THE AUDITORY BULLA IN SOME FOSSIL MAMMALS

With a General Introduction to this Region of the Skull

By C. J. van der KLAAUW

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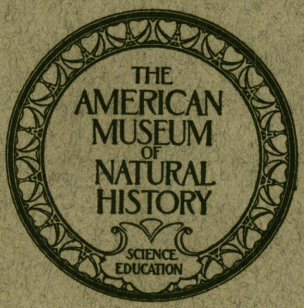

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Article I. — ON THE AUDITORY BULLA IN SOME FOSSIL MAMMALS, WITH A GENERAL INTRODUCTION TO THIS REGION OF THE SKULL

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CONTENTS

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PREFACE

My investigations during the past years on the development of the auditory bulla in recent mammals brought me into contact with the literature on this part of the skull and taught me the importance of the tympanic region both in comparative anatomy and as a factor in the determination of the relationships of genera and larger groups. It taught me also how little it has been described in fossil mammals in comparison with recent forms. Knowing how important the knowledge of the tympanic region in fossil mammals must be for the solution of many problems, I was therefore anxious to study the fossils myself, so I gratefully accepted the opportunity offered to me by the "Nederlandsch-Amerikaansche Fundatie," at The Hague, to visit the United States of America. During the short time of my sojourn (from the second of September until the twenty-fourth of November of the year 1923) the best I could do, I thought, was to study the fossil mammals in which the so-called ento-tympanic might be expected and to examine this material in as many museums as I could visit.

I wish to express my thanks to all who so generously opened the collections for my investigations and helped me in so many ways. In this respect I mention—following the route of my visits—in New York, Professor H. F. Osborn, Professor William K. Gregory, Dr. W. D. Matthew, of The American Museum of Natural History; in Washington, D. C., Drs. J. W. Gidley, C. W. Gilmore and R. Kellogg, of the United States National Museum; in Princeton, Professors W. B. Scott and W. J. Sinclair; in Cambridge (Mass.), Dr. G. M. Allen of the Museum of Comparative Zoölogy at Harvard; and in New Haven, Professor R. S. Lull, Drs. M. R. Thorpe, E. L. Troxell, and G. F. Eaton of the Peabody Museum at Yale University. I mention here also my wife, Mrs. A. M. van der Klaauw-Bruins, who not only helped me with literature during my trip but also made the line-drawings of the specimens I studied, under my direction.

As Van Kampen's paper, which gives a detailed description of all the characters of the bulla and its neighborhood, family after family, retains its high value, I have treated the matter from another point of view, which in my opinion may be valuable for palæontologists and mammalogists as well. Thus, I have discussed each character of the bulla through all orders and families of mammals.

As a rule, I have not contradicted remarks in literature that seem to me to be incorrect. I have only referred to them, giving the description that in my opinion is correct.

With a few exceptions only, I have not discussed or described figures of bullæ given in the literature. My experience in this respect, taken from the specimens I have seen or described, is that in many cases the figures do not allow of this.

It was also too difficult, if not impossible, for me to give the last adopted species and genus names. As a rule, I mention only the names given in the cited literature.

I wish to express my hearty thanks to Professor P. N. Van Kampen for his kindness in reading and criticising the manuscript of this paper.

A REVIEW OF THE TYMPANIC REGION

Early Development of the Tympanic

In the early development we find the (ecto) tympanic as a small bony plate in the corner of the cartilage of Meckel and the malleus, later on forming the well-known bony ring (Van Kamp.[1]; Zittel, 1893, p. 16; 1923, p. 409). Sometimes it is triradiate (Palmer, 1913*a*, p. 513). In this stage the tympanic is never totally a closed ring and, therefore, the name "ring-like tympanic" and "annulus tympanicus" ought to be changed to "semi-circular" or "horseshoe-shaped tympanic" and "arcus tympanicus," but the first-mentioned names are so commonly used that it is better to keep them (Van Kamp.; Winge, 1893*b*, p. 20, where he says that it is better to call it "three-quarters of a ring").

The tympanic is present in all recent mammals and all later investigations agree that it develops as bone and never as cartilage. One might say that this is the case only in the recent mammals and that it is possible that in the early fossil mammals it was cartilaginous or not yet developed. There are a few theories that homologize the (ecto) tympanic with a cartilaginous element in the lower vertebrates. I mention that of Gadow (tympanic = quadratum; Van Kamp.; Gaupp, 1913, p. 72; Gregory, 1913*a*, p. 35) and that of Winge (1888, pp. 168, 198, 199; 1893*b*, p. 142; tympanic = one of the cartilaginous rings of the external ear). These theories allow us the view that in the early fossil mammals the (ecto) tympanic remained cartilaginous and that this is the reason we do not find it in these mammals.

There are a few theories (Gaupp, 1913, p. 74) that the (ecto) tympanic is a neomorph. These theories allow us the view that in the early fossil mammals the tympanic was not yet developed. There is, however, strong evidence to believe that Van Kampen's view is the right

[1]Van Kamp. This abbreviation is used throughout this paper to refer to Van Kampen's works of 1904, 1905, and the works listed therein.

one: namely, that the (ecto) tympanic has been derived from one of the bones of the lower jaw of the lower vertebrates (Van Kampen, 1904, p. 365; 1905, p. 706; Gaupp, 1913, pp. 72–79; Gregory, 1913*a*, p. 35; Palmer, 1913*a*, pp. 513, 514). Accepting this as true and knowing no cases in recent mammals in which the tympanic has secondarily disappeared, we have good reason to believe that all mammals at least had a bony tympanic ring and that there are other reasons why we do not find it in so many fossil mammals.

In the early developmental stages the tympanic ring lies nearly horizontal and also the tympanic cavity is then nearly horizontal and very flat. It lies at a very short distance under the petrosal. With Van Kampen we can distinguish as bordering on this tympanic cavity: first, the morphological lateral wall formed by the tympanic and the tympanic membrane; and secondly, the morphological medial wall, which is opposite the lateral wall and extends over the petrosal and sometimes also over a part of the alisphenoid and the squamosal.

In the adult skull the (ecto) tympanic sometimes shows these ontogenetic characters, especially in the lower mammals.

Ring-Form of the Tympanic

The ring-form of the tympanic is preserved in many adult mammals. This is generally considered to be a primitive condition (Van Kamp.; Steinmann-Döderlein, 1890, p. 686; Zittel, 1893, p. 22; 1911, p. 334; 1923, p. 412; Gregory, 1910, pp. 151, 155, 156, 253, 265, 279; Stromer von Reichenbach, 1912, pp. 151, 161; Abel, 1920, p. 414).

Of course it is not necessary to conclude that in all cases where the annular tympanic is preserved we have a primitive condition, as a secondary one may be present. According to this, Van Kampen (1904, pp. 129, 136; 1905, pp. 454, 461) suggests that the annular tympanic of *Pteropus* is not a primitive but a secondary feature among the Pteropodidæ.

A ring-like tympanic in adult specimens is described for the monotremes (Van Kamp.; Winge, 1888, pp. 168, 199; 1893*b*, p. 74; Bondy, 1907, p. 393; Gaupp, 1908, pp. 663, 759, 760, 780; Gregory, 1910, p. 151) and for the marsupials (Zittel, 1893, pp. 16, 88, 558; 1923, pp. 409, 428; Stromer von Reichenbach, 1912, pp. 151, 175; Scott, 1913, p. 628). Many of these notes seem to imply that all marsupials have a ring-like tympanic, but according to Van Kampen this is only the case among the recent forms in the Didelphyidæ (Van Kamp.; Winge, 1893*b*, p. 20, *Grymæomys;* p. 35, *Philander;* pp. 37, 41, *Didelphys;* pp. 57, 59, *Hemi-*

urus). An annular tympanic is also described for the fossil Sparassodonta (Sinclair, 1906, pp. 336 and 397, especially *Amphiproviverra*); in *Ptilodus* we have, according to Broom (1914, p. 123), probably the same condition as in *Ornithorhynchus*.

A ring-like tympanic is described for adult insectivores (Van Kamp.; Schlosser, 1887, p. 81; Zittel, 1893, pp. 16, 558; 1923, pp. 409, 443; Stromer von Reichenbach, 1912, p. 175). According to these notes, at least for the larger part, one would suppose that all insectivores have an annular tympanic, but this is not always the case. According to Van Kampen, among the recent mammals, we find a ring-like tympanic in all insectivores except in some of the Talpidæ, Chrysochloridæ and Macroscelidæ. Thus, we find it in the Soricidæ (Van Kamp.; Bondy, 1907, p. 393, but see also the restriction on p. 310; Gregory, 1910, pp. 263, 265; Zittel, 1893, p. 567; Schlosser, 1887, pp. 81, 121); it is also in the Tupaiidæ (Van Kamp.; Gregory, 1910, pp. 274, 279; 1913*b*, p. 248; Matthew, 1909, p. 504; the same notice for the Macroscelidæ is not right; Winge, 1893*a*, p. 43).

In many other insectivores the tympanic is slightly expanded to the medial or to the lateral side, which only more thorough investigations can show. According to this, the following so-called annular tympanics are to be understood: *Centetes* (Schlosser, 1887, pp. 81, 110), *Erinaceus* (Schlosser, 1887, pp. 81, 94, 95), Solenodontidæ (Schlosser, 1887, p. 113), and perhaps also *Microgale* (Schlosser, 1887, p. 111) and the Potamogalidæ (Schlosser, 1887, p. 112). The fossil *Palæoryctes* (Matthew, 1913, pp. 310, 313), in which the tympanic is said to accord with that of *Solenodon*, also probably showed a broad ring.

In this way, also, we must understand the remark of Van Kampen cited above, on the presence of a ring-like tympanic among insectivores. Yet it would be much better to restrict the term ring-like tympanic or annulus tympanicus to the cases where there is neither a medial nor a lateral expansion of the tympanic. Sometimes the term ring-shaped tympanic is used with the addition "broad," which evidently means that it is expanded to the medial or the lateral side (Gregory, 1910, p. 246, *Solenodon;* p. 264, *Myogale*). If it is only said that the tympanic is expanded (Gregory, 1910, pp. 257, 267, *Chrysochloris*), it cannot be determined which of the two expansions is present.

Thus, it is impossible to say from many descriptions whether the tympanic has been a primitive ring or a broad ring, in many cases. It is, however, very probable that the first placental insectivores had a narrow annulus tympanicus in the primitive sense (Schlosser, 1887,

p. 91). Nor is it impossible that the primitive Chroptera are derived from insectivores with a primitive narrow annulus tympanicus (Winge, 1893*a*, pp. 41, 86). According to Van Kampen this is, however, an exception among the recent forms, among which only *Pteropus* showed this primitive ring, while allied genera show an expansion of the tympanic. Thus, we have also in the Chiroptera to take the term ring-like tympanic in the broader sense (Gregory, 1910, p. 319; Bondy, 1907, p. 318, *Miniopterus;* Winge, 1893*a*, p. 43, especially the Pteropodidæ, often a narrow ring).

A thick tympanic ring is found also in *Orycteropus* (Van Kamp.; Owen, 1842, p. 26; Turner, 1851, p. 220; Gregory, 1910, p. 335; Winge, 1915, p. 222); it resembles that of the Sirenia; although it is thick, it forms neither a bony recessus meatus nor a part of the "ventral" wall. On the other hand, the anterior leg of the tympanic in *Orycteropus* is plate-like, broadened, the lateral margin ending ventrally with a short process, while the top of the posterior leg is very thin and hooked at its extremity (Van Kamp.; Owen, 1840, pp. 59, 60).

In *Cholœpus*, in contrast with *Bradypus*, we find a narrow horseshoe-shaped tympanic, showing only a small thickening in the neighborhood of the auditory tuba (Van Kamp.; Turner, 1851, p. 207).

In the Gravigrada the tympanic is in general a horseshoe-shaped, narrow element, in which, according to Van Kampen, a bony recessus meatus is lacking, but which in a few cases is a little broadened in the "ventral" wall. A narrow tympanic is present in *Megatherium* (Turner, 1851, p. 209, not inflated; Reinhardt, 1878, p. 277), in *Nothrotherium* (=*Coelodon*, Reinhardt, 1878, pp. 277, 336, supposed to be so), in *Hapalops* (Scott, 1903*b*, p. 220; 1904, p. 254; Winge, 1915, p. 246; my own investigations), in *Pelecyodon cristatus* (Scott, 1904, p. 310; see also my own investigations). In *Analcimorphus giganteus* (Scott, 1904, p. 285) the tympanic is, according to my own investigations, a little broader. This broadening lies in the "ventral" wall and does not form a bony recess, as the auditory meatus is large and irregular, the same as in *Hapalops* (Scott, 1903*b*, p. 220). A narrow horseshoe-shaped tympanic is found again in *Mylodon* (Turner, 1851, p. 210; Owen, 1842, p. 26; Reinhardt, 1878, p. 277; Allen, 1913, p. 323; Stock, 1914, p. 324; see also my investigations), in *Scelidotherium* (Turner, 1851, p. 210; Reinhardt, 1878, p. 277) and in *Glossotherium* (Owen, 1842, p. 26). In *Lestodon* we find a partly broadened tympanic ring, forming a part of the bony ventral wall (see Van Kampen's and my investigations).

All recent Dasypodidæ show a narrow horseshoe-shaped tympanic,

except *Chlamydophorus*, *Dasypus* and *Zaëdyus* (Van Kamp.; Turner, 1851, p. 212, *Tatusia;* p. 215, *Priodontes;* p. 215, *Xenurus;* p. 216, *Tolypeutes;* Osborn, 1904, p. 164, *Tatusia;* Winge, 1915, pp. 8, 37, *Xenurus duodecimcinctus;* pp. 8, 67, *Dasypus novemcinctus;* Matthew-Granger, 1918, p. 625, *Cabassous*). Among the fossils a narrow ring is described for *Proeutatus* (Scott, 1903*a*, p. 44, a large irregular meatus, which means at all events no bony recess; Winge 1915, p. 228), for *Stenotatus* (Winge, 1915, p. 228), for *Chlamydotherium* (Winge, 1915, p. 94, supposed to be so), while in *Stegotherium* it is a little broadened (Scott, 1903*a*, p. 16; see also my investigations).

In the rodents we do not find a ring-like tympanic and according to Winge (1888, pp. 103, 110, 184) the earliest rodents already no longer possessed such a tympanic.

As to the Creodonta, Van Kampen supposed that in most cases the tympanic was narrow and horseshoe-like. His addition, "probably as in *Paradoxurus* and *Nandinia*," shows that he thought the tympanic was broadened. Winge (1895*b*) supposed a ring-like tympanic in *Stypolophus* (pp. 48, 49), probably as in the recent *Nandinia*, and described a small narrow ring-like tympanic in *Amphictis* (p. 52; Van Kamp.; Pohle, 1917, pp. 404, 405) and compared it with that of *Nandinia*. Winge (1895*b*, p. 50) mentions a very small ring-like tympanic for *Mesonyx*. *Hyænodon cruentus* shows a mere ring of ossification of the tympanic in contrast with allied forms (Matthew, 1906, p. 217). In my opinion it is not improbable that in this case only a part of the tympanic is preserved (see my investigations). The delicate tympanic ring described for *Nimravus debilis* by Eaton (1922, p. 449) is not in its place, if it be the tympanic ring at all (see my investigations).

The ancestors of the Carnivora among the insectivores had, according to Winge (1895*b*, pp. 43, 123), a ring-like tympanic, while according to Van Kampen the ancestors had a broadened tympanic. Yet it is not necessary to conclude that the difference between these two authors is a principal one. Winge adds to the above cited remark: "as one can find still among the Carnivora." Even the often chosen examples of a ring-like tympanic among the recent carnivores, the genus *Nandinia* (Van Kampen; Winge, 1895*b*, pp. 48, 49, 52) and the genus *Paradoxurus* (Van Kampen) have a broadened tympanic ring. In this way no doubt we must understand Matthew's remark (1909, p. 315) on the ring-shaped tympanic in the later Carnivora. Every tympanic is ring-like to a certain degree, even the tympanic that forms a broad bony ventral wall and a well-developed bony recessus meatus, and it would not be difficult to

give examples taken from the literature. Therefore, it is important that such descriptions should be clear as to whether a narrow primitive tympanic ring is meant or not.

Winge (1906, pp. 66, 158, 173) supposes that the most primitive and many other primitive ungulates possessed a ring-like tympanic. According to him (1906), *Pantolambda* (p. 73), the Mœritheriidæ (p. 173), and *Arsinoitherium* (p. 164) must have had a ring-like tympanic. His remark (1906, p. 147) that the Perissodactyla possess a ring-like tympanic, such as *Tapirus* shows (p. 158) and to which the Equidæ form an exception (p. 147), indicates that in his descriptions he does not make a difference between the primitive narrow tympanic ring and the broadened one.

In the recent Sirenia the tympanic ring, though thick, is a primitive ring, for it forms neither an expansion in the "ventral" wall nor a bony recessus meatus (Van Kamp.; Zittel, 1893, p. 191; Winge, 1906, p. 173; Dilg, 1909, p. 100, *Manatus;* Stromer von Reichenbach, 1912, p. 221). The fore and under parts are especially thickened. The tympanic in *Manatus* is thicker than that in *Halicore.* An extensive description of the tympanic in *Halicore dugong,* in the adult form, and its development is given by Freund (1908, pp. 617, 618, 619, 621, 622). In the youngest embryo of his material (p. 617) the caudal end of the tympanic is orocaudally prolonged and flattened; then narrowing, the tympanic becomes broader in the ventral part. The external surface of the tympanic lies in a conical surface. The tympanic does not form an expansion in the ventral wall, as the tympanic membrane is attached near the thickened mesial margin. In the further development (pp. 619, 621) the tympanic has grown irregularly. The oral part is considerably thickened oromesialward and connected by a relatively thin bridge to the caudal part. The dorsocaudal end of the tympanic becomes broad, hoe-shaped. The caudal leg lengthens to a round bony rod. The oral leg is broadened in the sagittal plane. In the adult *Halicore* (p. 622) the still more broadened hoe-shaped end of the caudal leg forms an angle with the caudal leg itself. The rostral leg is considerably broadened in the oro-ventral direction.

The tympanic ring in *Rhytina* (Claudius, 1867, p. 8) showed the same features as those of the recent genera. The transverse section of the middle part of the ring shows an elliptical figure, of which the long diameter goes from the upper to the under side. On the basis of the hind leg, where the tympanic is much narrower, the ellipse of the transverse section turns inward. There the long diameter of the ellipse runs fore-mesially

to back-laterally; then the tympanic broadens downward. The anterior leg is small and short; the hind leg is better developed and shows a backwardly directed process, lying in proximity to the hyoid arch.

The fossil *Halitherium schinzi* (Lepsius, 1882, p. 35) shows the general sirenian conditions as well: it shows neither a bony ventral wall nor a bony recessus meatus. The tympanic consists of the middle part that forms a thick, sharp head, and two well-developed legs. The anterior leg is much shorter than the hind leg. The latter is long, becoming gradually narrower because of a broad groove (p. 36), and ends with a large, flat foot (p. 35).

Hay (1916, p. 387) describes in the fossil *Desmostylus hesperus* a ridge running obliquely forward and inward, wedged in between the glenoid fossa and a part of the alisphenoid in front and the exoccipital behind, which evidently corresponds with the tympanic bulla, according to Hay. If this is true, it corresponds probably to the middle part of the tympanic ring, if the conditions agree with those in the other Sirenia at all.

Among the recent Prosimiæ we find a narrow ring-like tympic in the Malagasy forms. It is found in the recent lemurs (Van Kamp.; Gregory, 1910, p. 322; 1915, p. 426; 1920, pp. 163, 164, 165), in the Chirogaleinæ (Gregory, 1915, p. 426), in *Propithecus* (Gregory, 1915, p. 426; 1916, p. 264), and in the Indrisinæ (Gregory, 1915, p. 426). The recent Chiromyidæ show a thin narrow tympanic ring as well (Van Kamp.; Gregory, 1915, p. 426). For the fossils allied to these Prosimiæ a narrow primitive tympanic ring is mentioned several times: for *Notharctus* (Gregory, 1915, p. 426; 1920, pp. 164, 165, 218, 220, 224, 227, 232); for *Adapis* (Forsyth Major; Van Kamp.; Gregory, 1915, pp. 422, 426; 1920, pp. 164, 165, 220); for the Adapidæ in general (Zittel, 1923, p. 639); for the Megaladapinæ (Gregory, 1915, p. 426); for the Archæolemurinæ (Gregory, 1915, p. 426); and for *Nesopithecus* (Forsyth Major, cited by Van Kampen). All these recent and fossil genera and groups are brought together in one larger group: the Lemuriformes (Gregory). It is easily understood, that the fact that they possess a narrow primitive ring-like or horseshoe-like tympanic is given as a general character of these Lemuriformes (Gregory, 1915, pp. 426, 432; 1920, p. 220; Zittel, 1923, p. 638). Without doubt it was also a character of the ancestral protoadapine stock (Gregory, 1920, p. 232). This form of the tympanic is the more primitive one among the Primates (Gregory, 1915, p. 426).

In none of the other Prosimiæ does the tympanic show this primitive form.

Some Peculiarities of the Primitive Narrow Tympanic

Sometimes the primitive narrow tympanic shows processes. We have already mentioned a short process of the ventral part of the tympanic in *Orycteropus*, the thickening in the neighborhood of the auditory tube in *Cholœpus* and the backwardly-directed process of the hind leg in *Rhytina*. We can add *Chiromys*, in which a sharp process on the fore part of the under margin of the tympanic runs forward toward the ostium tympanicum tubæ of the bulla (see Van Kampen's paper). A very remarkable condition is found in the Sirenia. In these mammals the front leg of the tympanic bifurcates into two processes. The mesial or oral process is the crista tympanica and is connected with the skull. Between the two processes we find the sulcus malleolaris with the Folian process of the malleus. The caudal or lateral process is free (Van Kamp.; Freund, 1908, p. 617, etc.; Lepsius, 1882, p. 35; Claudius, 1867, p. 8). A detailed description is given for *Halicore dugong* by Freund (1908, pp. 617–619, 621). The caudal or lateral process in its early development is rounded and flattened and runs in the dorsolateral direction (p. 617); afterwards it becomes triangular and its caudal end develops a sharp oval wing (p. 619); finally it is broad and sharp (p. 621). The oral or mesial process of the front leg of the tympanic in its early development is thin and flattened (p. 618). In *Rhytina*, Claudius (1867, p. 8) describes a prominent bony ridge between the two processes of the rostral leg of the tympanic, with which the Folian process of the malleus is fused. According to Lepsius (1882, p. 35), in *Halitherium schinzi* the Folian process is fused with the caudal process, which shows many longitudinal folds, remains of the attachment of the Meckelian cartilage.

The narrow tympanic ring can show on its mesial side a curve in the form of half a circle and in front of this a small bony process in the lateral wall of the auditory tube. I found this condition in *Hapalops* and allied genera, less distinct in *Mylodon*. It seems to be present in those cases where the tympanic and the entotympanic lie close together. Freund (1908, pp. 618, 622) described a sulcus pro tuba Eustachii on the mesial surface of the oral or mesial process of the front leg of the tympanic ring in *Halicore dugong*.

By exception, the narrow tympanic is not horseshoe-shaped or C-shaped. The form of an irregular ridge in *Megatherium mirabile* (Leidy, 1855, p. 52; Van Kampen notices that Leidy's auditory process forms the tympanic) could perhaps be an artificial condition. This is probably not the case in the V-shaped tympanic with the tuberous apex in *Mega-*

lonyx jeffersonii (Leidy, 1855, pp. 9, 10; according to Van Kampen the auditory process is the tympanic), here the "horseshoe" is ventrally pointed. Further, I may refer to the description of the tympanic in the Sirenia given above. It shows that the primitive horseshoe-like tympanic is not necessarily a simple structure—which is one of the reasons for giving such a detailed description.

Incomplete and Complete Tympanic Ring

We have seen that originally the tympanic is an incomplete or semicircular or horseshoe-like ring which is open above. Sometimes you will find it said that the tympanic ring is open on the under side (Zittel, 1893, p. 22; 1911, p. 334; 1923, p. 412; Abel, 1920, p. 414). This no doubt means that the tympanic is not expanded to the morphological ventral side of the tympanic cavity, which lies medially to the under side of the tympanic ring. How ambiguous the expression "unten offen" is can be seen in Abel (1920, p. 414), where the specialized opposite character is given: "tympanic a closed bony ring." Thus, it is much better to limit the expression, that the tympanic is open, to the incomplete tympanic ring itself.

Sometimes the tympanic is closed above or nearly closed. In still other cases a closed tympanic is figured; according to Van Kampen (1904, pp. 101, 102; 1905, pp. 424, 426) this is due to the fact that the caput mallei is figured as a part of the tympanic annulus. A similar case I saw in a specimen of *Stegotherium tesselatum* Amegh. (Princeton, No. 15566), figured in Scott (1903*a*, Pl. III, fig. 6). One can see very clearly here, what is probably also the case in the above-mentioned instances, that the head of the malleus does not lie in the same plane as the tympanic ring. This is due to the situation of the head of the malleus which lies inside the tympanic membrane. That we find such cases even in fossils is due to the fact that the tympanic is often firmly connected with the anterior process of the malleus, a fact that is not astonishing, if we consider the ontogeny and phylogeny of the two elements (Van Kamp.; Gregory, 1910, pp. 151, 155, 156; Bondy, 1907, p. 302, etc.).

There are some examples of a tympanic that is closed all around. In *Sorex* opinions differ. According to Parker it is closed, to Winge (1878, cited by Van Kampen) open, while Bondy (1907, p. 310) found that it was closed with the exception of a very narrow space.

In the Microchiroptera, according to Van Kampen (1904, p. 133; 1905, p. 457), the tympanic ring as a rule is closed all around, but is sometimes open. Bondy (1907) gives more extensive information: sometimes

it is open above (p. 313, *Vesperugo noctula*), even very wide (p. 318, *Miniopterus schreibersi;* p. 320, *Rhinolophus hipposideros*). The opening above can amount to one-third mm. (p. 321, *Rhinopoma microphyllum*), to about 100 mikra (p. 315, *Vesperugo serotinus*) or even 60–70 mikra (p. 317, *Vespertilio murinus*). In the last two cases the top of the hind leg has already moved a little dorsally in relation to the top of the rostral leg, and in still other cases the hind leg lies for a short distance dorsally above the top of the rostral leg, connected with it by dense connective tissue (p. 319, *Plecotus auritus;* p. 319, *Rhinolophus ferrum equinum*), so that the tympanic ring is totally closed.

Among the edentates the tympanic is closed all around, almost totally in *Manis* and in the Myrmecophagidæ.

In many rodents the auditory meatus is closed all around by the tympanic itself; in other cases it is difficult to determine, as the tympanic is fused with the periotic. In the cases where the cylindrical auditory meatus is totally, or almost totally, lacking the tympanic is nearly closed all around. In this order of mammals as well, Bondy (1907) gives us more extensive information: the legs of the tympanic touch each other (p. 393, *Myoxus avellanarius, Cricetus*), cross each other (p. 393, *Myoxus glis, Arvicola arvalis*) or even coössify on more advanced age (p. 393, Sciuridæ, Caviidæ). In *Sicurus vulgaris* (p. 325) the tympanic is closed all around, the two legs are fused, and the place of fusion is indistinct; probably the hind leg lies against the lateral side of the front leg. A similar mutual relation of the tops of the two legs is found in the closed tympanic of *Cavia cabaya* (p. 345). In *Arvicola arvalis*, also, (p. 334) the tympanic is totally closed; the top of the rostral leg partly covers the caudal leg, connected to it by connective tissue. In *Myoxus glis* (p. 330) Bondy found a similar condition. In *Myoxus avellanarius* (p. 328) and in *Cricetus frumentarius* (p. 332) the tops of the two legs nearly touch each other. In other rodents which Bondy investigated the tympanics were more or less open above: *Mus decumanus* (p. 336 opening about 3 mm.), *Mus minutus* (p. 342, opening about 250 mikra), *Mus musculus* (p. 338), *Mus silvaticus* (p. 340), and his remarkable "Feldmaus" (p. 343).

Among the Carnivora, Bondy (1907) notices a tympanic closed all around in *Viverra zibetha* (p. 363), nearly totally closed in *Canis familiaris* (p. 352), while it is probably also closed all around in *Fœtorius vulgaris* (p. 355) and in *Mustela foina* (p. 361). As to the condition in the Phocidæ, the remarks in literature differ. According to Van Kampen, in contrast to older authors, the tympanic does not close the cylindrical external

auditory meatus all around. The opinion of Bondy (1907, p. 368) is that in *Phoca vitulina* the tympanic is totally or nearly closed, though it was difficult to find the suture against the squamosal.

In *Cervus capreolus* Bondy (1907, p. 376) found a small opening in the tympanic, lying far backward. This is due to the fact that the rostral leg is much longer than the caudal one. In *Cervus elaphus* (p. 377) the rostral leg is shorter and the opening in the tympanic much larger. Studying the development of the tympanic ring in *Sus domestica*, Bondy (1908, pp. 594, 596, 597, 599) found that the distance between the tops of the two legs diminished more and more. In the oldest embryo it was 1 mm., the diameter of the tympanic membrane being 7 mm.

In the Sirenia the dorsal opening of the tympanic is very large, and the tympanic is often called in descriptions a semi-ring. Lepsius (1882, p. 36) tells us that in *Halitherium schinzi* the distance between the tops of the two legs was 11 mm., while the diameter of the ring was about 16 mm.

In *Tarsius* the tympanic is nearly closed (Van Kampen's paper).

In *Macacus nemestrinus* it is, according to Bondy (1907, p. 383), evidently not closed.

Inclination of the Annulus Tympanicus

The nearly horizontal tympanic ring is found in many of the lower mammals. This small inclination of the tympanic membrane and of the tympanic ring is generally considered to be a primitive character for monotremes, marsupials, and placentals (Van Kamp.; Gregory, 1910, pp. 156, 253, 426). A nearly horizontal position of the tympanic ring in adult mammals is found in the monotremes (Van Kamp.; Gaupp, 1908, pp. 663, 681, 759, 760; Gregory, 1910, pp. 425, 151). This horizontal position is probably the primitive condition and not secondary (Gregory, 1910, p. 151). It is also found in the Soricidæ (Van Kamp.; Gregory, 1910, p. 263). According to Broom (1914, p. 123) we have in the fossil *Ptilodus* probably the same conditions as in *Ornithorhynchus*. A small inclination of the tympanic ring is found in the following forms: (1) in adult Centetidæ (in *Hemicentetes* and *Microgale* it is still more horizontal than in *Centetes* and *Ericulus;* this is in connection with the development of the tympanic wing of the basisphenoid as we shall see later; Van Kamp.; Gregory, 1910, pp. 246, 426); (2) in Erinaceidæ (in *Gymnura* more oblique than in *Erinaceus*, also probably in connection with the development of the processus tympanicus basisphenoidei); and (3) in Talpidæ (according to Van Kampen, nearly horizontal in

different genera of this family, but Bondy, 1907, p. 306, determines the angle between the tympanic membrane and the sagittal plane as 45°). In all other mammals the position of the tympanic is a more oblique or a more vertical one. Of course there are transitions; for example, in *Chrysochloris* the inclination is only a little larger than in *Talpa*.

In other orders adult specimens show a tympanic membrane with a more vertical position. A few examples will suffice. In *Orycteropus* the tympanic shows a small inclination; in the Myrmecophagidæ a large one; in *Cholœpus* it is nearly vertical. In those Gravigrada which Van Kampen investigated (*Glossotherium, Lestodon*), the tympanic was lying in a still more vertical plane than in *Cholœpus*. In *Lestodon* the tympanics were loose, but Van Kampen replaced them exactly, guided by a distinct groove in the squamosal. According to my own investigations the tympanic is nearly vertical in *Mylodon*, but in *Hapalops* with its related genera, in *Lestodon*, and *Stegotherium* the inclination is about 45°.

In the rodents the tympanic membrane lies vertically or nearly vertically. According to Gray (1913, p. 400) the tympanic membrane in *Lepus cuniculus* is set more nearly in the vertical plane than that of man.

Among the carnivores, Van Kampen emphasizes a nearly vertical plane in *Phoca grœnlandica*.

In the adult cetacean genus *Megaptera* (Ridewood, 1922, p. 225), the plane of the attachment of the tympanic membrane to the tympanic is transverse or oblique (we have to describe it in this way, as the tympanic membrane has the form of a glove-finger).

In the recent Sirenia the tympanic is nearly vertical. In the fossil *Halitherium schinzi*, on the other hand, Lepsius (1882, pp. 34, 36) describes the tympanic as nearly horizontal.

Among the Prosimiæ, Van Kampen emphasizes the nearly vertical position of the tympanic membrane in *Tarsius*, while in *Lemur mongos* the tympanic membrane inclines a little.

That the tympanic ring lies in a nearly horizontal plane is, as we have seen, an exception in adult mammals. The more oblique position is due to two factors: first to the inflation of the cochlea, which we always find to a certain degree, except in *Echidna*, but especially to the enlargement of the space between the medio-ventral part of the tympanic ring and the under surface of the petrosal. To a certain extent there is a relation between this space and the inclination of the tympanic ring and membrane and the inflation of the bulla. We can imagine this space to

be formed by turning the tympanic annulus around a horizontal axis going through the lateral open part of this ring. Through the enlargement of the space between the medio-ventral part of the tympanic ring and the under surface of the petrosal a new wall of the tympanic cavity is formed, which Van Kampen has called its morphological ventral wall. According to this author, this wall is a neomorph element and developed during the phylogeny of the mammals, in relation to which it develops late in ontogeny. This wall can be flat or inflated; the latter is the case if a so-called hypotympanic sinus of the tympanic cavity is formed. In the recent mammals we nearly always find bone in this ventral wall, sometimes cartilage. It is membranous by exception only.

A membranous ventral wall among the recent members is found only in Soricidæ, in *Orycteropus* and in Sirenia (Van Kamp.; Claudius, 1867, p. 8; Freund, 1908, pp. 617, 621).

Membranous Ventral Wall

Further, we will consider in this respect the many cases in which the auditory bulla in fossils is said to be incompletely ossified. In my opinion, in most of these cases if not in all, an entotympanic has been present, which has fallen out or, as it was cartilaginous, has not been preserved. These cases are quoted in the chapter on the entotympanic.

Winge's view (1895*b*, pp. 43, 123), in contrast with the opinion of Van Kampen, is that the ancestors of the Carnivora among the insectivores had a membranous ventral wall. It is not overlooked that Winge also calls a cartilaginous wall "membranous" (pp. 43, 45, 123, 125): here he compares the auditory bulla in the fossil ancestors of the Carnivora with recent and with later Carnivora in general; the same is the case with the ventral wall in *Amphictis* and the Amphictidæ in general, which he compares with *Nandinia* (pp. 52, 59). In the Herpestoidei the ventral wall is, according to him (1895*b*, p. 60), either membranous or shows an "os" bullæ. Interesting in this respect is his remark (p. 59) that in the Amphictidæ the ventral wall was "membranous-cartilaginous." The most primitive ungulates, as well, possessed, according to Winge (1906, p. 66), a membranous or cartilaginous ventral wall.

The presence of a primitive narrow tympanic ring and a membranous, well-developed ventral wall is often judged to be a primitive character (Zittel, 1893, pp. 16, 22; 1911, p. 334; 1923, p. 412, if we may understand by "unten offen" that the morphological ventral wall is developed but is membranous, although this wall lies more on the medial than on the under side). The more specialized condition is, then, that the

tympanic is more tube-like (Stromer von Reichenbach, 1912, p. 161); or that the tympanic chamber is closed and even inflated (Steinmann and Döderlein, 1890, p. 686; Zittel, 1893, p. 22; 1911, p. 334; 1923, pp. 409, 412; Stromer von Reichenbach, 1912, p. 161; Abel, 1920, p. 414).

Terms "Bulla" and "No Ossified Bulla"

The skeletal ventral wall forms the larger part of the so-called auditory bulla; the other parts are as a rule the place occupied by the primitive tympanic annulus and the bony recessus meatus acustici externi.

The name "bulla" is in many cases not happily chosen in respect to the form which the word bulla will express. Therefore, Hagenbach has already proposed another name, but the name bulla is so generally used that it is impossible to replace it by another term. We shall in future use the name bulla also when the bulla is not inflated but flat, or when the skeletal ventral wall is flat or even when the bulla is concave.

The bulla contains more than the part that lies between the tympanic annulus and the petrosal (Steinmann and Döderlein, 1890, p. 682). We can distinguish three parts: the primary tympanic cavity, the hypotympanic sinus and the recessus meatus acustici externi. The transition between these as a rule is gradual. The hypotympanic sinus covers a part of the tympanic cavity that contains none of its principal elements, including the auditory ossicles and the fenestræ in the periotic. It is formed when the ventral wall loses its flatness and becomes inflated on the medial or caudal side.

Where the bulla is composite, the tympanic is not broadened in the ventral wall and the sutures are distinct; there the three different parts of the bulla can easily be distinguished. Where, on the other hand, the sutures in the composite bulla are not clear or have disappeared, the tympanic is broadened in the ventral wall or the bulla is built up by one element, there it is impossible to determine externally the place of the three parts. Sometimes there is a groove in the bulla, as in *Chrysochloris* and *Macroscelides* and in Hapalidæ, between the inflated hypotympanic sinus and the recessus meatus acustici externi. In other cases however a similar line lies between the recessus and the cylindrical part of the external auditory meatus. The transition between these two can easily be determined as a rule, as the latter is cylindrical and the former becomes narrower toward the lateral side. Still, by exception, even this transition can not be determined, as in *Phascolomys*, in the Ursidæ and Mustelidæ, where the outside is so much thickened that the two portions can only be distinguished by an investigation of the internal side. The

Phocidæ show a similar thickening; even a part of the cylindrical auditory meatus is externally a part of the bulla.

In other groups a very gradual external transition between the recessus meatus and the cylindrical auditory meatus is due to a horizontal extension of the hypotympanic sinus in the lateral direction covering the under side of the recessus meatus and more or less also the cylindrical auditory meatus, so that these seem to be inflated. An investigation of the inside of the bulla still shows the different parts. This cause of a gradual external transition between the recessus meatus and the cylindrical auditory meatus is emphasized for *Hyæna crocuta*, in which both tympanic chambers are extended laterally; and for the recent Camelidæ, where this feature causes a distinct inflation of the external auditory meatus, which is separated from the bulla, *s.s.*, by the vagina for the hyoid arch. In the Ursidæ this horizontal extension of the hypotympanic sinus, as well as the thickening of the under wall of the auditory meatus, causes the gradual external transition. Moreover, the Rodentia and also *Tragulus* show this gradual external transition. Also, *Procavia* shows externally a very gradual transition, while internally, as we shall see later on, a distinct vertical septum partly separates the recessus meatus from the cavity of the cylindrical external auditory meatus.

That there can be a well developed bulla without the presence of a large hypotympanic sinus is shown in *Galeopithecus*, where the bony ventral wall is only very little concave but the recessus is very large and practically forms the bulla.

We shall call this bulla the "auditory bulla" or the "bulla tympani," or "bulla tympanica," or "bulla acustica." The name "bulla ossea" is not always well chosen, as the bulla is, by exception, sometimes partly cartilaginous. Nor would we use the term "tympanic bulla," as that sometimes seems to be identical with "true tympanic" or "(ecto) tympanic bulla," terms that imply either the part of the bulla formed by the tympanic or that the bulla is wholly formed by the (ecto) tympanic. It is also wise to omit the expression "false bulla," as it is much more important to state by which element or elements this false bulla is formed. It is taken for granted that the elements of the bulla can always be determined, but as this is often not the case it is much better to use the more neutral name "auditory bulla."

Dawkins (1878, p. 48) and Zittel (1911, p. 395; 1923, p. 476) call "bulla" in *Felis* and in the Viverridæ the part formed by the entotympanic. Matthew (1906, pp. 212, 213), on the other hand, seems to restrict the term bulla to "true tympanic bulla," saying that the bullæ are not

developed in marsupials nor in most Insectivora, in which groups "false bullæ" are frequently present.

If authors do not define what they mean by the term bulla it is not clear what is meant in regard to the tympanic region of an animal in which there is "no ossified bulla," as is sometimes stated in palæontological papers.

In this respect I refer to the following papers. "No bulla" or "bulla absent" is said to occur in:

Among the Mammals:

Nearly all Eocene mammals, Primates alone excepted (Matthew, 1901, p. 30; 1909, p. 510; Teilhard de Chardin, 1922, p. 40).

Among the Insectivora:

The first placental insectivores (Schlosser, 1887, p. 91); Hyopsodontidæ (Matthew, 1909, pp. 507, 510, 514; Zittel, 1923, p. 448); Pantolestidæ (Matthew, 1909, pp. 508, 525; Zittel, 1923, p. 449).

Among the Rodents:

Paramys (Matthew, 1910*b*, p. 47).

Among the Creodonta:

Most Creodonta (Matthew, 1909, pp. 326, 327, 345, 408, 414; Zittel, 1911, pp. 375, 379; Stromer von Reichenbach, 1912, p. 182; Scott, 1913, p. 556; Zittel, 1923, p. 454).

Thryptacodon (Matthew and Granger, 1915, p. 10).

Arctocyon and *Triisodon* (Matthew, 1901, p. 30, rudimentary or absent).

Pachyæna (Winge, 1895*b*, pp. 49–50).

Mesonyx (Matthew, 1901, p. 30, rudimentary or absent).

Oxyænidæ (Matthew, 1909, pp. 408, 414).

Patriofelis (Matthew. 1909, p. 425).

Some of the Hyænodontidæ (Matthew, 1909, p. 465; Zittel, 1911, p. 379; 1923, p. 459).

[redacted] *Sinopa* (Wortman, 1902*b*, p. 439; Matthew, 1906, pp. 212, 230; 1909, p. 470).

Tritemnodon (Matthew, 1909, p. 476).

Stypolophus (Winge, 1895*b*, pp. 49, 50).

Limnocyon (Wortman, 1902*a*, p. 202; Matthew, 1909, p. 435).

Neohyænodon (Thorpe, 1922*b*, p. 280).

Miacidæ (Matthew, 1909, pp. 345, 355; Zittel, 1911, p. 383; Scott, 1913, p. 557; Pohle, 1920, pp. 50, 56, 57, 61; Zittel, 1923, pp. 463, 466).

Miacis (Matthew, 1909, p. 371).

Viverravus (Matthew, 1909, pp. 345, 358; Teilhard de Chardin, 1915–1916, p. 14).

Uintacyon (Matthew, 1909, p. 345).

Vulpavus (Matthew, 1909, pp. 345, 392).

Phlaodectes (Matthew, 1909, p. 392).

Among the Carnivora:

The primitive Carnivora (Matthew, 1909, p. 315; Thorpe, 1923, p. 242).
The European *Cynodictis* (Carlsson, 1914, p. 228; Teilhard de Chardin, 1914–1915, p. 20, also footnote, pp. 29, 53, 88; Zittel, 1923, p. 466).

Among the Condylarthra:

Periptychus (Matthew, 1901, p. 30, rudimentary or absent).
Pleuraspidotherium (Teilhard de Chardin, 1922, p. 40).

Among the Litopterna (see Stromer von Reichenbach, 1912, p. 202, bulla almost never present):

Theosodon (Scott, 1910, p. 115).
Proterotheriidæ (Scott, 1910, pp. 9, 10).
Diadiaphorus (Scott, 1910, pp. 15, 18).

Among the Perissodactyla (see Stromer von Reichenbach, 1912, p. 202, bulla almost never present):

Hyracodon (Scott, 1896, p. 358).

Among the Artiodactyla (see Stromer von Reichenbach, 1912, p. 196, nearly always a bony bulla; Stehlin, cited by Sinclair, 1914, p. 284):

Most Anthracotheriidæ (Lydekker, 1885*a*, p. 70).
Helohyus (Sinclair, 1914, p. 284; Zittel, 1923, p. 565).
Dichobune (Sinclair, 1914, p. 284).
Homacodon (Sinclair, 1914, p. 286; Zittel, 1923, p. 569).
Oreodon culbertsoni (Marsh, cited by Scott, 1890, p. 339).
Several Merycoidodontidæ (Thorpe, 1923, pp. 242, 245).
Protoceratinæ (Zittel, 1923, p. 584).
Protoceras (Marsh, 1891, p. 82).
Camelomeryx (Scott, 1899, pp. 70, 73).

Among the Amblypoda:

Pantolambda (Winge, 1906, p. 73).

What is the meaning of the expression "no ossified bulla," "no bulla," "bulla absent," in these different examples? (1) Does it mean that no skeletal element is present either in the morphological lateral or in the ventral wall? (2) Does it mean that there is only a primitive annular tympanic and no ventral wall? (3) Does it mean that there is such a tympanic with a well-developed membranous or cartilaginous ventral wall in which so-called tympanic wings of neighboring skeletal elements are lacking? (4) Does it mean that the tympanic is expanded in the ventral wall, but not enough to be called a bulla, while other elements in the ventral wall are absent, so that the bulla is incompletely ossified? (5) Does it mean that there is a totally closed skeletal tympanic chamber, but that the form is not that of a bulla in the

common sense? It is important to know which of these five cases is indicated.

(1).—No doubt in the majority of cases it means that no skeletal element at all is present, either in the lateral or in the ventral wall of the tympanic cavity. In my opinion this is due to the loose attachment to the skull, so that in maceration these elements have fallen out.

Often the authors suppose that this is really the reason, that the bulla is absent (Matthew, 1910*b*, p. 47, *Paramys;* Wortman, 1902*b*, p. 439, *Sinopa;* Matthew, 1906, p. 212, *Sinopa;* Carlsson, 1914, p. 228, *Cynodictis intermedius;* Pohle, 1920, pp. 56, 57, Miacidæ; Scott, 1910, pp. 9, 10, Proterotheriidæ; p. 15, *Diadiaphorus;* p. 115, *Theosodon;* Scott, 1896, p. 358, *Hyracodon;* Matthew, 1909, p. 487, *Pachyæna* and *Mesonyx;* Winge, 1895*b*, pp. 48, 49, *Stypolophus;* Schlosser, 1921, p 121, *Pleuraspidotherium;* Zittel, 1923, p. 223, *Pleuraspidotherium;* Winge, 1906, p. 73, *Pantolambda*).

Thus, it is easily understood that it is seldom preserved (Adams, 1896, p. 421, *Hoplophoneus primæeus*) and that in some species or genera given in the list it is found later, or in other specimens (Scott, 1895*a*, p. 312, *Protoceras;* 1910, p. 115, *Theosodon;* on bulla in *Protoceras*, Van Kamp.; Osborn and Wortman, 1892; Scott, 1899).

But in other cases they give also as a possibility that there was no ossified bulla ever present (Wortman, 1902*b*, p. 439, *Sinopa;* Matthew, 1906, p. 212, *Sinopa;* Thorpe, 1922*b*, p. 280, *Neohyænodon;* Teilhard de Chardin, 1914–1915, p. 20, footnote, *Cynodictis*). Here we can add the remark of Pohle, that the bulla in *Amphictis* is cartilaginous (1920, p. 50). One would suppose that in these specimens nothing can be preserved, but Pohle (1920, pp. 57, 61) calls "bulla" only the ventral wall and the place occupied by the tympanic is excluded.

This feature (that no ossified bulla was ever present) is often called a primitive mammalian feature (Matthew, 1906, p. 230; 1909, p. 350; 1901, p. 30; Thorpe, 1923, pp. 242, 245). Those authors who think that the loose attachment is the reason that the auditory bulla is not preserved may also call the absence of an auditory bulla in macerated skulls a primitive condition, as the free condition of the tympanic is primitive and the fastening to the skull secondary (see farther on).

Another possibility is that the bulla is so fragile that it is practically always broken away in fossils. There is every reason to consider this also as a possibility in some cases, as we have the same in recent mammals. Among others, these exceedingly thin and fragile bullæ are mentioned in Notoryctidæ and in Microchiroptera (Zittel, 1893, p. 572;

1923, p. 451, says that the bulla in Chiroptera is strongly ossified, but this is not true) and this is perhaps the reason that Anthony (1917, p. 567) noticed that in the fossil bats he studied the bullæ were unknown. Filhol (1883, p. 30) notices the very fragile walls of the bulla in *Amphicyon*, so that they were broken. That these are really the reasons that the bulla is absent in many cases can be seen in the fossil *Ictops*, where the tympanic bulla is delicate and loosely attached to the skull, so that it is only occasionally preserved (Matthew-Granger, 1918, p. 607; Matthew, 1909, p. 514).

Here we can add a few remarks on the other extreme condition, that of the very dense and thick bulla. This condition is due to aquatic life. It is a well-known fact in the bulla of the Cetacea (Van Kamp.; Zittel, 1893, pp. 162, 163; 1923, p. 485; Lillie, 1910, p. 781, *Balænoptera;* Schulte, 1917, p. 394, *Kogia*), though the different parts can show a different thickness; the mesial lip especially can be thickened (Delphinidæ, Balænopteridæ). Also the tympanic ring in the Sirenia is very dense. Further, the Otariidæ show a thin-walled bulla (Winge, 1895*b*, pp. 73, 74); among the Phocidæ the less highly organized species (p. 72) show also a thin-walled bulla which, however, is already more dense than that in the Otariidæ, while the more specialized Phocidæ show a bulla which resembles that of the Cetacea (p. 72). Palmer (1913*b*, p. 884) remarks that the bulla in *Anoplotherium* is very thick as well.

(2, 3, and 4).—Another possibility is that the expression "no bulla" means: the tympanic is narrow or more or less expanded in the ventral wall, which, if present, is totally or for the larger part membranous or cartilaginous. I refer to such expressions as: the tympanic is not ossified into an otic bulla (Wortman, 1902*a*, p. 202, *Limnocyon*); the tympanic is not expanded into a bulla (Matthew, 1909, p. 414, Creodonta). We can add here a remark on the meaning of the expression "bulla not ossified" in the paper of Pohle. This author calls the ventral wall "bulla" and the place occupied by the primitive tympanic ring is excluded (see Pohle, 1920, pp. 57, 61).

It is also possible that, in the cases where there is "no ossified bulla," the bony ventral wall has totally or for the larger part fallen out. This is easy to understand in every case where we find an entotympanic.

For example, the entotympanic is cartilaginous in *Tatusia novemcincta;* the very small ossified part, which is not connected by bone to one of the neighboring elements, will also fail in the dry skull. A totally ossified entotympanic is also sometimes so loosely fastened that it is often absent in the dry skull, as Van Kampen found in *Priodontes*

giganteus. Burmeister (cited by Van Kampen) notices that the element, which according to Van Kampen can be nothing else than the entotympanic, is sometimes loose in the Gravigrada. In the fossil edentates that I could investigate the entotympanic was as a rule present, except in *Stegotherium*, but there is every reason to believe that this animal had an entotympanic either cartilaginous or ossified and loosely attached.

(5).—Still another possibility is that the expression "no bulla" means: the form of the skeletal element in the lateral and ventral wall of the tympanic cavity is not that of a bulla, in its common sense of inflated. In this respect I refer here to the following examples, in which a bulla in the broad general sense is present and even described by the author, and yet there is said to be "no bulla": *Synoplotherium* (Cope, 1873*a*, pp. 555, 557; 1873*b*, pp. 205, 206: tympanic chamber small and narrow); *Liops* (Gidley, 1906, p. 165: flat bulla); *Palæopropithecus* (Standing, 1908, pp. 73, 74, 80–81: surface smooth concave; therefore he gives as a character of the family Indrisidæ on p. 72 and of the subfamily Indrisinæ on p. 73; auditory bullæ generally present); the Catarrhina (Flower, cited by Van Kampen; Stromer von Reichenbach, 1912, p. 191); the Anthropoidea (Standing, 1908, p. 160). The remark of Gray (1913, p. 398), that in man the bulla is practically non-existent, has another meaning, as Gray calls "bulla" the general cavity of the bulla, the cellulæ being excluded.

Tympanic Free; Bulla Free

Now let us consider the fact that the tympanic and also the bulla in some cases are so loosely fastened to the skull that in a great many cases they easily fall out. The ontogeny teaches us that the tympanic develops independently of the neuro-cranium, a fact that agrees with the theory that it is one of the elements of the lower jaw of lower vertebrates. So, in many cases in the adult skull it remains loosely attached to the cranium and easily falls out in the dry skull. The connection with the Folian process of the malleus, which occurs in monotremes (Van Kamp.; Bondy, 1907, p. 302) and in *Orycteropus*, and others in which the tympanic is free, is of no use in this respect, as the auditory ossicles also easily fall out.

Correctly, this free tympanic is judged to be a primitive character, while the more specialized condition is that the tympanic is coössified with the cranium (Stromer von Reichenbach, 1912, p. 161; Steinmann and Döderlein, 1890, p. 686; Zittel, 1893, p. 22; 1911, p. 334; 1923, p.

412; Abel, 1920, p. 414; that the tympanic is coössified with the periotic is not true in general, as we shall see later on).

As this free condition of the tympanic is a primitive one, it is evident that it occurs in many groups and therefore it is advisable to be very prudent in using this character in questions of affinity (see Owen, 1840, pp. 59, 77: here the loose condition of the tympanic in *Glossotherium* and *Scelidotherium* is interpreted as evidence of closer affinity to *Orycteropus* than to the armadillos).

In many mammals the bulla is partly formed by dependent plates of the neighboring elements, which of course remain, if they do not break off, even if the other loosely attached elements fall out. The (ecto) tympanic and the entotympanic may be loosely fastened to the skull and easily fall out in the dry skull or can be fused with the skull.

In the marsupials the tympanic is often permanently separate from the other elements, though not always, as one would suppose from some of the notes (Zittel, 1893, p. 88; 1923, p. 428; Scott, 1913, p. 628); but this is very clear only in the Didelphyidæ, Peramelidæ, *Phascolarctus*, *Phascolomys* and the Macropodidæ. According to Sinclair (1906, pp. 336, 349, *Borhyæna;* p. 364, *Prothylacinus;* p. 397, *Amphiproviverra*), the tympanic is also unfused with the adjacent elements in the so-called Sparassodonta and therefore has not often been preserved; that it is still present in some genera with an alisphenoid bulla is perhaps due to the fact that this partly covers the tympanic, as is found in some recent marsupials (see below).

A free tympanic is also present in *Sorex* (Van Kamp.; Bondy, 1907, p. 310), where it lies only against the tympanohyal and the tegmen tympani. In *Erinaceus* it is also free; the hind leg lies also against the tympanohyal, but the rostral leg does not even touch the squamosal. In many Talpidæ, in contrast with other forms of this family, the tympanic is also free. It was also loosely united to the skull in the fossil *Ictops* (Matthew, 1909, p. 514; Matthew-Granger, 1918, p. 607) and perhaps also in *Hyopsodus* (Matthew, 1909, p. 514) and, in my opinion, in all the fossils in which the bulla (taken in the broader sense) is said to be absent.

Zittel (1893, p. 581) seems to think that in insectivores and marsupials there is cartilage between the bulla and the skull and that this is the reason that the bulla is not connected with the cranium in the dry skull. This is of course not true.

In Chiroptera the tympanic is also free, though it is connected sometimes by very dense connective tissue to the squamosal (Van Kamp.; Bondy, 1907, pp. 313–314, *Vesperugo noctula;* p. 316, *Vesperugo sero-*

tinus; p. 318, *Miniopterus;* p. 319, *Plecotus auritus*); or in the same manner to the so-called "Chordafortsatz," which in these cases forms a process of the basis of the processus hyoideus or of the periotic (Bondy, 1907, p. 318, *Miniopterus;* p. 320, *Rhinolophus hypposideros*).

In *Orycteropus* the tympanic is free, except its connection with the Folian process; the anterior leg lies against the squamosal just behind the fossa glenoidea without being connected with it, while the posterior leg is separated from the squamosal and lies only against the tympanohyal (Van Kamp.; Owen, 1840, pp. 59, 77; Turner, 1851, p. 220).

Also in *Manis* the tympanic is free and not coössified with other skeletal elements, as has been noticed somewhere in literature.

In *Cholœpus*, except in very old skulls, the tympanic is free in contrast to the adult *Bradypus*.

In the Gravigrada (Van Kamp.; Reinhardt, 1878, pp. 277, 336; 1879, p. 362) the tympanic is not attached to the skull, at least not as a rule, so that it is often absent. The loose condition is described for: *Glossotherium* (Owen, 1840, pp. 59, 77; Reinhardt, 1879, p. 362); for *Scelidotherium leptocephalum* (Owen, 1840, p. 77; Turner, 1851, p. 210); for *Mylodon robustus* (Turner, 1851, p. 210); for *Pelecyodon cristatus* (Scott, 1904, p. 310). The same loose condition is shown by my own investigations on *Lestodon*, where the tympanic, present on both sides of one skull, had a different place of attachment on both sides, so that it must have been movable. Sometimes the tympanic was partly present, partly absent in the material that the authors had under investigation, for example in *Nothrotherium texanum* (Hay, 1917, p. 118) and in *Grypotherium listai* (Woodward, 1900, pp. 66, 68). This also shows that it had not become ankylosed to the skull. In other cases it was absent in all the material. This was the case in *Mylodon robustus* (Owen, 1842, pp. 26, 28) and in *Megatherium americanum* (Owen, 1856, p. 573), in which the absence of any fractured surface indicated that it was not broken off as a mere process of the temporal, but that it was a loose element. It was absent in *Scelidotherium leptocephalum*, investigated by Owen (1858, p. 103) and by me; in *Nothrotherium* (=*Cœlodon*), investigated by Reinhardt (1878, p. 336), where also there are no indications that it has been broken off, so that it must have been a loose element which has fallen out (Reinhardt, 1878, pp. 336, 277). Finally, Brown (1903, p. 574) notices that the tympanic is lost in his material of *Paramylodon nebrascensis* and Scott (1904, p. 324) in that of *Planops magnus*.

Also, in the Glyptodontidæ the tympanic is unknown and, as there

are no fractured surfaces, the tympanic must have been loosely attached to the skull (Van Kamp.; Scott, 1903*b*, pp. 121, 123, *Propalæohoplophorus;* p. 159, *Metopotoxus*). Huxley's note (1865, p. 55) that in *Glyptodon* the bulla is broken away is not right, according to Van Kampen, while Huxley's tympanic is a part of the mastoid.

In the recent Dasypodidæ, except *Chlamydophorus, Dasypus* and *Zaëdyus*, the tympanic is not at all, or only feebly coössified with the skull. Thus, it is not true that in the dasypodes in general the tympanic bone soon becomes ankylosed with the other parts of the temporal as Owen says (1840, p. 59). A loose tympanic is emphasized, for example, in *Priodontes* (Turner, 1851, p. 215) and *Tolypeutes tricinctus* (Bondy, 1907, pp. 349, 350); in the latter species there is a connection only between the posterior leg of the tympanic with the "Chordafortsatz," which here forms a process of the periotic, while the anterior leg remains at a long distance from the skull. Among the fossils it was loosely attached in *Proeutatus robustus* (Scott, 1903*a*, p. 44). In *Chlamydotherium majus* (Winge, 1915, p. 94) the tympanic is unknown, but as there are no fractured surfaces the tympanic must have been loose.

In the primitive Rodentia the tympanic was free, as in the recent *Sminthus* or *Mus* (Winge, 1888, p. 110). It was loosely attached in the earlier genera of the family Ischyromyidæ (Matthew, 1910*b*, p. 44), in the genus *Sciuravus* (pp. 47, 60) and probably also in *Paramys* (p. 47).

Among the Creodonta the tympanic was free in most cases (Van Kampen). It is said or supposed to be free, loosely or not attached to the skull, in *Dissacus* (Matthew, 1909, p. 487), *Pachyæna* (Matthew 1909, p. 487), *Synoplotherium* (Matthew, 1909, p. 487), *Mesonyx* (Matthew 1909, p. 487), *Sinopa* (Wortman, 1902*b*, p. 439; Matthew, 1906, p. 212), *Stypolophus* (Winge, 1895*b*, pp. 48, 49), Miacidæ (Pohle, 1920, pp. 56, 57).

Among the recent Carnivora we find a loosely attached tympanic in *Nandinia* (Van Kamp.; Winge, 1895*b*, pp. 48, 49, 52; Pohle, 1920, pp. 56, 57), in *Paradoxus* (Van Kamp.; Pocock, 1916*a*, pp. 263, 264; Carlsson, 1920, p. 341) and in *Arctictis* (Carlsson, 1920, p. 341). A loosely attached or free tympanic is described in the fossil *Cynodictis intermedius* (Carlsson, 1914, p. 228), Amphicyoninæ (Zittel, 1923, p. 467), *Daphænus* (Matthew, 1906, p. 214; Scott, 1913, p. 526), *Daphænodon* (Scott, 1913, p. 525), so that it is rarely found in *Daphænus*, in *Cephalogale* (Filhol, 1883, p. 39), and in *Amphictis* (Winge, 1895*b*, p. 52; Pohle, 1917, p. 404).

In the Cetacea the tympanic is often not ankylosed or fused to the

periotic (Zittel, 1893, p. 162), as in the Odontoceti (Zittel, 1893, p. 169; Lydekker, 1887, p. 53) and in the Physeteridæ (Zittel, 1893, p. 177) or, which excludes a fused condition, the tympanic is said to articulate with the periotic, as in the Delphinidæ (Zittel, 1893, p. 175), in the Physeteridæ (Zittel, 1893, p. 177), and in *Diochotichus vanbenedeni* (True, 1910, p. 27). Later we shall see many examples of fusion in these groups. Schulte (1917) mentions in *Kogia* the absence of ankylosis between the tympanic and the periotic (pp. 383, 394) and describes in the mastoid region a facette for articulation with the processus petrosus of the tympanic (p. 396, no ankylosis as in *Phocæna*) but on the other hand mentions an ankylosis of the uncinate process on the rostral lip with the periotic (p. 396) and of a hooked process of the tympanic with the tegmen tympani (p. 396). In *Mesoplodon* the tympanic and periotic are not fused.

Among the Condylarthra the tympanic is said to be free in *Pleuraspidotherium* (Schlosser, 1921, p. 121; Zittel, 1893, p. 223).

In the Litopterna the tympanic is very loosely attached (Scott, 1910, p. 3). Scott (1910) notices it for the Proterotheriidæ (pp. 9, 10), the genus *Diadiaphorus* (pp. 15, 18) and *Theosodon* (p. 115), so that it was missing from all the skulls or was so in most cases.

In the Tapiridæ the tympanic is not ankylosed to the surrounding parts, so that it is rarely seen in dry skulls (Van Kamp.; Parker, 1882, p. 776); it is fused only with the Folian process of the malleus. In the fossil Rhinoceridæ the tympanic was also, in my opinion, loosely attached to the skull, so that it has easily fallen out (Scott, 1896, p. 358, *Hyracodon*). Therefore it is seldom figured, for example, in the many illustrations in the paper of Osborn (1893–1903); only Pl. XIIa of *Hyrachyus* shows a distinct bulla. Van Kampen found in an adult, though not a very old skull of *Rhinoceros sumatrensis*, that the tympanic was fused only with the Folian process, while in older skulls it is more firmly coalesced, as we shall see later. In the fossil *Palæotherium* (Cuvier, cited by Van Kampen, 1904, pp. 248; 1905, p. 581) the tympanic has also fallen out easily. In *Mesohippus* (Scott, 1891*b*, p. 306) as well, the tympanic is not ankylosed with the periotic and in most specimens has become detached and lost, though it was apparently coössified with the tympanohyal.

No doubt in the stem Perissodactyla the tympanic and the periotic had not coalesced (Gregory, 1910, p. 390).

In *Tragulus* and *Hyomoschus* the tympanic is loosely attached to the skull; neither is the bulla fused with the periotic, nor the external auditory meatus with the squamosal.

Also in the Cervidæ the tympanic is loosely attached to the skull. According to Bondy (1907), the two legs of the tympanic lie against the squamosal in *Cervus capreolus* (p. 376), while in *Cervus elaphus* (p. 377) the hind leg lies against the petrosal, but is separated from the free margin of the squamosal.

In the Bovidæ, as a rule, the tympanic is not coalesced with the skull; in other cases, however, they are fused.

Among the Amblypoda, the tympanic is supposed to be free in *Pantolambda* (Winge, 1906, p. 73).

In *Arsinoitherium* as well, the tympanic is loosely attached to the neurocranium (Winge, 1906, p. 164).

Tympanic and Bulla Attached

In many cases the tympanic is not loose but attached to the skull. It can be attached to the squamosal as a rule with two legs or with one leg, or it can be coössified with the other elements of the auditory bulla or, finally, it can coössify with one or more of the elements in the neighborhood. Thus the fusion with the periotic, though it sometimes occurs, does not happen in most cases, as one would suppose from some notes (Steinmann-Döderlein, 1890, p. 683).

a.—Tympanic Legs Attached to the Skull

The two legs of the tympanic ring growing upward become attached as a rule to the squamosal on the fore and hind part of the margo tympanicus squamosi. If the tympanic coössifies with the squamosal, usually first the hind leg, and often also the rostral leg, coösifies with the squamosal (Bondy, 1907, p. 301).

We find that among the marsupials the tympanic is coössified with the squamosal in all recent Phalangeridæ. So in the very old *Cholœpus* the hind leg of the tympanic is coössified with the cranium. In the adult *Bradypus* the tympanic is coössified with the squamosal, and also with the entotympanic, as we shall see later. In some Gravigrada where, as a rule, as we have seen, the tympanic is loose, this element can be attached to the skull. Perhaps this is due to the age of the specimen or to the species. This is perhaps the case in *Mylodon garmani* (Allen, 1913, p. 323; see also my own investigations) and in *Mylodon harlani* (Stock, 1914, p. 324, tympanic being "broken" away). In *Hapalops*, I found that the tympanic could be broken off, leaving the extremities attached to the skull, so there must have been a closer connection between the two. In *Megatherium mirabile*, which seems to differ from the other Gravigrada in the structure of the tympanic region, the tympanic was, according to Van Kampen, probably coössified with the skull and also with the entotym-

panic (Van Kamp.; Turner, 1851, p. 209, tympanic bone attached; Leidy, 1855, p. 52, the tympanic bone, called by Leidy the auditory process, extends from the outer extremity of the glenoid articular cavity to the apex of the mastoid process). In the Myrmecophagidæ the tympanic is coössified with the squamosal and also with the mastoid (Van Kamp.; Owen, 1840, p. 59).

Among the recent rodents the fusion of the tympanic with the periotic makes if often difficult or impossible to determine whether the auditory meatus is closed all around by the tympanic or not, and this includes the difficulty or impossibility of determining the place of the tops of the two tympanic legs.

According to Bondy (1907), the hind leg of the tympanic is fused with the periotic in *Mus silvaticus* (p. 340) and in his remarkable "Feldmaus" (pp. 343, 344), while in these species the rostral leg is free. In *Mus decumanus* (p. 336), the hind leg lies against a process of the periotic (which forms the basis of the "Chordafortsatz" and the lateral bony wall of the recessus epitympanicus) and the top of the front leg is connected with the tegmen tympani. Moreover, the bulla in rodents is sometimes coalesced with the mastoid, and the mesial lip often with the periotic (see below).

In the Creodonta the attachment of the bulla to the skull is probably often due to a fusion of the tops of the legs of the tympanic with the squamosal, as my own investigations in *Hyænodon* show. As the notes in literature do not mention the exact place of attachment, I will mention all these notes together when I sum up the connections of the bulla with the neighboring skeletal elements.

In the recent Felidæ the bulla is attached to the skull in one place only, where the hind leg of the squamosal and the lip of the tympanic, which forms the so-called external auditory meatus, are fused with the squamosal (Van Kamp.; Bondy, 1907, pp. 365, 366). According to Pocock (1916*a*, pp. 267, 268) there occurs also a fusion with the basisphenoid. In a specimen of *Canis familiaris* of about four months, the two legs of the tympanic are already fused with the squamosal (Bondy, 1907, p. 352).

In *Phoca vitulina* both legs of the tympanic are fused with the squamosal (Bondy, 1907, p. 368); moreover, the bulla shows still other fusions, as we shall see later.

These are the only exact data on the attachment of the tops of the two legs of the tympanic to the skull, which no doubt also occurs in other Carnivora.

In *Sus scrofa domestica*, the tops of both legs of the tympanic are ankyosed to the squamosal; first the caudal leg fuses, then the rostral (Bondy, 1908, p. 599). Bondy (1907, p. 371) mentions that in the lateral wall of the recessus epitympanicus of the adult *Sus scrofa domestica* it is difficult to separate squamosal and tympanic. Moreover, the bulla is fused in other ways with the skull, as we shall see later.

In the fossil *Anoplotherium* (Palmer, 1913*b*, pp. 881, 883, 884) the fusion of the bulla with the skull was perhaps due only to the attachment of the legs of the tympanic to the skull, which would explain that it falls out rather easily.

In the Sirenia both legs of the tympanic are fused with the periotic (Van Kamp.; Zittel, 1893, p. 191; Dilg, 1909, pp. 100, 141, *Manatus*). The mesial process, the crista tympanica, of the front leg is fused with the tegmen tympani, while the lateral process is free. The caudal leg is also fused with the periotic, in *Halicore* and *Manatus* also with the tympanohyal. Freund (1908) gives us more detailed information on *Halicore:* the mesial process of the rostral leg in the embryo is attached to the lamina parietalis (pp. 616, 617) on the caudal side of the incisure above the membrana Shrapnelli (p. 617); in the later developmental stages it is attached to the horizontal plate which is developed on the lamina parietalis (p. 621). The caudal leg in the embryo is also attached to the lamina parietalis (p. 616), on the caudal side of the incisure above the membrana Shrapnelli (p. 617); in the adult *Halicore* (p. 622) the mastoid shows a distinct place of attachment for the caudal leg. In *Rhytina stelleri* (Claudius, 1867, pp. 7, 8), also, the two legs of the tympanic are fused in the same way with the periotic; moreover the caudal process of the hind leg is coalesced with the periotic (p. 8). In *Halitherium schinzi* (Lepsius, 1882) the mesial or oral process of the front leg (p. 35) and the top of the hind leg are fused with the periotic (p. 34); moreover, the hind leg lies free against the pars mastoidea (pp. 34, 35) and is fused with the tympanohyal in a small place (p. 36). These are the only places where the tympanic is fused; the middle part of the tympanic is free from the surrounding bones and also from the periotic, with which only the ends of the two legs are fused. Therefore, Dilg (1909, p. 100) rejects the term "petrotympanic," which Lydekker (1887, p. 15) uses for *Rhytina gigas*. Probably Hay's note (1916, p. 387) that the tympanic in the fossil *Desmostylus hesperus* is not ankylosed to the surrounding bones, but that the sutures can not be distinguished, relates to the middle or ventral part of the tympanic ring.

A remarkable feature in respect to the conditions which are found

so typically among the Cetacea is the progressive loosening of the tympanic and the periotic. Dilg (1909, p. 127) describes the development of this feature in *Manatus:* in the early stages the tympanic and periotic are held in their place by the neighboring elements, the squamosal, basioccipital and exoccipital. Later on the skull grows, the foramina lacera anterius and posterius enlarge in size, while the tympanic and periotic show a relatively smaller growth, so that these elements become loose and nearly movable.

In the recent *Lemur* (Van Kamp.; Gregory, 1920, p. 163) the rostral leg of the tympanic is free, while the caudal leg is fused with the squamosal in only one part, viz., anteriorly to the stylomastoid foramen and also with the bulla, as we shall see later. In the recent *Chiromys* we have practically the same condition.

In the fossil *Notharctus osborni* (Gregory, 1920, p. 165) the tympanic ring was attached posteriorly to the junction of the posttympanic process of the squamosal with the outer wall of the bony carotid canal, at the postero-external angle of the bulla, anteriorly to the posterior wall of the entoglenoid region of the squamosal, internal to the postglenoid foramen. This position was substantially the same in *Adapis*, *Lemur* and *Propithecus* (Gregory, 1920, p. 165). In the fossil *Megaladapis edwardsi*, according to Lorenz von Liburnau (1905, p. 464), in contrast with the recent lemurs, the tympanic is not a free semi-ring but coössified with the lateral part of the roof of the tympanic cavity as in ruminants and other ungulates. According to Van Kampen (1905, not in edition 1904), perhaps it is possible that the note of Lorenz von Liburnau implies that the membrane, which in the recent lemurs connects the tympanic with the wall of the bulla, is ossified. In my view, it might imply also a firmer attachment of the tops of the tympanic legs to the skull.

In *Homo* the tops of both legs of the tympanic early coössify with the squamosal (Bondy, 1907, p. 387).

(*b*).—Tympanic Fused with Other Elements of the Bulla

Sometimes the tympanic coössifies with one or more of the other elements of the auditory bulla, often with the so-called false bulla, as often in the recent Phalangeridæ, in *Talpa* and in *Condylura*, and in the Notoryctidæ. In the Macroscelididæ (Van Kamp.; Carlsson, 1910*a*, p. 352; 1922, p. 231) the tympanic is coalesced with the entotympanic. Also in Chiroptera the tympanic is often connected with the osseous bulla (Gregory, 1910, p. 319). In the adult *Bradypus* the tympanic is coössified with the entotympanic and with the squamosal, as we have seen above.

In *Mylodon garmani* the tympanic is, according to Allen (1913, p. 323), solidly fused with the petrosum, with which my own investigations agree, with the exception that this element is not a part of the periotic but of the entotympanic. The same was perhaps the case in *Mylodon harlani* (Stock, 1914, p. 324, tympanic "broken" away). According to Van Kampen, in *Megatherium mirabile* the tympanic was probably coössified with the entotympanics as well as with the skull.

In the recent Carnivora where an entotympanic is found, the tympanic is practically always fused with the entotympanic. We find this in the Canidæ, Mustelidæ (Van der Klaauw, 1924*b*, *Meles*), most of the Viverridæ (Van Kamp.; Pocock, 1916*a*, p. 264), Hyænidæ, Felidæ (Van Kamp.; Winge, 1895*b*, p. 54) and the Phocidæ, Otariidæ and Trichechidæ. No fusion occurs in *Paradoxurus* (Van Kamp; Pocock, 1916*a*, p. 263), *Cynogale*, *Diplogale* (Pocock, 1916*a*, p. 264) and *Paguma larvata* (Pocock, 1916*a*, p. 263). The same is the case in the fossil mustelid *Palæoprionodon*, according to Winge (1895*b*, p. 54).

According to Owen (1859, p. 313), in the cat, dog, hyæna, civet, otter, and bear, the tympanic bulla is formed by the inflated petrosal with which the true tympanic has coalesced. Probably the entotympanic is signified by this "inflated petrosal," though the entotympanic is not known in all mentioned species.

In the old *Rhinoceros* the tympanic is fused with the entotympanic.

If in the recent Suidæ, an entotympanic is present, this is fused with the tympanic.

In the recent Procavia the tympanic is coalesced with the entotympanic, which in turn is fused with the skull, as we shall see later.

In the recent *Lemur* the caudal leg of the tympanic is not only fused with the squamosal but also with the margin of the bulla, though it is for the larger part free from the bulla (Van Kamp.; Gregory, 1920, p. 163; Carlsson, 1922, p. 231). In the recent *Chiromys* we have practically the same condition. In the fossil *Megaladapis edwardsi*, according to Lorenz von Liburnau (1905, p. 464), in contrast with the recent lemurs, the tympanic is not a free semi-ring but coössified with the lateral part of the roof of the tympanic cavity as in ruminants and other ungulates. According to Van Kampen (1905, not in addition 1904) it is possible that the note of Lorenz von Liburnau implies that the membrane which in the recent lemurs connects the tympanic with the wall of the bulla is ossified.

In the Lorisidæ, Galaginæ and Tarsiidæ the tympanic is fused with the processus tympanicus petrosi (Van Kamp.; Carlsson, 1922, p. 231). Also in the Hapalidæ, Cebidæ, Cercopithecidæ, Hylobatidæ and Anthro-

pomorphæ the tympanic is fused with the processus tympanicus of the petrosal. In his material of *Macacus nemestrinus*, Bondy (1907, p. 383) describes in the neighborhood of the caudal leg of the tympanic only connective tissue between the tympanic and the periotic. Gregory (1920, p. 181) speaks of a petrotympanic or fused petrosal and tympanic in man.

(*c*).—Tympanic or Bulla Fused with Neighboring Elements

The tympanic or the bulla in general may coössify with one or more of the elements in the neighborhood. In the Phalangeridæ it is coössified with the mastoid. In *Talpa* no sutures are visible (Van Kamp.; Bondy, 1907, p. 305). In *Galeopithecus* the bulla is rostrally coossified with the mesiocaudal margin of the fossa glenoidea, caudally with the mastoid and in older age also with the exoccipital; the bony cylindrical external auditory meatus is also ossified with the neighboring elements.

Among the recent Dasypodidæ the tympanic is firmly coössified with the skull in *Chlamydophorus, Dasypus* and *Zaëdyus;* in the two last-mentioned genera the cylindrical external auditory meatus is coössified with the squamosal and with the mastoid. As we have already noticed, Owen's remark (1840, p. 59), that in the dasypodes in general the tympanic bone soon becomes ankylosed with the other parts of the temporal bone, is not correct. Among the fossils, Scott (1903*a*, p. 90) mentions that in *Peltephilus* the bulla is firmly connected with the surrounding bones.

In the Myrmecophagidæ the tympanic is not only coössified with the squamosal but also with the mastoid (Van Kamp.; Owen, 1840, p. 59).

Among the recent rodents we often find a "petrotympanic." Then the mesial lip of the bulla is fused with the periotic (Winge, 1888, pp. 113, 114, 191, *Lagomys*). This, however, does not occur in *Lepus* (Van Kamp.; Winge, 1888, pp. 114, 191, *Lepus, Palæolagus*), *Pedetes*, most of the Muridæ or perhaps all Muridæ (Van Kamp.; Bondy, 1907, pp. 336, 340, 343, 344). In *Castor fiber* the bulla is fused with the tegmen tympani only. In other rodents, where the fusion with the periotic is lacking, the bulla can be coalesced with the mastoid. In *Lepus* this fusion is lacking as well.

Bondy gives us some information but unfortunately does not tell us the exact place of the fusion. As I suppose that the fusion of the bulla in general and not that of the tops of the two legs only is meant, I mention these notes here. In *Sciurus vulgaris* (Bondy, 1907, p. 324) and in *Spermophilus citillus* (p. 328) the elements of the os temporale are

so strongly fused that it was not possible to separate them nor to determine their sutures. In *Arvicola arvalis* (p. 334) the tympanic was still separated from the neighboring elements in its rostral part, while caudally it was fused. A similar incomplete information on the place of fusion is given in some palæontological notes. In *Ischyromys* (Matthew 1910*b*, p. 61) the bulla is always attached to the skull. In *Neoreomys* (Scott, 1905, p. 392) the tympanic is coössified with the periotic. In *Entoptychus* (Zittel, 1893, p. 533) the bulla is not distinctly separated from the mastoid.

A remarkable change in this respect occurs during the development of *Hydrochœrus capybara* (Preller, 1907). In the new-born animal (pp. 379, 387) the tympanic is coalesced with the periotic, but later (pp. 387, 411) the foramina lacera anterius and posterius enlarge in size and the bulla becomes movable as in *Paca*.

In the Creodonta the bulla is fused to the neighboring skull-elements, according to Zittel (1893, p. 581), but this is true for only a part of the creodonts. In *Harpagolestes*, *Dissacus saurognathus*, and *Pachyæna gigantea*, the tympanic is ankylosed to the squamosal (Matthew, 1909, pp. 486, 487). In *Synoplotherium* (Cope, 1873*a*, p. 555; 1873*b*, p. 205) a laminar expansion of the mastoid overlaps the posterior half of the external auditory tube, with which the tympanic was perhaps fused.

In the recent Ursidæ the cylindrical auditory meatus is fused with the squamosal and with the mastoid.

In the Mustelidæ the cylindrical auditory meatus is ankylosed to the mastoid and the posttympanic process. As a rule, it is separated from the postglenoid process, a feature related to the rostral position of the glenoid fossa; in *Mellivora* (Van Kamp.; Winge, 1895*b*, p. 67) and *Zorilla* the tympanic is fused with the processus postglenoideus. In *Zorilla*, *Pœcilogale*, and some species of the genus *Putorius* and *Ictidonyx* (Winge, 1895*b*, p. 67) the bulla has coalesced with the processus pterygoideus. Bondy (1907), in his material (*Fœtorius vulgaris*, p. 355; *Fœtorius putorius*, p. 358; *Mustela foina*, p. 361), mentions the lack of sutures in this region.

In the Herpestinæ the external auditory meatus is fused with the squamosal, in the Viverrinæ the tympanic itself. In *Paradoxurus* and *Arctictis* the rostral wall of the bulla is fused with the squamosal. In the Herpestinæ and *Cryptoprocta* the bulla is fused with the mastoid.

In the Hyænidæ the bulla is fused with the squamosal.

In the recent Felidæ the tympanic is often said to be attached to the squamosal with the caudal leg only, as we have seen, but according

to Pocock (1916*a*, pp. 267, 268) the anterior end of the bulla is immovably fused to the basisphenoid. In the fossil *Machairodus* (Winge, 1895*b*, pp. 55, 56) the external auditory meatus is fused to the mastoid process.

In the Phocidæ the cylindrical auditory meatus is fused with the squamosal and with the mastoid. In older specimens of the Otariidæ the bulla is fused to the mastoid and to the postglenoid process. In the Trichechidæ the bulla is fused with the postglenoid process and with the "mastoid process," which probably, also, contains the posttympanic and the paroccipital process in this group.

In the Delphinidæ and Phocænidæ the tympanic and periotic coössify rather early in development, as follows: the processus tubarius of the tympanic fuses with the processus anterior periotici of the tegmen tympani; the processus petrosus s. posterior of the tympanic coössifies with the processus tympanicus petrosi (the mastoid). The connecting part in this last-mentioned pedicle shows in some genera an apertura posterior for the sinus pneumaticus paroccipitalis, in others this aperture is lacking. This posterior process bears a groove for the facial nerve. The posterior pedicle is broad and massive; by exception only, as in *Globiocephalus*, long and pointed, resembling the condition in the Physeteridæ.

In *Platanista* the processus posterior is better developed than in the Delphinidæ.

In the Physeteridæ the processus posterior of the tympanic has been described as "mastoid," but according to Van Kampen this is not true; morphologically this process is the abnormally situated hind-lip of the external auditory meatus. This process of the tympanic does not seem to be fused with the mastoid. In *Hyperoödon* and perhaps also in other Physeteridæ, the apertura posterior is lacking. Schulte (1917, p. 396) mentions in *Kogia* an uncinate process on the rostral lip of the bulla which is received in a concavity of the periotic and is firmly ankylosed with that bone and a hooked process of the tympanic which is ankylosed to the tegmen tympani.

According to Hanke (1914, p. 506), in the Odontoceti the tympanic and periotic can be fused, moreover, by means of the processus sigmoideus and of the part of the upper border between the processus sigmoideus and the processus anterior bullæ, which, however, can also touch the periotic without being fused with it.

The petrotympanic in the Cetacea is often loosely attached to the skull, a feature easily understood in connection with the mode of hearing (see Matthes, 1912, pp. 596, 597). Yet the bulla does not easily fall out

in all cases as one would suppose according to some notes (Zittel, 1893, p. 162; 1923, p. 485; Stromer von Reichenbach, 1912, p. 184), as it is often firmly fused with the periotic and this petrotympanic is often held in its place by the neighboring elements and by its own processes.

The petrotympanic is, as a rule, loosely attached to the skull in the Odontoceti (Van Kamp.; Hanke, 1914, p. 522).

In the Delphinidæ and Phocænidæ the petrotympanic is not fused with the skull; they are connected by ligaments only, so it easily falls out in the dry skull (Van Kamp.; Matthes, 1912, pp. 594, 595, *Phocæna*).

In the dry skull of *Platanista* the petrotympanic does not fall out; it is held in its place by the processus falciformis (=pars entoglenoidea of the squamosal) and also by the pterygoid. An attachment to the skull by the processus posterior has also been described. Hanke (1914, p. 504) mentions *Platanista gangetica* as well as an exception to the other Odontoceti, in which the petrotympanic is connected to the skull by connective tissue only.

In the Physeteridæ the petrotympanic does not fall out either in the dry skull, as it is held in its place by the processus falciformis of the squamosal (=pars entoglenoidea) which holds the tegmen tympani in its place, and by the strongly developed processus posterior of the tympanic, which is connected with the squamosal and exoccipital. In *Kogia*, according to Schulte (1917, p. 394), this large lateral portion of the tympanic, which shows an irregular pyramidal form, fits between the squamosal, the exoccipital and the otocranial flange of the basioccipital, presenting its broad base in the lateral surface of the skull.

In general the two processes by which the petrotympanic is attached to the skull differ in the Odontoceti from those in the Mystacoceti, especially in size (Van Kamp.; Hanke, 1914, p. 505).

In the Mystacoceti the tympanic and periotic are connected (Zittel, 1893, p. 180; Lydekker, 1887, p. 16) by two narrow, very thin, bony bridges, thus differing from those of the Odontoceti (Hanke, 1914, p. 505). These two bridges are formed as follows (p. 505) : the processus anterior bullæ is fused with the periotic or with the processus anterior petrosi, forming together a rostrally directed process; the processus posterior bullæ is fused with the processus posterior petrosi, which together form a long characteristic process (Van Kamp.; Abel, 1912, p. 458). No other connections between the periotic and tympanic occur in the Mystacoceti (Hanke, 1914, p. 506), which thus differ from the Odontoceti. According to Lillie (1910, p. 778), in *Balænoptera* the anterior bony bridge connecting the anterior extremity of the tympanic with the inferior surface of the

periotic is longitudinally flattened; this pedicle, as well as the posterior, is thin (p. 781). In *Balænoptera sibbaldi*, Turner (1913, p. 14) describes a broad posterior pedicle connecting the upper border of the outer surface of the tympanic to the under border of the long, flattened, wing-like opisthotic process of the petrous bone; also the anterior pedicle (p. 16) connecting the upper border of the anterior part of the outer surface of the tympanic bulla with the petrous bone is broad. The investigations of Ridewood (1922, p. 242) on *Megaptera* show us that the fusion of both pedicles of the tympanic with the periotic develops rather late. *Balænoptera* does not show an apertura posterior. A groove for the facial nerve in the processus posterior is present (Van Kamp.; Hanke, 1914, p. 507). In *Balæna* the processus posterior is perhaps formed by the tympanic only, or together with the mastoid.

In the Balænopteridæ the petrotympanic is held in its place anteriorly by the processus falciformis and the pterygoid, posteriorly by the processus posterior. According to Hanke (1914, p. 504), the anterior attachment in the Mystacoceti is caused by the processus anterior petrosi, which lies in a pit of the squamosal. The posterior process is wedged in between the squamosal and the occipital without being fused with these elements (Hanke, 1914, pp. 504, 505, 523; Abel, 1912, pp. 458, 459; Ridewood, 1922, p. 240). Though not so firmly, as in many land-mammals, the petrotympanic of the Mystacoceti is much better attached to the skull than in the Odontoceti and is, as a rule, preserved in dry skulls (Hanke, 1914, pp. 504, 505, 523). According to Ridewood (1922, pp. 231, 236) the anterior and posterior extensions, which in the adult *Megaptera* hold the periotic in position, develop relatively late, also a process from the hind edge of the squamosal that meets the posterior pedicle of the tympanic.

As to *Protocetus atavus*, Van Kampen (1905) concludes from the literature that the neighborhood of the bulla was more like that in the Carnivora than like that in the recent Cetacea, and was also probably attached to the skull in another way from that in the recent Cetacea.

In the old *Rhinoceros* the tympanic is fused with the entotympanic, while the latter is coalesced with the periotic and sometimes also with the basioccipital.

In *Equus* the bulla is ankylosed with the petrosal (Van Kamp.; Scott, 1891*b*, p. 311), while in the fossil *Mesohippus* (Scott, 1891*b*, p. 306) the tympanic was not ankylosed with the periotic, and in most specimens has become detached and lost, as we have seen; it is apparently coössified with the tympanohyal.

In the recent Suidæ the bulla is not coalesced with the periotic. The bulla is held in its place, as the external auditory meatus is enclosed in a false auditory meatus formed by the strongly developed posttympanic process, which is coalesced with the hind wall of the fossa glenoidea. The false auditory meatus lies close against the lateral wall of the bulla and encloses the basis of the cylindrical external auditory meatus as well. *Dicotyles* shows only a canal between the under wall of the cylindrical and the false auditory meatus. The top of the posttympanic process runs downward along the lateral wall of the bulla, with which it is fused. The cylindrical auditory meatus in *Sus* is formed by the tympanic and the squamosal, which are fused without suture.

In the recent Hippopotamidæ as well, the cylindrical auditory meatus is fused with the squamosal, while the hind wall of the bulla is fused with the basis of the paroccipital process.

In the fossil *Anoplotherium* (Palmer, 1913*b*, pp. 883, 884) the tympanic is not ankylosed with the periotic, while the fusion with the squamosal is perhaps due only to the legs of the tympanic, as the bulla falls out rather easily (pp. 881, 884).

In the recent Camelidæ the cylindrical auditory meatus early fuses with the squamosal; in the adult skull the bulla is fused with the tympanohyal.

In the fossil *Poëbrotherium*, according to Scott (1891*a*, p. 16), the posttympanic process is closely united with the posterior lip of the meatus auditorius, while, according to Loomis (1910, p. 321), the bulla is fused to the paroccipital process. In the fossil *Stenomylus* (Loomis, 1910, pp. 302, 321) the postglenoid facet is closely appressed to the bulla, the tympanic bone is fused to the squamosal and also to the paroccipital process for most of its length. In the fossil *Alticamelus altus* (Matthew, 1893–1903, p. 430) the bulla is in the same condition as in the modern species, except that the paroccipital process is less firmly soldered to the bulla.

In the recent Giraffidæ the thickened rostral wall of the external auditory meatus is united with the postglenoid process.

In *Bos taurus* the inner lip of the bulla is fused with the periotic, while in the Bovidæ in general, as a rule, the bulla is not coalesced with the skull.

In the fossil Typotheria, according to Scott (1912, p. 292), the tympanic is ankylosed with the mastoid (posttympanic of Roth). In *Interatherium* (Sinclair, 1909, p. 51) the squamosal is firmly coössified with the auditory meatus. In *Hegetotherium*, according to Sinclair (1909,

pp. 71, 74), the postglenoid process is closely fused with the auditory meatus; usually the suture between the squamosal and the auditory meatus has been obliterated, so that the latter is frequently fused with the squamosal. According to Scott (1912, p. 290), the tympanic in *Hegototherium* is ankylosed with the thin, compressed plate which is called the mastoid or protuberancia petrosa (Roth). In the fossil *Protypotherium* (Sinclair, 1909, p. 22) the bulla is more or less completely fused with the basioccipital. In *Typotherium cristatum* Van Kampen found that the auditory meatus was coössified without suture with the squamosal.

In the Toxodonta (Scott, 1912, pp. 291, 292) the tympanic is fused with a thin plate which ends in a well-defined process and which seems to be the mastoid (protuberancia petrosa), but may in fact be an outgrowth of the tympanic. According to Van Kampen's own investigations, the tympanic portion of the cylindrical auditory meatus in *Toxodon* fuses early with the squamosal; later on the posttympanic process is fused with the cylindrical auditory meatus.

In the recent *Procavia* the anterior part of the mesial margin of the bulla is fused with the periotic, the posterior part remaining free; later on the tympanic coössifies with the tympanohyal.

In *Elephas* the bulla is not fused with the squamosal but is fused with the periotic and the tympanohyal only. A groove marks the place of fusion between the tympanic and the periotic.

The fusion in the fossil *Mastodon* is perhaps similar to that in the recent *Elephas* (Weithofer, 1890, p. 114), though it is not clear whether the bulla is fused with the periotic or with the basis cranii.

In old skulls of the fossil *Mesopropithecus* (Standing, 1908, p. 93) there is a fusion of the postglenoid process with the bulla. In the modern Lemuridæ as a rule the outer wall of the bulla is fused with the processus postglenoideus. In the recent *Nycticebus* and *Loris* the cylindrical external auditory meatus is fused with the postglenoid and with the posttympanic process.

In the Cercopithecidæ as well, the external auditory meatus is fused with the squamosal. Bondy (1907, p. 383) mentions that in *Macacus nemestrinus* the tympanic could not be separated from the squamosal.

Form and Size of the Auditory Bulla

At the beginning of this chapter we can mention the remark given by Cope (1882, p. 472; 1883, p. 113) for the Carnivora, but which has general value. Cope says: "Although the degree and form of inflation

are characteristic of various groups, they cannot be used in a systematic sense, because, like all characters of proportion merely, there is no way of expressing them in a tangible form. For, if the forms in question pass into each other, the gradations are insensible and not sensible, as is the case with an organ composed of distinct parts." Yet these characters are often used and they are no doubt valuable if they are based on the comparison of a great many specimens of different age and sex with those of allied species or groups. If this is not the case, as sometimes occurs, especially in fossils, the notes on the degrees of inflation, lacking remarks on the differences with allied forms, have little value.

The form of the bulla is very different, even in closely allied animals. For example, among the Phalangeridæ the bulla is low in *Phalanger*, for the rest, inflated, and in the genus *Pseudochirus* varying with the species. Among the Macropodidæ the form of the bulla is also very variable, even in the same genus; it can be strongly inflated, flat, or even concave. This shows that the systematic value of this character can be unimportant in distinguishing larger groups. Thus the form of the auditory bulla in *Phascolarctus* resembles that of *Sus;* in both, the bulla is very high and laterally compressed so that it shows a medial and a lateral flat wall sharply bending round.

Among the insectivores the bulla is, as a rule, flat. So the uninflated bulla in the fossil Tillodontia is one of the reasons for classifying this group with the insectivores instead of with the Rodentia, where the bulla is in general large and inflated (Gregory, 1910, p. 293; Zittel, 1893, p. 507; 1923, p. 450). Among recent insectivores, for example in *Talpa europæa*, the bulla is so flat that the tympanic membrane is nearly horizontal and the bulla is hardly to be discerned from the vicinity, especially before and behind, the inner wall alone being a little more distinct (Van Kamp.; Zittel, 1893, p. 563; 1923, p. 445). In *Chrysochloris* the bulla is strongly protuberant and resembles in its hemispherical form that of the fossil *Xenotherium* (Gregory, 1910, p. 258). *Rhynchocyon* shows a strongly inflated bulla and the bulla of *Macroscelides* also is extraordinarily large (Van Kamp.; Schlosser, 1887, p. 116); in the latter genus it is especially due to the inflation of the tympanic wing of the alisphenoid. In contrast to the greatly inflated bulla in *Rhynchocyon* and *Macroscelides typicus*, the bulla in the genera *Elephantulus* and *Nasilio* is small (Carlsson, 1910*a*, p. 353). Also in *Tupaia* the bulla is large but in the allied *Ptilocercus* it is smaller and narrower, resembling a broad semicircular ring, and is in this respect more primitive than *Tupaia* (see also: Gregory, 1910, p. 272; Carlsson, 1910*a*, p. 352).

In the Microchiroptera the bullæ are inflated to a different degree. There is said to be a correlation between the inflation of the auditory bulla and the size of the external ear, but there are exceptions to this rule (Van Kamp.; Wing, 1893*b*, p. 13 *Vesperugo*). Thus the bulla is not always very much inflated as one would suppose according to Zittel (1893, p. 572). The so-called cochlea-like form of the bulla in the Chiroptera (Schlosser, 1887, p. 137) is perhaps due to the fact that the two parts of the bulla (the tympanic and the entotympanic) resemble a cochlea.

Among the Dasypodidæ the bulla in the fossil *Prozaëdius* (Scott, 1903*a*, p. 71) is very much like that of *Dasypus* and *Zaëdyus*, but is not so large as in these two modern genera, while in the fossil *Peltephilus* (Scott, 1903*a*, p. 90) the bulla is relatively as large as in *Dasypus*. Now according to Van Kampen the bulla in *Dasypus* and *Zaëdyus* is low in comparison to that in *Chlamydophorus*, where it is wide and oval, resembling the bulla in rodents.

In the recent rodents the bulla shows different sizes. Sometimes it is very small (Van Kamp.; Winge, 1888, p. 49, *Calomys saltator;* p. 56, *Rhipidomys mastacalis;* p. 59, *Nectomys squamipes;* p. 124, *Cricetus;* Preller, 1907, pp. 390, 411, *Hydrochœrus*), the tympanic in that case being but a slightly broadened semi-ring, which is sometimes nearly flat in the transversal direction. In all other cases the bulla is more inflated (Van Kamp.; Winge, 1888, p. 23, *Sigmodon vulpinus;* p. 33, *Habrothrix lasiurus;* p. 19, *Hesperomys expulsus;* p. 53, *Calomys laticeps;* p. 77, *Dactylomys amblyonyx;* p. 83, *Loncheres armatus;* p. 92, *Nelomys antricola;* p. 98, *Carterodon sulcidens;* p. 110, primitive rodents, *Sminthus, Mus;* p. 113, *Lagomys;* p. 118, *Pedetes;* p. 119, *Sminthus;* p. 120, *Scirtetes;* p. 123, *Graphiurus,* p. 123, *Platacanthomys;* p. 124, Gerbilli; p. 128, Hystricini; Preller, 1907, p. 411, *Dinomys*), and is sometimes even large (Van Kamp.; Gregory, 1910, p. 329; Zittel, 1893, p. 515; Van Kamp.; Winge, 1888, p. 41, *Scapteromys labiosus;* p. 95, *Mesomys spinosus;* pp. 120, 121, *Dipus;* p. 134, *Habrocoma*); it has then the form of a semi-globe or it is lengthened in the longitudinal direction. Sometimes the bulla is distinctly narrowed in the rostral part and can be more or less pear-shaped in that case (Van Kamp.; Winge, 1888, p. 19, *Hesperomys expulsus;* p. 35, *Calomys laticeps;* p. 56, *Rhipidomys mastacalis;* p. 59, *Nectomys squamipes;* Preller, 1907, pp. 387, 411, *Hydrochœrus capybara*). This narrow rostral part of the bulla is differently developed in these examples, but in *Calomys laticeps* (Winge, 1888, p. 53) this protuberance of the bulla is individually vari-

able; it can be large or small or even almost absent. Perhaps this protuberance described by Winge contains also the processus styliformis.

Sometimes the bulla is large, but very little inflated in the downward direction. According to Winge (1888, pp. 68, 69) the bulla in *Cavia porcellus* shows important differences in size and inflation, which are independent of age. Also Kellogg (1912, p. 163) mentions great variation in the size of the bullæ of *Erethizon epixanthum*, while according to Allen (1904*b*, p. 383) *Erethizon godfreyi* differs from *Erethizon epixanthum* in the greatly reduced bullæ. The bulla in rodents resembles in form that of the ungulates; for example, the bulla in *Castor* resembles that in the artiodactyls.

As to the fossil rodents, the best we can do is to include a summary of the descriptions given in the literature.

In *Ischyromys* the auditory bulla is large, while in allied genera it is incomplete (Matthew, 1910*b*, p. 61). In *Steneofiber simplicidens* the bullæ are rather small, intermediate between *nebrascensis* and the later forms (Matthew, 1907, p. 206). In *Entoptychus formosus* (Matthew, 1907, p. 212; Zittel, 1893, p. 533) the bullæ are somewhat smaller than in *Thomomys* and more like those of *Heteromys*. In *Steiromys* (Scott, 1905, p. 414) the bullæ are far smaller than in *Erethizon* or *Cœndou*. In *Sciamys* (Scott, 1905, p. 421) and in *Spaniomys* (Scott, 1905, p. 410) the bullæ are greatly inflated. In *Neoreomys* (Scott, 1905, p. 392) the inflated bulla is large, not unlike that of *Dasyprocta*, but has a still closer resemblance to that of *Cavia*. In the different species of *Perimys* (Scott, 1905, pp. 435, 439, 441, 444, 446) the bullæ are very greatly inflated, larger than in *Viscaccia* (pp. 435, 444) and more spheroidal in shape (p. 444), and in *Perimys puellus* it is larger than in any other species with which Scott (1905, p. 446) was able to compare it. In *Prolagostomus* (Scott, 1905, p. 451) the bulla was, like that in *Perimys*, greatly inflated. The bulla of *Eocardia* (Scott, 1905, p. 463) is of only moderate size and is relatively less inflated than that in *Dolichotis*. In *Schistomys* (Scott, 1905, p. 480) the bullæ are smaller than in *Dolichotis*, especially in the transverse diameter. In *Citellus beecheyi captus* (Kellogg, 1912, p. 165) the bullæ are relatively long and narrow.

The note of Zittel (1893, p. 581), that the bulla in the Creodonta is usually rather inflated, must be considered with prudence, as the bulla in many creodonts is yet unknown, and as there are also examples of a flattened condition. In *Harpagolestes* (Wortman, 1901, p. 288; Matthew, 1909, p. 486) the small, slightly inflated bulla is apparently depressed as in the Ursidæ. Also in *Synoplotherium* (Cope, 1873*a*, pp.

555, 557; 1873*b*, pp. 205, 206) the small tympanic chamber is narrow and even less expanded than that in the bears, which it resembles more than that of any carnivorous type. In *Dromocyon* (Wortman, 1901, p. 294; Gregory, 1910, p. 303) the inflated bulla is of moderate size. According to Schlosser (1890, p. 71) the bulla in *Hyænodon brachyrhynchus* in contrast to that of *Pterodon* shows no depression of the hind and inner part of the bulla.

The bulla in *Hyænodon crucians* (see my own investigations) was small and inflated.

In the Fissipedia the bulla is very different, as we shall see, and not always of important size (Zittel, 1893, p. 608; Stromer von Reichenbach, 1912, p. 151); also the degree and form of inflation is very different (Van Kamp.; Cope, 1882, p. 472; 1883, p. 113).

In the Canidæ in general the bulla is well inflated (Van Kamp.; Reynolds, 1909, p. 10), usually but little longer than broad, seldom very oblong.

In the recent Canidæ the auditory bulla is extended less backward than in the recent Felidæ, so that the porus acusticus externus lies halfway in the lateral wall of the bulla and not in the rostral half. The maximal height lies nearly in the middle of the bulla, a little mesialward. The bulla is inflated to a different degree, sometimes enormously inflated (Van Kamp.; Zittel, 1893, pp. 608, 620, 632, *Otocyon*, Schlosser, 1899, p. 116; Scott, 1913, p. 520). Examples of these differences in form and inflation are given by Winge (1895*b*). The bulla in *Icticyon piscivorus* (Winge, 1895*b*, pp. 28, 116) is a little larger than in *Icticyon venaticus* (pp. 30, 117), where the bulla resembles the short but much inflated bulla in *Canis cancrivorus* (pp. 23, 114). In both species of *Icticyon* the bulla is smaller than in *Canis azaræ* (pp. 28, 116; 30, 117). A relatively small bulla is shown in *Canis jubatus* (pp. 25, 114) and *Canis azaræ* (pp. 18, 112), where the bulla is less inflated than in other allied Canidæ. Winge supposes that the bulla in *Canis azaræ* may show variations similar in form to those in *Canis vulpes* and other dogs (pp. 18, 112) and in *Canis vetulus* (pp. 21, 113), where the bulla may be as small as in *Canis azaræ* but may also be extraordinarily large sometimes. The bullæ in wolves are larger than in dogs (Reynolds, 1909, p. 23). Also in the fossil *Tephrocyon rurestris* (Merriam, 1906, p. 7) the bullæ are very large.

As to the fossil Cynodictinæ we find extremely large bullæ in *Temnocyon* (Cope, 1879, p. 181; 1880*a*, p. 95; Scott, 1895*b*, p. 66), which are much more prominent than those in *Cynodesmus thoöides* (Scott, 1895*b*, p. 66), in which the large inflated bullæ equal in actual

size, and therefore proportionally exceed in size those in *Canis latrans*. According to Cope (1881*b*, p. 389) the bulla in *Canis* (*Cynodemsus*) *brachypus* is not very large, but is much swollen; also in *Cynodesmus thomsoni* (Matthew, 1907, p. 187) the bulla is of moderate size. In *Mesocyon* (Thorpe, 1922*a*, pp. 170, 171) the bullæ are narrow and ovate, differently ovate in different species. In *Nothocyon* (Wortman and Matthew, 1899, p. 125; Scott, 1913, p. 529) the bullæ are large and inflated. In *Nothocyon latidens* and *lemur* (Wortman and Matthew, 1899, p. 127; Matthew, 1907, p. 182) the bulla is very large. In *Nothocyon* (*Galecynus*) *geismarianus* (Wortman and Matthew, 1899, p. 127; Matthew, 1907, p. 182) though still large, it is of more moderate size, while in the variety *mollis* (Merriam, 1906, p. 13) the bulla is relatively as large as in *Nothocyon lemur* and much larger than in *Cynodictis* (?) *oregonensis*. In *Nothocyon gregorii* (Matthew, 1907, p. 183) the bullæ are larger and closer together than in "*Galecynus*" *geismarianus*. In *Procynodictis* (Scott, 1913, p. 529) and in the North American *Cynodictis* (Scott, 1913, p. 529; Teilhard de Chardin, 1914–1915, p. 29; Zittel, 1923, p. 466) the bullæ are large and inflated. In *Philothrox condoni* (Merriam, 1906, p. 31) as well, the bulla is large.

In the fossil *Amphicyon* (Filhol, 1883, pp. 30, 84, 85, 96) the bulla seems to have been inflated, resembling that of *Cynodictis* (pp. 85, 96), much more inflated than that in *Ursus*, (p. 85) and resembling that in *Canis* (pp. 30, 84), being only relatively a little longer and narrower than that in *Canis*. In *Enhydrocyon crassidens* (Matthew, 1907, p. 191) the bulla is large, longitudinally oval. Extraordinarily remarkable are the conditions in *Daphænus* (Leidy, 1853, p. 393; Zittel, 1893, p. 625; Scott, 1895*b*, p. 73; 1913, p. 526; Matthew, 1906, p. 214) where the anterior true tympanic bulla only is ossified or preserved so that these skulls show a small bulla. In *Pliocyon medius* (Matthew, 1918, p. 194; see also my own investigations) as well, the anterior small bulla only is practically preserved. Perhaps in *Daphænodon* we have a similar condition; in this genus the bulla is less reduced than in *Pliocyon* (Matthew, 1918, p. 194) and is smaller than in the wolf (Scott, 1913, p. 525). The peculiar conditions found in *Daphænus* are perhaps the reason that Zittel (1923, p. 467) mentions as a character of the Amphicyoninæ in general that the bulla is usually small.

As to the fossil Cynodontinæ, the description by Filhol (1883, p. 39) of *Cephalogale* states that the bulla is longitudinally elongated, the inner wall vertical; the general form more closely resembles that in the Viverridæ than that in *Canis*. In *Dinocyon* (?*Borophagus*) *gidleyi* the bulla is inflated, but smaller than typical Canidæ and propor-

tionally smaller than in the wolf (Matthew, 1902*a*, pp. 131, 132). In *Cynodon* (*Plesiocyon* of Schlosser) the bullæ are very much inflated (Teilhard de Chardin, 1914–1915, p. 41). In *Plesiocyon* (Teilhard de Chardin, 1914–1915, p. 53) the bulla is large. In *Paracynodon* (Schlosser, 1899, pp. 115, 116, 144; Teilhard de Chardin, 1914–1915, p. 52) the ossified bullæ were convex, but very small, smaller than in the Canidæ in general. The bullæ in *Pachycynodon* (Schlosser, 1899, p. 114; Teilhard de Chardin, 1914– 1915, pp. 40, 41) though better developed than in the Ursidæ, were small and very convex or even flattened as in *Cynodon* (Teilhard de Chardin, 1914–1915, p. 41).

In the recent adult Ursidæ the bulla is not large, and little or not at all inflated (Van Kamp.; Zittel, 1893, pp. 608, 639; Filhol, 1883, p. 85; Matthew, 1902*a*, p. 131; Schlosser, 1899, pp. 116, 144; Reynolds, 1906, p. 10; Scott, 1913, p. 548; Zittel, 1923, p. 470). Yet there are differences in inflation among the species of the genus *Ursus*. In *Ursus malayanus*, but also in *Ursus brasiliensis* and *U. bonariensis*, the bullæ are rounded, though to a different degree (Winge, 1895*b*, pp. 32, 33, 118, 119), though not more inflated than in young specimens of *Ursus arctus* and *maritimus*, in which generally the bulla is larger and more inflated, resembling more that in the Canidæ (Van Kamp.; Winge, 1895*b*, pp. 33, 119). In *Æluropus* the bulla resembles that in the Procyonidæ, though it is more flattened (Gregory, 1920, p. 196). The bulla is more or less triangular, the broad mesial margin is nearly straight. From this mesial margin the bulla suddenly rises to its greatest height. As the erected margin of the basi-occipital lies closely against the bulla, the latter seems to be lower than is really the case. According to Brown (1908, p. 184) the bulla in the fossil specimens of *Ursus americanus* is large and arched.

In the recent Procyonidæ the vertical axis of the bulla is larger than in *Ursus;* the bullæ often resemble those in the Mustelidæ; in proportion to the size they are strongly inflated, more than in *Ursus* (Van Kamp.; Zittel, 1893, p. 644), though in the different genera they are inflated to a different degree; they are never very much prolonged longitudinally. In *Nasua* (Wortman and Matthew, 1899, p. 134) the bulla is reduced and peculiarly shaped, different from that in *Phlaocyon.* In *Phlaocyon* (Zittel, 1923, p. 472; Wortman and Matthew, 1899, fig. 10; Matthew, 1893–1903, fig. 7) the bulla is large and inflated. Also in *Pseudobassaris riggsi* (Riggs, 1898, p. 258; Pohle, 1917, p. 408) the bulla is well inflated resembling that in *Jentinkia* (*Bassariscus*); the meatus externus enters at the middle of the bulla.

Typical for the bulla of the recent Mustelidæ is that the mesial side suddenly rises to the greatest height and descends toward the meatus externus, but this character is found in many other Carnivora as well. It is emphasized for the fossil *Mustela palæattica* (Weithofer, 1888, p. 227). For the rest the form of the bulla is very variable.

The greatest height lies in or in front of the middle of the longitudinal axis. In exceptional cases only, the caudal part is a little higher than the rostral part, for instance, as in the smaller species of the genus *Putorius* and perhaps also in *Helictis*.

The bulla in the recent Mustelidæ is oval, and in relation to the slight vertical height it shows a considerable horizontal extension forward and backward (Van Kamp.; Matthew, 1909, pp. 138, 139, *Mustela, Putorius*). Also the allied fossils show an elongated bulla. In *Mustela transitoria* (Gaillard, 1899, p. 57) the bulla is longitudinally elongated. In *Putorius cicognanii angustidens* the small, narrow and subcylindrical bulla is shorter than that in *P. cicognanii* (Brown, 1908, p. 181); in *Putorius gracilis* (p. 182) the subcylindric bulla is narrower and longer than in *P. angustidens*. Also in the fossil *Oligobunis* (Thorpe, 1921*a*, p. 481) the bulla is oval in outline. In *Bunælurus* on the other hand (Matthew, 1902*b*, pp. 138, 139; Scott, 1913, p. 551), the bulla, which is said to be of primitive character, is short. As the fossa glenoidea lies far forward, the bulla extends far along the basisphenoid in recent Mustelidæ. The caudal extension behind the auditory meatus and the stylomastoid foramen can be as large as in Viverridæ and Felidæ; this is enormously developed in species of the genus *Putorius*, in which the bulla resembles that of the Herpestidæ, and also in *Lutra* and *Aonyx*, in which this caudal part is much narrowed. Winge (1895*b*) emphasizes an abnormally large forward inflation and sac-like backward prolongation in *Ictidonyx* (p. 67) and *Pœcilogale* (p. 67). The bulla in *Mustela sarmatica* (Winge, 1895*b*, p. 96) is not bulged out backwardly. Also the bulla in *Martes* is not especially extended (p. 66). In *Mellivora* (p. 67) the bulla shows a remarkable extension on the caudal side of the postglenoid process. Thus, in my opinion, probably the meatus externus will not enter at the middle of the bulla in all mustelines, as Riggs notices (1898, p. 258).

Though inflated, the bulla in the mustelids is as a rule but little inflated and often small (Van Kamp.; Zittel, 1893, pp. 645, 646; 1911, p. 392; 1923, p. 473; Reynolds, 1911, p. 12; Scott, 1913, p. 550); though showing important differences in the different groups (Van Kamp.; Zittel, 1893, p. 646). Gregory (1920, p. 196) emphasizes the great difference in size and degree of inflation in *Latax* and *Putorius* and in

Latax and *Zorilla*. According to Zittel (1911, p. 392; 1923, p. 473) the elder mustelids show a large inflated bulla. In *Bunælurus* (Scott, 1913, p. 551; Matthew, 1902*b*, pp. 138, 139; 1907, p. 194; Teilhard de Chardin, 1914–1915, p. 74) the bulla is large, strongly inflated and prominent and, according to Matthew (1902*b*, pp. 138, 139), of a primitive character. In *Plesiogale felina* the thin bullæ are inflated, while in *Plesiogale robusta* the thick bullæ are flattened (Teilhard de Chardin, 1914–1915, p. 79). The bulla in *Palæoprionodon* is abnormal for a mustelid, as we shall see later.

In the fossil *Palæogale* the bulla was also large (Teilhard de Chardin, 1914–1915, p. 74). The bulla in the recent species of the genus *Putorius*, though different in the various species, is as a rule more or less flattened (Van Kamp.; Matthew, 1902*b*, pp. 138, 139). According to Brown (1908, p. 181) the bulla in the fossil *Putorius cicognanii angustidens* is not inflated as much posteriorly as it is in the recent species, a feature which gives the skull less vertical depth at this point.

The bulla in *Gulo*, though variable, is little inflated (Reynolds, 1911, p. 13). The bullæ in *Megalictis* (Matthew, 1907, pp. 196, 198) are small, inflated and show the flattening in an incipient stage characteristic of the mustelid family; the bullæ are flattened marginally at the borders. They are intermediate between the simple inflated cynoid type of Oligocene Mustelidæ and the flattened form characteristic of most modern members of the family. Thus the type of bulla in *Megalictis* is very similar to that of the Pinnipedia, according to Matthew (1909, p. 415).

In the fossil *Plesictis* the bulla is large and inflated (Matthew, 1907, p. 194) and the form resembles much more that of a mustelid than that of a viverrid (Teilhard de Chardin, 1914–1915, p. 59, also footnote 58 on on p. 59, *Viverra schlosseri* = *Plesictis robustus*). In the fossil *Oligobunis* (Thorpe, 1921*a*, pp. 480, 481; Van Kamp.; Matthew, 1907, p. 194) the bullæ were probably moderately inflated. In *Mustela* the bulla is more or less inflated (Van Kamp.; Zittel, 1893, p. 646), sometimes even considerably inflated (Reynolds, 1911, p. 13). In *Mustela palæattica* (Weithofer, 1888, p. 227) the bulla is strongly inflated and prominent, in *Mustela transitoria* (Gaillard, 1899, p. 57) it is rather prominent; in *Mustela robusta* the bulla is less inflated than in *Mustela martes* (Reynolds, 1911, p. 5); sometimes they may be called flattened (Matthew, 1902*b*, p. 139). In *Amphictis* (Matthew, 1907, p. 194) the bulla is supposed to be large and inflated. In *Lutra* the bulla is but very little inflated and much flattened (Zittel, 1893, p. 652; Reynolds, 1911, p. 13). In *Potamotherium* (Zittel, 1923, p. 475) as well, the bulla was flat.

In the Melinæ the bulla is moderately inflated (Zittel, 1893, p. 650). *Taxidea* shows an intermediate condition (Matthew, 1907, p. 198).

As a rule the bulla is relatively larger in the smaller species than in the larger species (see Van Kampen's paper), though there are many exceptions. The large *Meles taxus* shows a large bulla, for example, and in the Lutrinæ the bulla is very much flattened, but this is due to the flattening of the skull in general and the aquatic life. Pocock (1921), to whom we owe many remarks on the flatness and form of the bulla in many mustelids (p. 479, etc.), gives as his opinion that the flattening of the bulla in *Pœcilogale* and *Lutra* has been independently acquired (pp. 485, 486).

In the recent Viverridæ the bulla is much elongated, large and inflated (Van Kamp.; Zittel, 1893, p. 655; 1911, p. 395; 1923, p. 476). In *Galidia* (Carlsson, 1910*b*, pp. 566, 597) the height of the bulla is low and smaller than in allied Herpestinæ.

In the Herpestinæ generally, both chambers of the bulla are about equally high. In *Herpestes* (Carlsson, 1910*b*, p. 566) both chambers are of about the same height; in *Galidia* (pp. 565, 566) and in *Crossarchus fasciatus* (p. 566), however, the tympanic part is lower than the entotympanic chamber, while in *Hemigalidia* (p. 566) the tympanic is more inflated.

In the Cryptoproctinæ (Van Kamp.; Carlsson, 1910*b*, p. 567; 1911, p. 425) the greatest height of the bulla lies far backward; from this point the bulla descends gradually forward.

In the Viverrinæ as a rule (Van Kamp.; Winge, 1895*b*, p. 56; p. 57, *Paradoxurus;* p. 58, *Hemigale;* Carlsson, 1910*b*, pp. 566, 567; 1911, p. 425) the greatest height of the bulla lies far backward; from this point the bulla descends gradually forward; this point lies about in the center of the entotympanic part of the bulla or a little before the center. In *Nandinia binotata* the entotympanic part is only very little more prominent than the tympanic chamber, thus differing from the majority of the Viverrinæ, which show a rather great difference in inflation. Small differences in the form and degree of inflation are used in systematics.

In *Genetta* only the tympanic chamber is more inflated than the small entotympanic chamber.

In *Eupleres* the entotympanic chamber is much more inflated than the rostral part, as in the Viverrinæ, thus differing from the Herpestinæ.

In the recent Hyænidæ the bulla shows remarkable differences. In *Proteles* the bulla resembles that of the Viverridæ; it is large and oval; the greatest height lies in the caudal part and is formed by the caudal

chamber. In *Hyæna* the bulla resembles much more that in the Felidæ; it is shorter and less prolonged, especially behind the porus acusticus externus. In *Hyæna crocuta* the top of the bulla is formed by the rostral chamber, whose caudal margin on the surface of the bulla lies far backward. In *Hyæna crocuta* the bulla is considerably more inflated than in *Hyæna striata* (Reynolds, 1902, p. 7). According to Zittel (1893, p. 660) the bulla in the Hyænidæ in general is caudally much inflated, rostrally narrowed.

In the recent Felidæ the bulla is rounded, very prominent (Van Kamp.; Zittel, 1893, pp. 608, 663, 664; 1911, p. 397; 1923, p. 478), in the smaller species as a rule proportionately more than in larger ones. The greatest height lies in the center; from this point the bulla strongly descends especially in the lateral and mesial direction. Though the bulla is not constant, it is often more prominent toward its inner than toward its hinder border, which would be a difference from the Viverridæ.

The bulla in the recent *Felis* also shows individual and specific differences. Winge (1895*b*) mentions these individual variations in length and form in *Felis tigrina* (pp. 7, 8, 106), in *Felis macrura* (pp. 9, 106) and in *Felis eïra* (pp. 11, 107). According to Winge (1895*b*, pp. 9, 106) the bulla in *Felis macrura* is much larger than in *Felis tigrina*. In the fossil *Felis atrox* var. *bebbi* the bulla is much smaller than in either the lion or the tiger, and is smaller than the bulla of any modern feline known to Merriam (1909, p. 296); the entotympanic portion is much less inflated than in the lion and the tympanic region is much flattened. In the fossil *Dinictis* (Riggs, 1896*b*, p. 237; Scott, 1889, p. 214) the bullæ are very large and well inflated and the external shape is rather feline. In the Nimravidæ (Scott, 1889, p. 238) the bulla is inflated and is more prominent toward its inner than toward its hinder border.

In the fossil *Smilodon* (Matthew, 1910*c*, p. 298, fig. 6; Scott, 1913, p. 533) the bulla is large and inflated and shows a peculiar form and construction, quite unlike *Felis* or any living fissiped. In *Hoplophoneus primævus* (Adams, 1896, p. 421) the bulla is apparently moderately expanded. In *Machairodus* (Zittel, 1893, p. 673; Scott, 1913, p. 535) the bulla is large and but moderately inflated.

In the Pinnipedia the bulla is inflated (Van Kamp.; Zittel, 1893, p. 681), though it shows different degrees of inflation. In general appearance it resembles the arctoid rather than the æluroid type (Van Kamp.; Gregory, 1910, p. 314), especially the Ursidæ and Mustelidæ (Van Kamp.; Matthew, 1909, p. 414).

In the Otariidæ the bulla resembles more those of the Arctoidea,

especially that in *Ursus*, than we will find in the Phocidæ and in the mustelid *Enhydra lutris* (Van Kampen). In contrast with the bulla in the Phocidæ, that in the Otariidæ is proportionally small and flat (Van Kamp.; Winge, 1895*b*, p. 73). The form of the bulla is triangular; the greatest height lies on a line parallel with and at a short distance from the mesial margin of the bulla.

In the recent Phocidæ the bulla resembles that of the Arctoidea, especially that of the Ursidæ and larger Mustelidæ (Van Kamp.; Matthew, 1909, p. 414), but is always much larger than in this group. As a rule the bulla in the Phocidæ is large and very much inflated (Van Kamp.; Winge, 1895*b*, *Erignathus*, *Phoca*, p. 75, Monachi; p. 76, *Monachus*, *Lobodon*, *Pœcilophoca* sive *Leptonyx*, *Cystophora*), though there are differences in the degree of inflation between species of the same genus, and sometimes the bulla is even small. The bulla in the Phocidæ is more inflated than in any known species of the Otariidæ (Winge, 1895*b*, pp. 72, 74). According to this author also, the inflated bullæ in the fossil seal described by Wyman (1850, p. 229) indicate an affinity to the Phocidæ.

In the Trichechidæ the bulla is more or less inflated, but always low; it shows a triangular outline, which in the young is more quadrangular, as in that case the porus acusticus externus is still very wide.

In the Cetacea in general the bulla is large and inflated (Van Kamp.; Stromer von Reichenbach, 1912, p. 151).

In the different genera and species of the Cetacea (Van Kamp.; Zittel, 1893, p. 163) the bulla is more or less inflated, elongated or rounded, sometimes flattened or angular. These differences are used in systematics, also in the palæontological literature, as the bulla is often found separate. As these differences are for the larger part of little morphological value, I have not tried to be complete in my review of the literature, but will give only a few notes.

Already in the fossil *Zeuglodon* (see Van Kampen, 1905, not in edition 1904) and in the fossil *Protocetus* (Gregory, 1910, p. 419; Abel, 1912, fig. 388 on p. 509; 1919, fig. 556 on p. 748; 1920, fig. 642 on p. 424) the bulla was inflated and shaped as in later Cetacea. According to Gregory (1910, p. 419) the bulla in *Protocetus* is more expanded than in any known creodont. This however is an aquatic adaptation seen also in the Pinnipedia, and it may be of little phylogenetic significance. Thus, even in the earliest odontocetes, the bulla was most certainly inflated (Gregory, 1910, p. 417).

In the recent Delphinidæ and Phocænidæ the bulla is elongated and

has more the shape of a gutter than of a bladder. The rostral part is spout-like and prolonged in relation to the shape and size of the orificium tubæ, differently in different species. This causes the position of the porus acusticus externus in the caudal half of the outer wall of the bulla. The caudal part of the bulla is divided into two lobes by a deep longitudinal groove in the under wall.

In the recent Platanistidæ the rostral part of the bulla is also pointed, to a different degree in different genera.

In some recent genera of the Physeteridæ we find the two lobes at the posterior end also; in other genera they are indistinct or absent. This depends on the development of the groove on the surface. According to Schulte (1917, p. 395) the bulla in *Kogia* is rather short and broad; its ventral surface has the shape of an irregular parallelogram; the mesal spout-like portion of the tympanic is short and not much narrower than the lateral portion (the long axis of the bulla is nearly transverse).

In the fossil *Diochotichus vanbenedeni* (True, 1910, p. 26) the bulla is small in proportion to the size of the skull; in form, as well as in size, it so closely resembles the bulla of *Schizodelphis crassangulum* (Case) that had it been found separately, it might have been supposed to belong to that species. Viewed from below, the bulla is triangular in outline, the posterior border being deeply emarginated or bilobed and the anterior abruptly acuminate. The inferior surface of both lips is convex except for a depression near the anterior end.

In the recent Mystacoceti the groove in the under wall of the posterior part of the bulla is lacking, so that the bulla is not bilobed (Van Kamp.; Hanke, 1914, p. 505). The form of the bulla shows differences, which are used to distinguish genera and species (Van Kamp.; Zittel, 1893, p. 163).

In the Balænopteridæ, according to Zittel (1893, p. 181; 1923, p. 493), the bulla is elongated, greatly inflated and rounded on all sides. According to Lydekker (1887, p. 31) the bulla varies in different individuals of the same species in the balænopterine section much less than in the balænine section. In *Balænoptera* (Zittel, 1893, p. 182; Lillie, 1910, p. 779), the bulla is moderately inflated, the mesial wall is flattened, the under side is narrowly elliptical, and the outer side is rounded with the convexity pointing outward. In *Megaptera* (Zittel, 1893, p. 183) the bulla is greatly inflated and the mesial surface is convex. In *Plesiocetus* (Zittel, 1893, p. 181) the bulla is elongated, egg-shaped, the under wall being flattened.

In the Balænidæ (Zittel, 1893, p. 183; 1923, p. 493) the bulla is

nearly quadrangular, and angular, little inflated. In *Balæna primigenia* (Lydekker, 1887, p. 20) the bulla presents many variations, but as they all seem to pass into one another, these variations cannot apparently be considered of specific value, according to Lydekker.

The bullæ in the fossil Condylarthra were supposed by Van Kampen to be all, or partly, much like the bulla in *Tapirus* and *Rhinoceros*. According to Matthew (1901, p. 30) they are rudimentary if not absent in *Periptychus*.

The bulla in the Litopterna was supposed by Van Kampen to resemble that in the artiodactyls, but Scott (1910, pp. 3, 7; 1912, p. 137) describes the tympanic as imperfectly ossified, not forming a bulla, but remaining merely a small scale-like plate. In the Macrauchenidæ and probably also in the Proterotheriidæ (Scott, 1910, pp. 10, 106) the tympanic was very small, scale-like and flattened and could hardly be said to form a bulla, as the author mentions, especially in the genus *Theosodon* (pp. 115, 118).

In the Perissodactyla we usually find a bulla (Van Kamp.; Scott, 1910, p. 7), which in the stem perissodactyls was probably small (Gregory, 1910, p. 390).

The bulla in the modern *Rhinoceros* is very small. The nearly vertical lateral wall is formed by the extension of the small tympanic in the ventral wall; the entotympanic forms the vertical inner and caudal wall and the inclined rostral upper wall. The two elements do not constitute a simple bulla but a somewhat complicated structure, which is probably also present in allied fossils, as can be judged from a notice by Toula (1902, p. 74) on *Rhinoceros* (*Ceratorhinus*) *hundsheimensis* and perhaps also from figures given by Pavlow (1893, Pl. IV, fig. 1*a*) and by Cope and Matthew (1915, p. cxxvii, *Aphelops*). Also, Depéret (1892, p. 66) mentions that the bullæ in *Rhinoceros* are not prominent. Scott (1896, p. 358) supposes that the bulla in *Hyracodon* is large but not inflated. The tympanic in *Triplopus cubitalis* forms a bulla, according to Cope (1881*c*, p. 384).

In the recent tapir the small tympanic has the same form as in *Rhinoceros*, but a normal bony entotympanic is absent in the dry skull; it is either fused with the periotic, forming a crest on this bone (Van Kampen), or it remains partly cartilaginous (see Parker, 1882, p. 776), or a free bone that is lost in the dry skull.

In the recent *Equus* we find quite another condition. Here we find a simple, small, not much inflated bulla. The lateral wall is flat and vertical, the inclined inner wall is a little convex; both walls meet each

other with a sharp angle. According to Winge (1906, p. 147), even in the oldest Equidæ the bulla is small and not ring-like but scale-like, and remaines practically unchanged. Thus in *Mesohippus* (Scott, 1891*b*, p. 306) the tympanic is very small and forms a minute bulla. In *Anchitherium bairdii* (Leidy, 1854, p. 69) the bulla is relatively slightly more dilated than in the horse.

In the Chalicotheriidæ, according to Zittel (1893, p. 310), the bulla is cylindrical. In *Macrotherium grande* (Depéret, 1892, pp. 66, 75; Zittel, 1893, p. 311) the bullæ are enormously inflated and show the form of a curved cylinder, having the concavity behind and in front. As to the shape of the bulla in *Eomoropus*, see my own investigations.

In the recent Suidæ the bulla is always well developed (Van Kamp.; Zittel, 1893, p. 367), largest in *Sus* and *Babirussa*. As a rule the bulla is longest in the vertical direction, the longitudinal axis running a little obliquely and the top of the bulla lying more rostrally than the basis. In *Dicotyles* (Van Kamp.; Winge, 1906, p. 38), however, the bulla is low, about as high as broad and not laterally compressed. In all other recent genera the bulla is more or less compressed laterally (Van Kamp.; Gidley, 1921, p. 654). The top of the bulla is slightly pointed as a rule in *Dicotyles*, *Sus* and *Babirussa*, sharply pointed in *Potamochœrus* and crest-like in *Phacochœrus*, where the bulla is strongly compressed laterally. The fossil *Perchœrus* in contrast with modern peccaries shows a simple round bulla (Matthew, 1907, p. 216).

The bulla in the fossil *Elotherium* (Leidy, 1869 and Scott, 1898, both cited by Van Kampen) is small. The bulla in *Archæotherium mortoni*, according to Leidy (1854, p. 61), appears to have been broad and convex, but compared to those in recent suilline animals was feebly developed. Also in *Archæotherium clavus darbyi* (Troxell, 1920*b*, p. 369) the bulla is only slightly convex.

In the recent Hippopotamidæ the form of the bulla resembles that of the Suidæ, but the bulla is not compressed in a direction nearly perpendicular on the longitudinal axis of the skull but rather from caudo-mesially toward rostro-laterally, also showing a rather sharp under margin.

As to the fossil Anthracotheriidæ, we find in the American *Ancodus* (*Hyopotamus*), according to Scott (1895, cited by Van Kampen), a large inflated bulla, considerably more inflated than in the European species and of a somewhat different shape. The form is oval, with a marked depression on the ventral surface, internal to the median line. This gives it a very different appearance from the regular, almost spheri-

cal bulla of *Eporeodon*. A similarity with a striking feature in oreodonts is emphasized by Schmidt (1913, p. 26) for the genus *Brachyodus* (*Bothriogenys*). In different species of this genus and sometimes even in different specimens of the same species the bulla is very differently developed; it can be small, intermediate, large and even enormously large (Schmidt, 1913, pp. 21, 22, 24, 25). In this way these differences in size have little systematic value according to Schmidt (1913, pp. 26, 101). A similar feature is described for *Elomeryx armatus* by Marsh (1894, p. 177), in which the type specimen has a small bulla and the other a larger one. According to Troxell (1921*a*, p. 333), we have to look to the immature animal for the greatly inflated bulla, while a specimen of *Elomeryx armatus angustus* (p. 334) just reaching maturity shows moderate bullæ. The bulla in *Hyopotamus brachyrhynchus* (Osborn and Wortman, 1894, p. 221) is well inflated as in the peccary, but is lower, more rounded, and more elongated anteroposteriorly. Also in *Æpinacodon deflectus* (Troxell, 1921*a*, p. 338), the bulla is elongated anteroposteriorly.

In the fossil Anoplotheriidæ (Zittel, 1893, p. 367), the bulla is always well developed, sometimes very large and much inflated. In *Anoplotherium* (Leidy, 1854, p. 32; Depéret, 1892, p. 66; Winge, 1906, p. 94; Palmer, 1913*b*, p. 884), the bulla is small, round, and inflated according to Winge and uninflated according to Palmer. According to Turner (1849, cited by Van Kampen), the inflation of the bulla covers also the under wall of the external auditory meatus, as in Camelidæ.

The bulla in *Cænotherium* (Lydekker, 1885*a*, p. 65; Zittel, 1893, p. 377; Winge, 1906, p. 96) is very large and much inflated, showing the form of a semi-globe. According to Van Kampen it shows a great likeness to the bulla in *Tragulus*.

The bulla in *Oreodon* and allied genera shows a very different size and degree of inflation (Scott, 1890, p. 322, etc.; Douglass, 1907, p. 810).

In *Oreodon culbertsoni* Leidy the bulla is very small and uninflated (Leidy, 1854, p. 55; 1856, p. 164; Marsh, 1875, p. 250; Scott, 1890, pp. 339, 372; Osborn and Wortman, 1894, p. 216; Loomis, 1920, p. 288; Thorpe, 1921*b*, p. 104). The bulla in the very small *Oreodon gracilis* (Leidy, 1854, p. 55; 1856, p. 164; Osborn and Wortman, 1894, pp. 216-218; Scott, 1890, p. 339) shows a somewhat greater inflation than that in *O. culbertsonii*.

In *Eporeodon* (*Oreodon*) *bullatus* (Scott, 1890, p. 339; Osborn and Wortman, 1894, pp. 218, 219; Thorpe, 1921*b*, p. 104) the bullæ are much more inflated than in either *O. culbertsonii* or *O. gracilis;* they are, moreover, extended backward. The bullæ in *Eporeodon occidentalis* (Thorpe,

1921*b*, p. 104) are nearly the same size as in *Eporeodon bullatus;* the same is true of the bullæ in *Eporeodon condoni* (idem, p. 104), which in this species are called small, while those in *Eporeodon occidentalis* (Thorpe, 1921*b*, p. 96) are called large. The bullæ in *Eporeodon perbullatus* (Thorpe, 1921*b*, p. 106) are relatively enormous and are nearly twice the size of those in *E. leptacanthus*, which are also called large (p. 98).

In *Eporeodon* (*Oreodon*) *major* the bullæ are large and greatly inflated (Leidy, 1856, p. 164; Scott, 1890, pp. 339, 372; Matthew, 1893–1903, p. 396; Osborn and Wortman, 1894, p. 218).

In *Eucrotaphus* (*Oreodon, Eucrotaphus*) *auritus* the bullæ are also very large and inflated (Scott, 1890, p. 372; Leidy, 1854, pp. 56, 57). According to Leidy (1854, p. 57) the bullæ in *Eucrotaphus* are relatively as large as in the Californian deer.

In different specimens of *Eporeodon leptacanthus pacificus* (Thorpe, 1921*b*, p. 99) the bullæ are different in size, according to Thorpe, probably due to age and sex. In *Eporeodon trigonocephalus* (Thorpe, 1921*b*, p. 101) the bullæ are small, while in the subspecies *parvus* are large (p. 102).

Thus, the above-mentioned species have been brought together under three different genera, named *Oreodon, Eporeodon* and *Eucrotaphus*, which are distinguished by the size of the auditory bulla (Leidy, 1856, p. 164; Marsh, 1875, p. 250; Lydekker, 1885*b*, p. 208; Scott, 1890, pp. 339, 372), a character which is sometimes judged to be doubtful as a sufficient basis for distinction (Lydekker, 1885*b*, p. 208; Loomis, 1920, p. 288). Then we can limit the name *Oreodon* to the species with a small, uninflated or little inflated bulla (Leidy, 1854, p. 32; Marsh, 1875, p. 250; Lydekker, 1885*b*, p. 207; Scott, 1890, p. 372; Zittel, 1893, pp. 353, 354; Matthew, 1893–1903, p. 395; Loomis, 1920, p. 286), while in *Eporeodon* and *Eucrotaphus* the bulla is large and more inflated (Marsh, 1875, p. 250, *Eporeodon;* Lydekker, 1885*b*, p. 208, *Eporeodon;* Scott, 1890, p. 372; Zittel, 1893, pp. 353, 354, 355, *Eucrotaphus;* p. 355, *Eporeodon;* Loomis, 1920, p. 286, *Eucrotaphus, Eporeodon;* p. 288, *Eucrotaphus*).

We owe a critique on this distinction based on the size of the bulla to Scott (1890). According to this author (pp. 322, 339, 373) it is easy to find intermediate stages and even in the same species a wide variability often occurs.

According to Scott (1890, pp. 372, 373, 383; Zittel, 1893, p. 349) the highly inflated bulla is the primitive condition, which is secondarily reduced in many species, as is the case in most of the White River species. Scott gives the following reasons (pp. 372, 373): (1) in all other

genera of the Oreodontinæ and also in all Agriochœrinæ the bulla is well developed; (2) the oldest known species of *Oreodon* from the lowest White River show a large bulla; (3) in a large series of skulls of oreodonts all intermediate stages are found.

Marsh (1875, p. 249) thought that *Oreodon* and *Eporeodon* occurred in a somewhat different horizon of the Miocene. According to Scott (1890, p. 339) this is only partly true. According to this author (Scott, 1890, p. 339) the species with small and those with large bullæ do not occur in separated strata of the White River Formation; in the lowest horizon we find those with large bullæ only, while both occur in the higher horizons. None of the John Day species shows a reduced bulla (Scott, 1890, pp. 340, 373), which seems to be a character that did not last long. In contrast to Scott's opinion, Osborn and Wortman (1894, p. 219) found that the greatly inflated bulla type comes only from the upper or *Protoceras* Beds, while the species in which the bullæ are little or not at all inflated are confined to the lower part of the *Oreodon* Beds. The single example of the transitional form, *O. bullatus*, has a position exactly intermediate in respect to its vertical distribution. According to Osborn and Wortman (1894, p. 219) the range in time corresponds with the evolution of the bulla, so that the large rounded form occurs in the later species (p. 216). According to Van Kampen the reduction of the bulla in Oreodontidæ resembles that in the Cervidæ, with which the differences in general also agree and, as in that family, seem to coincide with the differences in size.

In form the bulla is often laterally compressed (Leidy, 1854, p. 57, *Eucrotaphus auritus;* Thorpe, 1921*b*, p. 96, *Eporeodon occidentalis;* pp. 98, 99, *Eporeodon leptacanthus*; p. 104, *Eporeodon condoni*, in which it is less compressed; according to Van Kampen the bulla is also compressed in *Oreodon bullatus* and *major*, but not in *Cyclopidius emydarius*). In *Oreodon* (Leidy, 1854, p. 57) the bulla is slightly swollen at the inner termination of the vaginal crest of the auditory process. In *Eucrotaphus jacksoni* (Leidy, 1854, p. 57; Loomis, 1920, p. 288) it is a large simple mammillary eminence, being more like *Eporeodon* than is *Oreodon*. In *Eporeodon trigonocephalus* (Thorpe, 1921*b*, p. 101) the bulla is ovoidal, in the subspecies *parvus* (p. 102), triangular. The bullæ in *Eporeodon perbullatus* is ovate (Thorpe, 1921*b*, p. 106).

In *Protoreodon* (Scott, 1890, pp. 362, 371; 1899, p. 90) the bulla was not well preserved in any of the specimens of Scott's material; it is almost certain, however, that the bulla was very small, much as in *O. culbertsoni*.

In *Mesoreodon longiceps* (Douglass, 1907, p. 814) the bulla is large.

In *Mesoreodon chelonyx* (Scott, 1895*b*, p. 129) the bullæ vary in size, being in some specimens much more prominent and inflated than in others. This is perhaps a sexual character, the bullæ in the male being more largely inflated than in the female. In *Paroreodon marshi*, as well (Thorpe, 1921*b*, p. 109), the bullæ are very large and robust.

Also in the genus *Merycochœrus* (Scott, 1890, pp. 340, 374) the bullæ are differently developed. In some species they are large and strongly inflated, in others they are relatively small and compressed, though they are never so much reduced as in many species of the genus *Oreodon*.

In the genus *Merychyus* Leidy (*Ticholeptus* Cope) the bullæ are large and well inflated (Scott, 1890, pp. 348, 374; Zittel, 1893, p. 355), though they never attain the enormous size of the bulla in *Leptauchenia* (Scott, 1890, p. 348). In *Ticholeptus brachymelis* (Douglass, 1907, p. 816) the bulla is quite large, but smaller than in *Ticholeptus breviceps* (Douglass, 1907, pp. 816, 817). In *Ticholeptus rusticus*, on the other hand, the bulla is small and not inflated (Loomis, 1920, p. 283).

In *Leptauchenia* the bulla is enormously inflated (Scott, 1890, pp. 353, 375, 383; 1913, pp. 381, 382; Zittel, 1893, p. 355). The same is the case in *Cyclopidius* and *Pithecistes* (Scott, 1890, pp. 353, 383; Zittel, 1893, p. 356).

Protagriochœrus (Scott, 1899, p. 103) probably possesses a small tympanic bulla, judged from the form of the paroccipital process and the shape of the basioccipital. In the different species of *Agriochœrus* the bulla varies much (Scott, 1890, pp. 372, 376; Zittel, 1893, p. 352; Wortman, 1895, pp. 147, 177, 178; Thorpe, 1921*c*, pp. 112, 116–118); it is described as being greatly inflated, much inflated, less inflated, flattened, large, moderately large, small. Also the shape of the bulla in the different species is very different (Wortman, 1895, pp. 177, 178; Thorpe, 1921*c*, p. 117): it may be mammiform, ovoid, quadrate, triangular in outline, or, in a few cases, elongate in the direction of the length axis of the skull or very obliquely directed; it may be constricted in the middle or medially and it may be inferiorly keeled in the transverse plane. We may finish with the description given by Thorpe (1921*c*, p. 116) of the bulla in *Agriochœrus bullatus:* the bulla has a flat, nearly vertical surface facing inward and backward; antero-externally a ridge runs forward and inward beyond the middle of the glenoid articular surface; the inferior surface of the bulla is keeled, the keel running transversely from the postglenoid tubercle to the lower border of the internal plane face; a form of bulla which, according to Thorpe, does not occur in any other species of this genus.

In the recent Camelidæ the bullæ are high and inflated, in *Lama* sometimes more inflated than in *Camelus*. In *Lama* the bulla is bladder-like, inflated, while in the camel it is strongly compressed (Scott, 1890, p. 390; 1891*a*, p. 54). According to Winge (1906, p. 11) the bulla in the young *Auchenia major* is more compressed from in front backward than in the old *A. lama* and pushed farther backward against the jugular process around the groove for the stylohyal.

In the fossil *Protylopus* (Scott, 1899, pp. 27, 28) the bulla seems to be a short, transversely placed, and slightly swollen tube, which is perhaps the entire bulla, but this could not definitely be decided, as the bulla is not very well preserved in any of the specimens. This bulla is very much smaller than that in *Poëbrotherium* (Scott, 1899, pp. 27, 28, 44, 113, 118). According to Winge (1906, p. 98), in the otherwise very primitive members of the family of the Camelidæ, the bulla is large and inflated.

In the fossil genus *Poëbrotherium* the bulla is of a large size (Scott, 1891*a*, p. 57; Loomis, 1910, p. 321; Troxell, 1917, p. 381), relatively larger and more rounded than in modern Camelidæ (Scott, 1891*a*, pp. 15, 56), and greatly inflated (Scott, 1891*a*, p. 15; Zittel, 1893, p. 362; Wortman, 1898, p. 115). According to Wortman (1898, p. 115) it is relatively low. The bulla in *Poëbrotherium wilsoni* is inflated and of large size (Leidy, 1847, p. 324; 1854, p. 21; Scott, 1891*a*, p. 14) and according to Leidy (1847, p. 324) comparatively larger than in *Bos bovis*, *Cervus rufescens* or any other ruminant with which this author was acquainted; relatively the bullæ are not longer than in the musk deer but their transverse and anteroposterior diameters are rather greater; externally they are convex, internally they are vertical and slightly convex or nearly plane (Leidy, 1854, p. 21). In the small *Poëbrotherium wilsoni* the bullæ are larger and less compressed than in *P. labiatum* (Scott, 1891*a*, pp. 14, 15) in which the bullæ are of more moderate size, so that the basioccipital is quite a broad plate, while in *P. wilsoni* the basioccipital is reduced to a mere rod by the enormously inflated bullæ. While in *Poëbrotherium labiatum* and in *Poëbrotherium* in general the bulla is rounded, that in *P. andersoni* is roughly subtriangular, resembling in this respect the later camels (Troxell, 1917, pp. 381, 387).

Also in *Stenomylus* (Loomis, 1910, pp. 302, 321) the bullæ are large and greatly inflated. In *Pseudolabis* (*Paralabis*) *matthewi* (Lull, 1921, p. 392) the bulla is less rounded than is that of *Poëbrotherium*, although fully as large.

The bony ventral wall is extended lateralward along the under surface of the external auditory meatus, so that this under wall is swollen,

and the external auditory meatus is not tube-like, but a mere opening in the bulla (Scott, 1899, p. 27, *Poëbrotherium*) and the bulla externally projects beyond the meatus externus (Leidy, 1847, p. 324, *Poëbrotherium*).

The bulla of the Camelidæ is highly characteristic (Van Kamp.; Leidy, 1847, p. 324, *Poëbrotherium;* Wortman, 1898, pp. 115, 116; Troxell, 1917, pp. 381, 382, *Poëbrotherium*), consisting of two swollen portions united rostrally so that the bulla is V-shaped, and separated posteriorly by the vagina processus hyoidei, which in the adult skull is sometimes closed behind. The mesial part is the true bulla, the lateral leg of the V is the inflation of the under wall of the external auditory meatus. The side walls of the bulla are nearly vertical. The mesial part is longitudinally directed (Wortman, 1898, pp. 115, 116) and often laterally compressed. Wortman (*loc. cit.*) describes the lateral part as an outer vertical buttress, which joins the inner part at an angle, and at the upper limit of which is placed the external auditory meatus. In *Poëbrotherium andersonii* according to Troxell (1917, pp. 381, 382) the upper end of the outer portion envelops the external auditory meatus. In *Poëbrotherium* (Wortman, 1898, p. 116) the inner portion is much the larger; in *Gomphotherium* (Wortman, 1898, p. 116; Troxell, 1917, p. 388) the outer and inner parts of the bulla are about equal in size; in *Pseudolabis* (*Paralabis*) *matthewi* (Lull, 1921, p. 392) the inner lobe is narrower, more as in the later camels. In the living genera *Camelus* and *Auchenia* (Van Kamp.; Wortman, 1898, p. 116) the inner part of the bulla is much reduced.

Also in the fossil *Eotylopus reedi* (Matthew, 1910*a*, p. 36) the bulla is of the camelid type, which is "folded upon itself."

In the Tragulidæ (Van Kamp.; Scott, 1891*b*, p. 358; Zittel, 1893, p. 382; Winge, 1906, p. 107) the bulla is large, high, a little laterally compressed, resembling the greatly inflated type of the bulla of the Cervidæ.

In the Hypertragulidæ, according to Zittel (1923, p. 578), the bulla is usually large. In *Leptomeryx* (Leidy, 1853, p. 394; Zittel, 1893, p. 389; Scott, 1899, pp. 16, 112; Matthew, 1902*c*, p. 313; Winge, 1906, pp. 106, 108) the bulla is small. In *Leptomeryx evansi* the bulla is small (Scott, 1891*b*, pp. 349, 359), much smaller than in *Moschus* (= *Tragulus*) *javanicus* (Leidy, 1853, p 394) and also very much smaller in every dimension (especially in the vertical direction) than that of the tragulines (Scott, 1891*b*, p. 346; 1895*a*, p. 313). The bulla in *Leptomeryx evansi* is still more inflated than that in *Leptomeryx obliquidens* (Lull, 1922, p. 116). The bullæ in *Leptomeryx* are more inflated than those in *Blastomeryx* (Matthew, 1908, p. 553) in which the bulla is small, but nearly round and

strongly inflated (Matthew, 1908, p. 536). The bulla in *Hypertragulus* is somewhat larger than in *Leptomeryx* (Matthew, 1902*c*, p. 315). The bulla in *Allomeryx* is small (Lull, 1922, p. 114).

The bulla in *Leptomeryx obliquidens* (Lull, 1922, p. 115) is laterally compressed, elongated oval in shape. According to Matthew (1908, p. 553) the bullæ in *Leptomeryx* are quite different from the types characteristic of *Tragulus* and of the camels, but agree according to Scott (1891*b*, p. 360) with the Pecora.

In the recent Cervidæ the bulla shows different degrees of reduction and flattening (Matthew, 1908, p. 538). We can distinguish two types, connected by very few intermediate stages.

As a rule, in the deer the bulla is small, not compressed, extending little or not at all beneath the under wall of the external auditory meatus. Sometimes the bulla is very small, as in *Moschus* (Van Kamp.; Scott, 1895*a*, p. 313; Winge, 1906, p. 110). Many other genera belong to this type showing a different size and inflation even in different species of the same genus (e.g., Winge, 1906, p. 19, *Subulo campestris* and *rufus*). Even in this type the bulla may called strongly developed, as Bondy (1907, p. 375) calls the bulla in *Cervus capreolus*. Some species of the genus *Cariacus* show a greatly inflated bulla, leading toward the other type of bulla, the greatly inflated, laterally-compressed bulla, resembling that in *Tragulus*. We find this type in *Cervus kuhlii* and *porcinus* (while other species of this genus belong to the first-mentioned type or are intermediate) and in *Hydropotes* (Van Kamp.; Winge, 1906, p. 110). In this last-mentioned type the bulla seen from below is more or less kidney-shaped, due to the shape of the vagina processus hyoidei.

As the bulla in the artiodactyls is generally strongly inflated, probably in the Cervidæ, as in the Oreodontidæ, the small bulla must be derived from the more inflated one (Van Kampen). In the fossil *Dromomeryx* (Scott, 1895*b*, p. 171, *Blastomeryx*) the bulla is small and of the shape usual in the antelopes. In the fossil *Protoceras* (Osborn and Wortman, 1892, pp. 353, 358; Scott, 1895*a*, pp. 310, 312, 320; 1899, p. 20) the bulla is uninflated and very small, much smaller than the bulla in *Leptomeryx* (Scott, 1895*a*, p. 313). The bulla in *Protoceras* is simple, scale-like (Winge, 1906, p. 106) and much like that in *Moschus* (Scott, 1895*a*, p. 312). Also the bulla in the fossil *Camelomeryx* (Scott, 1899, p. 70) was probably very small, smaller even than in *Leptomeryx*.

Also in the modern Giraffidæ the bulla is small. It is pointed forward and downward, and resembles the inflated bulla of the Cervidæ also in the characters of the vagina processus hyoidei which runs along the side-wall of the bulla.

In the fossil *Hypisodus* (Matthew, 1893–1903, p. 440; 1902*c*, pp. 311, 312; Winge, 1906, pp. 107, 108; Loomis, 1910, p. 321; Troxell, 1920*a*, p. 393) the bullæ are exceptionally large. According to Thorpe (1920*a*, p. 393), they occupy over a third of the vertical height of the skull in *Hypisodus alacer* and according to Matthew (1893–1903, p. 440), the enormous size was equalled only by the little antelope *Madoqua* among the modern skulls that he was able to examine.

The bulla in *Merycodus osborni* (Matthew, 1904, p. 110) is much larger than in the pronghorn (*Antilocapra*), almost as large as in the gazelle; in this respect it approximates the young *Antilocapra* more than it does the adult and probably retains more of the primitive character of the group. This character of the young animal is perhaps also the reason that the bulla in a specimen of *Merycodus furcatus* is larger than in *M. osborni* (Matthew, 1904, p. 111). Lull (1920, p. 96) mentions also a marked difference in shape and degree of inflation in his skull material of *Aletomeryx gracilis*.

In the modern Bovidæ we find, as in the Cervidæ, two types of bullæ, but in the Bovidæ the small bulla is exceptional. Also in contrast with the Cervidæ, these two types show no other differences than that in size: the "small type" is nothing else than a small "large bulla."

The small type occurs, for example, in *Rupicapra tragus*, in *Nemorrhædus* (Van Kamp.; Winge, 1906, pp. 123, 127; Andrews, 1915, p. 286) and in *Protagoceros* (Winge, 1906, pp. 117, 127). Of course there are specific differences in the degree of inflation (Winge, 1906, p. 117, *Protagoceros*). Probably also the fossil *Liops* (Gidley, 1096, p. 165) shows this small type; the tympanic is said to be flat, with no bulla. The allied *Ovibos* forms a transition to the large type, which is the general type in the Bovidæ. Sometimes the bulla is enormously inflated, as in the modern *Madoqua* (Matthew, 1893–1903, p. 440), in *Tragelaphus* (Winge, 1906, p. 118) and in *Neotragus* and *Nanotragus* (Winge, 1906, p. 122).

Moreover, we may give the following examples of this large type: *Bos taurus* (Van Kamp.; Bondy, 1907, p. 381), *Tragelaphus* and *Damaliscus* (Winge, 1906, pp. 118, 119, 127), *Gazella* (Van Kamp.; Zittel, 1893, p. 417; Matthew, 1904, p. 110; Winge, 1906, pp. 120, 127). There are of course specific and generic differences. In *Ovis*, for example, the bulla is as a rule smaller than in *Capra*, though in both genera showing important specific differences.

In the modern skulls of both types the bulla is laterally compressed. Also in the fossil *Myotragus balearicus* (Andrews, 1915, p. 286) the bulla

is strongly compressed. In the fossil *Liops*, on the other hand, the bulla is roughly triangular in shape and flat (Gidley, 1906, p. 165).

The bulla in the Amblypoda is supposed to agree with that in *Rhinoceros* and *Tapirus* by Van Kampen, judged by the literature.

In the common ancestors of the toxodonts, typotheres, interatheres and hegetotheres, according to Gregory (1910, p. 378), the bulla became inflated very early.

In *Protypotherium* and *Interatherium* (Sinclair, 1909, pp. 22, 51) the bulla is pear-shaped; anteriorly, where most prolonged, the bulla is greatly flattened in the horizontal plane. In *Hegetotherium* (Lydekker, 1893, cited by Van Kampen; Sinclair, 1909, p. 74) the bulla is large, heart-shaped, convex in all dimensions and tapering to a point anteriorly. Also in *Pachyrukhos* (Sinclair, 1909, p. 89) the bulla is heart-shaped, pointed anteriorly, but considerably flatter inferiorly than in *Hegetotherium*. Van Kampen concluded from figures given by Lydekker and Ameghino (1889) that the bulla in *Pachyrukhos typicus* and *Icochilus extensus* agrees with *Typotherium*.

According to Van Kampen's own investigations, the bulla in *Typotherium cristatum* resembles that in the artiodactyls in form. The bulla is large and high (Van Kamp.; Lydekker, 1893, cited by Van Kampen). The horizontal outline is nearly quadrangular with rounded angles. The bulla is a little flattened in the direction from mesiocaudally toward laterorostrally. Thus it has two curved sides only, which meet in a rounded under margin, running from the lateral caudal angle mesialward and forward. This under margin ends caudally in a short process against the paroccipital process, rostrally in the styliform process. In front the bulla shows a point lying against the basisphenoid. In *Archæohyrax* Winge, 1906, p. 87) the bulla is well developed, bladder-shaped.

Also in the fossil *Rhynchippus* (Winge, 1906, p. 89) the bulla is bladder-shaped. In *Nesodon* (Scott, 1912, pp. 134, 137) the bullæ are unduly small, but mammillate (Scott, 1912, p. 292, Toxodonta in general) as their principal diameter is dorsoventral, somewhat as in the pig, but not in such an exaggerated degree; this form in the adult skull differs from that in the young specimen. Van Kampen concluded from the plates given by Lydekker (1893) that the bulla in *Nesodon* was little or not laterally compressed and rounded on the under side, thus differing from *Toxodon*. In *Toxodon platensis* Van Kampen describes the bulla showing the type of the artiodactyls; it is high and, especially in adult skulls, laterally compressed with a sharp under margin. According to Van Kampen, Owen's tympanic in *Toxodon* (1840, p. 24, a thin plate,

wedged in between the occiput and glenoid cavity) is nothing else than the crest on the under surface of the external auditory meatus.

In the Entelonychia (Scott, 1912, pp. 260, 262, 265, 293) the bulla, though agreeing in essentials with that of *Nesodon*, has a very different appearance. The inflated bulla is very large, much larger than in *Nesodon* and in the Toxodonta in general, especially in the anteroposterior dimension, which clearly distinguishes it from that of the Toxodonta and Typotheria, so that in ventral view the bulla forms an elongate, narrow oval. Thus in the Entelonychia the principal diameter of the bulla is in the anteroposterior direction (Scott, 1912, p. 293), while in the Toxodonta the principal diameter is dorsoventral (*loc. cit.*, p. 292). Also in the Notostylopidæ (Gregory, 1910, p. 375) the bullæ were much inflated.

In the recent Hyracoidea the bulla is scale-like (Winge, 1906, p. 166) and resembles the bulla in *Galeopithecus*, being small and flat. The mesial wall is rather steep, gradually passing lateralward into the external auditory meatus.

In the recent *Elephas* (Van Kamp.; Gregory, 1903, p. 389; Winge, 1906, p. 173) the bulla in the young skull is relatively large and inflated; later on it flattens down and becomes closely appressed to the skull in the old specimen, which is caused by the progressive brachycephaly of the skull. The bulla in the adult elephant is not laterally compressed, but in the anteroposterior direction. Viewing the skull from below, we see the hind wall of the bulla, the front wall lying against the under surface of the skull. These two walls show a rather sharp transition. The bulla points obliquely downward, forward, and inward, a condition already found, though less developed, in the artiodactyls and especially in the Suidæ. Also in the fossil *Mastodon arvernensis* (Weithofer, 1890, p. 114) the bulla in the old skull is much flattened. This bulla is triangular, the broad basis lying against the basis cranii, the top lying laterally against the mesial end of the fossa glenoidea.

In the recent *Lemur mongos* the bulla has nearly the shape of half a globe; the point of largest height lies about in the center, the outer wall runs up rather steeply leading to a very short tube, which is probably a very short external auditory meatus. The bulla is prolonged forward in an unswollen point. In the other recent lemurs the bulla is more or less swollen. For example (Gregory, 1920, p. 209), the bulla is large in *Mixocebus* and *Microcebus* (Van Kamp.; Gregory, 1920, p. 196), small in *Atililemur*, *Chirogale*, and *Myoxicebus*. In the Indrisidæ (Standing, 1908, pp. 73, 93; Gregory, 1915, p. 434) the bulla is typically much expanded

and prominent. Thus in *Propithecus* the bulla is said to be fairly large (Gregory, 1920, p. 215) and of moderate size (Gregory, 1916, p. 264). Sometimes the bulla is so much more elongated in the anteroposterior direction, that the line connecting the most caudal margin of the left and right bulla may pass the rostral margin of the foramen magnum or even lie behind this margin. Also in the recent *Chiromys* (Van Kamp.; Gregory, 1915, p. 435) the inflated part of the bulla is oblong; the forwardly directed point is little developed; perhaps it is partially inflated and thus causes the enlargement of the inflated part and the oblong shape.

The bullæ in the fossil *Notharctus* are greatly inflated (Wortman, 1904, cited by Gregory, 1920, p. 59; Gregory, 1915, p. 433; 1920, pp. 162, 188, 194, 224) but they are smaller than in *Lemur* (Gregory, 1913*b*, p. 251; 1920, pp. 169, 178) and smaller than in *Propithecus* (Gregory, 1920, p. 169) and less extended anterointernally (Gregory, 1920, p. 169), so that they are hemispherical swellings (Gregory, 1920, p. 224). Therefore, no doubt, the bulla in *Notharctus* is sometimes called small (Gregory, 1920, pp. 215, 218).

Also, in *Notharctus* the bulla shows specific differences (Gregory, 1920, p. 166); in *Notharctus venticolus* the bullæ are but little inflated, as compared with those of *Adapis;* those of *Notharctus crassus* were probably wider and more inflated than in *N. venticolus;* the conditions in *N. osborni* are intermediate.

In *Adapis*, as well, the bullæ are greatly expanded (Zittel, 1893, p. 695; Winge, 1895*a*, p. 37; Wortman, 1904, cited by Gregory, 1920, p. 59; Stehlin, 1912, cited by Gregory, 1920, p. 188; Gregory, 1915, p. 433; 1920, pp. 162, 194). According to Zittel (1893, p. 693), the large inflated bulla in *Adapis* is oval and anteriorly narrowed.

Also in *Adapis* we find specific differences in the shape and proportion of the bulla (Stehlin, cited by Gregory, 1920, p. 166): in *Adapis parisiensis* var. *schlosseri* the bulla is very wide, in *Adapis magnus* narrower, in *Adapis magnus* var. *leenhardti* smaller. The latter, which is one of the older varieties of *Adapis*, approaches *Notharctus* in the general appearance of the auditory region (Gregory, 1920, p. 166). In *Notharctus* the bulla is frequently less expanded than in the typical Lemuridæ (Gregory, 1920, p. 208), while in the Adapinæ it is more expanded (*loc. cit.*, p. 208). In *Adapis parisiensis*, for example, the bulla is larger than in modern Lemuridæ; this character is somewhat less pronounced in *Adapis* (*Leptadapis*) *magnus* var. *leenhardti* (Stehlin, 1912, cited by Gregory, 1920, p. 209).

Also, in *Aphanolemur gibbosus* (Granger and Gregory, 1917, p. 857), the bullæ are prominent and subsperical.

In *Mesopropithecus* as well, the bulla is prominent, large, similar in shape and proportions to those of recent Indrisinæ (Standing, 1908, pp. 83, 93).

According to Gregory (1915, p. 439), the earliest true lemurs probably had expanded bullæ. Gregory (1915, p. 440) is convinced that such changes as expanded bullæ becoming deflated have been frequent in the history of the Lemuroidea. Also, Standing (1908, p. 153) considers this as a secondarily acquired character and says that it cannot be urged as an argument for specially connecting *Palæopropithecus* with the Cercopithecidæ and higher apes. In *Palæopropithecus* (Standing, 1908, pp. 80–82, 153; Gregory, 1915, p. 440; 1920, p. 176) the vestigial bullæ are deflated and flattened in a vertical direction or even concave. Also, in *Megaladapis* (Lorenz von Liburnau, 1905, p. 463; Standing, 1908, pp. 108, 153; Gregory, 1920, p. 190) the bulla is by no means very prominent; it is moderately prominent only and the otherwise very spacious tympanic cavity is prolonged in the rostral process of the bulla (Lorenz von Liburnau, 1905, pp. 463, 464).

With these exceptions, a prominent inflated auditory bulla can be called a character of the majority of the lemuroids (Lorenz von Liburnau, 1905, p. 463; Standing, 1908, pp. 80, 108, 153, 160; Gregory, 1920, p. 183), although the bulla is usually of moderate size (Gregory, 1915, p. 432) and the inflated portion of the bulla is not greatly produced forward and inward toward the midline (Gregory, 1920, p. 183).

In *Archæolemur edwardsi* (Standing, 1908, pp. 97, 100) the bulla is large and prominent, but shows considerable variety in shape and size.

In the recent *Perodicticus potto* the bulla resembles that in *Lemur*, but is less prominent; oromesialward it gradually descends toward a pointed process, which may be compared with the forward prolongation of the bulla in the lemurs.

In *Galago crassicaudatus* the bulla is a little more prominent than in allied forms and in this respect agrees more with the Lemuridæ. Thus, according to Gregory (1915, p. 435), the bulla in the Lorisiformes is of moderate to large size.

In the Tarsiiformes (Gregory, 1915, p. 437) in general the bulla is of very large size, much extended antero-internally.

In the recent *Tarsius* (Van Kamp.; Winge, 1895*a*, p. 15; Wortman, 1904, cited by Gregory, 1920, p. 59; Gregory, 1915, pp. 426, 430, 442; 1920, p. 180) the bulla is greatly inflated. This bulla consists of two

portions, a rostral broader and more inflated portion and a caudal narrower and smaller portion, separated by an indistinct groove; the tympanic is fused with the caudal portion. Also in the allied fossils the bulla is large and greatly inflated, as in *Anaptomorphus* sive *Tetonius* (Zittel, 1893, p. 697; Winge, 1895*a*, p. 15; Wortman, 1904, cited by Gregory, 1920, p. 59; Gregory, 1915, pp. 426, 430, 442), in *Hemiacodon* (Gregory, 1915, p. 426), in *Necrolemur* (Winge, 1895*a*, p. 15; Gregory, 1915, pp. 426, 430, 442; 1916, pp. 462, 265) and in *Microchœrus* (Gregory, 1915, p. 426).

Also in *Anaptomorphus* (Zittel, 1893, p. 697) the bulla is oval.

The bulla in the recent Hapalidæ resembles that in *Tarsius;* it also extends in front of the porus acusticus externus, but it is less inflated and narrower and there is no distinct limit between the rostral and caudal portion. The bulla gradually descends in the anterior and in the mesial direction.

The bulla in the recent Cebidæ resembles that in *Hapale* but is broader and as a rule lower (see Winge, 1895*a*, p. 5, on difference between *Mycetes seniculus* and *niger*). Generally we find that the inflation is larger in the smaller species than in the larger ones.

In the generalized Platyrrhine, according to Gregory (1920, p. 218), the bulla is elongate anteromedially and the hypotympanic sinus is reduced.

According to Van Kampen there is no sharp difference in inflation between the Old World monkeys and the New World monkeys, as was formerly emphasized. Thus, in the Cercopithecidæ the bulla very much resembles that in the Cebidæ, and is perhaps very little less inflated.

Of course there is a great difference between the degree of inflation in the Cercopithecidæ and higher apes and the lemurs on the other hand (Standing, 1908, p. 153), though possibly the ancestral Catarrhinæ resembled these Prosimiæ in the swollen bullæ (Gregory, 1916, p. 265).

In the recent Hylobatidæ and Anthropomorphæ the bulla is less inflated than in the Cercopithecidæ. Only the small species of *Hylobates* show a still distinct bulla, while in the other genera and also in *Hylobates syndactylus* the bulla is flat. As a rule, however, the bulla is so flat and small that we find it noticed as an "anthropoid" character that there is "no bulla" (Van Kamp.; Standing, 1908, p. 160). In *Homo* the bulla is still less inflated, while the tympanic plate, which is elongate and spout-like in the lower anthropoids, is abbreviated in man (Gregory, 1916, p. 280).

Bullæ Touching Each Other in the Median Line of the Skull

The bullæ sometimes touch each other in the median line of the skull, in other cases they nearly do so.

In *Hemicentetes* and *Microgale* the tympanic processes of the basisphenoid nearly touch each other. In a part of the species of the genus *Erinaceus* we find the same, as the tympanic wing of the basisphenoid is much enlarged at the expense of the horizontal part of the basisphenoid, so that this part, lying in between the two bullæ, is very narrow.

In all Talpidæ the tympanic wing of the basisphenoid meets its fellow of the opposite side in the sagittal line of the under side of the skull, and in the young *Myogale* this also happens with the tympanic process of the alisphenoid (Van Kamp.; Gregory, 1910, p. 264).

In *Rhynchocyon* and *Macroscelides* the bullæ nearly touch each other in the median line, while in *Petrodromus* the distance between the bullæ is larger, as the rostral entotympanic is smaller (Van Kamp.; Carlsson, 1910*a*, p. 353).

In the rodents the bullæ sometimes touch each other in the median line beneath the basis cranii by means of the processus styliformes (Van Kamp.; Winge, 1888, p. 120, *Dipus*).

In the fossil *Hypisodus* (Matthew, 1893–1903, p. 440; 1902*c*, p. 312; Troxell, 1920*a*, p. 393) the bullæ are separated widely posteriorly, but in front they are closely in contact and connate in the median line of the skull, covering up almost all of the basisphenoid.

The rostral portions of the bullæ in *Tarsius* nearly touch each other in the median line. According to Van Kampen it is not true that the bullæ in *Nycticebus* and *Loris* touch each other in the median line, as has been formerly described.

Growth of the Bulla

It is of interest to know that the form of the bulla may change during growth and therefore it is important to know the stage of development of the skull in all cases where the form of the bulla is used as a character. How this alteration of the form is attained is very little known. The ossified wall may be excavated and also the outer wall may be thickened, while on the inside of the bulla resorption occurs.

In many cases the bulla inflates more and more as the animal grows older. Well-known examples are *Bos*, *Sus*, Prosimiæ and Carnivora. The conditions in *Centetes ecaudatus* are worth mentioning. According to Van Kampen, in this species and in this species alone, the strongly developed fore part of the tympanic cavity that lies in front of the tym-

panic and the periotic is secondary; in the young skull it is much smaller and hardly extends in front of the periotic and the tympanic.

In the young *Solenodon paradoxus*, there is a large open foramen lacerum medium, which seems to be covered by the tympanum in the adult skull (Gregory, 1910, p. 247).

In the new-born *Hydrochœrus capybara* (Preller, 1907, pp. 379, 387) the bulla is, as in many other Rodentia, large and inflated; but later the bulla grows less than the rest of the skull (p. 387), so that in the adult *Capybara* (pp. 390, 411) the bulla is relatively very small. This is explained (Preller, 1907, p. 387) as an adaptation to aquatic life. The shape of the bulla changes markedly, becoming much compressed laterally, the rostromesial part sharply pointed (Preller, 1907, p. 387).

According to Kellogg (1912, p. 163) the bulla in the young *Erethizon epixanthum* is unusually long anteroposteriorly and inflated, but shrinks and contracts with age, so that the general shape of the bullæ rather than their size would constitute a dependable character.

In *Felis domestica* the entotympanic portion of the bulla in the new-born specimen is flat; later it inflates and forms a globular hypotympanic sinus.

In the young *Ursus* the bulla is much more inflated, rounded, and larger than in the adult.

The same condition as in *Ursus* is emphasized for *Monachus tropicalis*, while in *Phoca* and *Cystophora* the bulla in the young specimen is relatively as large as in the adult.

In the young *Sus* the bulla is relatively much larger and thus more normal than in the adult.

In the young *Hippopotamus* the bulla is not yet compressed and then resembles that in *Dicotyles*.

In the fossil *Elomeryx* (Troxell, 1921*a*, p. 334) the immature animal shows greatly inflated bullæ, while in the animal just reaching maturity the bulla is moderate.

In the young modern Camelidæ the bulla is less abnormal than in the adult specimens, though the under wall of the auditory meatus is already inflated in the young animal.

In the young *Antilocapra* (Matthew, 1904, pp. 110, 111) the bulla is larger than in the adult. This is perhaps also the case in the fossil *Merycodus* (Matthew, 1904, p. 111).

In all young antelopes, as well, the bulla is larger than in the adult (Matthew, 1904, p. 111).

In the very young *Nesodon* (Scott, 1912, p. 137) the bulla is large,

oval, thin-walled and moderately inflated, with the long axis directed anteroposteriorly, while in the adult skull (Scott, 1912, pp. 134, 137) it is unduly small, but mammillate as the principal diameter is dorsoventral.

In the young *Elephas* (Gregory, 1903, p. 389) the bulla is relatively large and inflated, thus differing from that in the adult.

Also in the young Hylobatidæ and Anthropomorphæ the inflation of the bulla is relatively larger than in the old skulls.

Position of the Longest Horizontal Axis of the Tympanic and of the Bulla

The longest horizontal axis of the tympanic and of the bulla can be very differently directed. A few examples may be mentioned here.

The plane of the tympanic annulus runs as a rule anterointernally.

In the Trichechidæ the tympanic membrane is almost exactly sagittal. In *Phoca grœnlandica*, on the other hand, the declination of the tympanic membrane is rather large, perhaps due to the strong development of the mastoid.

In the recent Felidæ the longest horizontal axis of the bulla is nearly sagittal, a little anterointernally directed.

In the fossil *Cephalogale* (Filhol, 1883, p. 39) this long axis runs nearly in the sagittal direction.

In *Mesocyon drummondanus* the long diameter of the bulla is less oblique to the sagittal plane than in *Mesocyon josephi secundus* (Thorpe, 1922*a*, p. 171).

In *Kogia* the long axis of the bulla is transverse, nearly at right angles to its direction in *Phocæna* (Schulte, 1917, p. 395).

In *Agriochœrus bullatus* (Thorpe, 1921*c*, p. 116) the long axis of the bulla lies at an angle of about thirty-five degrees from the sagittal plane.

In *Poëbrotherium wilsoni* and *labiatum* (Scott, 1891*a*, p. 15) and in *P. andersoni* (Thorpe, 1917, p. 382) the long diameter of the inner parts of the bullæ are nearly parallel to each other and to the long axis of the skull, while in the modern Camelidæ (Scott, 1891*a*, p. 15) the long diameter of the bulla is placed at a wide angle with the cranial axis.

In *Tarsius* (Van Kamp.; Gregory, 1920, p. 227) and in the fossils *Anaptomorphus*, *Hemiacodon*, *Necrolemur* (Van Kamp.; Gregory, 1916, p. 264) and *Microchœrus* the bullæ are extended anterointernally toward the midline (Gregory, 1915, p. 426), while in the fossil *Notharctus* the inflated portions of the opposite bullæ are not extended inward toward the midline.

In the primitive Platyrrhinæ (Gregory, 1916, p. 266) the bullæ

are obliquely elongate; in the primitive Catarrhinæ (Gregory, 1916, p. 266) they are transversely extended and also in the Anthropoidea they are extended inward toward the midline (Gregory, 1920, p. 227).

Size of the Bulla in Relation to the Development of the Epitympanic Sinuses and to Other Factors

Perhaps there is a relation between the size of the auditory bulla and the development of the epitympanic sinuses. The conditions of these two are, however, very variable.

As to the possible relation between the hypotympanic and the epitympanic sinuses, we see that in general the more primitive mammals show a well-developed epitympanic sinus, as many marsupials, edentates and Galeopithecidæ, while the more specialized mammals show well-developed hypotympanic sinuses, as most Rodentia, Ungulata, and Carnivora. *Elephas* has a relatively small bulla but the tympanic cavity shows an exceptional extension in the exoccipital. Often one excludes the other; for example, *Procavia*, the only recent ungulate with a well-developed epitympanic sinus, has a small bulla. *Typotherium*, on the other hand, shows a large bulla and probably also a well-developed epitympanic sinus. Among the Prosimiæ and primates, going from the more primitive to the more specialized, we find that the epitympanic sinus becomes larger and larger, while the bulla diminishes in size (Van Kamp.; Gray, 1913, pp. 397–398, on the relation between the "mastoid cells" and the size of the cavity of the bulla). Exceptions, on the other hand, are not rare; we find them in many Rodentia.

So *Manis* and many other edentates, for instance, many Gravigrada (see my own investigations) do not show a hypotympanic sinus; the Myrmecophagidæ and *Chlamydophorus* show only a hypotympanic sinus. Some of them show, on the other hand, a well-developed epitympanic sinus (Van Kamp.; Gray, 1910, p. 338).

There may be other influences as well: for example, nocturnal life perhaps. It is a well-known fact that the bulla in nocturnal animals sometimes reaches enormous proportions (Scott, 1913, p. 66). There is often a relation between the size of the animal and that of the bulla, sometimes also between the size of the bulla and that of the external ears, as in Canidæ. Another influence is perhaps the presence of strongly developed air sacs starting from the pharynx and the Eustachian tube, as in the Chiroptera, which perhaps indicate the absence of accessory cavities of the tympanic cavity, while these are present in all other flying mammals. Air sacs starting from the Eustachian tube are also present in *Equus*, *Tapirus*, and *Procavia*, in which the bullæ are small.

Epitympanic Recess

Epitympanic sinuses are accessory cavities of the tympanic cavity lying in the squamosal or in the mastoid, which contain no essential parts of the tympanic cavity and which start from the recessus epitympanicus.

The recessus epitympanicus, atticus tympanicus, or aditus ad antrum, is that part of the primary tympanic cavity which in the mammals was added to this cavity when the elements of the joint of the jaw in the lower vertebrates were received into this cavity with the function of auditory ossicles. A recessus epitympanicus is wanting in *Ornithorhynchus*, which is a reminiscence of conditions in lower vertebrates. In *Ornithorhynchus* there is a so-called atticus tympanicus; this contains all the auditory ossicles, except the manubrium mallei; the membrana Shrapnelli lies under it, while the crista facialis is found on its external side. The absence of the bony recessus epitympanicus in *Ornithorhynchus* is probably the reason that the tympanic fossa, i.e., the roof of the tympanic cavity, is very small in *Ornithorhynchus*, while it is very large in *Echidna* (Gregory, 1910, p. 158). Formerly, in *Echidna*, that part of the tympanic cavity was also called recessus epitympanicus, which is larger than the true one, as it contains the malleus, except the manubrium, the incus, the stapes and the fenestra vestibuli and cochleæ, while the true recessus epitympanicus, which is only a part of the above-mentioned cavity, only contains parts of the malleus and incus. A similar condition is found in *Manis*, where the epitympanic sinus originates from the upper part of the tympanic cavity, which contains more than the true epitympanic recess and therefore may be compared with the "atticus tympanicus" of the monotremes.

The recessus epitympanicus is covered on the medial side by the tegmen tympani of the periotic, which is also a neomorph in the mammals, also by the squamosal, while the lateral wall is very differently developed.

Membrana Shrapnelli

The lateral wall of the recessus epitympanicus lies above the level of the true tympanic membrane or the so-called pars tensa, so that this lateral wall is formed as a rule by the pars flaccida of the tympanic membrane, or the membrana Shrapnelli, which according to Bondy (1907, p. 399) is a much better name, as it does not form a part of the tympanic membrane. The membrana Shrapnelli lies between (a) the skeletal element that closes the "Tympanicumdefekt" (the hiatus lying between the two "Tympanicumschenkel"), (b) these "Tympanicum-

schenkel" themselves and (c) the arcus terminalis; the latter is the band of connective tissue that connects the spinæ tympanicæ posterior and anterior and lies between the pars tensa of the tympanic membrane and the membrana Shrapnelli (Bondy, 1907, p. 301).

The size of the membrana Shrapnelli is very variable (Bondy, 1907, p. 396); it depends on the position of the spinæ tympanicæ on the tympanic ring and therefore on the length of the crista tympanica (Bondy, 1907, p. 395); it depends also on the length of the "Tympanicumdefekt" and on the distance between the arcus terminalis and the under margin of the lateral bony wall of the recessus epitympanicus (Bondy, 1907, p. 396). The membrana Shrapnelli is limited (see Bondy, 1907, pp. 396, 397) on the ventral side by the arcus terminalis and sometimes also by the dorsal margin of the two legs of the tympanic ring; on the dorsal side by the skeletal element that closes the "Tympanicumdefekt" and partly also by the legs of the tympanic ring. If the tympanic ring is closed all around, both "Tympanicumschenkel" alone limit the membrana Shrapnelli dorsally. Finally, in all cases where the lateral wall of the recessus epitympanicus is not bony but membranous, as in *Echidna*, *Erinaceus*, *Sorex* and Chiroptera (Bondy, 1907, pp. 397, 398, 399), a sharp limit cannot be defined except in *Echidna*, where the attachment of the cartilaginous external auditory meatus makes this possible.

In *Tolypeutes tricinctus* (Bondy, 1907, p. 350) the anterior leg of the tympanic remains at a great distance from the skull. Therefore the membrana Shrapnelli is not distinctly limited in this part but the limit is indicated by the connective tissue between the tympanic and the skull.

The membrana Shrapnelli is not always attached to the free margin of the elements that limit it. Thus, dorsally, (see Bondy, 1907, p. 396), the membrana Shrapnelli is not always attached to the free under margin of the bony lateral wall of the recessus epitympanicus, but on its lateral surface. This can occur over the whole length of the bony lateral wall of the recessus epitympanicus, as is the case in some Carnivora and Ungulata; then the free under margin of this bone projects into the cavity of the recessus epitympanicus (Bondy, 1907, p. 396). In other cases, as in *Sus* (Van Kamp.; Bondy, 1907, pp. 371–375) and also in *Fœtorius putorius* (Van Kamp.; Bondy, 1907, pp. 359, 360, sac-like diverticle behind the malleus; pp. 361, 362, *Mustela foina*), and in *Viverra* (Van Kamp.; Bondy, 1907, p. 363, attachment to the lateral side of the totally closed tympanic) the membrana Shrapnelli is partly free from the free under margin of the bony lateral wall of the recessus epitympanicus, so that protuberance of this recessus is formed, lying between the membrana

Shrapnelli and the lateral bony wall of this recessus. A transitional condition is shown in *Erinaceus* with a number of sacs (Bondy, 1907, p. 396). On the ventral side (Bondy, 1907, p. 397), there is sometimes, as in a few Chiroptera (Bondy, 1907, pp. 316, 317, 320) a small recessus as well between the lateral surface of the tympanic cavity and the medial surface of the membrana Shrapnelli; in this place the arcus terminalis projects into the tympanic cavity.

The membrana Shrapnelli is never absent, according to Bondy (1907, p. 397), although it may be very small. Van Kampen, on the other hand, emphasizes its absence in *Manis*.

Now we shall sum up some further remarks on the condition of the membrana Shrapnelli, which may illustrate the differences in size, mode of attachment, and so forth.

In the modern rodents the incisura tympanica may be absent or present. Even a bony lateral wall of the recessus may be totally absent, as is the case in the Muridæ. In *Dipus* the incisura tympanica does not form half a circle but nearly a whole circle, showing a very small defect only.

In *Lepus cuniculus*, according to Bondy (1907, p. 322), the membrana Shrapnelli is very small, as the defect in the crista tympanica is very small, while, according to Gray (1913, p. 400), the membrana Shrapnelli is relatively much larger than in the human subject and consequently the notch of Rivini forms a comparatively large break in the tympanic ring. In *Lepus timidus* (Bondy, 1907, p. 324), still a part of the space present in *Lepus cuniculus* is covered by the periotic, to which the membrana Shrapnelli is attached. In *Cricetus frumentarius* (Bondy, 1907, pp. 332, 333) and in *Myoxus avellanarius* (*loc. cit.*, p. 329) the membrana Shrapnelli lies between the arcus terminalis and both legs of the tympanic, which is closed all around. As in the latter species the spinæ are highly attached, the membrana Shrapnelli is small. In *Sciurus vulgaris* (Bondy, 1907, p. 326) the membrana Shrapnelli is very narrow, in *Spermophilus citillus* (*loc. cit.*, p. 328) it is a little larger; also in *Cavia cobaia* (*loc. cit.*, p. 347) it is a narrow sickle while in *Dasyprocta aguti* (*loc. cit.*, p. 348) it is broader than in *Cavia*. In *Arvicola arvalis* (*loc. cit.*, p. 335) there is no distinct membrana Shrapnelli.

In *Mus decumanus* (Bondy, 1907, p. 337) the rather broad membrana Shrapnelli is limited ventrally by the arcus terminalis, dorsally by the rostral leg of the tympanic and the tegmen tympani, caudally by a process of the periotic. In *Mus musculus* (Bondy, 1907, p. 339) the membrana Shrapnelli is very large, the sulcus tympanicus occupying

but little more than half the ring. Also in *Mus silvaticus* (*loc. cit.*, p. 341) the membrana Shrapnelli is very large, about half as large as the tympanic membrane. In both these species of *Mus* (pp. 339, 341) the membrana Shrapnelli is limited dorsocaudally by the hind leg of the tympanic, while dorsorostrally it is less distinctly limited; in the neighborhood of the rostral leg of the tympanic we find a recessus lying between the tympanic on the mesial side and the membrana Shrapnelli on the lateral side. In *Mus minutus* (*loc. cit.*, p. 343) the rather large membrana Shrapnelli lies between the arcus terminalis, both legs of the tympanic and a cartilaginous process of the tegmen tympani on the dorsal side. In the "Feldmaus" (Bondy, 1907, p. 344) the rather large membrana Shrapnelli lies between the arcus terminalis, both legs of the tympanic and the periotic.

In *Felis domestica* (Bondy, 1907, p. 366) the membrana Shrapnelli is limited by the arcus terminalis, both legs of the tympanic and the portion of the squamosal that covers the defect of the tympanic. In *Canis familiaris* (*loc. cit.*, p. 353) it is limited by the arcus terminalis, caudally by the lateral surface of the "Chordafortsatz," dorsally by both legs of the tympanic.

In *Fœtorius vulgaris* (Bondy, 1907, p. 356) the membrana Shrapnelli lies between the arcus terminalis and the totally closed tympanic.

In *Phoca vitulina* (*loc. cit.*, p. 368) it is narrow.

In the Mystacoceti the membrana Shrapnelli as well as the membranous lateral wall of the sinus epitympanicus forms the sac-like so-called tympanic membrane. In the Delphinidæ the membrana Shrapnelli is bagged out and forms the so-called sinus pneumaticus epitympanicus, which communicates by means of the apertura petro-tympanica s. hiatus epitympanicus with the epitympanic recess. There is a communication between the porus acusticus externus and the hiatus epitympanicus; this communication is wider in the Physeteridæ than in the Delphinidæ and thus more as in the Balænidæ.

In *Equus caballus* (Van Kamp.; Bondy, 1907, p. 369) the membrana Shrapnelli lies between the arcus terminalis and the incisura tympanica, which is formed by the incisure in the dorsal wall of the external auditory meatus; this incisure, which is closed by the membrana Shrapnelli, corresponds with the defect in the crista tympanica.

In *Sus* (Bondy, 1907, pp. 371–375) the membrana Shrapnelli is attached to the arcus terminalis, to the ends of both legs of the tympanic and to the lateral surface of the squamosal and not to the free under margin of this bone, forming the lateral wall of a diverticle of the epi-

tympanic recess. This attachment to the lateral surface of the squamosal occurs higher up than two-thirds of the length of the external auditory meatus.

In *Cervus capreolus* according to Bondy (1907, p. 376) the membrana Shrapnelli is attached to the arcus terminalis, to the ends of both legs of the tympanic and between these two legs on the lateral surface of the squamosal. Between the lateral wall of this part of the squamosal and the membrana Shrapnelli lies a recess of the tympanic cavity. The membrana Shrapnelli is not much smaller than the tympanic membrane itself, as the crista occupies half the tympanic only.

In *Cervus elaphus* (Bondy, 1907, p. 378) the membrana Shrapnelli is attached to the arcus terminalis, the rostral leg of the tympanic, the squamosal and a mass of connective tissue between the squamosal and the caudal tympanic leg, which lies at a large distance from the squamosal. Thus the end of the caudal leg of the tympanic projects into the membrana Shrapnelli. The membrana Shrapnelli is large, as the crista is short and the defect of the tympanic large.

In *Capra hircus* (Bondy, 1907, p. 380) the membrana Shrapnelli is not attached over its whole length to the free margin of the squamosal, but over a short distance on its lateral surface, covering a flat recess. The height of the membrana Shrapnelli is about one-fourth of that of the tympanic membrane.

In *Bos taurus* (Bondy, 1907, p. 381) and in *Ovis aries* (*loc. cit.*, p. 383) the attachment of the membrana Shrapnelli is the same as in *Cervus capreolus*, but it is smaller, and its size in *Ovis aries* is half that of the tympanic membrane.

In *Macacus nemestrinus* (Bondy, 1907, p. 385) the membrana Shrapnelli is low, and lies between the arcus terminalis and the under margin of the bony lateral wall of the epitympanic recess.

In man, according to Gray (1913, p. 400), the membrana Shrapnelli is smaller than in many other mammals.

Bony Lateral Wall of the Epitympanic Recess

The bony lateral wall of the recessus epitympanicus may also be variously formed. When the tympanic ring is closed all around, this lateral wall is practically formed by the tympanic, as the parts of the os temporale, which lie above it, only take part in it to a small degree (Bondy, 1907, p. 393). In most cases, however, the tympanic is not closed all around and then the bony lateral wall of the recessus epitympanicus is formed by the skeletal element which closes the "Tympanicum-

defekt" and the tympanic does not take part in it or only to a very small degree (Bondy, 1907, p. 393). As a rule, this skeletal element is the squamosal (Bondy, 1907, p. 393), viz., the so-called planum epitympanicum of the squamosal, which planum forms the inferior part of the facies epitympanica. Exceptionally it is the periotic, as is the case in *Erinaceus*, *Tolypeutes* and Rodentia (Bondy, 1907, pp. 350, 393). According to Van Kampen the recessus epitympanicus in *Erinaceus europæus* is laterally covered not only by the membrana Shrapnelli and the squamosal but also by the mastoid, while in the allied *Gymnura* and *Hylomys*, just as in *Centetes*, the mastoid is lacking in this lateral wall, a feature that is probably related to the development of the posterior part of the squamosal (the posttympanic process). In *Sorex*, according to Bondy (1907, p. 310), the tegmen tympani of the periotic forms a part of the lateral wall of the recessus epitympanicus.

In *Echidna* (Gaupp, 1908, p. 657) the squamosal forms the lateral wall and the largest part of the roof of the epitympanic recess, the mesial part of this roof being formed by the crista parotica.

In the rodents we do not find the squamosal in the lateral wall of the epitympanic recess, but the petrotympanic. This small development of the caudal portion of the squamosal is a characteristic feature in rodents and causes the total absence of the squamosal in the walls of the tympanic cavity and its accessory cavities. As the tympanic and the periotic are fused, it often can hardly be said which of the two forms the lateral wall of the epitympanic recess. Also the bony lateral wall can be totally absent. An incisura tympanica may be absent or present. In *Dipus* the incisura does not form a half circle, but nearly a total one, showing a small defect only.

According to Van Kampen, probably the tympanic, by means of the upper wall of the external auditory meatus, often forms the larger part of the lateral wall of the epitympanic recess. According to Bondy (1907) the fused legs of the tympanic form this lateral wall in *Sciurus vulgaris* (p. 325), while in *Myoxus avellanarius* (p. 329) and *Myoxus glis* (p. 331) both legs lie in this wall. In this lateral wall lies the long rostral leg of the tympanic in *Arvicola arvalis* (Bondy, 1907, p. 334), the broad caudal leg in *Mus silvaticus* (p. 340), *Mus minutus* (p. 342) and in the "Feldmaus" (p. 344).

According to Van Kampen, this lateral wall in *Lepus* is partly formed by the downwardly turned margin of the tegmen tympani. According to Bondy (1907, p. 324) in *Lepus timidus* we find a part of the periotic in the place where in *Lepus cuniculus* a part of the membrana Shrapnelli

is found. In *Mus decumanus* (Bondy, 1907, p. 336) the lateral wall of the epitympanic recess is formed by the prolongation of a bony process of the petrosal. In *Cavia cobaya*, Bondy (1907) describes the petrosal in this lateral wall (pp. 345–346) and a bony plate connected with the petrosal and with the crista (pp. 346–347).

In *Viverra zibetha*, according to Bondy (1907, p. 363), the tympanic, which is closed all around, forms the lateral wall of the epitympanic recess.

In the Delphinidæ, Van Kampen emphasizes the absence of the squamosal in the lateral wall of the epitympanic recess, which is perhaps due to the development of the sinus pneumaticus epitympanicus: the margin of the tegmen tympani forms the limit of the space found in the dry skull.

In *Equus* (Van Kamp.; Bondy, 1907, p. 369) the bony lateral wall of the epitympanic recess is formed by the dorsomesial wall of the bony external auditory meatus, as the epitympanic recess is still extended dorsalward above the attachment of the membrana Shrapnelli. The squamosal seems to form the upper wall only. Also in the modern *Rhinoceros* and *Tapirus* the squamosal is absent in this lateral wall; probably a similar condition occurs as in *Equus*.

In *Sus scrofa domestica* (Van Kamp.; Bondy, 1907, pp. 371–373) the lateral bony wall of the epitympanic is formed by the squamosal, though it is very difficult to limit it from the tympanic, with which it is fused in the adult skull. This bony lateral wall shows a deep incision by which the epitympanic recess communicates with its lateral diverticle, which in turn is covered laterally by the membrana Shrapnelli.

In the modern Camelidæ the epitympanic recess does not extend along the bony external auditory meatus.

In the Tragulidæ the lateral bony wall is formed by the squamosal and tympanic; there is no open incisura tympanica.

In the recent Cervidæ this lateral wall is incompletely formed by the squamosal.

In *Procavia* the squamosal covers the epitympanic recess laterally.

In *Rhytina* (Claudius, 1867, p. 8) the petrosal shows a deep incisura above the place of attachment of the tympanic and above the malleus. In *Manatus* the epitympanic recess lies in the thick tegmen tympani, which is excavated like a basin. In *Halicore* the squamosal participates in the covering of the recess. Freund (1908, pp. 616, 617) describes an incisure above the tympanic membrane in the lamina parietalis of the fœtal *Halicore*.

According to Gregory (1920, p. 170) the anterosuperior sinus of the epitympanic recess in *Notharctus* extends between the squamosal and the periotic, exactly as in *Lemur*.

Bondy (1907, p. 383) could not decide whether the bony lateral wall of the epitympanic recess in *Macacus nemestrinus* is formed by the petrosal or by the squamosal.

Membranous Lateral Wall of the Epitympanic Recess

Another exceptional condition occurs when the bony lateral wall is less developed, so that this wall is partly membranous, as is the case in *Echidna*, *Sorex*, and Chiroptera (Bondy, 1907, pp. 393, 395, 396). This membranous lateral wall of the recessus epitympanicus is to be distinguished from the membrana Shrapnelli, the latter being covered by the epithelium of the external auditory meatus, while the former is not covered by this epithelium, but by subcutaneous tissue (Bondy, 1907, pp. 304, 305, 395, 396). Of course, in the dry skull it is impossible to make out where the membrana Shrapnelli ends and where the membranous lateral wall of the recessus epitympanicus begins. So Van Kampen thought that in *Echidna* the true recessus epitympanicus was laterally covered by the membrana Shrapnelli, but Bondy (1907, pp. 304, 305) found that this covered only the under part of the so-called false recessus epitympanicus (see above), while the lateral wall of the true epitympanic recess was membranous and not covered by the epithelium of the external auditory meatus.

Size and Shape of the Recessus Epitympanicus

The size of the recessus epitympanicus is variable, sometimes even in allied mammals. For example, *Chrysochloris aurea* shows an enormously developed recessus epitympanicus, probably in relation to the large caput mallei and corpus incudis, while in other species the recessus epitympanicus is smaller or even absent, though the species which do not show a recessus epitympanicus in the dry skull are sometimes separated from this genus under the names *Amblysomus* or *Chalcochloris*.

Sometimes the epitympanic sinus and the epitympanic recess are not distinctly separated, so that the epitympanic recess forms a part of the combined cavity. This happens in *Orycteropus* and in *Bradypus*. In different Gravigrada (see also my own investigations on *Scelidotherium*) there is a rather large and deep recessus epitympanicus, but, except in *Nothrotherium* and perhaps in *Mylodon*, an epitympanic sinus in the squamosal is lacking. Also in the Dasypodidæ an epitympanic sinus

rarely originates from the epitympanic recess. In the Glyptodontidæ the epitympanic recess, which as usual lies between the periotic and the squamosal, is rather deep. In *Myrmecophaga* we find a small and deep recessus epitympanicus.

In *Plecotus auritus* (Gray, 1913, p. 409) the attic consists only of a cone-shaped bulging of the upper portion of the tympanum.

In the modern rodents the recessus epitympanicus is sometimes deep, so that it has been described as an epitympanic sinus, which is not correct according to Van Kampen. According to Gray (1913, p. 401) the attic of the tympanum in *Lepus cuniculus* is a well-marked cavity, extending for a considerable distance above the malleo-incudal articulation, being narrowest at the lower wall and a little flattened from without inward.

In *Felis* and *Canis* the epitympanic recess is rather deep. Also in *Herpestes griseus* (Gray, 1913, p. 403) the attic is comparatively large and roughly pear-shaped, the broad end being directed forward, while the posterior extremity is formed by the rudimentary antrum.

In *Phoca* (Van Kamp.; Bondy, 1907, p. 368) the epitympanic recess is very high and spacious, a fact that is related to the size of the incus; this enlargement is caused by a small concavity of the planum epitympanicum, which may be called a small accessory sinus. In the Otariidæ, in which the incus is not abnormally large, the epitympanic recess is smaller than in the Phocidæ. In the Trichechidæ, on the other hand, the epitympanic recess is smaller than in *Phoca*, notwithstanding the large size of the incus.

Thus, in the Sirenia as well, the epitympanic recess is wide, the auditory ossicles also being large.

In *Equus* the recessus epitympanicus is rather large. That in the modern Camelidæ and Tragulidæ is small.

In the fossil *Notharctus*, according to Gregory (1920, p. 170), the epitympanic recess comprises a small posterior sinus containing the malleus and incus, and a much larger anterosuperior sinus, which extends dorsad between the squamosal and the periotic, exactly as in *Lemur*.

Epitympanic Sinuses

As a rule, the presence of epitympanic sinuses may be suggested externally, if the region of the bulla is swollen. A species of the genus *Phascolomys* shows that this is not necessary. There different swellings are present, while not all contain accessory sinuses.

Perameles shows that it may be impossible in the dry skull to distinguish an accessory sinus in the tegmen tympani of the periotic from an extraordinarily developed fossa muscularis major.

In the monotremes and in the Didelphyidæ epitympanic sinuses are lacking. The marsupials in general show well-developed sinus epitympanici in the squamosal. The epitympanic sinuses in the superficies meatus squamosi show remarkable differences in place. In *Phascolomys*, where the depth of the epitympanic sinus in the superficies meatus squamosi shows remarkable differences in the various species, this epitympanic sinus is divided by a transversal ridge into a fore and a hind part, which communicate with the recessus epitympanicus by the foramen supratympanicum Cope (this is the opening between the squamosal and the upper wall of the external auditory meatus). The fore part lies in the same place as the epitympanic sinus in *Phascolarctus*, where it is rather large and also extends into the postglenoid process and the root of the processus zygomaticus, communicating with the tympanic cavity by a foramen pneumaticum, Cope's so-called foramen postzygomaticum, which is according to Van Kampen not homologous with Cope's foramen postzygomaticum in the monotremes. The large concavity in the Macropodidæ lies in this place as well and has a foramen postzygomaticum and communicates with the recessus epitympanicus through the foramen supratympanicum. The air-cells in the squamosal in *Thylacoleo* (Owen, 1859, p. 316) lie, according to Van Kampen, in the same place also and not so far behind as in the Dasyuridæ, with which Owen compares it. All this concerns the fore part of the epitympanic sinus in *Phascolomys* and the epitympanic sinuses which agree with it in place.

The hind part of the epitympanic sinus in the superficies meatus squamosi in *Phascolomys* lies in the same place as the epitympanic sinus in the Polyprotodontia, i. e., the Dasyuridæ, and probably also in the Peramelidæ, though in this family it is lacking in a few species. In the same place lies the small hind concavity in the Macropodidæ. Especially in the Phalangeridæ the epitympanic sinuses are well-developed (Van Kamp.; Winge, 1893*b*, p. 100); they communicate with the tympanic cavity through the foramen supratympanicum, which lies on the same place as this opening in the Macropodidæ; except for the strongly developed epitympanic sinus in the squamosal. *Trichosurus* also shows one in the mastoid, while in *Phalangista* and *Petaurus* the accessory sinuses extend into the processus jugalis and the condyli occipitales.

Among the Erinaceidæ, some species show a small epitympanic sinus, others a large or even a very large one. In *Erinaceus europæus*, we find a small epitympanic sinus in the mastoid and in the hind wall of the postglenoid process of the squamosal. In *Macroscelides*, but not in all species, we find large accessory cavities in the squamosal, parietal and mastoid,

which communicate with the tympanic cavity (Van Kamp; Carlsson, 1910*a*, p. 353). Among the insectivores we find epitympanic sinuses in *Erinaceus*, *Chrysochloris*, and *Macroscelides* and hypotympanic sinuses in the Talpidæ and Chrysochloridæ. They seem, however, except perhaps those in the Talpidæ and Chrysochloridæ, to have originated independently. The epitympanic sinus is wanting in the Chiroptera (Van Kamp.; Gray, 1913, pp. 409, 413).

In *Galeopithecus* the air-cells lie in the mastoid, squamosal, even in the postglenoid process, often even in the under wall of the external auditory meatus; the epitympanic sinus shows resemblances to that in the Phalangeridæ; the foramen pneumaticum, which lies between the alisphenoid and the squamosal, has a similar place to that of *Manis*.

The epitympanic sinus lying in the squamosal occurs in many edentates, but also among other mammals, which according to Van Kampen (1904, p. 144; 1905, p. 469) can only be regarded as due to convergence.

In *Orycteropus* (Van Kamp.; Winge, 1915, p. 222) the epitympanic sinus in the squamosal is not large; the walls are smooth, except for a few ridges; the foramen pneumaticum is very large, so that there is a gradual transition between the epitympanic recess and the epitympanic sinus, as we have mentioned above. According to Van Kampen the epitympanic sinus does not form a continuation in the alisphenoid, as is sometimes noted. In *Manis* (Van Kamp.; Gregory, 1910, p. 338; Winge, 1915, pp. 223, 224) the epitympanic sinus is larger than in *Orycteropus*. It lies in the hinder part of the squamosal and fills this up as far as the upper margin; the posttympanic process is swollen; the foramen pneumaticum is large; the wall of the epitympanic sinus is smooth with a few low ridges. The above-mentioned communication of the two tympanic cavities by means of cavities in different bones of the skull in *Manis* probably does not exist, according to Van Kampen. In *Bradypus* the epitympanic sinus is very large, indistinctly separated from the recessus epitympanicus; the epitympanic sinus originates from the facies epitympanica and lies in the swollen squamosal as far as the processus jugalis; the walls are smooth. In *Cholœpus hoffmanni* the sinus epitympanicus is practically absent, the facies epitympanica slightly concave and only at its fore part a little more excavated; according to Van Kampen this is perhaps individual. The alleged connection of the cavity in the squamosal with that in the pterygoid in some Bradypodidæ is, according to Van Kampen, an error, and therefore is probably an error also in *Nothrotherium* (=*Cœlodon*) (see Van Kamp.;

Reinhardt, 1878, pp. 276, 277). According to Van Kampen an epitympanic sinus is lacking in most genera of the Gravigrada, except probably in *Nothrotherium* (=*Cœlodon*) (Van Kamp.; Reinhardt, 1878, p. 277) and perhaps in *Mylodon* (Owen, 1842, p. 26), if this is not the recessus epitympanicus. In *Myrmecophaga* the epitympanic sinus in the squamosal is small. In the Dasypodidæ (Van Kamp.; Winge, 1915, p. 225, who denies the presence of an epitympanic sinus) an epitympanic sinus is rarely found. Perhaps it is present, but then inconstant in *Xenurus* (=*Lysiurus*) *unicinctus;* further in *Dasypus* a little accessory cavity is found, perhaps lying in the squamosal, but Van Kampen, is not sure about that. In the Glyptodontidæ, according to Van Kampen, the cavities in the squamosal do not communicate with the recessus epitympanicus, as Burmeister mentions.

In the modern rodents the epitympanic sinus is as a rule present. Sometimes it is absent, and then a wide epitympanic recess only is found. It lies neither in the squamosal nor in the tympanic, but is totally enclosed in the periotic, according to Van Kampen. According to Bondy (1907, p. 345), however, in *Cavia cobaya* it is covered by the tympanic and the periotic. The foramen pneumaticum often lies rostrally in the epitympanic recess and the tegmen tympani in relation to the oralward extension of the mastoid. According to Bondy (1907) a bony plate, formed by the petrosal, separating the tympanic cavity from the cellulæ epitympanicæ anteriores and forming their floor, is present in *Cavia cobaya* (p. 347) and in *Dasyprocta aguti* (p. 348). In *Lepus cuniculus* (Gray, 1913, pp. 401, 413) the antrum opens out of the posterior, inferior wall of the attic and there is a constriction marking the boundary between the two. The epitympanic sinus is very differently developed. Among the Sciuridæ it is most strongly developed in the flying species, as is often the case in flying mammals (except in the Chiroptera), as in Phalangeridæ and *Galeopithecus.*

The epitympanic sinus may be subdivided by one or more septa; sometimes externally a deep groove corresponds with this subdivision (Van Kamp.; Scott, 1895, cited by Van Kampen, *Protoptychus*). In *Sciurus vulgaris* we find three bulgings one behind the other. In other rodents there are many septa (Van Kamp.; Bondy, 1907, p. 345, *Cavia cobaya*); then the sinus is cellular (Van Kamp.; Sinclair, 1909, p. 11) or spongy, or, exceptionally, contains osteophytes. The fossil *Protoptychus* (Scott, 1895, cited by Van Kampen) shows incomplete septa. In *Lepus cuniculus* (Van Kamp.; Gray, 1913, pp. 401, 413) the small epitympanic sinus is of about the same size as the epitympanic recess; it is

roughly cone-shaped, the rounded point of the cone being the posterior extremity of the cavity; there is no further development in the direction of other air-containing cells. All conditions found in the epitympanic sinus also occur in the cavity of the auditory bulla, but not always in the same animal in the same way.

In many rodents the mastoid above and before the porus acusticus externus, (in other rodents also in the hinder portion) is more or less distinctly inflated. Sometimes it is so strongly inflated that the inflation is visible on the occipital plane and also on the dorsal side of the skull; then they may even strongly reduce the occipital. Sometimes the caudal portion of the squamosal as well has a convex surface.

As to this inflation of the mastoid, the rodents differ from the ungulates; but also in the Typotheriidæ occurs an inflation of the caudal part of the skull, resembling that in some rodents (Van Kamp.; Sinclair, 1909, p. 11; Gregory, 1910, p. 374).

This inflation of the mastoid is very differently developed (Van Kamp.; Matthew, 1910*b*, p. 70), as a rule, in relation to the size of the epitympanic sinus.

Mostly a large bulla mastoidea is accompanied by a large auditory bulla and in many cases also by a widened auditory meatus. This so-called mastoid bulla may even be larger than the true auditory bulla.

The degree of inflation of the mastoid among the modern rodents is independent of the systematic subdivision. The degree of inflation is used in some cases to characterize genera and species. While among the Sciuridæ (Van Kamp.; Matthew, 1910*b*, p. 70) the mastoid is little or not at all inflated, it is rather strongly inflated in the flying species.

In the fossil *Protoptychus hatcheri* (Scott, 1895, cited by Van Kampen) the inflation of the mastoid resembles that in the Heteromyidæ (Van Kamp.; Matthew, 1910*b*, p. 70) where the "mastoid bulla" is as a rule very large. In the fossil *Pleurolicus* and *Entoptychus* (Scott, 1895, cited by Van Kampen) the mastoid is less inflated than in *Protoptychus*. According to Matthew (1907, p. 212) the mastoid swelling in *Entoptychus formosus* is greater than in *Thomomys*, less than in *Heteromys*.

The above described communication between a sinus in the basisphenoid and the opposite bullæ in *Lepus* is, according to Van Kampen, not correct, as the bullæ do not even touch the basisphenoid.

In the Felidæ (Van Kamp.; Dawkins, 1878, p. 48), Canidæ, and Viverridæ there is no epitympanic sinus.

Among the mustelids we find different conditions.

In *Meles meles* (Pocock, 1921, p. 478) and in *Pœcilogale* (Pocock,

1921, pp. 480, 485) the tympanic cavity is closed behind and does not communicate with a chamber hollowed out in the mastoid. According to Winge (1895*b*, pp. 70, 128) the pars mastoidea is not extraordinarily shaped in *Meles*, *Arctonyx* and *Mydaon*. Also in *Helictis* (Winge, 1895*b*, p. 68; Pocock, 1921, p. 480) there is no air-filled mastoid. In the Lutrini (Winge, 1895*b*, p. 69) the mastoid is flatly extended.

In species of the genera *Gale*, *Mustela* and *Putorius* (Van Kamp.; Pocock, 1921, p. 480) there is no definite hollow space in the external portion of the periotic, but this bone is spongy and porous and its spaces communicate with the cavity of the bulla.

In many other genera, there is a hollowed mastoid. Winge (1895*b*, p. 68) describes it in *Mephitis*, while in *Taxidea* the mastoid is inflated (*loc. cit.*, pp. 68, 70, 128). Pocock (1921, pp. 481, 482, 484, 485) describes a hollowed mastoid in *Mellivora*, *Pœcilictis*, *Taxidea*, *Grisonella*, *Ictonyx*, *Lyncodon*, *Mephitis*, *Spilogale*, *Conepatus*, *Mydaus* (see Van Kampen). They show differences in the size of the epitympanic sinus and also in the size and other features of the passage connecting with the tympanic cavity (Pocock, 1921, pp. 484, 485).

In *Herpestes griseus*, Gray (1913, pp. 403, 413) describes an antrum. It is very small and rudimentary and can hardly be said to exist as a special cavity, as it consists merely of a small backward prolongation of the attic and as there is no line of constriction separating it from the attic. It lodges the short process of the incus, which is bound to its lower wall. There is no further development in the direction of air-containing cells.

In the Phocidæ we find a small concavity of the planum epitympanicum, thus there is a small accessory sinus. As it is no doubt related to the large size of the incus, it can better be called an enlarged epitympanic recess.

In the majority of the ungulates there is no epitympanic sinus. This absence is emphasized for the Litopterna (Gregory, 1910, pp. 371, 379, 384, squamoso-periotic region not inflated), *Sus* (Van Kamp.; Scott, 1912, p. 290), *Tragulus*, and others.

Gray (1913, pp. 398, 407, 408, 413) describes in *Ovis aries* a distinct antrum. It is distinctly differentiated from the attic and there is a constriction marking the boundary between the two, though the constriction is not so marked as in the rabbit. In the sheep the antrum is in wide communication with the attic and from this point the cavity projects outward and backward. There is no further development in the direction of air-containing cells.

In the Notoungulata (Scott, 1912, pp. 241, 289; Stromer von Reichenbach, 1912, p. 213; Zittel, 1923, pp. 604, 605) the region behind the ear-region is broadened and inflated, the cavity of which is connected with that of the auditory bulla. The cavity of this inflated region is often filled with cancelli. There are great differences in the degree of inflation (Zittel, 1923, p. 605).

In the Astrapotherioidea (Gregory, 1910, pp. 371, 374, 384; Stromer von Reichenbach, 1912, p. 212; Zittel, 1923, p. 605) this inflation of the squamoso-periotic region is absent.

Thus this peculiar inflation occurs in the Typotheria, Toxodonta and Entelonychia, each of these three suborders showing its particular modification of the general plan (Scott, 1912, p. 241).

This inflated element, according to Roth (Scott, 1912, pp. 289, 290 (Van Kamp.; Sinclair, 1908, pp. 67, 68; 1909, pp. 3, 11), is homologous with the mastoid in man, but not with the element so designated in other ungulates and which Roth calls the protuberancia petrosa. According to Scott (1912, p. 290) Roth gives no convincing reason for regarding this element as homologous with the human mastoid and Roth does not make clear his conception of the relation between the pars Serrialis of the squamosal and the pars mastoidea of the periotic. According to Scott (1912, p. 290) it is the pars Serrialis or post-tympanic portion of the squamosal which is inflated, as clearly appears in those typotheres in which the two are separate. Scott (1912, p. 290) refers to Sinclair's figure of *Hegetotherium*, in which the element in question is divided by a transverse suture into dorsal and ventral portions; the former is the inflated pars Serrialis of the squamosal and the latter is a thin, compressed plate ankylosed with the tympanic, which is the homologue of the similar plate in the skull of *Nesodon*, called the mastoid or protuberancia petrosa.

Among the Typotheria in general (Sinclair, 1908, pp. 67, 68; 1909, pp. 3, 11; Gregory, 1910, p. 384; Scott, 1912, p. 292; Zittel, 1923, p. 606) the inflation in the squamoso-mastoid region of the back of the skull shows a different development; it is either hollow or filled with cancelli, showing in either case a direct communication with the cavity of the auditory bulla. According to Sinclair the inflation is formed by the mastoid (Van Kamp.; Zittel, 1923, p. 607), according to Scott (1912, p. 292) it is formed by the pars Serrialis of the squamosal and even the root of the zygomatic process has a very inflated appearance externally.

In *Protypotherium* according to Sinclair (1909, pp. 19, 20) the root of the temporal process of the squamosal and a large part of the cranial

expanse of the same element is dilated, the chambers communicating with each other as well as with the tympanic cavity; the dilatation extends also to the mastoid with which the squamosal is closely fused.

In *Interatherium* (Sinclair, 1909, pp. 50, 51) the squamosal is dilated as in *Protypotherium*, the distention involving the mastoid as well. In *Hegetotherium* according to Sinclair (1909, p. 71) the mastoid is dilated; the sutures between the mastoid and the squamosal, however, have been completely obliterated by fusion.

In *Hegetotherium* and *Protypotherium* the post-tympanic process is not extensively developed and occupies relatively little of the occipital surface (Scott, 1912, p. 137). *Pachyrukhos*, however, shows an extraordinary specialization (Scott, 1912, p. 137; Lydekker, 1893, cited by Van Kampen).

The extension and inflation of the squamoso-mastoid region attains in *Pachyrukhos* the highest degree among all notoungulates (Zittel, 1923, p. 606).

According to Sinclair (1909, p. 88) the most prominent feature of the back of the skull of *Pachyrukhos* is the greatly distended "mastoid bulla," which projects posteriorly beyond the condyles; these bullæ show but slight contact with the squamosal anteriorly and are separated from the parietal by a groove, opening into the cerebral chamber.

According to Lydekker (1893, cited by Van Kampen) these inflations, erroneously called "tympanic bullæ" by Lydekker (see Van Kampen) reach the dorsal surface of the skull, where they are separated by the narrowed parietals and supra-occipitals.

In *Typotherium cristatum* Van Kampen describes a strong inflation of the side-wall of the skull, above the porus acusticus externus, very probably formed by the squamosal.

This inflation is sometimes filled with cancelli, as in *Protypotherium* (Sinclair, 1909, pp. 19, 20; Gregory, 1910, p. 363), in *Interatherium* (Sinclair, 1909, p. 50) and in the Interatheriidæ in general (Sinclair, 1909, p. 11; Zittel, 1923, p. 607). In *Hegetotherium* (Sinclair, 1909, pp. 71, 88; Zittel, 1923, p. 607) there is a large, oval chamber connected by a canal with the tympanic cavity. In *Pachyrukhos* (Sinclair, 1909, p. 88; Scott, 1912, pp. 290, 292) as well, they are internally hollow and connected by a canal with the tympanic cavity. Much more commonly, however, in the Santa Cruz Typotheria they are filled with cancelli, obviously a secondary condition (Scott, 1912, pp. 290, 292).

Also *Archæohyrax* (Winge, 1906, p. 87) shows an air-filled inflated pars mastoidea.

In the suborder Toxodontia (Gregory, 1910, p. 384; Zittel, 1923, p. 610) the squamoso-mastoid region is inflated, though not extraordinarily.

In the fossil *Nesodon* (Scott, 1912, pp. 133, 136) a highly characteristic feature is the great prominence of the post-tympanic process (Roth's mastoid), in which the dorsal portion is inflated, at the supero-external angles of the occiput. In the young *Nesodon* (Scott, 1912, p. 136) the post-tympanic process is relatively much smaller than in the old specimens. The post-tympanic process in *Nesodon* (Scott, 1912, p. 137) is more extensively developed and occupies much more of the occipital surface than in the small Typotheria of the Santa Cruz (except the extremely modified genus *Pachyrukhos*). In *Adinotherium robustum* (Scott, 1912, pp. 231, 232) the post-tympanic portion of the squamosal is inflated so as to form a protuberance on the occipital surface, which is more conspicuous than in any of the other species, indeed, than in any other known member of the suborder Toxodontia.

The inflated dorsal portion of the post-tympanic process in *Nesodon* (Scott, 1912, pp. 136, 137) contains a large oval cavity above the long, tubular auditory meatus; this cavity is filled with coarsely cancellous bone; at the antero-internal corner of this cavity is a small, tubular passage, which communicates with the cavity of the auditory bulla through the inner end of the auditory meatus. Also in *Adinotherium robustum*, Scott (1912, p. 231) mentions an auditory chamber in the inflated post-tympanic process. Thus it is given as a general character of the suborder Toxodontia (Scott, 1912, pp. 113, 290) that the post-tympanic portion of the squamosal (Roth's mastoid) contains a large, oval cavity, which communicates with the cavity of the auditory bulla by a small canal. In *Toxodon platensis*, according to Van Kampen, the squamosal shows a cavity which, however, probably does not communicate with the tympanic cavity (see also Roth, cited by Van Kampen).

In the Entelonychia (Scott, 1912, pp. 241, 261, 262) the inflated post-tympanic region of the squamosal makes up less of the occipital surface than in the Toxodonta; the lack of prominence in the region of the swollen post-tympanic process is especially noticeable in the ventral view of the skull, and in the superior view of the skull no trace of it is visible, while in the Santa Cruz typotheres and Toxodonta the swollen post-tympanics form the postero-external angles of the skull. In *Homalodotherium* (Gregory, 1910, p. 374) as well, the squamoso-periotic region is slightly dilated. Also in the Entelonychia (Scott, 1912, p. 290) the post-tympanic process (Roth's mastoid) contains a large cavity which communicates with the cavity of the auditory bulla by a small canal. No

doubt in the common ancestors of toxodonts, typotheres, interatheres and hegetotheres the squamoso-periotic region became inflated (Gregory, 1910, p. 378).

In the recent *Procavia* we find a rather large sinus in the squamosal. It contains a hollow chamber which, at least in the dry skull, opens into small cellulæ in the remainder of the squamosal and in the postglenoid process. Externally an inflation of the postglenoid process only is visible; internally, i.e. in the cavum cranii, the squamosal itself protrudes. According to Scott (1912, p. 291), however, the mastoids are large and inflated and their cavities are filled with cancellii, while Gregory (1910, p. 363) mentions a cancellous dilation of the squamoso-periotic.

In *Lemur mongos* the deep epitympanic sinus is probably bounded by the mastoid and the squamosal. In species of the genera *Lepilemur* and *Chirogale* the mastoid is inflated and probably pneumatized, starting from the epitympanic recess, as in the Nycticebidæ. Thus, in the typical Lemuridæ, the mastoid is sometimes inflated (Gregory, 1920, p. 208: *Lepilemur*, *Microcebus*). Such an inflation of the mastoid is wanting in all other recent Lemuridæ. In *Avahis laniger*, *Lepilemur* and *Propithecus* the caudal portion of the squamosal is inflated.

In the fossil *Notharctus* (Gregory, 1920, pp. 208, 233) the mastoid is not inflated, though the interior is pneumatic (*loc. cit.*, p. 161). In the ancestral protoadapine stock as well (Gregory, 1920, p. 233), the mastoid was not inflated. In *Adapis* the mastoid is inflated Gregory, 1920, p. 208) and thoroughly pneumatic, like that of *Lepilemur* (Gregory, 1920, p. 209). A similar cavity is mentioned by Lorenz von Liburnau (1905, pp. 463, 464) in *Megaladapis*. Thus in the primitive Lemuriformes the mastoid region is sometimes inflated (Gregory, 1915, p. 426). In *Chiromys* an epitympanic sinus is present, containing a few vertical septa.

In *Perodicticus potto* there is, externally, a strong inflation of the mastoid and of the caudal portion of the squamosal, containing a large cavity in the diploë of the pars mastoidea and the squamosal. The squamosal seems to participate little in the boundary of this cavity, but this point can scarcely be decided from the early fusion of the elements. This cavity communicates with the caudal bulging of the mesial portion of the bulla and more forward with the epitympanic recess. In the young skulls the former communication is not yet present. In the accessory cavity is found one nearly horizontal septum, which divides it incompletely. In all Galaginæ (Van Kamp.; Gregory, 1915, p. 441), Lorisidæ (Van Kamp.; Gregory, 1915, pp. 427, 436) or Nycticebidæ (Van Kamp.; Winge, 1895*a*, p. 17, *Otolicnus*) the mastoid is inflated and contains a

cavity, which is always connected with the tympanic cavity by means of the epitympanic recess but perhaps not always by means of the aperture in the medial sinus of the bulla (Van Kamp.; Gregory, 1915, pp. 427, 436). In one of these forms the cavity of the mastoid has formerly been described as absent (*Otolicnus senegalensis* = *Galago galago*, according to Hyrtl).

In the recent *Tarsius* there is no epitympanic sinus. In the Tarsiidæ in general (Gregory, 1915, p. 438) the mastoids are not at all or but little inflated. In the fossil *Microchœrus* and *Necrolemur* (Gregory, 1915, pp. 438, 441) the mastoid is much inflated, the sinus in the mastoid perhaps opening into the bulla, thus foreshadowing the conditions in the Lorisidæ (Gregory, 1915, p. 427).

Gregory (1915, p. 441) inclines to the opinion that the inflation of the mastoid has developed independently in the Lorisiformes and in the Tarsiiformes.

In *Midas rosalia*, one of the modern Hapalidæ, a distinct foramen pneumaticum in the tegmen tympani opens into the "cellulæ mastoideæ"; these extend into the caudal portion of the squamosal and into the mastoid which is fused with the squamosal, the two being somewhat inflated externally. The slightly developed cellulæ in the squamosal are nearly completely separated from the much more extended cellulæ in the mastoid; only within the foramen pneumaticum do they mutually cohere. The mastoid cellulæ communicate by means of a larger cavity, the "antrum mastoideum," with the foramen pneumaticum, though this connection is not so distinct as in *Homo*. There is no extension in the wall of the bulla as in the Lorisidæ.

In the modern Cebidæ the external inflation of the mastoid is small or sometimes absent. In *Ateles* the cellulæ mastoideæ fill up the mastoid and the caudal part of the squamosal. There is no antrum mastoideum. The cellulæ are distinctly separate from the epitympanic recess. The cellulæ in the mastoid and those in the squamosal seem to remain separate, though incompletely so. The cellulæ petrosæ and the cellulæ mastoideæ approach each other immediately at the boundary of bulla and mastoid; there is no communication, though in other specimens or species a communication may be present. In the New World monkeys the cellulæ petrosæ and mastoideæ are separate; in the Old World monkeys there may exist a communication which, if present, is probably secondary and due to a larger extension.

In the modern Cercopithecidæ, as a rule, the inflation of the squamosal and especially that of the mastoid is very distinct externally.

The foramen pneumaticum is so wide that the recessus is not sharply separate from the cellulæ. There is a spacious antrum mastoideum, which by means of smaller apertures opens into further cellulæ. The cellulæ in the squamosal and those in the mastoid are almost completely separated from each other. Those in the squamosal extend far forward, in some species even as far as the basis of zygomatic process. Moreover, there are separate apertures in the tegmen tympani, which also is provided with cellulæ. Apertures are found also in the caudal wall of the tympanic cavity. Probably there are more systems of cellulæ, which do not cohere. Perhaps they cohere directly, that is, without intervention of the tympanic cavity.

In the modern Hylobatidæ and Anthropomorphæ, together with the reduction of the auditory bulla, the inflation of the mastoid and of the caudal end of the squamosal increases. In the gorilla the cellulæ show a larger extension than those in man. They occur in the whole mastoid, in the mastoid process, in the tegmen tympani, in the largest part of the squamosal and even in the under wall of the external auditory meatus. The cellulæ in the mastoid radiate from the antrum mastoideum toward the periphery. The cellulæ petrosæ and mastoideæ are not separate. Also there are many small apertures in the tegmen tympani, etc.

In *Homo* and in the orang-outan, the cellulæ of the os temporale are for the larger part still covered by a layer of spongiosa, the pneumatization being less complete. The extension of the cellulæ in the orang-outan and in the chimpanzee is in the main the same as in the gorilla. In *Homo* the cellulæ mastoideæ are still further extended by the development of the mastoid process (Van Kamp.; Gray, 1913, pp. 397, 411, 412, 413). According to Gray (1913, p. 413) the development of the mastoid process with its cellulæ has clearly occurred in comparatively recent times in the course of evolution. Reasons for this belief are that the mastoid process and cells are found only in man and the anthropoid apes, not even in other branches of the primates; secondly, that the mastoid process and cells develop rather late in ontogeny.

Neighboring Elements Touching the External Surface of the Bulla

In general we can say that the external surface of the bulla touches the foramen lacerum posterius, the exoccipital, the paroccipital process, the mastoid, the tympanohyal, the squamosal, the alisphenoid, the foramen lacerum anterius s. medium, sometimes the basisphenoid, the pars petrosa of the periotic or the basioccipital.

According to Winge (1906, p. 66) in the ungulates originally the tympanic is totally free and its form is unaffected by the neighboring skeletal elements. In the later forms the jaw-muscles and the neck-muscles cause the appression of the bulla to the neighboring elements, which can be more or less affected in form by the bulla.

We can add here a remark on the exceptional condition found in a few Rodentia, where a process of the supraoccipital, the so-called processus lateralis ossis occipitis, reaches the external auditory meatus; this process divides into two the oral extension of the mastoid above the external auditory meatus.

Another exceptional condition is found in the modern Phocidæ, where the large bulla even touches the palatinum, a feature perhaps caused by the large development of the mastoid.

The Foramen Lacerum Posterius

In the case of a small bulla the foramen lacerum posterius will be visible externally, but a large bulla can cover this foramen more or less. If the upper margin of the bulla bends round, it is possible that this margin is to be seen from the cavum cranii through the foramen lacerum posterius, as in *Elephas* and *Toxodon*. Scott (1895, pp. 66, 67) mentions that in the fossil *Cynodesmus thoöides* the shape and development of the bulla produce some differences in the disposition of the foramina in its neighborhood; thus the foramen lacerum posterius extends less around the hinder end of the bulla and is confined to its postero-internal angle, running almost parallel to the basicranial axis. In *Felis* the foramen lacerum posterius is partly covered by the bulla, so that the inwardly bent upper margin of the bulla is visible from the cavum cranii through the foramen lacerum posterius, and of course also through the fissure between the petrosal and the basioccipital. In *Hyæna* the foramen lacerum posterius forms a deep groove in the bulla.

The Exoccipital

That the bulla can touch the exoccipital can easily be understood. Sometimes the tympanic cavity is extended so far backward that it forms a hypotympanic sinus in the exoccipital, as in *Phascolomys* and in *Elephas*.

In the Notoryctidæ the bulla abuts against the anterior half of the occipital condyles, a condition probably due to the very narrow exoccipital, in such a manner that the occipital condyles occupy the whole breadth. In *Typotherium cristatum* according to Van Kampen the bulla

adjoins the exoccipital. In *Elephas* the exoccipital covers the wall of the caudal part of the bulla. In *Lemur mongos* the bulla adjoins the exoccipital; they are partly separated by the foramen lacerum posterius. In *Perodicticus potto* they are for the larger part separated by this foramen. In *Tarsius* the caudal portion of the bulla adjoins the exoccipital.

The Paroccipital Process

Among the marsupials it is a matter of systematic value as to whether or not the tympanic wing of the alisphenoid reaches the paroccipital process. Details will be given later, describing the alisphenoid part of the bulla. I only mention here that in the Phalangeridæ and the Macropodidæ the tympanic process of the alisphenoid touches the paroccipital process. In the Macropodidæ with an uninflated bulla the alisphenoid runs downward along the paroccipital process.

In *Cholœpus* the bulla, and especially the entotympanic, reaches the paroccipital process. We find this character again in many Gravigrada, as Van Kampen already has shown and for which I also refer to my own investigations (*Hapalops* and allied genera *Mylodon*, *Scelidotherium*). In many cases there is no distinct suture between the entotympanic and the paroccipital process and it is easily understood that this is one of the reasons for the entotympanic not being recognized as an independent element. In a few cases, on the other hand, a distinct suture is found (see my own investigations on *Scelidotherium*). In a few other Gravigrada the entotympanic does not reach the paroccipital process. According to Van Kampen this is the case in *Mylodon gracilis* and in *Lestodon*. In *Lestodon* (see also my own investigations) the foramen lacerum posterius separates the short entotympanic from the processus paroccipitalis. In *Mylodon garmani* (see my own investigations) there is no suture between the entotympanic and the paroccipital process.

Among the modern Rodentia we find different conditions of the paroccipital process and its relation to the auditory bulla. In the few genera with a very small bulla there is a space between the paroccipital process and the bulla. As a rule, however, the basis of the paroccipital process touches the hind surface of the bulla. The paroccipital process can be short (Van Kamp.; Winge, 1888, pp. 134, 193, Bathyergini, Hystricini) or long (Van Kamp.; Winge, 1888, pp. 135, 193, Capromyini, Dasyproctini, Eriomyini). Thus *Hydrochœrus capybara* is distinguished from the other Caviidæ by a much longer paroccipital process (Preller, 1907, pp. 378, 384, 385). This long paroccipital process can be straight or nearly straight (Van Kamp.; Winge, 1888, pp. 130, 134, 135,

193, Capromyini, Dasyproctini, Eriomyini; Preller, 1907, p. 378, Caviidæ), while in other cases as in *Hydrochœrus capybara* the distal part is curved oralward, the proximal part being vertical and lying against the bulla (Preller, 1907, pp. 384, 385). In *Lepus*, for example, the paroccipital process lies with a greater part of its length against the bulla. In *Nelomys antricola* (Winge, 1888, p. 91) the paroccipital process is extended leaf-like; in *Carterodon sulcidens* (Winge, 1888, p. 98) it is less extended.

In the fossil family Ischyromyidæ (Matthew, 1910*b*, p. 65) the paroccipital process is short and backwardly directed, which according to Matthew (*loc. cit.*) is a primitive eutherian character common to nearly all Eocene mammals. In the later rodents (Van Kamp.; Matthew, 1910*b*, pp. 65, 66) the position and direction of the paroccipital process is changed. In the fossil *Neoreomys* (Scott, 1905, p. 392) the paroccipital process has about the same relative development as in *Dasyprocta*, but is more closely applied to the bulla. In *Spaniomys* as well, the paroccipital processes are attached to the bullæ (Scott, 1905, p. 410). In the Octodontidæ (Winge, 1888, pp. 130, 134, 135, 193; Zittel, 1893, p. 542) the paroccipital process is curved oralward beneath the auditory bulla.

The primitive type of the paroccipital process in the Carnivora is, according to Matthew (1909, p. 315), short, spatulate and directed backward.

In all Creodonta (Matthew, 1909, pp. 316, 416), the paroccipital process is short, stout and directed backward. According to Wortman (1906, cited by Matthew, 1909, pp. 415, 416) the creodonts are distinguished by exceptionally robust paroccipital processes, but according to Matthew (1909, p. 416) they are neither peculiar to inadaptive creodonts nor characteristic of the majority of the genera; they are found only in certain of the large powerful forms (*op. cit.*, p. 424). According to Matthew (1910*c*, pp. 297, 298) in all Eocene creodonts this process is directed backward and is free from the bulla. This backward direction of the paroccipital process has been mentioned by Matthew (1909) for: the Oxyænidæ (p. 408), *Viverravus minutus* (p. 358), *Miacis uintensis* (p. 371), *Vulpavus* (*Phlaodectes*) *ovatus* (p. 393), *Limnocyon* (pp. 434, 435), and *Tritemnodon agilis* (pp. 476, 477). In *Dromocyon* (Wortman, 1901, p. 294) the paroccipital process has more of a backward and outward than a downward direction. According to Matthew (1901, p. 30) the paroccipital process in *Triisodon heilprinianus*, *Arctocyon* and *Mesonyx* is stout, not long, and confluent with the mastoid, projecting laterally rather than downward. In *Sinopa* (Wortman, 1902*b*, p. 439; Matthew, 1906,

p. 214) the paroccipital process is broad, flattened, shows a sharp point and has a marked outward and backward direction. In *Viverravus angustidens* (Teilhard de Chardin, 1915–1916, p. 14) the paroccipital process is long and horizontal. According to Pohle (1920, p. 57) the paroccipital process in the Miacidæ is not broadened; it is free and backwardly directed. Also in *Stypolophus* (Pohle, 1917, p. 404) the paroccipital process is free from the bulla. Probably also in *Palæonictis* (Winge, 1895*b*, pp. 46, 126) this process is not at all or very little broadened against the bulla. According to Riggs (1898, p. 258) the paroccipital process in the creodonts is directed backward, downward and outward, and is free from the bulla. The same is the case in the early carnivores (Riggs, 1898, p. 258). In the more generalized or primitive Carnivora (Scott, 1889, p. 234; Matthew, 1910*c*, p. 297) the paroccipital process is directed backward and free from the auditory bulla, while in modern Carnivora (Matthew, 1906, p. 214) the tip of this process usually extends farther downward and is soldered to the bulla. In the most primitive Fissipedia, according to Matthew (1909, p. 416), this process is backwardly directed as it is in the Arctoidea generally.

The relation of the paroccipital process to the bulla and the form of this process caused thereby, and the absence or presence of a prominent free top, show characteristic differences in the families of the modern Fissipedia, which are used in systematics. In the allied fossils, however, the paroccipital process often does not show the feature characteristic of the modern forms of the same family (Van Kamp.; Cope, 1880*c*, p. 834; 1882, p. 472; 1883, p. 113; Schlosser, 1889, p. 232; Zittel, 1893, p. 664). More thorough investigation of the modern forms has shown the limited value of these characteristic features (Van Kampen, Viverridæ).

According to Wortman (1906, cited by Matthew, 1909, pp. 415, 416) there occurs no robust paroccipital process in the true Carnivora, but according to Matthew (1909, p. 416) it occurs in many of the larger Fissipedia.

In the Canidæ, as a rule, the paroccipital process (Zittel, 1893, p. 620; 1911, p. 386; 1923, p. 466; Matthew, 1907, p. 199; Reynolds, 1909, pp. 10, 11) is prominent, slender, directed downward, and closely approximate to the bulla, with which it is in contact. Though it is appressed to the bulla, it retains more of the primitive form than in other Carnivora (Matthew, 1909, p. 393).

In the recent Canidæ, as a rule, the paroccipital process (Van Kamp.; Zittel, 1893, pp. 608, 664; Scott, 1895*b*, p. 66) is long, prominent, and very salient both in the vertical and backward direction; its

anterior edge is closely applied to the back part of the auditory bulla; the process, however, is not spread out but is laterally compressed. According to Matthew (1918, p. 194) the primitive backward direction is completely lost in the modern *Canis*. *Otocyon*, for example, forms an exception to the general rules. In *Fennecus zerda*, according to Van Kampen, the paroccipital process is not laterally compressed but is spread over the bulla, thus resembling the Herpestoidea. As in *Fennecus zerda*, in contrast to the majority of the Canidæ, the bullla shows a large backward extension; this condition is an indication that there is a relation between the flattening of the paroccipital process and the backward extension of the bulla. In the fossil *Tephrocyon rurestris* (Merriam, 1906, p. 7) the paroccipital process is prominent.

According to Scott (1895*b*, p. 66), in contrast with the existing *Canis*, the paroccipital process in *Cynodesmus* and *Temnocyon* is much longer, more compressed and more curved downward and backward; its free portion is much more widely separated from the bulla, with which the process is connected by a narrow bridge of bone which expands anteriorly so that the contact surface between the two is about as in the existing genus. In *Temnocyon coryphæus* (Cope, 1879, p. 181; 1880*a*, p. 95) the paroccipital process is directed backward at an angle of 45° and is rather elongate and acute; it caps the bulla posteriorly. In *Temnocyon altigenis* (Merriam, 1906, p. 24) the paroccipital process is shorter and less acute and not directed downward as much as in *Temnocyon ferox*. In *Cynodesmus thomsoni* (Matthew, 1907, p. 187) the paroccipital process is much closer to the bulla than in *Cynodesmus thoöides*, projecting downward at the tip. The paroccipital process in "*Canis*" (*Cynodesmus*) *brachypus* is, according to Matthew (1907, p. 186), more primitive than in *Cynodesmus thoöides*, notably in the backward direction. In this "*Canis*" *brachypus* (Cope, 1881*b*, pp. 389, 390; Van Kamp.; Cope and Matthew, 1915, Pl. CXIX*b*) the paroccipital process is well developed and projects backward nearly as far as the posterior face of the occipital condyles; it is connected with the auditory bulla by a plate of bone, which, with the process, is larger than that of the wolf. According to Cope (*loc. cit.*) "*Canis*" *brachypus* differs in this respect from all the Truckee and White River species, where the paroccipital process is either in contact with the bulla or but little separated from it. In *Nothocyon gregorii* (Matthew, 1907, p. 183), the paroccipital process is more closely united with the bulla than in *Galecynus* (*Nothocyon*) *geismarianus* and its tip directed downward instead of partly backward as in *Galecynus geismarianus*. In *Cynodictis* (Matthew, 1906, p. 214; Carls-

son, 1914, p. 228) the paroccipital process projects backward and has been separated from the bulla; in no case has it been spread over the hinder surface of the bulla. In *Cynodictis gracilis* (Scott, 1889, p. 233) this process is not in contact at all with the bulla. In *Philotrox condoni* (Merriam, 1906, p. 31) the paroccipital process is slender.

In *Amphicyon* (Filhol, 1883, pp. 18, 82) the paroccipital process is long and prominent; its anterior edge is more "oblique" forward than in *Canis*, its posterior edge is more concave. In *Daphænus* (Matthew, 1906, p. 214) the paroccipital process is broad and flattened and curves downward at the tip. In *Pliocyon medius* (Matthew, 1918, p. 194) this process is short, spatulate and directed backward and very slightly downward. In *Daphænodon* (Matthew, 1918, p. 194) the primitive backward direction is partly lost. In *Dinocyon* (*?Borophagus*) *gidleyi* (Matthew, 1902*a*, p. 131) the paroccipital process is moderately long and coössified with the bulla. In *Enhydrocyon crassidens* (Matthew, 1907, p. 191) the paroccipital process lies close to the bulla at the base and projects beyond it backward and downward in rather a long trihedral spine.

In the modern Ursidæ (Van Kamp.; Scott, 1889, p. 214; Zittel, 1893, p. 608) the hind margin of the bulla touches the paroccipital process, which, thanks to the slight development of the bulla, for the larger part, freely projects. According to Matthew (1909, pp. 316, 393) this process is short, stout, round and directed backward. Also according to Zittel (1893, pp. 608, 639) the paroccipital process is strongly developed. Matthew, (1902*a*, p. 131) calls this process in the bears reduced. In a fossil specimen of *Ursus americanus* (Brown, 1908, p. 184) the paroccipital process is long and slender. In the modern Procyonidæ the paroccipital process is not spread over the bulla, but for the larger part is free from it (Van Kamp.; Carlsson, 1920, p. 372), resembling that in the mustelids. It is well developed (Van Kamp.; Zittel, 1893, p. 644); in the smaller species it is less developed.

In the fossil *Pseudobassaris riggsi* (Riggs, 1898, pp. 258, 259, *Amphictis;* Pohle, 1917, pp. 405, 408) the paroccipital process is free from the bulla and is directed backward, downward and outward and resembles that in the mustelines.

In the recent Mustelidæ the paroccipital process shows important differences.

As a rule this process is small and not always well developed, as one would suppose according to Zittel (1893, pp. 646, 664). Thus, in *Pœcilictis* (Pocock, 1921, p. 485) it is nearly obsolete. In the larger mustelids, according to Matthew (1909, p. 316) the paroccipital process is short,

stout and directed backward. In *Martes* (Winge, 1895*b*, p. 66) this process is considerable, in *Mustela*, however, (*loc. cit.*, p. 67) strongly reduced. In *Taxidea* (Pocock, 1921, p. 485) this process is stout and projecting. These differences even occur in the same genus; for example, in *Galictis barbara* the paroccipital process is better developed and prominent, while in *Galictis intermedia* and *vittata* it is much reduced and shows no free prominent tip (Winge, 1895*b*, pp. 39, 40, 121, 122).

As a rule the paroccipital process is free from the bulla. In *Lutra* (Zittel, 1893, p. 652; Pocock, 1921, pp. 480, 484) the slightly developed bulla, posteriorly, is far in advance of the paroccipital process. In *Mephitis*, *Spilogale* and *Conepatus* (Pocock, 1921, p. 484) this process is placed some distance behind the bulla; in Taxidea (Pocock, 1921, p. 485) the bulla does not reach the paroccipital process. Although the remoteness of the paroccipital process from the bulla is well marked in many genera (Van Kamp.; Pocock, 1921, p. 373), it is not always free from the bulla and not always prominent, as one would suppose according to some authors (Scott, 1889, p. 214; Zittel, 1893, p. 645; 1911, p. 392; 1923, p. 473). In *Putorius*, with its strongly inflated backwardly extended bulla, the paroccipital process does not project outside the bulla, against which it is slightly spread out. In *Helictis* and *Grison* the paroccipital process is as closely applied to the posterior end of the bulla as in typical Felidæ, and it is even more confluent with the bulla in *Pœcilictis* than in *Mustela* (Pocock, 1921, pp. 473, 474, 485). Also in *Pœcilogale* (Pocock, 1921, p. 485) the bulla abuts against the paroccipital process behind. In *Galictis intermedia* and *vittata* (Winge, 1895*b*, pp. 39, 40, 121, 122) the paroccipital process is applied against the posterior wall of the bulla and shows no free prominent tip.

In the fossil *Palæoprionodon* the paroccipital process is better developed than in *Viverra* (Teilhard de Chardin, 1914–1915, p. 78) and the cartilaginous hind chamber of the bulla exerts little influence on its form (Winge, 1895*b*, p. 54). In the fossil *Stenoplesictis cayluxi* (Scott, 1889, p. 232) the paroccipital process is small and is in contact with the bulla, but does not enclose the latter as in a capsule. In *Bunælurus* (Matthew, 1902*b*, p. 138) this process is stout and entirely free of the short bulla. In the fossil *Megalictis* (Matthew, 1907, p. 196; 1909, p. 415) the paroccipital process is short, stout, spatulate, prominent, projecting backward and partly downward and well separated from the bulla. According to Matthew (1907, p. 199) the primitive form and position of the paroccipital process is equally characteristic of the family to which *Megalictis* belongs.

In the fossil *Amphictis* (Winge, 1895*b*, pp. 46, 56, 126; Pohle, 1917, pp. 404, 405) this process is primitive, free from the bulla.

In the modern Æluroidea as a rule (Matthew, 1909, p. 393; Reynolds, 1909, pp. 10, 11) the paroccipital process is laterally expanded and applied to the posterior face of the bulla.

In the modern Viverridæ (Van Kamp.; Zittel, 1893, p. 608; Winge, 1895*b*, pp. 47, 56, 57, 59, 126, *Paradoxurus;* Scott, 1889, pp. 232, 239; Matthew, 1907, p. 199; Carlsson, 1910*b*, p. 566; 1914, p. 228; 1920, p. 372; 1921, p. 71; Pohle, 1920, p. 57) the paroccipital process is leaf-like and spread out over the posterior surface of the bulla. According to Zittel (1893, p. 646) the paroccipital process is not strongly developed.

In the majority of the modern Viverrinæ (Van Kamp.; Zittel, 1893, p. 608; Carlsson, 1910*b*, pp. 566, 567; 1911, p. 425; 1920, p. 341, *Arctictis binturong*) the paroccipital process projects more or less beneath the bulla. An exception among the Viverrinæ in this respect is found in the genera *Viverricula, Prionodon* and *Poiana* (Van Kamp.; Carlsson, 1910*b*, p. 566; Teilhard de Chardin, 1914–1915, p. 80, *Prionodon*).

In the Herpestinæ there is no free tip of the paroccipital process (Carlsson, 1911, p. 425; 1910*b*, pp. 566, 567, *Galidia, Hemigalidia,* Herpestinæ in general, *Fossa*). In *Cryptoprocta* the relatively short paroccipital process does not project beneath the bulla (Carlsson, 1910*b*, p. 567; 1911, p. 425). Thus, often in the Viverridæ the paroccipital does not project outside the bulla (Zittel, 1893, p. 655).

In *Nandinia* (Van Kamp.; Pohle, 1920, p. 57; Carlsson, 1921, p. 71) the paroccipital process is not broadened; it is caudally directed and free from the cartilaginous posterior chamber of the bulla.

In the modern Hyænidæ (Van Kamp.; Winge, 1895*b*, pp. 47, 59, 126; Pohle, 1920, p. 57) the paroccipital process is leaf-like, spread out over the caudal surface of the bulla. Thus, the paroccipital process covers, for the larger part, the external surface of the posterior chamber which is limited to the caudal superior corner of the bulla (Van Kamp.; Pocock, 1916*e*, p. 306).

In *Proteles* a free tip of the paroccipital process is wanting, which in *Hyæna*, on the other hand, is developed probably in relation to the size of the bulla. According to Zittel (1893, p. 660) the paroccipital process in the Hyænidæ is "vorragend."

In the modern Felidæ (Van Kamp.; Cope, 1880*c*, p. 834; Scott, 1889, p. 239; Schlosser, 1890, p. 37; Zittel, 1893, p. 608; Winge, 1895*b*, pp. 46, 53, 54, 56, 126; Matthew, 1907, p. 199; 1910*c*, pp. 297, 312; Pohle, 1920, p. 57) the paroccipital process is a little broadened, flattened,

and spread out over the caudal wall of the bulla, but rather retains its primitive form and is not at all leaf-shaped and directed downward.

In the larger species the tip is free, in the smaller species there is only a small knob or edge (Van Kamp.; Zittel, 1893, p. 608). In the fossil *Felis atrox* var. *bebbi* (Merriam, 1909, p. 296) the paroccipital process is relatively prominent, owing largely to the reduction in size of the auditory bulla.

According to Winge (1895*b*, p. 53) in the primitive Felidæ the basis of the paroccipital process can touch the caudal surface of the bulla, though in that case the latter can change the form of the paroccipital process; this never becomes leaf-shaped but retains its primitive form and its free top.

In all modern and Pleistocene Felidæ, according to Zittel (1893, p. 664), the paroccipital process is closely applied to the auditory bulla, while in the older fossils this process is very strongly developed. Cope (1880*c*, p. 834) emphasized the difference in the paroccipital process between the recent and the fossil Felidæ.

Thus in the Nimravidæ (Scott, 1889, pp. 238, 239), the paroccipital process projects backward and does not touch the bulla. In *Dinælurus crassus* (Eaton, 1922, p. 446) this process is similar in size and direction to that of *Nimravus*.

In *Dinictis* (Cope, 1879, p. 177; 1880*a*, p. 45; Scott, 1889, p. 214; Zittel, 1893, p. 669; Riggs, 1896*b*, p. 237; Matthew, 1910*c*, p. 297) the short paroccipital process is directed backward and free from the bulla, from which it is separated by a considerable interval.

According to Riggs (1896*b*, p. 237) this process is slender in *Dinictis*; Scott (1889, p. 214) calls it almost rudimentary.

In the Machairodinæ, according to Zittel (1893, p. 668), the paroccipital process is free and prominent. In *Hoplophoneus* (Matthew, 1910*c*, p. 297) this process is directed backward and free from the bulla. In *Smilodon* (Matthew, 1910*c*, p. 297) it is neither free from the bulla nor directed backward.

As to the pinnipeds, according to Zittel (1893, pp. 681, 682), the paroccipital process is slightly developed and hardly prominent. According to Wortman (1906, cited by Matthew, 199, pp. 415, 416) the paroccipital process is exceptionally robust, and directed backward. This is not true, however, and Matthew (1909, p. 416) mentions that the large robust process is not found in the smaller seals, while in the larger Pinnipedia (Matthew, 1909, p. 316) it is short, stout and directed backward.

In the Otariidæ and Trichechidæ there is no separate paroccipital process; perhaps it is fused with the mastoid process.

In the Phocidæ the paroccipital process as a rule is rudimentary. In *Erignathus*, however, it is considerable, while in *Phoca* it is more or less reduced (Winge, 1895*b*, p. 75). In the Phocidæ the paroccipital process is separated by a wide fissure from the bulla.

In the modern *Rhinoceros* the bulla in old skulls reaches, as a rule, the base of the paroccipital process, while in young skulls they are separate.

In the Suidæ (Van Kamp.; Gidley, 1921, p. 654) the bulla is closely appressed to the base of the paroccipital process; in *Dicotyles*, however, there is a space between the two.

In the modern Hippopotamidæ the caudal surface of the bulla is fused with the inner root of the paroccipital process.

In the fossil *Ælpinacodon deflectus* (Troxell, 1921*a*, p. 338) this process joins the bulla at its base. In the allied *Elomeryx armatus* (Marsh, 1894, p. 177) the paroccipital process is long.

In the Oreodontidæ, the posterior portion of the bulla touches the paroccipital process, as may be derive d from the following notes. It is emphasized for *Oreodon* (Leidy, 1854, p. 32), *Oreodon culbertsonii* (Osborn and Wortman, 1894, p. 216), *Oreodon bullatus* (Osborn and Wortman, 1894, p. 218), *Eporeodon major* (Osborn and Wortman, 1894, p. 218), *Eucrotaphus jacksoni* and *auritus* (Leidy, 1854, p. 57), *Eporeodon leptacanthus pacificus* (Thorpe, 1921*b*, p. 100), *Eporeodon trigonocephalus* (Thorpe, 1921*b*, p. 101), and *Mesoreodon chelonyx* (Scott (?), 1895*b*, p. 129).

In these examples the paroccipital processes are said in *Oreodon culbertsonii* to be connected with the bulla by prominent ridges (Osborn and Wortman, 1894, p. 216); in *Eporeodon leptacanthus pacificus* (Thorpe, 1921*b*, p. 100) the contact with the bulla is only at the base, while in *Oreodon bullatus* (Osborn and Wortman, 1894, p. 218) they are largely in contact. In *Paroreodon marshi* (Thorpe, 1921*b*, p. 109) the paroccipital process abuts against the bulla for two-thirds of its length. In *Leptauchenia* (Scott, 1890, p. 353) the paroccipital process is very broad and flattened, being closely applied to the bulla.

In *Agriochœrus*, according to Scott (1890, p. 358), the paroccipital process and the bulla are more widely separated than in *Oreodon*. In my opinion this perhaps refers to the free top of this process and not to the base, as in *Agriochœrus antiquus dakotensis* and *Agriochœrus bullatus* (Thorpe, 1921*c*, pp. 113, 116) the bulla is in contact with the paroccipital process.

In *Proagriochœrus* (Scott, 1899, p. 103) the anterior face of the paroccipital process is concave, as though it had partly embraced the bulla.

In the modern Camelidæ the posterior portion of the bulla joins the paroccipital process. In the fossil *Alticamelus altus* (Matthew, 1893–1903, p. 430) this process is less firmly soldered to the bulla than in modern species. In *Protylopus* (Scott, 1899, pp. 28, 44) the bulla does not come into contact with the paroccipital process at all, but is entirely contained within the notch between the postglenoid and posttympanic processes. In the fossil *Poëbrotherium* (Leidy, 1854, p. 21; Scott, 1891*a*, p. 14; 1899, p. 27; Loomis, 1910, p. 321; Troxell, 1917, p. 382) a broad irregular surface of the bulla is closely applied and fused to the paroccipital process; the latter is united suturally with the bulla for most of its length. In *Stenomylus* (Loomis, 1910, pp. 302, 321) the bulla is fused to the paroccipital process for most of its length.

In the modern *Tragulus* and *Hyomoschus* the bulla joins the paroccipital process.

In the modern Cervidæ the bulla adjoins the base of the paroccipital process. In the fossil *Dromomeryx* (Scott, 1895*b*, p. 171, *Blastomeryx*) the base of this process is closely applied to the bulla. The same character is found in the Giraffidæ.

In the Antilocapridæ (Matthew, 1893–1903, p. 440) the paroccipital process is fused to the bulla except near the tip. The same condition is found in the fossil *Hypisodus* (Matthew, 1902*c*, p. 312; Loomis, 1910, p. 321; Troxell, 1920*a*, p. 394).

In the fossil *Myotragus balearicus*, according to Andrews (1915, p. 286), the bulla is firmly united to the paroccipital process posteroexternally.

In the Typotheria, Scott (1912, p. 114) mentions the junction of the paroccipital process with the bulla. According to Van Kampen the bulla in *Typotherium cristatum* adjoins the base of the long paroccipital process. The same condition, according to Van Kampen, is seen in *Toxodon platensis*.

In old skulls of *Procavia* (*Hyrax*) the bulla abuts against the paroccipital process.

Mastoid and Mastoid Process

In *Erinaceus* the mastoid lies between the two legs of the tympanic. The auditory bulla often lies closely against the mastoid. Among the edentates this is emphasized in *Myrmecophaga*, where the tympanic is coössified with the mastoid and for *Prozaedius*, where, according to Scott (1903*a*, p. 71), the mastoid process is closely applied to the tympanic. In the Gravigrada the bulla (in these cases the entotympanic)

is in contact with the mastoid (see my own investigations on *Scelidotherium* and *Lestodon* and on *Hapalops*, where it is not so distinct).

In the modern Rodentia the posterior surface of the bulla joins the mastoid, with which it is sometimes fused. In rodents with a very small bulla there is a space between the bulla and the mastoid. The mastoid practically always, except perhaps in *Castor* and in the Bathyergidæ, forms a prolongation in the oral direction between the tympanic and the squamosal, covering the auditory meatus dorsally; sometimes this prolongation is divided into two, as it is laterally partly covered by a portion of the squamosal or by a process of the supraoccipital. The mastoid process can be absent (Van Kamp.; Preller, 1907, pp. 379, 387, development in *Hydrochœrus;* Gray, 1913, p. 401, absence in *Lepus cuniculus*) or it is more or less developed. In that case it lies against the bulla or projects freely, if strongly developed. In *Mesomys spinosus* according to Winge (1888, p. 95) the bulla has pushed aside the mastoid, which is very small, and thus the bulla lies in an incisure of the occipital.

In the fossil *Entoptychus* (Zittel, 1893, p. 533) the bulla is not distinctly separate from the mastoid.

The fossil Creodonta, according to Wortman (1906, cited by Matthew, 1909, pp. 415, 416) are characterized by exceptionally robust mastoid processes. According to Matthew (1909, p. 416), however, these large robust mastoid processes are neither peculiar to inadaptive creodonts, nor characteristic of the majority of the genera; they are found only in certain of the large powerful forms (Van Kampen, *loc. cit.*, pp. 424, 434). In *Limnocyon verus* (Matthew, 1909, p. 435) the mastoid process projects outward and somewhat downward. In *Sinopa agilis* (Wortman, 1902*b*, p. 439) the mastoid is prominent.

In the primitive carnivorous skull the mastoid process is free from the bulla (Scott, 1889, p. 234) and distinct but small (Matthew, 1909, p. 315).

The relation of the mastoid process to the bulla and the form of this process caused thereby and the absence or presence of a prominent free top show characteristic differences in the families of the modern Fissipedia which are used in systematics. In the allied fossils, however, the mastoid process sometimes does not show the feature characteristic of the modern forms of the same family (Van Kamp.; Cope, 1880*c*, p. 834). As a rule the mastoid process in the Fissipedia is little developed (Zittel, 1893, p. 608; Wortman, 1906, cited by Matthew, 1909, pp. 415, 416). In many of the larger Fissipedia, however, the mastoid process is robust (Matthew, 1909, p. 416).

In the modern Canidæ the mastoid process is little developed (Van Kamp.; Zittel, 1893, p. 664). In the fossil *Dinocyon* (?*Borophagus*) *gidleyi*, according to Matthew, 1902*a*, p. 131), this process is small. In the fossil *Pliocyon medius* (Matthew, 1918, p. 194; see also my own investigations) the mastoid process is prominent, stout, constricted at base; the mastoid border is reflected over the postero-external margin of the bulla; the mastoid process is more prominent and robust than in *Daphænodon*.

In the recent Ursidæ the bulla is for the larger part separated from the mastoid by the stylomastoid foramen and the groove for the tympanohyal. Thus the mastoid projects freely (Van Kamp.; Scott, 1889, p. 214). The mastoid process in the bears (Zittel, 1893, p. 639; Matthew, 1902*a*, p. 131) is strongly developed and much enlarged. In the fossil specimen of *Ursus americanus* (Brown, 1908, p. 184) the mastoid process is long but not directed forward as much as in recent specimens, and is of about the same size.

In the modern Procyonidæ the mastoid process is not extended upon the surface of the bulla and for the larger part is free from it. It is well developed (Van Kamp.; Brown, 1908, p. 644), but in smaller species less so, and resembles that in the mustelids. The same is emphasized for the mastoid process in the fossil *Pseudobassaris* (Riggs, 1898, pp. 258, 259, *Amphictis*), where this process is blunt and inconspicuous, lies close to the meatus, and forms part of its posterior wall.

In the recent Mustelidæ (Van Kamp.; Zittel, 1893, pp. 645, 646, 664) the mastoid process is well developed and prominent and resembles that in *Ursus* and in the Procyonidæ. It is directed forward, which probably causes the similar direction of the cylindrical auditory meatus. In the fossil *Mustela palæattica* (Weithofer, 1888, p. 227) the mastoid process is strong and laterally prominent. In the fossil *Megalictis* (Matthew, 1909, p. 415) as well this process is prominent.

In the modern Viverridæ the outer surface of the bulla abuts against the mastoid, with which it is fused in the Herpestinæ and in *Cryptoprocta*. It does not project freely, or only a very little (Van Kamp.; Scott, 1889, pp. 238, 239; Zittel, 1893, pp. 646, 655). In *Nandinia* only, with its small bulla, it shows a free margin.

Among the modern Hyænidæ the mastoid is flattened against the bulla. In *Hyæna* it still shows a free projecting top, which is wanting in *Proteles* and thus depends on the extension of the bulla in the caudal direction, which is larger in *Proteles* than in *Hyæna*. The mastoid partly covers the caudal chamber, which is limited to the caudal superior corner of the bulla.

In the recent Felidæ the posterior portion of the bulla adjoins the mastoid. The mastoid process (Van Kamp.; Cope, 1880*c*, p. 834; Scott, 1889, pp. 238, 239; Zittel, 1893, p. 664; 1911, p. 399; 1923, p. 480; Matthew, 1910*c*, p. 312) lies more or less against the bulla and is small, vestigial or obsolete. In the larger species there is a free top, but in the smaller species, in which the bulla is strongly inflated, it projects but little freely. Thus it is merely a small convex rugosity (Matthew, 1910*c*, p. 296).

Also in the Pleistocene Felidæ, according to Zittel (1893, p. 664), the mastoid process is closely applied to the bulla, while in the older fossil forms it is strongly developed.

In the Nimravidæ (Scott, 1889, pp. 238, 239) the mastoid process is very prominent. In *Dinælurus crassus* (Eaton, 1922, pp. 440, 446) the form, size, position and direction is similar to those in *Nimravus*. The mastoid process in *Pogonodon serrulidens* (Eaton, 1922, p. 435) in point of size, resembles *Nimravus* rather than *Dinictis* but it is directed a little more forward than in *Nimravus*, in this respect being more like *Dinictis*. The mastoid process in *Nimravus* is less prominent than that in *Dinictis* (Matthew, 1910*c*, p. 296). In *Dinictis* (Scott, 1889, pp. 213, 214; Zittel, 1893, p. 669; Matthew, 1910*c*, p. 296) the mastoid process is strong, heavy and prominent, but small; it projects downward and is not in contact with the bulla, though it shows an anterior position and the distance between it and the postglenoid process is very short. In the Machairodontinæ (Zittel, 1893, p. 668) the mastoid process is free and prominent. In *Hoplophoneus* (Matthew, 1910*c*, p. 296) the mastoid process is of larger size than in *Dinictis* and more prominent, but similar in form and position. In *Machairodus* (Winge, 1895*b*, pp. 55, 56; Matthew, 1893–1903, p. 386; 1910*c*, p. 296; Scott, 1913, p. 535) this process is greatly increased in size and prominence and is shifted forward and outward to a position close to the postglenoid process curving under the external auditory meatus, the bulla being still conspicuous in the side view of the skull. In *Smilodon* (Matthew, 1910*c*, p. 296; Scott, 1913, pp. 533, 535) the mastoid process is still larger and more prominent than in *Machairodus* and reaches the maximum of distance in front of the occipital condyles; the bulla is not visible from the side, being covered externally by this process.

The Pinnipedia, according to Wortman (1906, cited by Matthew, 1909, pp. 415, 416), show exceptionally robust mastoid processes, but this is not true, according to Matthew (1909, p. 416), in the smaller seals. According to Zittel (1893, pp. 681, 682) the mastoid process in the Pinnipedia is little developed and hardly prominent.

In the modern Phocidæ the bulla is separated from the mastoid by a depressed groove. The mastoid process, or better the mastoid itself, is inflated and to this inflation the neighborhood of the posttympanic process contributes. Also in the fossil seal described by Wyman (1850, p. 229), the mastoid process is very large, rounded and prominent, nearly equalling the tympanic bone in size.

In the Otariidæ the bulla is fused with the mastoid, but both project strongly from the common suture, enclosing a deep groove, which perhaps caused the formerly described separation of the bulla and the mastoid described above. The mastoid process is differently developed in various Otariidæ, but is always quite strong. Probably it has appropriated the post-tympanic process and perhaps also the paroccipital process.

In the Trichechidæ as well the bulla is fused with the "mastoid process," separated by a shallow groove only and by the stylomastoid foramen. This difference in the separating groove between the Otariidæ and the Trichechidæ depends on the form of the bulla and the place of the mastoid process on the mastoid. To this "mastoid process" contribute probably the post-tympanic process and no doubt also the paroccipital process. The mastoid process is very large (Van Kamp.; Winge, 1895*b*, p. 73), according to Van Kampen nearly as large as in the Otariidæ. The mastoid process is downwardly directed and according to Winge (1895*b*, p. 73) extends beneath the external auditory meatus.

In *Equus* as well the bulla lies against the mastoid. In the recent *Lemur*, *Perodicticus* and in the Lorisidæ in general (Van Kamp.; Gregory, 1915, p. 436) the caudal wall of the bulla is continuous with the mastoid. In the fossil *Notharctus* and *Adapis* (Gregory, 1920, p. 165) the tympanic part of the bulla is separated from the mastoid by the carotid canal. In the modern *Tarsius* the bulla is distinctly separate from the mastoid. In the fossil Microchœridæ (*Microchœrus*, *Necrolemur*) (Gregory, 1915, p. 438) the mastoid inflation is demarcated from the bulla by a constriction.

In the South American monkeys (Gregory, 1920, p. 165) the tympanic part of the bulla is in contact with the mastoid.

In the anthropoid apes and man a distinct mastoid process is present (Van Kamp.; Gray, 1913, pp. 397, 411, 412, 413), the development of which, according to Gray (1913, p. 413), has occurred in comparatively recent times in the course of evolution. Reasons for this belief are (Gray, 1913, p. 413) that this process is found only in man and the anthropoid apes, not even in other branches of the primates, and that this process develops rather late in ontogeny.

The Tympanohyal

In many cases the bulla touches the tympanohyal.

Perhaps a strongly developed bulla causes the opisthotrematic condition of the hyoid, but *Echidna* shows that this can not be the only cause.

In *Centetes ecaudatus* the hind leg of the tympanic lies against the top of the tympanohyal, while in this species the tympanic cavity is so slightly developed in this region that the tympanohyal lies practically outside the tympanic cavity. In *Erinaceus* the tympanic lies against a small process of the processus mastoideus, which probably is the tympanohyal. In *Pteropus* the hind leg of the tympanic lies against the tympanohyal.

In *Orycteropus* the tympanic covers the tympanohyal laterally. In many Xenarthra there is a close connection between the entotympanic and the tympanohyal. In the representatives of this group in which the ontogeny of the entotympanic has been studied (Van Kampen, 1915; Van der Klaauw, 1922, 1924) a connection is found between these two elements. Also in the adult skull there is often a close connection between the entotympanic and the tympanohyal. In *Cholœpus*, for example, the entotympanic is often coössified with the tympanohyal, while in *Cholœpus hoffmanni*, it is often a mere process of the tympanohyal. Also in the Gravigrada which I could investigate the two elements lie close together, though I could not find a direct connection; which, on the other hand, could not be denied. Exceptions are found in *Lestodon* (see my own investigations) where the absence of this connection is sure, and in *Mylodon* (see my own investigations), where the tympanohyal lies closely against the entotympanic; this is perhaps not a natural condition but is affected by compression of the skull.

Among the Dasypodidæ there is a close connection between the entotympanic and the tympanohyal; in *Xenurus* (=*Lysiurus*) *unicinctus* they are fused together in the old skulls. In *Priodontes giganteus* the entotympanic does not reach the tympanohyal or barely reaches it, with a narrow process. In *Tolypeutes tricinctus*, where the entotympanic is less developed than in *Xenurus*, this element does not reach the tympanohyal, or does not do so invariably.

I refer also to the remarks in the chapter on the vagina processus hyoidei.

The Squamosal

As a rule the two legs of the tympanic are attached to the squamosal, but this will not engage our attention here.

In *Centetes ecaudatus* the fore leg of the tympanic lies along the processus entoglenoideus of the squamosal, while between the two legs lies the incisura tympanica of the squamosal and not the mastoid as in *Erinaceus*. In some of the species of the genus *Erinaceus* the tympanic lies against a medialward directed process of the postglenoid process. In *Solenodon paradoxus* the tympanic rests anteriorly against the postglenoid process of the squamosal in contrast to *Centetes* (Van Kamp.; Gregory, 1910, p. 246).

In the fossil *Philotrox condoni* (Merriam, 1906, p. 31) the bulla is almost entirely separated from the postglenoid process. In *Pliocyon medius* (Matthew, 1918, p. 194) the base of the bulla is reflected at its antero-external margin over the back of the glenoid articulation from the postglenoid foramen nearly to the eustachian canal.

In the mustelid genera *Galictis* and *Lyncodon* (Winge, 1895*b*, pp. 69, 127) the tympanic is entirely free from the postglenoid process, while in *Mellivora* the tympanic extends over the postglenoid process and fuses with it (Winge, 1895*b*, pp. 67, 70, 128).

In *Eucrotaphus auritus* (Leidy, 1854, p. 57) the bulla rests against the postglenoid tubercle, but such is not the case in *Eucrotaphus jacksoni*. In *Eporeodon leptacanthus pacificus* (Thorpe, 1921*b*, p. 99) the bullæ are separated from the postglenoid tubercles, while in *Eporeodon condoni* (Thorpe, 1921*b*, p. 105) the postglenoids and the bullæ are in contact. In *Agriochœrus guyotianus* (Wortman, 1895, p. 177) the bulla is widely separated from the postglenoid, while in *Agriochœrus trifrons* (*loc. cit.*, p. 177) the bulla joins the postglenoid internally. In *Agriochœrus antiquus dakotensis* and in *Agriochœrus bullatus* (Thorpe, 1921*c*, pp. 113, 116) the bullæ are in contact with the postglenoid tubercle.

According to Winge (1906) the bulla sometimes forms a part of the hind wall of the fossa glenoidea as in the Camelidæ (*loc. cit.*, p. 98), in *Bos bubalus* (*loc. cit.*, p. 125) and in the Tragulini (*loc. cit.*, p. 107), where the postglenoid process is said to have disappeared. A similar condition is probably present in *Anoa* (Winge, 1906, p. 125), where the bulla is said to touch the condylus of the lower jaw. In *Hypisodus* (Winge, 1906, p. 107) the enormously developed bulla seems to have spirited away the postglenoid process. In *Protoceras* and in *Leptomeryx* (Winge, 1906, p. 106), on the other hand, the bulla does not form the hind wall of the fossa glenoidea, as the postglenoid process is free and well developed.

In *Lemur*, *Propithecus*, and all other recent lemurs (Gregory, 1920, pp. 164, 165), the expanded portion of the bulla is in contact with the

inner side of the entoglenoid region of the squamosal. The same is the case in *Adapis* and *Notharctus* (Gregory, 1920, pp. 164, 165, 194).

In *Adapis* (Gregory, 1920, p. 166) there are differences in the width of the contact between the entoglenoid ridge and the bulla, which is very wide in *Adapis parisiensis schlosseri* and narrow in *Adapis magnus leenhardti*.

In the fossil *Palæopropithecus* Gregory (1920, p. 176) mentions a remnant of the space which once separated the outer expansion of the bulla from the entoglenoid process of the squamosal.

In the ancestral protoadapine stock, according to Gregory (1920, p. 232), the anterior end of the tympanic was in contact with the entoglenoid region as in *Notharctus*.

In the higher apes (Gregory, 1920, pp. 165, 220) the portion of the bulla formed by the processus tympanicus petrosi has lost its contact with the entoglenoid region of the squamosal, while the true tympanic portion has retained its ancient contact with the entoglenoid region and also with the post-tympanic process.

I refer also to the chapter in which the fusion of the bulla with the squamosal is discussed and to that on the squamosal participating in the bulla.

Alisphenoid and Foramen Ovale

In a great many mammals the alisphenoid takes part in the constitution of the bulla and I may allude here to that part of this article in which the alisphenoid portion of the bulla is described. Only a few additional remarks will be given here.

In *Tupaia javanica* the bulla is prolonged far forward over the alisphenoid and covers the foramen ovale for the larger portion, while in *Erinaceus* and *Gymnura* (Carlsson, 1922, p. 233) the foramen ovale is distinctly visible.

In the modern rodents the foramen ovale can be united with the foramen lacerum anterius, which in turn can be covered more or less by the bulla. The uncovered part of the foramen lacerum anterius can completely separate the bulla from the alisphenoid. According to Winge (1888) an extension of the oral margin of the bulla adjoins the caudal external corner of the ala magna in *Hesperomys expulsus* (p. 19), *Calomys laticeps* (p. 53), *Rhipidomys mastacalis* (p. 56), and *Nectomys squamipes* (p. 59).

The relation of the foramen ovale to the bulla in the modern Musteli-dæ shows large differences. According to Winge (1895*b*) the bulla is

freely prolonged forward under the foramen ovale in *Ictidonyx* and *Pœcilogale* (*loc. cit.*, pp. 67, 70, 128), while in *Galictis*, *Lyncodon* and *Mellivora* (*loc. cit.*, pp. 69, 127) this anterior prolongation of the bulla is absent. Pocock (1921, p. 476) concludes that the position of the foramen ovale with regard to the orifice of the Eustachian tube in the Mustelidæ varies in accordance with the length of the back of the skull and with the inflation of the anterior part of the bulla. They may be separated by a considerable space or only by a thin plate of bone.

In the fossil *Protoceras* (Scott, 1895*a*, p. 312) the ascending process of the alisphenoid internally to the glenoid cavity extends almost to the tympanic.

In *Elephas* the bulla extends forward under the alisphenoid, so that in the ventral view of the skull the foramen ovale is invisible.

In primitive placentals of the Eocene, according to Gregory (1920, p. 224), the pterygoid plate of the alisphenoid extended to the auditory bulla.

In *Lemur mongos* the front wall of the bulla, together with the caudal end of the processus pterygoideus alisphenoidei, forms a bridge over the foramen ovale, which thus is covered for the larger part by the bulla (Carlsson, 1922, p. 233).

According to Gregory (1920, p. 224) in certain lemurs the pterygoid plate of the alisphenoid extends to the auditory bulla in a somewhat reduced form in comparison with that in the fossil *Notharctus*.

According to Standing (1908, p. 81) a flat plate or bony bridge connects the outer pterygoid laminæ of the alisphenoids with the bullæ in *Propithecus* or *Indris*.

In *Avahis laniger* this connection is wanting, according to Van Kampen. According to Gregory (1920, p. 164) in all Malagasy lemurs the bulla is in contact with the pterygoid wing of the alisphenoid, and this author (1920, p. 183) gives this as a character of the lemuriformes in general. Also in *Notharctus* and *Adapis* (Gregory, 1920, pp. 164, 194, 224, 227), the elongate descending or pterygoid plate or wing of the alisphenoid is very large and extends back to the auditory bulla, which is situated immediately behind this pterygoid plate, with which it is in contact.

In *Lemur* and *Adapis*, according to Gregory (1920, p. 210), the processus styliformis is connected with the external pterygoid plate.

In *Notharctus* (Gregory, 1920, p. 218) the external pterygoid plate is connected with the anterolateral process of the bulla. Also in the ancestral protoadapine stock, according to Gregory (1920, p. 232), the

elongate pterygoid plate of the alisphenoid extends postero-externally to make contact with the antero-external process of the bulla.

In the fossil *Palæopropithecus* (Standing, 1908, p. 81; Gregory, 1920, p. 176) the bony bridge connecting the outer pterygoid lamina of the alisphenoid with the bulla is entirely absent and the pterygoid plate of the alisphenoid no longer extends to the bulla.

In *Megaladapis edwardsi* (Lorenz von Liburnau, 1905, p. 463) the anterior process of the bulla touches with its lateral margin the mesial margin of the pars spinosa of the ala magna.

In *Chiromys* as in *Lemur* the processus pterygoideus alisphenoidei is fused with the margo fissuræ of the squamosal. In *Perodicticus potto*, however, they do not reach each other, so that the foramen ovale is not bridged over. In *Galago crassicaudatus* on the other hand we find a bridge, though a very narrow one.

In *Tarsius* and *Anaptomorphus*, according to Winge (1895*a*, p. 15), the bulla curves rostralward, against the fossa pterygoidea, which thereby gets a remarkable form. In *Necrolemur* (Winge, 1895*a*, p. 15) the bulla does not seem to have affected the pterygoid fossa.

In the higher Primates (Gregory, 1920, pp. 224, 227) the pterygoid plate of the alisphenoid and the auditory bulla are generally separated by a considerable interval.

Gregory (1920, p. 218) also mentions it for the generalized Platyrrhine that the external pterygoid plate is separated from the anterolateral process of the bulla.

The Pterygoid

In a few cases the pterygoid lies in the ventral wall of the tympanic cavity, as we shall see later on. Here we will restrict ourselves to the cases where the auditory bulla touches the pterygoid.

In many Xenarthra the auditory bulla and especially the entotympanic reaches the pterygoid. We find this in *Cholœpus* and *Bradypus*. According to Van Kampen they touch each other or nearly touch each other in *Scelidotherium*, in *Nothrotherium* (=*Cœlodon;* Van Kamp.; Reinhardt, 1878, pp. 274, 336) and other Gravigrada. I could confirm this for *Scelidotherium*, *Hapalops* and allied genera, and probably it occurs also in *Mylodon*. In *Lestodon* (see Van Kampen's and my own investigations) the short entotympanic does not reach the pterygoid. In *Cycloturus* the ptyergoid covers the processus tympanicus basisphenoidei. Among the Dasypodidæ the entotympanic reaches the pterygoid in *Xenurus* (=*Lysiurus*) and sometimes also in *Priodontes giganteus*.

In many modern rodents belonging to different groups, the hamulus pterygoideus is connected by a bony bridge with the bulla just behind and beneath the processus styliformis. In other cases this bony bridge is probably represented by a ligament only. According to Preller (1907) in *Dinomys* (p. 411) the bulla touches the pterygoid, while in *Dasyprocta* (p. 379) this is nearly the case.

In the fossil *Steiromys* (Scott, 1905, p. 414) the pterygoids do not extend to the bullæ, also in *Perimys impactus* (*loc. cit.*, p. 444) the bulla is not suturally connected with the pterygoid, while the bulla in *Prolagstomus* (*loc. cit.*, p. 451) sends forward a process to connect with the pterygoid.

In the modern Mustelidæ the bulla sometimes touches the hamular process of the pterygoid (Van Kamp.; Winge, 1895*b*, p. 67, *Ictidonyx;* p. 96, *Mustela sarmatica* and *larvata;* Pocock, 1921, p. 485, *Ictonyx* and *Pœcilictis*), while in *Taxidea* (Pocock, 1921, p. 485), for example, the bulla ceases in front far behind the hamular process of the pterygoid.

In the recent Phocidæ as well the large bulla touches the pterygoid, perhaps in consequence of the large development of the mastoid.

In the embryo of the Mystacoceti, according to Hanke (1914, p. 519), the bulla touches the processus digitiformis of the pterygoid, while in later ontogenetic stages they are widely separated.

In the fossil *Ancodus* (*Hyopotamus*) (Scott, 1895, cited by Van Kampen) the bulla extends toward the pterygoid, with which it is in contact.

In the fossil *Agriochœrus bullatus* (Thorpe, 1921*c*, p. 116) the anterior portion of the bulla approaches the pterygoid process.

In *Elephas* the bulla extends over the pterygoid. It lies against the pterygoid process, a feature which is emphasized by the strongly vertical development of this process.

In the Lemuriformes, according to Gregory (1920, p. 183), the true pterygoid is usually nearly in contact with the bulla. Also in *Notharctus* (Gregory, 1920, p. 166) the anterointernal extensions of the bullæ are closely appressed to the true pterygoids.

Foramen Lacerum Anterius Sive Medium

Just as in the case of the foramen lacerum posterius, the foramen lacerum anterius s. medium also can be visible externally or covered by the bulla in relation to the development of the auditory bulla. In the latter case the upper margin of the bulla, if bent round, can be seen from the cavum cranii.

In the adult *Solenodon paradoxus* the roof of the tympanum covers the foramen lacerum medium completely, while in the young skull this foramen is open. Also in *Centetes* this foramen is obliterated by the hypertrophy of the tympanic wings of the ali and basisphenoid (Gregory, 1910, p. 247).

In nearly all Dasypodidæ the entotympanic forms a sulcus or canalis caroticus; in the latter case the foramen lacerum anterius is covered. This is individually variable, even on the right and on the left side of the same skull. A similar condition with the same variability is found in *Bradypus*. Also in the fossil *Hapalops* I found a similar condition. In what seemed to be the best preserved specimens, there was a canalis caroticus with a foramen caroticum posterius. It is possible that *Hapalops* shows a similar variability and that in the other specimens, where this described condition is lacking, it is not broken off, but that they show the natural condition.

In the modern Rodentia the bulla can cover the foramen lacerum anterius totally or nearly totally; then the bulla participates in the covering of the cavum cranii. The uncovered part of the foramen lacerum anterius varies in size; it can be very large (many Hystricomorphæ; Van Kamp.; Preller, 1907, pp. 387, 411, *Hydrochærus capybara*, difference during the development). Sometimes there is a relation to the size of the bulla (Van Kamp.; Winge, 1888, p. 49, *Calomys saltator;* p. 91, *Nelomys antricola;* p. 95, *Mesomys spinosus;* p. 98, *Carterodon sulcidens* and *Nelomys;* Preller, 1907, p. 411, *Dinomys*).

In the modern Canidæ the bulla covers the foramen lacerum anterius. In the modern Procyonidæ the bulla hardly covers this foramen, a feature which no doubt is related to the large vertical but little horizontal extension of the bulla. In the modern Mustelidæ the far forwardly extended bulla covers the foramen lacerum anterius. In the recent Hyænidæ this foramen, with the exception of a small aperture, is covered by the bulla.

In the modern Viverridæ we find different conditions. Pocock (1916*a*, p. 268) concludes that the orifice by which the carotid enters the skull may be entirely cut off from the rest of the foramen lacerum medium and fully exposed on the basisphenoid (*Mungos, Cryptoprocta, Fossa, Galidictis, Arctogalidia;* see also, *loc. cit.*, pp. 264, 265), or it may be continuous with the foramen lacerum medium behind and form a deeper or shallower notch in the basisphenoid, the anterior end of this notch being sometimes plainly visible in front of the bulla (*Arctictis, Diplogale, Paradoxurus;* see also, *loc. cit.*, pp. 263, 264), sometimes overlapped by

it and only visible by looking beneath the bulla (*Genetta, Viverricula, Nandinia*; see also, pp. 262, 263, 265). This complete concealment of the foramen lacerum medium is caused by the fusion of the bulla to the basisphenoid (Pocock, 1916*a*, p. 268).

In the modern Felidæ the bulla covers the foramen lacerum anterius. According to Pocock (1916*a*, pp. 267, 268), the orifice by which the carotid enters the base of the skull always notches the basisphenoid but it is never visible from the surface, because the overlying portion of the bulla, forming here a bony contact or fusion with the basisphenoid, conceals the foramen lacerum medium completely.

In the fossil *Dinictis* (Riggs, 1896*b*, p. 237) the foramen lacerum medium is large.

In the modern Phocidæ the bulla partly covers the foramen lacerum anterius s. medium.

In the recent Otariidæ and Trichechidæ this foramen is not covered.

According to Winge (1906, p. 38) there is a difference in the degree of covering of the foramen lacerum medium in *Dicotyles labiatus* and *torquatus*.

In *Elephas* the bulla covers the foramen lacerum anterius. Thus the bulla and also the carotid canal in the mesial wall of the bulla are visible from the cavum cranii through this foramen and through the fissure between the periotic and the basis cranii as well.

In *Lemur mongos* (Van Kamp.; Winge, 1985*a*, p. 38, *Lemur collaris*) the anterior process of the bulla covers the foramen lacerum anterius nearly totally. According to Gregory (1915, pp. 431, 433), in the Lemurinæ in general the foramen lacerum medium is roofed over. In *Lichanotus* (*Avahi*), according to Gregory (1920, p. 176), the anterointernal process of the bulla covers the region of the foramen lacerum medium. In *Chirogale milii* the foramen lacerum anterius is not covered. Within the genus *Microcebus* different conditions occur (Van Kamp.; Gregory, 1920, p. 179). In *Microcebus furcifer* the foramen lacerum anterius is widely open, while in the other species of *Microcebus* this foramen is more or less roofed over by the anterointernal extension of the bulla.

In the fossil Megaladapinæ as well this foramen is roofed over (Gregory, 1915, p. 434). In *Palæopropithecus*, according to Gregory (1920, p. 176), in contrast with Standing's opinion the foramen lacerum medium is a small opening between the foramen ovale and the Eustachian foramen. Standing's "foramen lacerum medium" (1908, p. 81) widely exposed in consequence of the concave surface of the bulla, according to Gregory (1920; p. 176) is the foramen ovale.

In *Mesopropithecus* (Gregory, 1920, p. 176) the foramen lacerum medium is closed.

In *Adapis* (Stehlin, cited by Gregory, 1920, p. 178) and in *Notharctus* (Gregory, 1920, pp. 166, 178) there is no foramen lacerum medium.

In the fossil *Archæolemur* (Gregory, 1920, p. 177) the foramen lacerum medium is roofed over.

In the modern Chiromyidæ (Van Kamp.; Gregory, 1920, p. 177) the bulla totally covers the foramen lacerum anterius.

In the recent *Perodicticus potto* this foramen is not covered by the bulla. According to Gregory (1915, p. 430; 1920, p. 179) this foramen is widely open in the Lorisidæ or Nycticebidæ.

In the Tarsiidæ (Gregory, 1915, p. 430; 1920, p. 180) there is no foramen lacerum medium, this region being completely closed by the anterointernal extension of the bulla. The same is the case in the fossil *Necrolemur* (Gregory, 1915, p. 430; 1920, p. 180) and in *Anaptomorphus* (*Tetonius*) *homunculus* (Gregory, 1915, p. 430).

In the Old and New World monkeys (Van Kamp.; Gregory, 1920, p. 181) the foramen lacerum anterius is closed by the bulla; at the utmost there is a very narrow fissure. In *Homo* only this foramen is uncovered, which no doubt is secondary (Van Kamp.; Gregory, 1920, p. 181) in consequence of the reduction of the bulla.

The Basisphenoid

In the insectivores the basisphenoid can form a tympanic wing, as we shall see later.

Sometimes the bulla touches the basisphenoid, a feature that depends on the development of the bulla in the longitudinal direction. This is the case for example in *Tupaia javanica*, where we have a bulla prolonged far forward.

In *Manis gigantea* and in this species alone, the mesial margin of the entotympanic touches the basisphenoid. In *Scelidotherium* (see also my own investigations) and in many other Gravigrada the entotympanic touches the basisphenoid, as Van Kampen notes. In *Lestodon*, according to my own investigations, the entotympanic does not touch the basisphenoid. In the recent dasypodid *Xenurus* (=*Lysiurus*) *unicinctus* the inner margin of the entotympanic touches the basisphenoid.

In modern Rodentia the processus styliformis of the bulla sometimes just reaches the basisphenoid. In the rodents with a very large bulla, the basisphenoid is compressed and narrowed (Van Kamp.; Wing 1888, p. 95, *Mesomys spinosus;* p. 98, *Carterodon sulcidens*); in a few

cases the opposite bullæ even touch each other. According to Gregory (1910, p. 329) the lateral margins of the basisphenoid are often raised and more or less excavated on each side for the very large inflated bulla.

Among the Canidæ in *Fennecus zerda*, which shows an enormously large bulla, the caudal portion of the basisphenoid adjoins the bulla. Also in the fossil *Temnocyon coryphæus* (Cope, 1879, p. 181; 1880*a*, p. 95) the borders of the sphenoid descend on the inner side of the bullæ.

In the modern Ursidæ the foramen lacerum anterius separates the bulla from the basisphenoid.

In the recent Procyonidæ the bulla lies along the basisphenoid though not for so long a distance as in Mustelidæ as a rule; this probably in consequence of the larger inflation in the vertical direction.

In the modern Mustelidæ, as a rule, the bulla for a considerable distance lies along the basisphenoid, a feature which is probably related to the small vertical extension and the large horizontal one, and which is possible as the fossa glenoidea lies far forward.

In the recent Viverridæ, according to Van Kampen, there is no anterior process of the bulla along the basisphenoid, except in *Cryptoprocta*. In *Galidia*, according to Carlsson (1910*b*, p. 566) the tympanic portion of the bulla lies along the basisphenoid only and not along the basioccipital, as we shall see.

In the hyænas (Pocock, 1916*e*, pp. 306, 307) the bulla is fused anteriorly to the basisphenoid.

In the modern Felidæ (Van Kamp.; Pocock, 1916*a*, pp. 267, 268; 1916*e*, pp. 306, 307) there is a bony contact or fusion of the narrow anterior portion of the bulla to the basisphenoid.

In the recent Phocidæ the very large bulla extends rostrally along the basisphenoid and touches this, perhaps in consequence of the large development of the mastoid. In the Trichechidæ the bulla just adjoins the basisphenoid; the same is perhaps the case in the Otariidæ, but probably here it does not touch the basisphenoid at all.

The bullæ in *Leptauchenia* (Scott, 1890, p. 353) compress the basisphenoid and also the basioccipital, so much that they are reduced to narrow ridges.

In the fossil *Hypisodus* (Matthew, 1893– 1903, p. 440) the bullæ, which meet anteriorly in the median line of the skull, cover up almost all of the basisphenoid.

In the fossil *Typotherium serratum*, according to Van Kampen, the short narrow anterior process of the bulla touches the basisphenoid. Sinclair (1909, p. 74) also mentions in *Hegetotherium* a suture between

the tympanic and the basisphenoid at the elongated anterior extremity of the bulla.

In *Lemur* (Van Kamp.; Gregory, 1920, p. 210) the uninflated anterior process just touches the basisphenoid. In the fossil *Megaladapis edwardsi* (Lorenz von Liburnau, 1905, p. 463) the anterior process of the bulla lies mesially against the hind part of the basisphenoid. In the fossil *Notharctus* (Gregory, 1920, pp. 166, 178, 210, 224) the processus anteromedialis, into which the bulla is extended anterointernally, articulates with and is closely appressed to the hinder edge of the basisphenoid. In *Notharctus* (Gregory, 1920, pp. 161, 178) the anterointernal extensions of the bulla do not extend in front of the suture between the basioccipital and the basisphenoid, as they do in *Lemur*. In *Adapis* (Stehlin, 1912, cited by Gregory, 1920, p. 161) the basioccipital-basisphenoid suture is considerably behind the front ends of the bullæ.

In *Perodicticus potto* probably the bulla lies along the basisphenoid as well. In *Tarsius* the rostral portion of the bulla compresses the caudal part of the basisphenoid.

According to Gregory (1920, p. 220) in the ancestors of the Platyrrhinæ the bulla remained fastened to the postero-external corner of the basisphenoid.

The Basioccipital

The result of an enlargement of the auditory bulla in the horizontal direction will be that toward the median line the petrosal will be covered and that the bullæ will touch the basioccipital or even partly cover this and in the most extreme condition even meet each other in the median line (see elsewhere in this article).

In *Manis gigantea* and in this species of *Manis* alone the mesial margin of the entotympanic touches the basioccipital and also the basisphenoid, as we have seen above. In *Bradypus*, also, the entotympanic portion of the bulla touches the basioccipital. In *Scelidotherium*, too, (see Van Kampen's and my own investigations) the entotympanic reaches the basioccipital. According to Van Kampen this would likewise be the case in *Lestodon*, but I did not find it in the specimen I investigated. On the other hand, Van Kampen notes that in *Mylodon gracilis* the entotympanic does not reach the basis cranii, but it does so in my specimen of *Mylodon garmani*. These may be specific differences, but in *Mylodon garmani* it may be due to the compressed condition of the skull. In *Xenurus* (=*Lysiurus*) *unicinctus* the entotympanic touches the basioccipital and also the basisphenoid, as we have seen above.

In the modern Rodentia the bulla adjoins the basioccipital, except in those with a very small bulla. Large bullæ narrow and compress the basioccipital (Van Kamp.; Winge, 1888, p. 95, *Mesomys spinosus;* p. 113, *Lagomys;* p. 120, *Scirtetes* and *Dipus;* p. 98, less in *Carterodon sulcidens*). Sometimes even the opposite bullæ touch each other.

In the fossil *Perimys erutus* (Scott, 1905, p. 439) the bulla is closely appressed to the basioccipital. In *Schistomys* (Scott, 1905, p. 480) the bullæ are smaller than in *Dolichotis*, especially in the transverse diameter, so that they narrow the basicranial axis less.

In the Fissipedia the bulla is adjacent to the basioccipital.

In the recent Canidæ the bulla adjoins the basioccipital, separated posteriorly by the foramen lacerum posterius.

In the modern Ursidæ the mesial wall of the bulla lies against the erect border of the basioccipital, separated posteriorly by the foramen lacerum posterius.

In the recent Mustelidæ the bulla lies along the basioccipital and the basisphenoid, separated posteriorly by the foramen lacerum posterius. In the fossil *Bunælurus* (Matthew, 1902*b*, p. 138) the short bulla leaves a much larger surface of the occipitals and sphenoids exposed than in *Mustela* and *Putorius*. In *Palæoprionodon* (Teilhard de Chardin, 1914–1915, p. 78) the cartilaginous posterior chamber of the bulla probably lies against the circular bony crest on the border of the basioccipital.

In the modern Viverridæ the bulla adjoins the basioccipital, separated posteriorly by the foramen lacerum posterius. In the Viverrinæ, *Eupleres* and *Cryptoprocta* this is totally or almost entirely the entotympanic portion.

In *Civettictis* (Pocock, 1916*a*, p. 262) there is a small bridge of bone jutting inward from the bulla to the anterolateral angle of the basioccipital.

In the Herpestinæ (Van Kamp.; Carlsson, 1910*b*, p. 566), however, the entotympanic as well as the tympanic adjoin the basioccipital. In *Galidia* (Carlsson, 1910*b*, p. 566), in consequence of the extraordinary shortness of the basioccipital, the tympanic does not adjoin the basioccipital.

In the recent Felidæ the bulla lies against the basioccipital, posteriorly separated from it by the foramen lacerum posterius; the bulla covers even the lateral border of the basioccipital, together forming the carotid canal and with its involute margin lying beneath the fissure between the basioccipital and the petrosal. In *Felis spelæa* (Dawkins, 1878, p. 49) the bulla is in contact on the inside with the external and

lower border of the basioccipital. In *Dinictis felina* (Scott, 1889, p. 214) the basioccipital has sharp prominent edges which abut against the sides of the bullæ and thus give the bone a deeply concave shape from side to side.

In the Phocidæ, as a rule, the bulla is separate from the basioccipital by a wide fissure. In *Phoca barbata,* only the mesial margin of the bulla adjoins the basioccipital along a rather long distance. In the Otariidæ and in the Trichechidæ also the mesial margin of the bulla is adjacent to the basioccipital.

In old skulls of *Rhinoceros* the entotympanic lies against the basioccipital, which is not yet the case in young skulls.

In *Equus* and *Tapirus* bulla and basioccipital remain separate.

In *Eomoropus amarorum* (Cope, 1881*c*, p. 390; Osborn, 1913, fig. 1 n°. A^3; see also my own investigations) perhaps the entotympanic (i.e. Cope's inner longitudinal ridge of the inferior surface of the petrous bone, and Osborn's periotic) is in close contact with the basioccipital.

In *Hippopotamus* there is a wide fissure between the bulla and the basis cranii. In the fossil *Anoplotherium* (Palmer, 1913*b*, p. 884), as well, the bulla does not meet the basioccipital.

In the Cænotheriidæ (Winge, 1906, p. 96) the large bulla compresses the basioccipital.

In the Oreodontidæ with large bullæ these touch the basis cranii, while small bullæ are separated from the basis cranii by a fissure. In *Eucrotaphus jacksoni* and *auritus*, according to Leidy (1854, p. 57), the bulla rests with its base internally upon the margin of the basilar process and the conjunction of this with the sphenoidal body. In *Leptauchenia* (Scott, 1890, p. 353) the bullæ push aside the basioccipital and also the basisphenoid so much that these bones are reduced to narrow ridges.

In the modern Camelidæ the bulla joins the basioccipital. The same happens in *Tragulus* and *Hyomoschus.*

In the recent Cervidæ there remains a fissure between the bulla and the basioccipital, through which a part of the petrosal is visible. In *Cervus porcinus* and *kuhlii* only, with their strongly inflated bullæ, these can touch the basioccipital.

In the modern Giraffidæ there occurs a narrow fissure between the bulla and the basioccipital. Also in the fossil *Protoceras* (Scott, 1895*a*, pp. 310, 313) the very small bulla does not encroach upon the basioccipital, though their approximation in the natural condition is too close to allow the periotic to be seen.

In the recent Bovidæ as a rule the mesial margin of the bulla reaches the basioccipital.

In *Typotherium cristatum*, according to Van Kampen, the bulla immediately adjoins the basioccipital. In *Protypotherium* (Sinclair, 1909, p. 22) the bulla is fused with the basioccipital. In *Toxodon platensis*, according to Van Kampen, the top of the bulla only adjoins the basioccipital; moreover, the bulla covers the considerable space between the periotic and the basioccipital. In *Nesodon*, as Van Kampen concludes from Lydekker's plates (1893, Pl. XIV–XVI), the bulla joins the basioccipital.

In *Procavia* the bulla touches the basioccipital for a short distance only, being separated from it posteriorly by the foramen lacerum posterius, antericrly by the wide foramen lacerum anterius.

In the modern Lemuridæ (Van Kamp.; Gregory, 1920, p. 164) the bulla lies against the basioccipital. According to Gregory (1920, p. 210) the bulla articulates with its processus anteromedialis, with the basioccipital, and the basisphenoid.

In the fossil *Adapis* and *Notharctos* (Gregory, 1920, p. 164), as well, the expansion of the bulla is limited internally by the basioccipital. In *Adapis*, according to Gregory (1920, p. 210), the bulla articulates by means of its processus antercmedialis with the basioccipital and basisphenoid. This feature is probably also described by Winge (1895*a*, p. 37). A similar condition is found in *Notharctus* (Gregory, 1920, p. 224). In *Notharctus* (Gregory, 1920, p. 161) the lateral border of the basioccipital is raised into recurved alæ overlapping the medial base of the bullæ after the fashion of the tympanic processes of the basioccipital of insectivores. In *Adapis*, on the other hand, these flanges are absent, or but faintly indicated (Stehlin, 1912, cited by Gregory, 1920, p. 161).

In the recent adult *Perodicticus potto* the mesial margin of the bulla adjoins the basioccipital; in the young skull, however, a considerable part of the promontorium still remains uncovered.

In the modern *Tarsius* (Van Kamp.; Winge, 1895*a*, p. 15) the rostral portion of the bulla compresses the basioccipital, while the caudal portion does not reach the basioccipital as a result of the rostralward displacement of the foramen magnum.

In the fossil *Anaptomorphus* (Winge, 1895*a*, p. 15) the bulla rostrally compresses the basioccipital, which does not seem to happen in *Necrolemur* (Winge, 1895*a*, p. 15).

In the ancestors of the Platyrrhinæ, according to Gregory (1920, p. 220), the bulla remained fastened to the side of the basioccipital.

The Pars Petrosa of the Periotic

A small bulla will leave a part of the pars petrosa of the periotic free, while a larger bulla will cover this part more or less, or touch the basioccipital, or even cover a part of the basioccipital. Later we shall see that the petrosal can also form a tympanic wing of the bulla.

In *Sorex araneus* an important part of the pars petrosa behind the processus tympanicus petrosi is uncovered by the tympanic cavity.

In *Tupaia javanica* a small margin of the periotic is visible behind the bulla, between the bulla and the exoccipital and a very small margin between the bulla and the basioccipital. *Ptilocercus* shows a smaller and more primitive bulla than *Tupaia* and uncovers a larger part of the periotic between the bulla and the basioccipital, but not behind the bulla (Van Kamp.; Gregory, 1910, p. 272).

In the Microchiroptera also the promontorium is partly uncovered, generally less covered the more the bulla is inflated. According to Revilliod (1917, p. 21) in the fossil Palæophyllophora the bulla, properly speaking, only partly covers the petrosal the mesial half being left uncovered, as in the recent Chiroptera. In my opinion, however, this "bulle proprement dite" does not contain the entotympanic portion, or this portion is only partly preserved.

According to Van Kampen the periotic is visible in *Cholœpus* between the entotympanic and the basioccipital, but in the few skulls I could investigate, it seems to me that, just as in many fossil Gravigrada (see my own investigations), this space is dorsally covered by a part of the entotympanic that forms the roof for the sulcus caroticus. Perhaps it is individually variable. In the fossil *Lestodon* (see my own investigations) the short and small entotympanic uncovers a large part of the periotic. In *Priodontes giganteus* the entotympanic seems to let free a part of the periotic and not to reach the basis cranii, as in *Xenurus unicinctus*.

In the few modern rodents with a very small bulla the petrosal is externally visible.

In *Civettictis* (Pocock, 1916*a*, p. 262) the periotic appears for a small space on the surface of the skull between the bulla and the basioccipital, while in *Viverra zibetha*, *V. tangalunga* and *Viverricula malaccensis* the periotic does not reach the surface of the basis cranii.

On the ventral surface of the skull in the modern Phocidæ a narrow strip of the periotic is visible, which occupies the space between the bulla and the exoccipital and forms the thickened, inflated hind margin of the periotic and the mesialward prolongation of the inflation of the mastoid.

In the modern Trichechidæ the petrosal is only just visible behind the bulla, while in the recent Otariidæ the periotic is not at all visible.

In the recent Mystacoceti (Hanke, 1914, p. 507) the periotic and the tympanic together form the ventral surface of this region of the skull, while in the Odontoceti the petrosal in this view is nearly covered by the bulla.

In the fossil *Theosodon* (Scott, 1910, p. 115) the large periotic is concealed by the tympanic, though this is very small and can hardly be said to form a bulla at all.

In the ventral view of the skull in *Equus* a considerable part of the petrosal is visible.

In the fossil *Eomoropus amarorum* Cope (1881*c*, p. 390) describes and Osborn (1913, p. 268) describes and figures a part of the inferior surface of the petrosal, which the tympanic leaves exposed. In my opinion (see my own investigations) this is perhaps an entotympanic.

In the fossil *Leptomeryx evansi*, according to Scott (1891*b*, p. 347), there appears to be a broad surface of the periotic exposed between the squamosal and the occipital, which lies entirely in the occipital plane and not on the side. In *Allomeryx planiceps* (Lull, 1922, p. 114) the bulla is separated from the basioccipital by an outgrowth of the petrosal. In the fossil *Blastomeryx* (Matthew, 1908, p. 536) there is a depressed channel next to the basioccipital, at the bottom of which appears the petrosal.

In the modern Cervidæ a part of the petrosal is visible between the bulla and the basis cranii. In *Moschus* (Scott, 1895*a*, p. 313) this part of the petrosal is visible, when viewing the base of the skull, for nearly the entire length of the bulla from in front backward. According to Matthew (1908, p. 538) in most of the modern deer the internal exposure of the inferior surface of the petrous bone is reduced, partly by widening of the basioccipital, partly by decrease of the petrous bone anterointernally.

The portion of the petrous bone described by Owen (1840, p. 22) in *Toxodon platensis* is, according to Van Kampen, a part of the bulla, the petrosal being invisible in the ventral view of the skull.

Surface of the Bulla

Sometimes the surface of the bulla is not smooth. Leidy (1855, pp. 9, 10) notes that in the tympanic of *Megalonyx jeffersonii* the bulla is rugged (according to Van Kampen, Leidy's auditory process is the tympanic). In *Hapalops* and allied genera I have found that the under

margin of the entotympanic is rough in contrast to the smooth outer surface of the tympanic.

The bulla in *Harpagolestes macrocephalus* is rugged (Wortman, 1901, p. 288); the bulla in *Dromocyon vorax* (*loc. cit.*, p. 294) is rugose.

In the adult Ursidæ the bulla is more or less rugged; in the young skull it is more smooth.

The surface of the bulla in the Otariidæ is more or less rugged, as well as that in the Trichechidæ.

In *Diochotichus vanbenedeni* (True, 1910, p. 26) the middle portion of the inferior surface of the bulla is rugose, differing in this respect from the bulla in *Schizodelphis crassangulum*, which it otherwise resembles very much.

In old skulls of *Rhinoceros* the bulla is rugged.

In *Oreodon culbertsonii* (Osborn and Wortman, 1894, p. 216) the bulla is rugged in contrast to the smooth form found in the later species.

In the modern Camelidæ as a rule the bulla is rugose; in *Lama*, however, it is sometimes smooth.

In the recent Cervidæ showing the small type of bulla this is more or less rugged, while in the other type with the strong inflation the surface of the bulla is smooth.

In the modern Giraffidæ as well, the bulla is rugged, while in the Tragulidæ, Bovidæ, and others, its surface is smooth.

The flat bulla of the Anthropomorphæ is rugged.

Crests on the Surface of the Bulla

The underwall of the long cylindrical external auditory meatus in *Castor* shows a vertical crest which ends against the lateral wall of the bulla, these together enclosing the groove for the hyoid arch and the facial nerve and thus resembling the similar crest in many artiodactyls.

In the fossil *Myopotamus priscus*, judging from the figure given by Ameghino (1889, Pl. v, fig. 2), there seems to be a crest on the under surface of the bulla which runs far forward. There seems to be no crest on the under surface of the external auditory meatus.

In *Pachycynodon* (Teilhard de Chardin, 1914–1915, p. 40) the bulla shows a strong keel.

In the old skulls of modern Otariidæ, but not in young skulls, we find an irregular broad crest parallel to the mesial margin of the bulla and running along the place of greatest height; caudally this crest ends in a process. In the Trichechidæ this crest and process are wanting.

In the modern Mystacoceti (Hanke,1914, pp. 507, 508) the under

surface of the bulla shows a distinct, though slightly developed longitudinal crest lying about in the middle of the bulla, thus dividing it into an inner and an outer lobe.

In other cases in the Cetacea a groove on the surface of the bulla may give rise to a keel, as we shall see later (Turner, 1913, pp. 13, 14, *Balænoptera;* Schulte, 1917, p. 395, *Kogia*).

In *Equus* the under surface of the bulla shows a sharp margin or crest, running from in front backward and resembling the crista petrosa of man.

In the modern Suidæ, in which the bulla is more or less laterally compressed, the top of the bulla is crest-like as in *Phacochœrus*, or strongly pointed as in *Potamochœrus*, or curved as in *Dicotyles*, *Sus* and *Babirussa*.

In the hippopotamus the compressed bulla shows a rather sharp under margin, ending caudally in a short process, rostrally in a generally long, oblique downwardly-directed process. This sharp under margin of the bulla continues on the entire length of the under wall of the cylindrical auditory meatus as a high crest which is visible through a cleft of the false auditory meatus.

In the fossil *Agriochœrus bullatus* (Thorpe, 1921*c*, pp. 116, 117) the bulla is keeled inferiorly in the transverse plane; the keel runs from the postglenoid tubercle to the lower border of the internal plane face.

In *Paroreodon marshi* (Thorpe, 1921*b*, p. 109) the bulla ends inferiorly in a sharp ridge.

In *Oreodon*, according to Leidy (1854, p. 32), the auditory process inferiorly forms a ridge-like vaginal process curving forward and inward to the auditory bulla, with which it is continuous, the bulla being surmounted by this ridge. This ridge is prominent in *Oreodon culbertsonii* and but feebly developed in *Oreodon gracilis* (Leidy, 1854, p. 55). In *Eucrotaphus*, and especially in *Eucrotaphus jacksoni*, Leidy (1854, p. 57) mentions a ridge-like vaginal process of the auditory process, with which the bulla is outwardly continuous. Thorpe (1921*b*, p. 101) describes on the bulla of *Eporeodon trigonocephalus* an external ridge enclosing a groove continuous with the stylohyal fossa. Van Kampen concluded, from a figure of *Oreodon bullatus* given by Scott, that the crest on the under wall of the cylindrical auditory meatus is not entirely wanting.

The modern Cervidæ and Giraffidæ show on the under wall of the cylindrical auditory meatus a longitudinal uninflated crest, which laterally bounds the vagina processus hyoidei. In the Cervidæ this crest is low; in the Giraffidæ it is more strongly developed.

In the modern Bovidæ this crest is diversely developed, sometimes

feebly, sometimes very strongly. The crest is always flat and never inflated. In a few Bovidæ it ends in a downwardly-directed process near the tympanohyal.

Perhaps the above-mentioned crest, which occurs in many artiodactyls and also in *Toxodon*, is a remnant of an inflation of the under wall of the cylindrical auditory meatus, similar to that found in the modern Camelidæ.

In *Toxodon platensis*, according to Owen (1840, p. 22), the tympanic bone consists of a rough, compressed vertical osseous plate, wedged in transversely between the occiput and the posterior part of the glenoid cavity. The internal extremity of this plate points inward and forward, representing the styloid process. According to Van Kampen this "tympanic bone" is nothing else but the crest on the under wall of the cylindrical auditory meatus, which bends rectangularly and runs on to the under surface of the bulla, ending in the processus styliformis. Van Kampen concluded from the description and figures given by Lydekker (1893) that in *Nesodon patagonicus* this crest is perhaps absent.

In *Typotherium cristatum* Van Kampen found along the under wall of the cylindrical auditory meatus two high crests or edges, one being probably the posttympanic process, the other being either the top of a very high postglenoid process or a crest homologous to that in *Toxodon* and many artiodactyls. This could not be decided, as the tympanic was firmly fused with the squamosal. The under wall of the bulla in *Typotherium cristatum*, according to Van Kampen, shows a rounded under margin, running from the caudo-external corner rostromesialward, ending in the processus styliformis. Caudally this ridge ends in a short process against the base of the paroccipital process, while in front of this a similar process is visible.

In *Elephas* the strongly flattened fore-wall and hind-wall of the bulla bend into one another with rather a sharp margin.

In the fossil *Megaladapis edwardsi* Lorenz von Liburnau (1905, p. 463) describes a pointed three-sided crista tympanica or crista petrosa, which projects oralward from the oral external margin of the tympanic behind the opening for the Eustachian tube.

In the Cercopithecidæ a short and low nearly sagittal ridge is found sometimes lying on the boundary of the caudal part of the bulla and the floor of the external auditory meatus. In *Macacus* this ridge is sometimes very distinct. It is a first indication of a crista petrosa. In the higher apes this crista is well-known. In *Hylobates*, however, it is still absent or slightly developed. In *Anthropopithecus* and *Gorilla* it is most

distinctly developed. According to Gregory (1916, p. 278), however, the tympanic spout in man develops an inferior crest, thus differing from the gorilla. This crista develops in consequence of the slight inflation of the bulla. Its ontogeny in man shows that this crista coincides with the line of fusion of the tympanic with the periotic. The crista runs from the foramen stylomastoideum on the lateral side of the foramen caroticum posterius toward the orificium tubæ.

Furrows on the Surface of the Bulla

In the Cetacea there occur furrows on the surface of the bulla.

The longitudinal furrow on the surface of the bulla is well known in the Odontoceti (see also Hanke, 1914, pp. 505, 507); it divides the under surface of the bulla into two lobes, a lateral and a mesial one.

In the modern Delphinidæ this furrow is deep; it lies in the caudal part of the under surface and is filled with connective tissue in the living animal.

In the modern Physeteridæ this furrow is differently developed in different genera; it can be well marked, scarcely apparent, or obsolete, and in consequence of this, the bilobate character of the posterior end of the bulla is more or less distinct or absent. According to Schulte (1917, p. 395) *Kogia* shows an oblique ridge or fold of the ventral surface, for it is visible entally as a groove, the only one present in this bulla. The mesal portion of the bulla is set off from the lateral portion by a groove ectally and a ridge entally. In the fossil *Diochotichus van-benedeni* (True, 1910, p. 26) the posterior border of the bulla is deeply emarginated or bilobed; the furrow between the outer and inner lips is straight and extends to within 10 mm. of the anterior extremity.

This longitudinal furrow of the Odontoceti is lacking in the Mystacoceti (Van Kamp.; Hanke, 1914, p. 505), which, in this place, show the above described longitudinal crest (Hanke, 1914, p. 507). The bulla in *Balænoptera sibbaldi* (True, 1913, pp. 14, 16) is keeled in its inferior surface; an oblique, strong, relatively wide, groove-like depression divides the convex outer surface into an anterior and a posterior part, the latter of which is the larger, as this depression lies at the front of the lip-like or mallear process of the tympanic. In *Balænoptera musculus* (Turner, 1913, p. 13) the outer surface of the bulla possesses a deep groove parallel and close to the posterior border, which gives to that border a more definite character than was the case in *Balænoptera sibbaldi*. On the other hand, it does not possess the long broad groove parallel to and bounding the outer side of the lower border, which gives rise in *Balænoptera sibbaldi* to a very prominent keel.

Thus the note of Zittel (1893, p. 182) that the bulla in *Balænoptera* shows no vertical furrow is not correct. On the other hand Zittel (1893, p. 183) mentions such a furrow in *Megaptera*.

Vagina Processus Hyoidei or Styloidei

In a few cases the hyoid lies so close against the external surface of the bulla that it forms a groove in its wall, or in the extreme condition even a canal, called the vagina processus hyoidei. Sometimes also the top of the stylohyal and the tympanostyloid cartilage is enclosed in this canal, which then is called vagina processus styloidei.

In the adult *Bradypus* the tympanohyal is enclosed in a vagina in the posterior wall of the bulla, which is formed entirely by the tympanic and surrounds the top of the tympanohyal.

Among the Rodentia, *Castor* shows a vagina for the hyoid arch, resembling that in the Artiodactyla.

Many modern Carnivora show a groove on the bulla for the tympanohyal, which, however, never attains the depth of that in most ungulates. In Van Kampen's paper it is mentioned for *Canis*, Hyænidæ, Ursidæ, *Felis*. Van Kampen found in a pullus of one of the Trichechidæ the tympanohyal lying in a vagina formed by the bulla. In young skulls of Phocidæ the tympanohyal lies in a little groove of the bulla; they soon fuse and the vagina encloses the tympanohyal. In a pullus of one of the Otariidæ Van Kampen describes a groove for the tympanohyal in the bulla connected with the stylomastoid foramen. In all modern Viverridæ, except in *Nandinia*, the tympanohyal lies in a distinct little groove in the entotympanic, which can be nearly (*Arctictis*) or entirely (*Herpestes*) separate from the foramen stylomastoideum. Carlsson (1911, p. 425) mentions in *Cryptoprocta ferox* a groove on the bulla for the stylohyal. In *Galidia* (Carlsson, 1910*b*, p. 568) the distal portion of the stylohyal lies in a groove between the bony auditory meatus and the proper tympanic. Braun (1906, p. 675) mentions in *Mustela martes* and *Mustela foina* on the surface of the bulla a groove for the hyoid arch. In *Putorius* this groove is absent (Braun, 1906, p. 675; Van Kampen, 1907, p. 696).

In *Rhinoceros* the tympanohyal partly sinks down into the broad vagina, which lies in the caudal and under wall of the tympanic. The extension in the ventral wall, as well as the external auditory meatus, contributes to this vagina, while on the mesial side the caudal end of the entotympanic completes it.

In *Tapirus* this vagina is very shallow and formed by the tympanic only.

The vagina processus hyoidei in *Equus* is so deep that the margins are closed around the tympanohyal, forming a tube. The vagina is formed by the tympanic, the mesial wall by the lateral wall of the bulla, the lateral and rostral wall by the cylindrical auditory meatus and an edge on the under wall of the proximal part of the auditory meatus. In *Mesohippus*, according to Scott (1891*b*, p. 306), the bulla encircles and apparently is coössified with the tympanohyal. In the fossil *Anchitherium bairdii*, according to Leidy (1854, p. 69), the base of the styloid process, alone remaining in the specimen, is embraced anterointernally by the os tympanicum.

In the modern Suidæ there may be a vagina which is deep or shallow, and which in *Dicotyles* is sometimes even closed.

In *Hippopotamus* the groove in the bulla for the tympanohyal is open.

In *Anoplotherium* Palmer (1913*b*, p. 884) describes a cylindrical hollow on the tympanic for the attachment of the tympanohyal, lying just in front of the stylomastoid foramen. This hollow is perhaps a vagina processus hyoidei or the foramen stylomastoideum definitivum, the stylomastoid foramen mentioned by Palmer being probably the primitive one.

Cænotherium filholi probably possesses a vagina which is closed all around, judging from the figures given by Lydekker (1885*a*, Fig. 1; 1885*b*, Fig. 22; see also my own investigations).

In *Mesoreodon chelonyx*, according to Scott (1895*b*, p. 130), the tympanohyal is inserted into a depression upon the outer side of the bulla. From this remark and from the figures given by Osborn and Wortman, Van Kampen concluded that this vagina shows the characters of that in the Cervidæ. Sometimes the tympanohyal seems to have been enclosed all around. Van Kampen concludes this from the figures and a remark in Osborn and Wortman (1894, p. 216), that the stylomastoid foramen is separated from the tympanohyal by a well-marked lamina of bone. Now in the recent Ruminantia these two are separated only if the vagina is closed.

In the modern Camelidæ (Van Kamp.; Winge, 1906, pp. 11, 98) the tympanic forms the vagina, which encloses the tympanohyal and the tympano-styloid cartilage (according to Winge, however, the stylohyal). In young animals the vagina is shallow, in adults it is deep and an entirely closed groove, the margins touching each other and fusing. This deep vagina lies on the boundary of the bulla proper and the inflated under wall of the auditory meatus. Thus the tympanic has the shape of a

V, one leg being formed by the compressed bulla proper, the other by the inflation of the external auditory meatus. While this vagina in the recent genera is very deep (Scott, 1891*a*, p. 54) and forms a deep circular pit surrounded by bone (Wortman, 1898, p. 116), the "styloid groove and pit" in the fossil *Poëbrotherium* (Scott, 1891*a*, pp. 15, 56) are shallower and more widely open behind, the pit being decidedly smaller and shallower and less distinctly separated from the groove than in *Auchenia*. In *Poëbrotherium* in general and especially in *Poëbrotherium wilsoni* (Leidy, 1847, p. 324; 1854, p. 21; Scott, 1891*a*, p. 15; Wortman, 1898, p. 116) the notch or groove, which on the postero-external angle of the tympanic separates the two ampullæ, is deep and ends below in a deep depression, the inconsiderable pit for the tympanohyal, which is enclosed by the bulla. In *Poëbrotherium andersoni* (Troxell, 1917, p. 382) the postero-exterior groove in the bulla, instead of following along the bottom of the bulla as in *Poëbrotherium wilsoni*, leads from the original pit upward. In *Gomphotherium* (Wortman, 1898, p. 116) the tympanohyal recess is much more pronounced. In *Pseudolabis* (*Paralabis*) *matthewi*, according to Lull (1921, p. 392), this recess is more widely open than in *Poëbrotherium* and more as in the later Camelidæ. According to Wortman (1898, p. 116), in all the camels the deep recess, where the hyoid arch is articulated to the skull, lies immediately behind the point of junction of the two parts of the bulla.

In the Tragulidæ the groove for the tympanohyal lies in the posterior wall of the tympanic between the bulla and the external auditory meatus and continues along the lateral wall of the bulla in the anterior downward direction. In *Tragulus*, probably in old specimens only, it is sometimes closed all around. The top of the tympanohyal does not reach the end of the vagina.

In the fossil *Leptomeryx evansi* (Scott, 1891*b*, p. 347) the postero-external angle of the bulla shows a rather wide and shallow "styloid" groove. In *Blastomeryx* (Matthew, 1908, p. 536) the stylohyoid pit is comparatively small.

In the modern Cervidæ (Van Kamp.; Matthew, 1908, p. 358) the vagina is deep or shallow. It lies posteriorly between the bulla and the auditory meatus, on the lateral side bounded by a ridge on the under wall of the cylindrical auditory meatus. In *Moschus moschiferus* only it is closed all around. In the deer with a much inflated bulla the vagina continues along the lateral wall of the bulla beneath the cylindrical auditory meatus downward and forward as in *Tragulus*. In this prolongation lies the tympano-styloid cartilage and the top of the stylohyal; the

vagina itself contains the tympanohyal. In the fossil *Dromomeryx* (Scott, 1895*b*, pp. 171, 172, *Blastomeryx*) the bulla shows a deep groove for the hyoid apparatus, a feature which is cervine rather than antilopine.

In the modern Giraffidæ the vagina is closed all around, closed on the lateral side by a ridge on the under wall of the cylindrical auditory meatus. It continues on the lateral wall of the bulla as an indistinct not sharply-bounded groove.

In the fossil *Protoceras* (Scott, 1895*a*, p. 312) the postero-external side of the bulla shows a deep pit for the tympanohyal.

In *Antilocapra* (Lull, 1920, p. 96) the groove for the attachment of the "stylohyoid" forms a deep pit. In *Aletomeryx gracilis*, according to Lull (1920, p. 96), this groove is hardly in evidence in one of the skulls of his material but better developed in two other skulls.

In the modern Bovidæ the groove for the hyoid arch continues in the lateral wall of the bulla in both types of bullæ. This groove is usually partly closed by the lateral wall of the bulla, which, extending lateralward, separates the tympanohyal from the paroccipital process and sometimes joins the external auditory meatus behind the vagina and thus encloses the tympanohyal all around. This latter condition is found especially in the larger Bovidæ as in the Bovinæ, Tragelaphinæ, *Ovibos* and others. The crest on the under wall of the cylindrical external auditory meatus also in this group forms a more or less complete lateral wall for the groove of the tympanohyal. In other Bovidæ, as in *Gazella*, *Ovis aries*, the tympanohyal is laterally practically uncovered, as this crest is poorly developed.

Also in the fossil *Myotragus balearicus* (Andrews, 1915, p. 286) immediately below the inner end of the auditory meatus the external face of the bulla is deeply grooved by the fossa for the tympanohyal.

In the Typotheria, according to Scott (1912, pp. 114, 292), a cylindrical fossa may be seen in some of the genera; it is a deep pit external to the paroccipital process of the outer side of the bulla near its posterior end, in consequence of the junction of the paroccipital process with the bulla. Sinclair (1909) mentions a deep pit for the tip of the "stylohyal" on the external side of the paroccipital process in *Hegetotherium* (p. 74) and a fossa in *Pachyrukhos* (p. 89). Probably this pit or fossa is the vagina processus hyoidei and not the stylomastoid foramen.

In *Toxodon platensis* Van Kampen describes rather a shallow vagina in the young specimen, but a very deep one in the adult one. This vagina approaches the sulcus tubarius and seems to divide the bulla into two parts. This feature is, according to Van Kampen, already figured by Owen (1840) and by Roth.

Elephas also shows a groove for the tympanohyal in the posterior wall of the bulla.

The bulla in *Lemur* shows a little groove, probably containing the top of the indistinct tympanohyal; it lies beneath the stylomastoid foramen and in front of the foramen caroticum posterius. In *Chiromys* the very distinct small groove in the bulla lies a little in front of and beneath the stylomastoid foramen. In *Perodicticus potto* out of the little groove beneath the stylomastoid foramen projects a small flat bony bar which is probably not the tympanohyal, but a rudimentary stylohyal fused with the skull. If this is really the case, it would approach the character of the processus styloideus, which occurs in a few Cercopithecidæ, in the orang-utan and in man. In *Simia, Gorilla* and *Anthropopithecus* we find a vertical groove in the tympanic, bounded by the crista petrosa and the sharp under margin of the external auditory meatus. In *Homo* this vagina is more developed.

Processes of the Bulla

We have already seen that the crest on the under surface of the bulla may end in a process. Such a caudal process we have mentioned for the Otariidæ, *Hippopotamus*, Bovidæ and *Typotherium*. The processus tubarius and the processus styliformis will now be considered.

Processus Tubarius

The processus tubarius, to which the cartilaginous Eustachian tube and the musculus tensor veli are attached, is known in some modern Carnivora, Cetacea and Ungulata.

In *Felis* the processus tubarius is hooked and lies at the level of the fissura Glaseri. In the Viverridæ this process resembles that in *Felis;* in the Hyænidæ it is little or not at all developed, while in the Canidæ it is lacking.

In the Delphinidæ the processus tubarius is formed by the inwardly bent margin of the bulla in front of the processus sigmoideus. This process, which is present in the Odontoceti is, according to Hanke (1914, pp. 508, 509), absent in the Mystacoceti, which is due to the fact that the Eustachian tube in the Mystacoceti does not reach the bulla but opens in an air-sac, the sinus pterygoideus, which lies between the petrotympanic and the processus digitiformis of the pterygoid.

Also in the modern Cervidæ we find a processus tubarius, an inwardly projecting hook, lying within the fore end of the sulcus tympanicus. A similar hook in a similar place is found in *Tapirus*, which is also perhaps a processus tubarius.

Processus Styliformis

The processus styliformis is a process on the fore end of the auditory bulla and forms the prolongation of the bony Eustachian tube. This process is sometimes called the processus styloideus (see Zittel, 1893, p. 16; 1923, p. 409), but as this name is generally used for the coössified tympanohyal and stylohyal, it is better to speak of it as the processus styliformis.

This process is not always formed by the tympanic, as one would infer from some notices (Zittel, 1893, p. 16; 1923, p. 409), but is formed sometimes by the entotympanic and by the periotic.

In *Tupaia* it is formed by the entotympanic. In *Galeopithecus* the short processus styliformis is formed by the (ecto) tympanic.

In many modern rodents the bulla shows a process which we have mentioned many times in the chapter on the form of the bulla. This process is perhaps homologous with the processus styliformis but it lies more mesialward than does this process in the Ungulata. In these rodents it is more or less distinct, always short and massive and does not project freely, but lies against the basis cranii, thus resembling the forward prolongation of the bulla in some Carnivora. It lies in the neighborhood of the orificium tubæ, and may, together with the petrosal, form a short tuba ossea, while in *Castor* and in a few Hystricomorphæ this process is perforated by the ostium tympanicum tubæ.

Sometimes in the modern Canidæ an indistinct processus styliformis is present. In the Mustelidæ the anterior part of the far forwardly extended bulla, which probably is not hollow, resembles a processus styliformis; it is very large in *Mydaus meliceps*, shorter in other recent mustelids. In some recent Felidæ the processus styliformis or processus bullæ spinosus anterior is distinct, small and pointed.

The old *Rhinoceros* shows a pointed processus styliformis, formed by a prolongation of the true tympanic side wall of the bulla; it lies on the lateral side of the ostium tympanicum tubæ.

In *Equus* this process is long, pointed, and directed oralward; it is a prolongation of the lateral wall of the bulla; it lies immediately lateral to the orificium tubæ. Also *Mesohippus* (Scott, 1891*b*, p. 306) shows in front of the bulla a short, sharp styliform process.

I do not know what to think about Cope's remark (1881*c*, p. 390) on the bulla of *Eomoropus* (*Triplopus*) *amarorum*, which opposite the stylomastoid foramen is turned forward and produced into a well-marked process; it encloses a groove in front of it which is continuous with the pterygoid fossa. Perhaps it is a styliform process.

In *Archæotherium* (*Elotherium*) *mortoni* Leidy (1854, p. 61; see also Leidy, 1869, cited by Van Kampen) describes a strong conoidal process, projected from the bulla anteriorly downward and forward, bounding the passage of the Eustachian tube externally and the foramen caroticum internally.

In *Oreodon* Leidy (1854, p. 32) mentions the bony process of the Eustachian tube. In *Eporeodon leptacanthus pacificus* (Thorpe, 1921*b*, p. 99) the bulla shows a small forward prolongation not seen in any other species of this genus. This is perhaps a styliform process, as perhaps is also the large anteriorly projecting process in front at the junction of the bulla with the skull in *Agriochœrus guyotianus* (Wortman, 1895, p. 177).

In the modern Camelidæ the processus styliformis is a very small point on the lateral margin of the orificium tubæ.

In *Hyomoschus* the styliform process is rather strongly developed, while it is absent in *Tragulus*.

In the modern Cervidæ with the small bulla the processus styliformis is a forwardly and downwardly directed plate; in those with the strongly inflated bulla it is small, sometimes hardly indicated.

In the recent Giraffidæ we find instead of the styliform process a vertical plate along the upper anterior wall of the bulla, ending downward at the point of the bulla.

In the fossil *Protoceras* (Scott, 1895*a*, p. 312) the bulla is produced anteriorly into a long, slender spine.

In the modern Bovidæ we find no difference in the styliform process between the two types of bullæ. The styliform process is absent or very small in *Rupicapra*, *Nemorrhædus*, *Antilocapra*, *Anoa*. Often in the inflated bullæ it is more distinct, as in Bovinæ, Bubalinæ, Tragelaphinæ and others. In *Ovis* and *Capra* it is a vertical plate lying closely against the basis cranii.

In *Typotherium cristatum* Van Kampen describes a styliform process, forwardly and downwardly directed, broken off in his material, but, according to him, figured by Gervais (1867–69). As we have already seen, this bulla itself is pointed anteriorly, and thus it is impossible to decide whether in many other Typotheria this process or the styliform process is described, a difficulty which of course applies as well to other groups. An anteriorly prolonged, elongated or pointed bulla has been described by Sinclair (1909) in *Protypotherium* (p. 22), *Interatherium* (p. 51), *Hegetotherium* (p. 74) and *Pachyrukhos* (p. 89).

The processus styliformis in *Toxodon* has been described in *Toxodon*

platensis by Owen (1840, p. 22) as "styloid process" (see Van Kampen) and perhaps also in *Toxodon burmeisteri* by Burmeister (1867, p. 262). According to Van Kampen it is also figured by Roth (1898). Van Kampen describes the styliform process in *Toxodon platensis;* it is pointed and directed downward and forward. As to *Nesodon*, Van Kampen concluded from the figures given by Lydekker (1893) that the processus styliformis is absent.

In the Santa Cruz genera of the Toxodonta and especially in *Nesodon* Scott (1912, pp. 114, 134, 141, 142, 207, 292, 293) describes a most exceptional character unique among mammals: the hyoid apparatus being attached to the anterointernal instead of to the posterior end of the bulla, and in the adult skull the stylohyal being firmly ankylosed in that position. In the adult *Nesodon* (*loc. cit.*, p. 141) this element is style-like, long and prominent, and according to Scott seems to represent the coalesced tympano-and stylohyals. In one very young skull of *Nesodon* (*loc. cit.*, pp. 141, 142) there are two elements: a very small, extremely short, cylindrical "tympanohyal" firmly attached to the anterointernal corner of the bulla, and a separate "stylohyal," which is long, slender, laterally compressed and moderately curved, with convexity behind, the proximal end being simple, without expansion or process, but on the posterior side near the distal end showing a low, roughened ridge. The homologization of these elements which are attached to the anterior end of the bulla as belonging to the hyoid arch does not seem to me very probable. Much more probably they constitute the styliform process. I grant that Scott's "stylohyal" in the very young skull probably does not belong to the styliform process. Scott remarks (1912, p. 141) that the "tympanohyal" in the very young skull cannot possibly represent the "coalesced tympano- and stylohyal" in the adult animal, but I notice also his other remarks (1912, pp. 134, 141) on the broken condition of this element.

In *Adinotherium* Scott (1912, p. 207) did not find a similar attachment or ankylosis to the anterior end of the bulla as in *Nesodon.*

In *Lemur* (Van Kamp.; Gregory, 1920, p. 210) there occurs a styliform process; sometimes it is rather long but in *Lemur mongos* it is short and blunt. Also in fossil *Adapis* (Gregory, 1920, p. 210) shows a processus styliformis. In the modern Chiromyidæ it is differently developed. In the Hapalidæ the processus styliformis is short and blunt and more or less distinct; in the Cebidæ it is as a rule very indistinct, while in the Cercopithecidæ as a rule it is nothing more than a short, blunt, rounded knob.

In the Hylobatidæ and Anthropomorphæ the styliform process is very distinct. In *Hylobates lar* it is blunt and thick; it is best developed in *Anthropopithecus* and *Gorilla*.

In the Hapalidæ and Anthropomorphæ Van Kampen mentions that it is probably formed by the tympanic, while in the Prosimiæ it is formed by the petrosal.

The Bony Eustachian Tube

Sometimes we find the tympanic part of the Eustachian tube surrounded by bone and this forms a short bony tube on the foreside of the auditory bulla.

In marsupials the Eustachian tube is frequently lodged in a groove on the internal side of the tympanic portion of the alisphenoid (Gregory, 1910, p. 223) and according to Van Kampen the opening for the Eustachian tube in the Macropodidæ is for a short distance tube-like, but we can hardly call this a pars ossea tubæ.

In the recent Rodentia a short tuba ossea can be formed by the periotic with the bent margin of the bulla or the processus styliformis.

In the modern Canidæ a rather long tuba ossea is formed by the alisphenoid and by a groove in the bulla. In the recent Ursidæ the alisphenoid in the upper wall of the tuba is present only in the young skulls, as in the older skulls the bent margin of the bulla pushes beneath the tegmen tympani, the long tuba ossea then being entirely formed by the tympanic. In the Procyonidæ as well there is a short tuba ossea formed by the bulla. In *Lutra* and *Putorius* the rather long bony tube is formed by the tympanic only, as in *Ursus*, the alisphenoid being excluded. In *Pœcilogale* and *Mustela*, Pocock (1921, p. 485) describes a short auditory tube. In the modern Viverridæ the short tuba ossea is formed by the tympanic and the alisphenoid, as in the Hyænidæ, where it is rather long. In *Felis* the short bony tube is formed by the bulla and the alisphenoid, according to some authors also by the petrosal.

Equus shows a short tuba ossea, the lateral wall of which is formed by the processus styliformis. This bony tube is absent in *Rhinoceros* and *Tapirus*.

In *Sus scrofa* the cylindrical tuba ossea is formed for the larger part by the bulla, a little bony plate forming the roof and the under wall being formed by the sulcus tubarius in the wall of the bulla.

In *Hippopotamus* the upper rostral wall of the bulla forms the under wall of the tube and shows an anterointernally directed sulcus; a low crest on the bulla forms the lateral wall.

The tuba ossea in the Oreodontidæ (Leidy, cited by Van Kampen) resembles that in the Cervidæ.

In the modern Camelidæ the tuba ossea is incomplete. A shallow longitudinal groove in the fore wall of the bulla partly forms the wall of the tuba ossea, which is partly closed dorsally by the alisphenoid.

In *Tragulus* the bulla shows a poorly developed sulcus tubarius.

In the modern Cervidæ with the small bulla the tuba ossea is formed by the processus styliformis, which partly forms its ventral and lateral wall. In the Cervidæ with the strongly inflated bulla we also find a groove on the bulla, lying on the mesial side of the processus styliformis, together forming the tuba ossea. In both types the alisphenoid covers the tuba ossea dorsally.

In the Giraffidæ the auditory tube is laterally bounded by a bony plate located on the place of the processus styliformis.

In the modern Bovidæ the proximal part of the tuba is bounded by the wall of the bulla. In *Ovis* and *Capra* the plate-like processus styliformis greatly narrows the tuba ossea.

In *Elephas* the rather long tuba ossea is formed all around by the bulla and ends with the orificium tubæ a little before the rostral point of the bulla.

In *Lemur mongos* the processus styliformis lies in the wall of the short tuba ossea. In *Perodicticus potto* the bulla forms a short tuba ossea. In *Tarsius* as well this tuba is formed by the bulla, and on the lateral side by the raised margo fissuræ and the processus pterygoideus alisphenoidei fused therewith.

Also in the Hapalidæ a short tube-like prolongation is present.

The Cylindrical External Auditory Meatus

The bulla sometimes shows a cylindrical lengthening toward the lateral side, which covers a part of the membranous external meatus. Its most proximal part, the recessus meatus acustici externi, is also covered by bone but this bone forms a part of the bulla. This is due to the fact that the diameter of the place where the recessus passes into the cylindrical meatus is much smaller than the diameter of the tympanic membrane and that this transition lies opposite to the upper part of the tympanic membrane. So the bony recessus and the cylindrical meatus can easily be distinguished by their form. Sometimes they are externally separated by a groove, as in *Macroscelides*. As the bony recessus forms a part of the bulla, often the cylindrical meatus is called the whole meatus. This is important to know, as sometimes the meatus acusticus is said to

be absent when only the cylindrical part of it is absent, while the bony recessus is developed.

The cylindrical part of the bony meatus acusticus externus will engage our attention just now, the bony recessus being described in another place.

The external auditory meatus is bounded dorsally by the superficies meatus of the squamosal, rostrally by the postglenoid process, if present, and caudally by the processus posttympanicus s. postauditorius of the squamosal, which is sometimes developed.

False External Auditory Meatus

A so-called false external auditory meatus or meatus acusticus externus spurius is formed in the cases where the posttympanic process is connected with the postglenoid process or with the fossa glenoidea beneath the true external auditory meatus. Generally the addition "false" or "spurius" is omitted, but to avoid confusion it is better to add it.

Cope (1880*c*, p. 854) describes in *Smilodon* a coössification of the posttympanic process with the postglenoid, thus closing the auditory meatus below. According to Winge (1895*b*, pp. 55, 56), however, in *Machairodus* the mastoid process grows forward beneath the external auditory meatus and approaches the postglenoid process. Also Van Kampen judges the same from the figure of *Smilodon* given by de Blainville. Such a false auditory meatus, in which the mastoid process participates, differs from the general rule, as in general the posttympanic process and not the mastoid process forms the caudal portion of the meatus spurius.

The postglenoid and posttympanic processes, which already in the stem Perissodactyla were large (Gregory, 1910, pp. 390, 391) remain separate in the modern Tapiridæ and Equidæ (Van Kamp.; Scott, 1891*b*, p. 306, *Mesohippus*). Among the Rhinoceridæ (Van Kamp.; Osborn, 1893–1903, p. 91, etc.; Winge, 1906, pp. 159, 160, 161, 162; Troxell, 1921*b*, pp. 22, 29) the distance between the tops of these two processes below the external auditory meatus is very different and thus also the degree of connection of these two processes, characters which are used in systematics. The degree of development of the meatus spurius is contrasted with that of the cylindrical external auditory meatus. The union of the post-glenoid and posttympanic processes in the Titanotheriidæ (Osborn, 1896, p. 172, etc.) parallels that which we observe in the rhinoceroses. In the modern Suidæ (Van Kamp.; Winge, 1906, p. 138; Scott, 1912, p. 291) the posttympanic process fuses with the hind margin

of the fossa glenoidea and not with the postglenoid process, which can be present but then freely projects. In the Hippopotamidæ (Van Kamp.; Winge, 1906, p. 139) even in the adult a narrow fissure remains between the tops of the posttympanic and the postglenoid processes, which do not touch each other beneath the external auditory meatus. In the fossil *Ancodus* (Scott, 1895, cited by Van Kampen) the tops of the postglenoid and posttympanic processes are separated by a narrow fissure only, the meatus spurius being nearly complete. In *Anthracotherium* (Winge, 1906, pp. 128, 131) the postttympanic process envelops the external auditory meatus, but has not overgrown it. Van Kampen concluded from figures given by Wortman, Scott, and others, that in the Oreodontidæ the tops of the strongly developed postglenoid and posttympanic processes show a similar variation in distance as in the Perissodactyla. The distance can be very large as in *Protoreodon, Leptoreodon,* a little smaller in *Agriochœrus,* much smaller in the Oreodontinæ in general, in *Merycochœrus* they nearly touch each other, while in *Leptauchenia* and *Cyclopidius* there seems to be a complete meatus spurius. Notwithstanding the agreement with conditions found in the Rhinoceridæ, the Oreodontidæ differ from the Rhinoceridæ in the unreduced condition of the cylindrical external auditory meatus. Also Winge (1906, p. 128) mentions that the posttympanic process in the Oreodontini envelops the cylindrical external auditory meatus, which in *Merycochœrus* (Winge, 1906, p. 133) is entirely enclosed by the surrounding bones. In the Camelidæ, as in the Ruminantia in general, the meatus spurius is reduced, there is no complete meatus spurius, the external auditory meatus is but partly surrounded by the postglenoid and the posttympanic processes. In the modern Tragulidæ the postglenoid process is wanting and the small postglenoid process only surrounds the external auditory meatus.

In the fossil *Pantolambda* (Winge, 1906, pp. 73, 74) there is a large space between the posttympanic and the free postglenoid processes for the external auditory meatus.

Typotherium cristatum, according to Van Kampen, probably shows a complete meatus spurius, resembling especially that in *Hippopotamus.* In *Protypotherium,* according to Sinclair (1909, pp. 19, 20), the mastoid is closely fused with the squamosal, resulting in the inclusion of the external auditory meatus in a puffy mass of bone extending from the postglenoid process to the base of the paroccipital. Perhaps the firm coössification of the squamosal and the mastoid in *Interatherium* (Sinclair, 1909, p. 51) has the same result. Zittel (1923, p. 606) mentions as a character of the Typotheria in general that the inflated squamosomastoid region surrounds the external auditory meatus. Perhaps in

these cases a meatus spurius is meant. According to Scott (1912, p. 137), however, the posttympanic and postglenoid processes in the Typotheria of the Santa Cruz are more widely separated than in *Nesodon*, while the auditory meatus in *Toxodon* (Scott, 1912, p. 143) is much more extensively exposed between the postglenoid and posttympanic processes than in *Nesodon* (Van Kamp.; Scott, 1912, pp. 260, 292). Also Van Kampen mentions that even in the adult *Toxodon* these two processes of the squamosal do not form a false auditory meatus. In the Entelonychia Scott (1912, pp. 241, 260, 266, 291) describes a tube formed by the junction of the postglenoid and posttympanic processes, which no doubt forms a meatus spurius, which seems to resemble that in the pig and in my opinion perhaps the posttympanic process is also fused with the hind margin of the fossa glenoidea and not with the postglenoid process which freely projects.

In the fossil *Arsinoitherium* (Gregory, 1910, p. 366) the postglenoid and posttympanic processes tend to bridge over the auditory meatus and form a tubular meatus.

In the adult *Elephas* (Van Kamp.; Winge, 1906, p. 169) a closed meatus spurius is present, forming a horizontal and transversal tube in the prolongation of the true cylindrical auditory meatus. The posttympanic process and the hind margin of the fossa glenoidea fuse in very old specimens. Thus the meatus spurius is not formed by the postglenoid process, as is sometimes noted (Van Kamp.; Gregory, 1910, p. 366). In *Mœritherium* (Gregory, 1910, p. 367) occurs a partial closure of the external auditory canal in palatal view by a backward prolongation of the postglenoid, which in *Eotherium* is widely open. The meatus in side view appears as a circular opening. According to Winge, (1906, p. 170) the posttympanic process in *Mœritherium* is pressed forward against the postglenoid process.

Thus among the ungulates in many groups no meatus spurius occurs and of those in which it occurs, more primitive allied genera do not show a complete meatus spurius. No doubt in the "Protoungulata" the tops of the postglenoid and posttympanic processes were not connected beneath the external auditory meatus. The meatus spurius develops independently in different groups in consequence of the brachycephaly of the skull.

True Bony Cylindrical Auditory Meatus

The true bony cylindrical external auditory meatus is nearly always formed by the tympanic, but sometimes as in *Tupaia* by the entotympanic and as in lemurs by the periotic.

There are great differences in the length of the bony cylindrical external auditory meatus, which are without constant rules but are often used to distinguish smaller groups.

The course of the cylindrical meatus is different among the mammals. In general it depends on the position (inclination, etc.) of the superficies meatus of the squamosal, against which it lies. Originally the tympanic membrane and the squamosal lie in the same plane, that is, in the side wall of the skull. In the phylogeny of the mammals much is changed in this respect. First, the tympanic membrane has turned; secondly, the squamosal is bent. It is easy to understand that these two changes have their influence on the course of the bony cylindrical external auditory meatus.

There are also differences in the degree in which the cylindrical meatus is closed above. Often it has the shape of a gutter which is open above, where we find the superficies meatus of the squamosal. In other cases it is closed dorsally and then we can distinguish two conditions. In the first, it is closed over the whole length also in the neighborhood of the tympanic ring. In this case the dorsal wall can lie immediately against the superficies meatus of the squamosal or there can be a space between the two, forming the so-called foramen supratympanicum of Cope, as is the case in *Phascolomys* and in *Macropus* and in all the recent Pecora (Scott, 1895*a*, p. 314). According to Bondy (1907, note at the bottom of p. 304) Van Kampen is not correct in thinking that in these cases the dorsal wall of the bony cylindrical external auditory meatus separates the pars tensa of the tympanic membrane from the membrana Shrapnelli, as this membrane is also covered by the epithelium of the external auditory meatus. In the second condition the bony cylindrical meatus is also closed all around except in the most proximal part; we find this in *Equus*, in ruminants and in some rodents.

After this general consideration of the bony cylindrical external auditory meatus, we state that it is absent in monotremes, where we find only a primitive ring-like tympanic.

Although nearly all marsupials show a bony recessus, only the diprotodonts have the cylindrical lengthening (Van Kamp.; Winge, 1893*b*, p. 100). In *Phascolomys* it is rather long and closed all around. In the Phalangeridæ it is nearly horizontal or a little sloping and lies between the postglenoid and the posttympanic process, often fused with the former. In *Trichosurus* the proximal part of the lateral expansion of the tympanic ring is closed all around and the meatus lies immediately against the superficies meatus. In the Macropodidæ the cylindrical

meatus is nearly transverse. In nearly all species of the genus *Macropus* and also in a species of the genus *Petrogale* the bony meatus is closed all around and shows above it a foramen supratympanicum. In a few other species of the genus *Macropus* and in practically all other genera of the Macropodidæ the bony meatus is not closed all around.

In the Insectivora we find a cylindrical meatus only in the Menotyphla. Its absence is emphasized for the fossil *Hyopsodus paulus* by Osborn (1902*b*, p. 186). In *Rhynchocyon* (Van Kamp.; Carlsson, 1910*a*, pp. 353, 389) it is relatively long and lies between the postglenoid process and the mastoid or the posttympanic process; it runs first in a transverse direction while the most distal part runs obliquely backward. In *Petrodromus* (Van Kamp.; Carlsson, 1910*a*, p. 389) it is shorter but wider than in *Rhynchocyon* and in *Macroscelides* it is still wider (Van Kamp.; Gregory, 1910, pp. 281, 284). In *Tupaia* we find a very short cylindrical meatus, which in the allied *Ptilocercus* (Van Kamp.; Carlsson, 1910*a*, p. 352) is lacking; it lies between the postglenoid process and the posttympanic process. In *Tupaia* it is totally formed by the entotympanic (Van Kamp.; Carlsson, 1910*a*, p. 352; 1922, p. 230), while in the Macroscelididæ it is formed by the tympanic (Van Kamp.; Carlsson, 1910*a*, p. 352).

In the Chiroptera there is generally no distinct bony recessus meatus (Van Kamp.; Winge, 1893*a*, pp. 41, 43, 86; Zittel, 1893, p. 572), but Van Kampen found in *Cynonycteris* not only a bony recessus but also a short cylindrical meatus with the shape of a gutter; and therefore *Cynonycteris* is more highly developed or probably less reduced than *Pteropus*.

In *Galeopithecus* there is a well-developed bony cylindrical meatus formed by the tympanic (Van Kamp.; Winge, 1893*a*, p. 43; Gregory, 1910, p. 317); it is formed like a gutter and in the older skulls is more or less fused with the postglenoid and the posttympanic process; it lies nearly transverse and since the under wall is horizontal, as the superficies meatus of the squamosal rises the cavity becomes wider and wider toward the lateral side. In *Galeopithecus philippinensis* the meatus is compressed from front to back, while in *Galeopithecus volans* it is nearly circular.

Formerly a cylindrical auditory meatus was described for the Gravigrada but Van Kampen did not find it in his material nor I in my own, while Woodward (1900, p. 66) emphasizes its absence in *Grypotherium listai*. Van Kampen shows that the auditory meatus described by Owen (1856) and by Leidy (1855, p. 52) for *Megatherium* cannot be anything else than the wall of the tympanic cavity.

Also in the Glyptodontidæ the cylindrical auditory meatus is described, but this, as well as the auditory bulla, is unknown. Van Kampen shows that Huxley's external auditory meatus (1865, p. 55: Owen calls this in his catalogue the perforated depression for the digastric muscle) is the foramen mastoideum and that Burmeister's external auditory meatus is the foramen stylomastoideum with the distal portion of the sulcus facialis.

Among the recent Dasypodidæ a cylindrical auditory meatus is present only in *Dasypus* and in *Zaëdius* (Van Kamp.; Scott, 1903*a*, p. 71) and a very short one in *Chlamydophorus*, completed externally by the ossified cartilaginous auditory meatus, as we shall describe later on. In *Dasypus* (Van Kamp.; Winge, 1915, pp. 8, 17, 229, 238, *Euphractus sexcinctus*) and *Zaëdius* the upper wall is formed by the superficies meatus; the rostral, the under, and in old skulls the caudal walls are formed by the tympanic. This develops rather late in life, so in a nearly adult skull of *Dasypus sexcinctus* the under wall is not yet ossified, while the caudal wall is formed by the processus mastoideus. This youth-stage of *Dasypus* agrees with the condition found in *Prozaëdius* (Scott, 1903*a*, p. 71), where the external auditory meatus is not a tube but an irregular opening, the anterior lip of which is formed by the tympanic and the posterior by the mastoid, which is closely applied to the tympanic, and by the posttympanic process. Winge (1915, pp. 228, 229, 238) says only that in *Prozaëdius* the tube-like auditory meatus is lacking; he mentions the same for *Stenotatus*, while *Macreuphractus* shows a tube, as *Euphractus* does. As to the external auditory meatus in *Peltephilus*, Scott (1903*a*, pp. 90, 91) says: "the external meatus is not so long as in the recent *Dasypus* and is a tube, the tympanic portion of which is incomplete, the dorsal wall being formed by the zygomatic process and the anterior by the postglenoid process, which is concave behind and very closely applied to the tympanic. Owing to this intimate connection, to the very low origin of the zygomatic process upon the side of the cranium and to the unusually anterior position of the opening, the meatus has the remarkable peculiarity of seeming to perforate the zygomatic arch in a manner that does not occur in any other known armadillo." According to Winge (1915, p. 94) in *Chlamydotherium majus* a long external auditory meatus is lacking. The larger species of *Metacheiromys* has a bony meatus such as *Dasypus* shows, while in the allied *Palæanodon* the bulla is without any ossified meatus (Matthew and Granger, 1918, p. 625).

In the modern Rodentia (Van Kamp.; Zittel, 1893, p. 515) as a rule a cylindrical auditory meatus formed by the tympanic is present. In

many Muridæ, *Spalax* (Van Kamp.; Winge, 1888, p. 122) and other Rodentia it is entirely absent. In the majority of cases (Van Kamp.; Winge, 1888, p. 136, Sciuridæ; Matthew, 1910*b*, p. 70, Sciuridæ) it is short or even hardly distinguishable from the recessus meatus; the under wall is then horizontal or directed obliquely upward (Van Kamp.; Winge, 1888, p. 23, *Sigmodon vulpinus;* p. 59, *Nectomys squamipes;* p. 77, *Dactylomys amblyonyx;* p. 91, *Nelomys antricola*). Occasionally, however, the tube is longer and more distinct (Van Kamp.; Winge, 1888, p. 113, *Lepus;* p. 115, Haplodontidæ; Matthew, 1910*b*, p. 70, Castoridæ, Geomyidæ, Heteromyidæ) and then it is often directed vertically upward, but a little lateralward and backward; sometimes the distal portion is bent. The various genera show differences in the length and the direction of the external auditory tube. In *Mesomys spinosus*, according to Winge (1888, p. 95), the projecting upper margin of the porus acusticus externus inclines downward, so that these pori look downward. This vertical upward direction of the cylindrical auditory meatus is due to the more vertical position of the superficies meatus. This superficies meatus in the rodents is formed by the mastoid and has a more vertical position than is found as a rule in a superficies formed by the squamosal. Instead of the squamosal, whose hind part is nearly always much reduced, the mastoid forms a rostral prolongation (except perhaps in *Castor* and in the Bathyergidæ) which forms the superficies meatus. In *Castor* (Van Kamp.; Winge, 1888, p. 136) and in the Geomyidæ the squamosal still forms a part of the superficies meatus, but this is more in consequence of the great length of the external auditory meatus. As a rule it is not possible to determine whether the cylindrical auditory meatus is closed all around by the tympanic itself, as the tympanic is fused with the periotic. In many cases no doubt the tympanic is closed all around. According to Bondy (1907, p. 322) in *Lepus* the external auditory meatus is directly connected with the two horns of the tympanic ring; this wall of the external auditory meatus shows a cleft which narrows laterally, corresponding to the defect in the tympanic ring.

In many cases a wide external auditory meatus is accompanied by a large auditory bulla and by a large so-called mastoid bulla. In *Dipus* the rostral wall of the external auditory meatus shows a shallow excavation. The entire external auditory meatus in this genus is very wide and bladder-shaped, forming a kind of bulla next to the proper auditory bulla. In *Sciurus bicolor* and in this species alone a similar excavation is found backward and upward. The vertical crest which runs along the under wall of the cylindrical external auditory meatus in *Castor*, even as similar

crests in other mammals, is already mentioned in the section on the crests on the surface of the auditory bullæ.

As to the fossil Rodentia I mention the following points. *Sciuravus* (Matthew, 1910*b*, p. 60) has no tubular meatus. In *Steiromys* (Scott, 1905, p. 414) the short irregular tube is much as in *Erethizon*, also in *Sciomys* (*loc. cit.*, p. 421) the tube is very short, and less prominent and less complete dorsally than in *Erethizon*. In *Neoreomys* as well (Scott, 1905, p. 392) the auditory meatus is a short, incomplete tube. *Eocardia* (Scott, 1905, p. 463) shows a quite short and incomplete tubular meatus similar to that in *Dolichotus*. In *Perimys* (Scott, 1905, p. 435) is found a short tube which, compared with that of *Viscaccia*, is directed more upward and outward, less backward.

A tubular external auditory meatus is seldom found in Creodonta (Scott, 1913, p. 559). It is present in *Mesonyx* (Scott, 1913, p. 559) and *Dromocyon* (Wortman, 1901, p. 294; Gregory, 1910, p. 303; Scott, 1913, p. 559), where it is quite long and tubular. In *Synoplotherium* Cope (1873*a*, p. 555; 1873*b*, p. 205) mentions that the tympanic bone is produced upward and outward and forms a tube with everted lips.

The meatus acusticus externus osseus in the Arctoidea as a rule, according to Pohle (1917, p. 407), is large; some of the oldest, however, form an exception.

In the modern Canidæ the cylindrical auditory meatus is very short. Also Reynolds (1909, p. 11) mentions a short but fairly prominent bony tube. Scott (1913, pp. 520, 551, 552), on the other hand, mentions as a character of the Canidæ in general: without tubular prolongation; external opening of the bulla is an irregular hole. Also the fossil *Enhydrocyon crassidens* (Matthew, 1907, p. 191) shows no ossified tube. In *Amphicyon* (Filhol, 1883, pp. 84, 85), however, the under wall of the external auditory meatus is moderately developed. *Pliocyon medius* (Matthew, 1918, p. 194) shows a considerable bony meatus external to the bulla.

In the modern Ursidæ the cylindrical external auditory meatus is very long (Van Kamp.; Scott, 1913, p. 548). Especially the inferior lip of the auditory meatus is considerably prolonged (Reynolds, 1906, p. 10; see also, Filhol, 1883, p. 85); it has the shape of a gutter and the superior wall is formed by the squamosal. The cylindrical auditory meatus very gradually passes into the bulla. It first runs horizontally and transversely, then as a rule a little upward and backward. In the fossil specimens of *Ursus americanus* (Brown, 1908, p. 184) the external auditory meatus is larger than in recent specimens of this species. In

Ursus brasiliensis and *bonariensis* (Winge, 1895*b*, pp. 33, 119) it is relatively long.

In the modern Procyonidæ (Winge, 1895*b*, pp. 63, 64; Pohle, 1917, p. 408) the bony cylindrical auditory meatus is long. The superior wall is formed by the squamosal. It is not at all or but little forwardly directed, notwithstanding the agreement in form and position of the mastoid process with that of the Mustelidæ. In the fossil *Pseudobassaris riggsi*, however (Riggs, 1898, pp. 258, 259, *Amphictis;* Pohle, 1917, pp. 407, 408), the external auditory meatus is very short and the inferior lip is wanting, the mastoid process forming part of the posterior wall of the auditory meatus as in certain mustelines.

In the modern Mustelidæ (Van Kamp.; Zittel, 1893, p. 646) the bony cylindrical external auditory meatus is nearly always rather long. There are, however, great differences in its length and width (see Van Kampen). Even species of the same genus may show important differences in length (Winge, 1895*b*, pp. 39, 40, 121, 122, *Galictis*). The cylindrical auditory meatus is longer than it seems to be; as its under wall is strongly thickened it seems to form a part of the bulla. It always runs horizontally and rather forward, probably in consequence of the obliquely downward and forward direction of the mastoid process. Probably the superior wall is not closed by the tympanic and according to Scott (1913, p. 550) the lower lip of the entrance is extended. Also in the fossil *Plesictis robustus*, according to Teilhard de Chardin (1914–1915, p. 59), the lower lip seems to be prolonged. *Bunælurus* (Scott, 1913, p. 551) shows no tubular entrance. This is present in *Mustela palæattica* (Weithofer, 1888, p. 227). The auditory meatus in *Megalictis ferox* (Matthew, 1907, pp. 196, 198) is long, tubular and partly flattened. In *Oligobunis darbyi* (Thorpe, 1921*a*, p. 481) it is quite large and directed forward.

In the modern Viverrinæ a cylindrical bony external auditory meatus is absent or very short (see also: Zittel, 1893, p. 655; Winge, 1895*b*, pp. 56, 58, 127; Riggs, 1898, pp. 258, 259; Carlsson, 1911, p. 425; 1920, p. 341, *Arctictis*). The same is found in *Eupleres*. Also *Cryptoprocta* shows a very short external auditory meatus (Van Kamp.; Winge, 1895*b*, pp. 56, 58, 127; Carlsson, 1910*b*, p. 567; 1911, p. 425). According to Carlsson (1920, p. 341) *Arctictis binturong* shows as in the Felidæ a lip-like broadening of the anterior wall of the external auditory meatus.

The Herpestinæ on the other hand show a more or less distinct bony external auditory tube (Van Kamp.; Winge, 1895*b*, pp. 56, 58, 59, 127; Carlsson, 1910*b*, p. 566). A very long bony tube is mentioned for *Suricata tetradactyla*, *Galidictis* (Winge, 1895*b*, p. 58; Carlsson, 1910*b*, p. 597),

Galidia (Winge, 1895*b*, p. 58; Carlsson, 1910*b*, pp. 566, 597) and *Hemigalidia* (Carlsson, 1910*b*, p. 597). In consequence of the presence of this external auditory tube the porus acusticus externus in the Herpestinæ is smaller than that in the other Viverridæ, in which this tube is absent. This external auditory tube is probably closed all around by the tympanic.

In *Hyæna* and *Proteles* (Van Kamp.; Winge, 1895*b*, pp. 59, 127) the cylindrical external auditory meatus is rather long. It is not entirely closed all around. The rostral wall is most prolonged and lip-like in contrast to that in the Herpestinæ.

In the modern Felidæ there is no cylindrical bony external auditory meatus (Van Kamp.; Zittel, 1893, pp. 663, 664; 1911, p. 397; 1923, p. 478) unless this name is applied to the lip, which in front of the porus acusticus externus laterally projects along the squamosal (Van Kamp.; Carlsson, 1920, p. 341). Thus the external auditory meatus can be called very short or imperfect (Cope, 1880*c*, p. 834). The superior wall of the porus acusticus externus is closed by the superficies meatus and the post-tympanic process. According to Zittel (1893, p. 664) the pleistocene Felidæ do not show a produced bony meatus. The same occurs in the Nimravidæ (Scott, 1889, p. 238) in which it is not imperfectly ossified below. Riggs (1896*b*, p. 238) mentions an external audtiory meatus in *Dinictis*, but according to Scott (1889, p. 214) there is no tubular meatus auditorius other than that formed by the notch between the mastoid and postglenoid processes, though the opening into the bulla is quite far removed from the surface.

In the modern Phocidæ the cylindrical external auditory meatus is rather long. Also here rather important differences occur even between species of the same genus (Van Kamp.; Winge, 1895*b*, p. 75, *Phoca*). The bony auditory tube is longer than it seems to be, as it is partly received in the bulla, which shows a large horizontal extension. In *Macrorhinus leoninus*, on the other hand, the bony tube is long and the bulla is small. As a rule the under wall runs transversely and a little upward. The caudal wall is longer than the under and rostral wall, so that the porus acusticus externus looks more or less forward. This is strongly the case in *Phoca grœnlandica*, in which the top of the caudal wall is bent forward or the cylindrical bony meatus is knee-shaped according to Winge (1895*b*, p. 75, *Pagophilus*) so that the porus acusticus externus is invisible in the lateral view. In *Ommatophoca*, according to a remark in the literature, contradicted by another, the rostral and caudal walls only are prolonged and not the floor. As a rule the tympanic forms the under and cauda

wall and partly the rostral wall. On the superior side where the squamosal lies it is open, and not closed by the tympanic, as has formerly been described (Van Kamp.; Bondy, 1907, p. 368).

Eumetopias at least among the Otariidæ shows no cylindrical external auditory meatus, which is also absent in the modern Trichechidæ.

In the modern Delphinidæ the cylindrical auditory meatus, if present, is nothing more than a short extension formed by the thickening of the walls of the recessus meatus. In *Platanista* the posttympanic process of the squamosal forms one-half of the upper boundary in young skulls and in adults the whole of the posterior wall of the external auditory meatus. In the modern Physeteridæ a part of a short cylindrical external auditory meatus is perhaps formed by an outgrowth of the caudal margin of the porus acusticus externus, i.e. the processus posterior (the mastoid of Flower and other authors).

In the Mystacoceti, according to Hanke (1914, p. 506) the processus sigmoideus and the processus medius are bent lateralward; the sigmoid process forms a rudimentary oral, the processus medius a rudimentary inferior wall of the bony external auditory meatus. Hanke does not mention whether they form more than a bony recessus meatus.

In the higher ungulates in contrast with the most primitive ones, according to Winge (1906, p. 66) the external auditory meatus of the tympanic is long. In the "Protoungulata" according to Van Kampen the tympanic probably formed the floor of the cylindrical auditory meatus only, which was superiorly closed by the squamosal.

In the fossil Litopterna (Scott, 1910, pp. 3, 106, 115, *Theosodon*) the auditory meatus is large, irregular and a mere hole; it is not at all prolonged into a tube.

In *Tapirus americanus* the short lip in the wall of the external auditory meatus forms a short horizontal gutter outside the recessus meatus. This gutter is open on the superior side only.

In *Rhinoceros sumatrensis* the tympanic forms in the lateral direction a long, rough and thick lip, which in the main lies in the under wall, partly also in the caudal wall of the external auditory meatus. The proximal part covers a small recessus meatus, the rest forms the cylindrical part. In other species of this genus this lip is also present, but less developed; it is least developed in *Rhinoceros sondaicus*. There is apparently a relation between the development of the true cylindrical external auditory meatus and that of the meatus spurius, which are contrasted in their degree of development. In *Triplopus cubitalis* according to Cope (1881c, p. 384) the large meatus auditorius externus is enclosed

anteriorly and below by the border of a wide element which may be the tympanic.

The cylindrical bony external auditory meatus in *Equus* (Van Kamp.; Stromer von Reichenbach, 1912, p. 202) is rather a long tube, running nearly transversely and a little upward, the under wall of the proximal part showing a somewhat greater inclination in relation to the vagina processus hyoidei. It is complete, closed all around, except dorsally, where we find an incisura tympanica, which corresponds with the defect in the crista tympanica and which is closed by the membrana Shrapnelli (Van Kamp.; Bondy, 1907, p. 369). *Mesohippus* also (Scott, 1891*b*, p. 306) shows an elongated tubular meatus.

In the Chalicotheriidæ (Stromer von Reichenbach, 1912, p. 202) a bony external auditory meatus is developed. In *Eomoropus* (*Triplopus*) *amarorum* according to Cope (1881*c*, p. 390) the inferior side of the tympanic bone is flat near the meatus, and according to Osborn (1913, p. 268) the wide external auditory meatus is closed by an osseous tympanic ring. These remarks perhaps bear upon a cylindrical auditory meatus, which seems to be figured by Osborn (1913, Fig. 1, n°. A^3).

The Artiodactyla, according to Stromer von Reichenbach (1912, p. 196), nearly always show an external auditory meatus.

In the modern Suidæ the cylindrical bony external auditory meatus is very long (Van Kamp.; Bondy, 1907, p. 371). It runs obliquely upward with a large inclination, so that the porus acusticus externus looks upward. In *Dicotyles* the tympanic forms the under and caudal wall only. In *Sus*, in which because of the indistinctness of the sutures between the squamosal and the tympanic this is very difficult to determine, the squamosal covers the dorsally open auditory tube (Van Kamp.; Bondy, 1907, p. 371). This dorsal wall shows just near the tympanic membrane a considerable incisura tympanica.

In the Elotheriidæ, according to Leidy (1854, p. 61), the auditory bullæ are externally prolonged into a broad and strong auditory process. The external auditory meatus is circular, relatively considerably larger than in the hog, and remarkable for the large infundibular expansion which leads to its entrance.

In the modern Hippopotamidæ the cylindrical bony external auditory meatus is very long and narrow and ends with an extremely small porus acusticus externus. It is closed all around by the tympanic. In the young specimen it is strongly directed upward. The same seems to be the case in the adult specimen, but here it is due to the form of the crest which runs along its under wall.

In the fossil *Ancodus* (*Hyopotamus*), according to Scott (1895, cited by Van Kampen), the auditory meatus is a quite elongate and incomplete tube, lacking the dorsal wall.

In *Anoplotherium*, according to Turner (1849, cited by Van Kampen), the under wall of the auditory meatus shows a similar inflation to that in the Camelidæ. According to Winge (1906, p. 94) the external auditory meatus in *Anoplotherium* is very long. Palmer (1913*b*, pp. 879, 884) describes it as an irregular mass of the tympanic which forms the floor of the external auditory meatus, the squamosal lying in its superior wall. According to Palmer (1913*b*, p. 879) there is no ordinary bony tube in *Anoplotherium*.

In *Cænotherium*, according to Van Kampen, the external auditory meatus shows a great resemblance to that in *Tragulus*.

In the Oreodontidæ in general, according to Zittel (1893, p. 349), the external auditory meatus is tubular and opens upward. In *Protoreodon* (Scott, 1899, p. 90) almost certainly the bulla was provided with a tubular meatus, much as in *Oreodon culbertsoni*. In *Oreodon*, according to Leidy (1854, p. 32), the auditory process constitutes the anteroinferior boundary of the meatus. In *Merychyus* Leidy (Syn. *Ticholeptus* Cope), according to Scott (1890, p. 348), the external auditory meatus is short, tubular, and opens a little backward. In *Merychyus zygomaticus* (Cope, cited by Scott, 1895*b*, p. 147) the external auditory meatus is directed posteriorly in a way quite peculiar, resembling somewhat the position seen in some of the hogs. In *Ticholeptus brachymelis* (Douglass, 1907, p. 816) it is a long straight tube directed upward more than outward or backward. In *Ticholeptus rusticus* (Loomis, 1920, p. 283) the auditory meatus is inclosed in a bony tube of moderate length and opens obliquely upward, but not nearly so high up as in either *Merycochœrus* or *Promerycochœrus*. In *Merycochœrus*, according to Scott (1890, p. 341), the long tubular auditory meatus runs upward, lateralward and backward and shows a position similar to that in *Hippopotamus*. In *Leptauchenia* (Scott, 1890, pp. 353, 375; Zittel, 1893, p. 355) the bony external auditory meatus forms a long tube running upward, lateralward, and backward, and ending with the porus acusticus externus high up, much higher than in *Oreodon*. According to Scott (1913, pp. 381, 382), the raised ear-openings in the *Leptauchenia* phylum are presumably in adaptation to an amphibious mode of life. Also in *Cyclopidius* (Scott, 1890, p. 356) the external bony auditory meatus is very long; it projects far from the wall of the skull and its external opening has a higher position than in the other genera. Cope (cited by Scott, 1890, pp. 357, 376) supposes an

aquatic habit of life such as that of the hippopotamus. Van Kampen concluded from the figures given by Scott, that the cylindrical auditory meatus was always closed all around, forming a point of agreement with *Hippopotamus* and with most ruminants with a large bulla. As to the crest on the under wall of the cylindrical external auditory meatus in *Oreodon bullatus*, I refer to the chapter on the crests on the surface of the bulla.

In the modern Camelidæ the external auditory meatus is inflated over its whole length. This inflation is separated from the proper auditory bulla by the vagina processus hyoidei. It is formed by the lateral extension of the hypotympanic sinus along the under wall of the cylindrical external auditory meatus. Thus there is no tubular prolongation of the bulla, as the cylindrical external auditory meatus is enclosed in this so-called lateral part of the bulla. In consequence of this the outer surface directly leads into the porus acusticus externus, which forms a mere opening in this so-called lateral part of the bulla. The auditory meatus is closed all around and rather long. The length-axis of its lumen first runs a little upward, while in the distal part it is nearly horizontal. There is no incisura tympanica. According to Winge (1906, p. 11) the porus acusticus externus in *Auchenia major* projects hardly at all as a tube, a condition which is found distinctly in the very young *Auchenia lama*. In *Poëbrotherium* occurs a similar condition. According to Scott (1899, p. 27) the auditory meatus in *Poëbrotherium* is not a tube, but a mere opening, with a raised lip, into the bulla. It is, according to Scott (1891*a*, p. 15), a closed ring, opening slightly upward and backward. Also in *Poëbrotherium andersoni* (Troxell, 1917, p. 382) the external auditory meatus is directed upward and backward as it leads from the bulla. According to Leidy (1854, p. 21) the auditory process in *Poëbrotherium wilsonii* resembles that of the musks, and the meatus auditorius externus, which holds the same relative position as in these, is subcircular. In *Stenomylus* (Loomis, 1910, p. 302) the external auditory meatus is a closed, slightly projecting ring. In *Protylopus* (Scott, 1899, p. 28) the meatus is relatively large and does not form a complete ring, only the anterior half of the lip being made by the tympanic, while the posterior half is made by the posttympanic process of the squamosal.

In *Tragulus* the cylindrical bony external auditory meatus is closed all around by the tympanic. It is not long; it runs backward and upward. In *Hyomoschus* on the superior side it is open.

In the fossil *Leptomeryx evansi* (Scott, 1891*b*, p. 347; 1899, p. 16) the auditory meatus is a long tube, with relatively very large diameter,

which extends more decidedly backward and less upward than in the tragulines. In *Blastomeryx* (Matthew, 1908, pp. 536–538) the auditory meatus is rather long, cylindrical and but slightly flattened on its inferior surface.

In the modern Cervidæ the cylindrical bony external auditory meatus is moderately long. Bondy (1907, pp. 375, 376) calls it considerable in *Cervus capreolus*. According to Matthew (1908, p. 538) the various modern deer show different degrees of reduction and flattening of the meatus. Nearly always it is gutter-shaped and open above (see also, Scott, 1895*a*, p. 313, *Moschus*). It is covered dorsally by the squamosal. In the few species with the very large bulla only it is nearly or entirely closed, this being another difference between the two types of the bullæ. It runs nearly transversely and a little backward only; in *Moschus*, however, a little upward and backward. The crest along its under wall is already mentioned in another chapter. In the fossil *Dromomeryx* (Scott, 1895*b*, p. 172, *Blastomeryx*) the auditory meatus is a long tube which is directed more posteriorly than in *Antilocapra*.

In the modern Giraffidæ the cylindrical bony external auditory meatus resembles that in the majority of the recent Cervidæ: it runs nearly transversely, is widely open above and behind, and shows a longitudinal crest along its under wall.

In the fossil *Protoceras* (Osborn and Wortman, 1892, pp. 357, 358; Scott, 1895*a*, pp. 312, 314) the auditory meatus is long and narrow; the tympanic does not form a complete tube, the upper part being covered by the squamosal, with which it is in contact in front, behind, and to some extent, above. In the fossil *Camelomeryx* (Scott, 1899, p. 70) the auditory meatus, if present, must have been of small size, much smaller than in *Protylopus*, which is indicated by the contracted space between the postglenoid and posttympanic processes of the squamosal.

In the fossil *Aletomeryx gracilis*, according to Lull (1920, p. 96), the external auditory meatus is a long tube, which is directed more posteriorly than in *Antilocapra*, forming an angle with the axis of the skull of about 60° in *Aletomeryx* to 70° in *Antilocapra*. The meatus in *Hypisodus* (Matthew, 1902*c*, p. 312) is long, prominent and enclosed. In *Hypisodus alacer*, according to Troxell (1920*a*, p. 393), the very large external auditory meatus is situated well forward and opens at an angle of 45° toward the rear.

In the modern Bovidæ the cylindrical bony external auditory meatus shows the common type of the Ruminantia. It is only longer than we find it in the Ruminantia as a rule. The distal portion runs nearly transversely

sometimes a little upward and backward. The under wall of the proximal portion as a rule descends in the mesial direction leading to the recessus meatus. Also here a crest along its under wall is present. It is mostly closed all around. In *Ovis*, *Capra*, *Antilope* and others the distal portion only is closed all around, the proximal one showing dorsally a triangular foramen. In many large antilope species, *Ovibos* and others, it is gutter-shaped. In the fossil *Myotragus balearicus* (Andrews, 1915, p. 286) the auditory meatus is narrow and as its walls are thick, the auditory opening is small.

In the common ancestors of the toxodonts, typotheres, interatheres and hegetotheres, according to Gregory (1910, p. 378), the tympanic very early became prolonged into a tubular meatus.

In the Typotheria in general (Scott, 1912, p. 137; Zittel, 1923, p. 606) the external auditory meatus is tubular, wide and upwardly directed. In the Santa Cruz Typotheria, according to Scott (1912, p. 292), the auditory meatus is tubular, long, its opening has a relatively low position and is directed backward rather than outward. In *Interatherium* (Sinclair, 1909, p. 51) the auditory meatus is long, tubular and directed almost horizontally. In *Hegetotherium* (Sinclair, 1909, pp. 71, 74) the auditory meatus is spout-like, long and tubular, posteriorly directed, with its orifice opening posteriorly. In *Pachyrukhos* (Sinclair, 1909, p. 89) the meatus is long, tubular and directed posteriorly, opening on a level with the postglenoid fossa. In *Pachyrucus typicus* (Lydekker, 1893, cited by Van Kampen) the external auditory meatus is somewhat tubular, with a backward and upward direction. In *Protypotherium* (Gregory, 1910, p. 363) the auditory meatus is tubular and upwardly directed. In *Typotherium cristatum*, according to Van Kampen, the cylindrical external auditory meatus is wide and runs nearly horizontally lateralward and backward. The under wall bears two high ridges, which are partly fused. One seems to be the posttympanic process, the other is either the top of a very high postglenoid process or a crest of the auditory meatus itself, as is found in many ungulates. In *Archæohyrax* (Winge, 1906, p. 87) the external auditory meatus is shifted far backward.

In the Toxodonta, according to Scott (1912, p. 113), the external auditory meatus has a more elevated position than in the other suborders of the Notoungulata. Also according to Zittel (1923, p. 610) the external auditory meatus in the Toxodonta opens obliquely upward. In *Rhynchippus* (Winge, 1906, p. 89) the external auditory meatus is shifted backward. In *Nesodon patagonicus*, according to Lydekker (1893, cited by Van Kampen), the external auditory meatus has an almost

horizontal direction. According to Scott (1912, pp. 133, 136, 137) the external auditory meatus in *Nesodon* is tubular and very long; a highly characteristic feature is the great prominence of the auditory meatus at the supero-external angles of the occiput. Its outer end in *Nesodon* (Scott, 1912, pp. 137, 291) passes upward, outward and backward to a very elevated termination, which has nearly the same relative position as in *Sus*. Thus this is in contrast with the above cited remark of Lydekker. Scott (1912, p. 136) mentions in *Nesodon* a communication of the epitympanic sinus with the tympanic cavity through the inner end of the auditory meatus.

In *Toxodon platensis*, according to Owen (1840, pp. 22, 23), the foramen aud. externum is only half an inch in diameter and gives passage to a long and somewhat tortuous meatus, which passes inward and slightly forward and downward, its direction being precisely the same as in *Hippopotamus*. Van Kampen has confirmed this in the same species. According to this author the agreement with *Hippopotamus* is in the main due to the presence of a high crest along the under wall of the auditory meatus. In consequence of this crest the cylindrical external auditory meatus seems to run up with a much greater inclination than is really the case. Also according to Lydekker (1893, cited by Van Kampen) the auditory meatus in *Toxodon* opens nearly vertically. According to Scott (1912, p. 143) the aperture of the tubular auditory meatus in *Toxodon* has the same elevated position as in *Nesodon*, which is in contrast to the description of Lydekker, as we have seen. In *Toxodon platensis*, according to Van Kampen, the porus acusticus externus in the adult skull is relatively smaller than in the young specimen. In the adult skull the rostral wall of the cylindrical bony external auditory meatus is a little thickened. In consequence of the fusion it could not be decided whether the tympanic closes it all around or whether the squamosal forms the superior and caudal part.

According to Scott (1912, p. 292) in the Toxodonta in general there is no visible tube leading to the external ear-opening, the passage being entirely concealed by the structures which probably constitute the meatus spurius. The opening has a very elevated position at the postero-external angle of the zygomatic arch, much as in the pig.

As to the Entelonychia (Scott, 1912, p. 241), the external auditory meatus is tubular in the Notostylopidæ and a mere hole in the Homalodontotheriidæ. The small size, inferior position and non-projecting form of the external auditory meatus are highly characteristic features and clearly differentiate it from that of the Toxodonta and Typotheria

(Scott, 1912, pp. 260, 261, 266, 293). Thus no trace of the external auditory meatus is visible in the superior view of the skull, while in the Santa Cruz Typotheria and Toxodonta the projecting tubular meatus forms the postero-external angles of the skull (Scott, 1912, p. 261). This lack of prominence is better displayed in the inferior view of the skull even than in the superior view (Scott, 1912, p. 262).

Though the external auditory meatus in the Entelonychia is far removed from the bulla, yet there is no visible connection between them, and according to Scott (1912, p. 266) it is uncertain whether there is any tube other than the meatus spurius. Its external porus is an irregularly circular opening without any projecting edge or lip (Scott, 1912, pp. 266, 293).

The modern Hyracoidea (Van Kamp.; Winge, 1906, p. 166; Gregory, 1910, p. 363; Stromer von Reichenbach, 1912, p. 215) show a bony cylindrical external auditory meatus which is upwardly directed. It is short and wide; in the young specimen it is relatively much narrower than it is later. The tympanic forms the under and caudal-wall, later on also the upper-rostral wall, which, however, during a long period is closed by the squamosal only. A lip-like prolongation projects the point lateralward from where the under wall passes into the caudal wall.

In *Elephas* the cylindrical external auditory meatus is not long; it runs transversely. It is open above. In an immature *Elephas africanus* it is for the greater part thin and leaf-like, the proximal part of the under wall only being thicker.

In *Lemur mongos* (Van Kamp.; Winge, 1895*a*, p. 39, *Lemur collaris*) there is probably a short cylindrical bony external auditory meatus formed by the petrosal part of the bulla. In *Propithecus diadema* it is hardly indicated. In the fossil Notharctidæ and Adapidæ (Gregory, 1920, p. 188) a bony external auditory meatus is absent. Standing (1908, p. 160) mentions as a "Lemuroid" character: no auditory meatus. Lorenz von Liburnau (1905, pp. 463, 464), however, describes in *Megaladapis edwardsi* a ca. 15 mm. deep, infundibuliform, external auditory meatus with strong walls. The porus acusticus externus is ca. 8 mm. in diameter; toward the mesial side it narrows considerably, being compressed in the dorsoventral direction and opens cleft-like into the bulla. According to Van Kampen (1905, not in edition 1904) it is formed either by the tympanic or the petrous bulla or by little accessory bones outside the true cylindrical external auditory meatus. In *Palæopropithecus* as well, according to Standing (1908, pp. 80, 82), a tubular external auditory meatus of considerable length (1 cm.) is present; its actual margin is

formed by the petrous portion of the squamosal and by the tympanic (or perhaps by the petrous bulla, in my opinion).

In the modern Chiromyidæ there is no bony cylindrical external auditory meatus.

In the Lorisiformes, according to Gregory (1915, p. 436), the tympanic is sometimes continued externally into a tubular meatus. In the Lorisidæ, according to this author (Gregory, 1915, p. 427), the tympanic does not form a protruding tubular auditory meatus, but merely a circular opening into the bulla. According to Van Kampen, *Nycticebus* and *Loris* show a distinct cylindrical external auditory meatus, which is probably closed above by the squamosal only. *Galago crassicaudatus* quite certainly does not possess a cylindrical external auditory meatus. In Van Kampen's specimen of *Perodicticus potto* it was also absent, but perhaps develops later on in life.

In the Tarsiiformes (Gregory, 1915, p. 437; Zittel, 1923, p. 644) the tympanic is continued externally into a tubular meatus. This is, according to Gregory (1915, p. 426), the case in *Tarsius* and its extinct relatives *Anaptomorphus*, *Hemiacodon* and their allies, and also in the fossil genera *Microchœrus* and *Necrolemur* (Van Kamp.; Gregory, 1916, pp. 264, 265). In *Tarsius* (Van Kamp.; Winge, 1895*a*, p. 15) the cylindrical bony external auditory meatus is short, rather shorter than longer in comparison with that in *Nycticebus* and *Loris*. Probably it is closed all around.

In the Platyrrhinæ there is no cylindrical bony external auditory meatus, or it is very short (Van Kamp.; Winge, 1895*a*, pp. 12, 21, 53; Osborn, 1902*b*, p. 186; Stromer von Reichenbach, 1912, p. 191; Scott, 1913, p. 583).

In the Catarrhinæ, however, it is well developed (Van Kamp.; Winge, 1895*a*, pp. 12, 53; Standing, 1908, p. 160; Stromer von Reichenbach, 1912, p. 191). Possibly the as yet undiscovered ancestral Catarrhinæ, according to Gregory (1916, pp. 265, 266), showed an elongated tubular meatus resembling that in *Necrolemur*.

In the modern Cercopithecidæ the cylindrical bony external auditory meatus is rather long. The under wall is directed a little backward and mostly also upward. In *Papio* it is longest and also most strongly backwardly directed. It is rather certainly gutter-shaped and open above (Van Kamp.; Bondy, 1907, p. 384, *Macacus nemestrinus*).

The cylindrical bony external auditory meatus in the Hylobatidæ and Anthropomorphæ shows but little differences from that in the Cercopithecidæ. In *Gorilla* it is a nearly closed tube or even entirely closed. In the others it is gutter-shaped, as in the lower monkeys and in *Homo*.

In *Hylobates* it is slightly directed forward; in the Anthropomorphæ it runs in the backward direction.

Accessory Small Bones

External to the bony meatus acusticus externus we find the meatus acusticus externus cartilagineus, which in a few cases partly ossifies and forms accessory small bones. This may be inconstant or constant. The latter is the case in the Macroscelidæ, Dasypodidæ and in Rodentia.

Among the Dasypodidæ an ossified cartilaginous external auditory meatus is best known for *Chlamydophorus*. In *Chlamydophorus* (Van Kamp.; Winge, 1915, p. 231) the long external auditory meatus is for the larger portion the ossified cartilaginous one, and is connected to the bulla with fibrous cartilage; it is composed of three pieces of which the middle one can remain cartilaginous. It is not impossible that a part of the external auditory meatus in *Dasypus* develops in the same way. In *Xenurus* (=*Lysiurus*) *unicinctus* Van Kampen found a thin half-ring lying against the external wall of the tympanic.

In some rodents (Van Kampen; Allen, 1904*a*, pp. 135–138) there occur one or two separate little pieces of bone outside the external auditory meatus. They are developed in cartilage, and sometimes similar cartilaginous pieces are found in adult rodents. This cartilage belongs to the cartilaginous external auditory meatus (see also, Winge, 1888, pp. 168, 198). These accessory bones are distinguished only by constant form and position from the ossifications of the cartilaginous external auditory meatus, which in other mammals, for example in the horse, often appear with older age.

Van Kampen (1905, not in edition 1904) mentions as a possibility that the exceptionally long external auditory meatus described by Lorenz von Liburnau in *Megaladapis edwardsi* is partly formed by similar accessory little bones outside the proper external auditory meatus.

Partly Membranous Wall of the Bulla

The bulla is not always closed. In larger or smaller degree skeletal elements can be absent, not mentioning the regular openings in the bulla for blood-vessels, nerves, Eustachian tube, etc.

(*a*).—In the Ventral Wall of the Tympanic Cavity

In the monotremes, *Echidna* is less primitive than *Ornithorhynchus*, as its tympanic cavity is much more surrounded by dependent plates of the adjacent bones (Van Kamp.; Winge, 1893*b*, pp. 82, 84), yet Van Kampen does not call it a bulla, as the pterygoid itself and not a special

process of it lies in the wall of the tympanic cavity. In *Echidna*, Gaupp (1908, pp. 662, 681, 757) gives a more detailed description of the fissura petropterygoidea between the pterygoid and periotic.

Also in the marsupials and the placentals, where we may speak of a bulla, this is not always totally closed but in these cases a larger membranous part is not necessarily a more primitive condition.

In many marsupials the ventral wall is for a larger or smaller part open. In *Phascolomys* it is totally or almost totally membranous (Van Kamp.; Winge, 1893*b*, p. 98). In the Didelphyidæ it is also open, to a different degree in different species (Van Kamp.; Winge, 1893*b*, p. 20, *Grymæomys;* p. 36, *Philander;* p. 54, *Hemiurus;* the membranous portion diminishes in the given order). Also in the Peramelidæ the membranous portion between the processus tympanicus alisphenoidei and petrosi is differently developed in relation to the development of these wings. In *Thylacinus*, as an exception among the Dasyuridæ, the bulla is open. The statement that in *Notoryctes* the bulla is extensively open (Scott, 1905, p. 370) is probably due to a specimen in which the exceptionally fragile bulla is broken. That there is an open space in the hinder part of the ventral wall in *Phascolarctus* was one of the reasons given by Winge (1893*b*, p. 100) for separating this genus from the Phalangeridæ; but according to Van Kampen, Winge is not right in saying that it is always the tympanic process of the alisphenoid that touches the paroccipital process and closes the bulla, since another element can be intercalated between the two. In the Macropodidæ the bulla is also totally closed.

Also in the insectivores the bulla is often partly open (Van Kamp.; Zittel, 1893, p. 558; 1923, p. 443). An extreme condition is found in *Sorex*, where practically the ventral wall is totally membranous (Van Kamp.; Schlosser, 1887, pp. 81, 121; Bondy, 1907, p. 310). Perhaps we have a similar condition in the fossil *Palæoryctes* (Matthew, 1913, p. 310 where there seems to be a broad tympanic ring, while false bullæ are absent. Also in other insectivores the bulla is partly open (Van Kamp.; Schlosser, 1887, p. 110, *Centetes;* p. 111, *Microgale;* p. 112, Potamogalidæ; pp. 81, 94, 95, 139, Erinaceidæ; p. 113, Solenodontidæ; p. 116, Macroscelidæ; p. 136, Myogalidæ). A part of the cited remarks of Schlosser are faulty, and even if they were correct, they are incomplete, as it is more important to know why the bulla is open, which elements of the bulla are not at all or little developed, and where the membranous part lies. For example, the part of the tympanic cavity in front of the periotic is much shorter in *Erinaceus europæus* than in *Centetes* and therefore not

open on the under side, but covered by the tympanic. In *Talpa* the bulla is closed (Van Kamp.; Zittel, 1893, p. 563; Schlosser, 1887, pp. 81, 125) and also closed or nearly so in Tupaiidæ (Van Kamp.; Schlosser, 1887, pp. 81, 115), Gymnuridæ (Van Kamp.; Schlosser, 1887, pp. 81, 93), Chrysochloridæ (Schlosser, 1887, p. 137) and in *Necrolestes* (Scott, 1905, p. 368). First I refer to the above-mentioned cases where there is "no ossified bulla" and where perhaps in many cases there was a partly open bulla.

That in the Chiroptera the bulla is not always ossified, as some remarks suggest (Zittel, 1893, p. 572; 1923, p. 451), we shall see later in the description of the entotympanic.

In some edentates also the bulla is partly open. An extreme condition shows *Orycteropus*, where the ventral wall is totally uncovered by bone and where a membrane connects the narrow tympanic ring with a crista of the promontorium. In *Manis* there is a narrow fissure between the tympanic and the periotic closed by membrane, in which caudally in some species a small loose entotympanic is found, which becomes lost in the dry skull. *Cholœpus* also shows a long narrow longitudinal fissure between the tympanic and the plate-like entotympanic. In *Bradypus* this fissure is lacking; in this genus, especially in young skulls, we find an open space between the tympanohyal and the bulla leading into the tympanic cavity. Perhaps a similar condition is found in the fossil *Prozaëdius* (Scott, 1903*a*, p. 71; see also my own investigations), where the bulla is so incomplete that it is deeply notched from behind in a very peculiar and characteristic manner. Among the Gravigrada that I could investigate, the bulla does not show analogous open fissures or spaces, as the tympanic lies in general closely against the entotympanic. *Lestodon* forms an exception (see Van Kampen's and my own investigations); here a large part of the auditory bulla in the dry skull is open, as the bony entotympanic is very small.

In the Odontoceti (Van Kamp.; Hanke, 1914, p. 506) we find on the lateral side, besides the porus acusticus externus, the somewhat larger hiatus epitympanicus, separated from each other by the fusion of the processus sigmoideus with the periotic. On the mesial side we find the fissura petrotympanica or tympano-periotica; in the living animal two cavities of the caudal system of air-sacs, viz., the sinus pneumaticus peribullaris and the sinus pneumaticus peripetrosus, communicate with the tympanic cavity through this fissure.

In the Mystacoceti we find similar conditions, with one exception only (Van Kamp.; Hanke, 1914, pp. 506, 507): the porous acusticus

externus and the hiatus epitympanicus are not separated, as the sigmoid process does not touch the periotic. This common aperture is bounded dorsally by the periotic and the processus posterior petrosi, rostrally bounded incompletely by the sigmoid process and the processus medius bullæ, caudally by the processus posterior bullæ. The fissura petrotympanica is broad (Hanke, 1914, p. 507).

In the recent Tapiridæ, Van Kampen found a rather broad cleft between the tympanic and the crest on the promontorium, which is perhaps an entotympanic. According to Van Kampen this cleft is closed by membrane, but perhaps it is closed by the entotympanic that Parker (1882) described.

In the adult, not very old *Rhinoceros sumatrensis*, Van Kampen describes the following openings in the bulla: 1. The cleft in the under wall of the bulla between the nearly vertical tympanic and the vertical middle part of the entotympanic; 2. rostrally the space between the tympanic and the rostral part of the entotympanic, while caudally the tympanic and the entotympanic touch each other; 3. caudally the fissure between the periotic and the upper margin of the caudal laterally directed extension of the entotympanic, while more rostrally, the periotic and the entotympanic touch each other. In old skulls the cleft in the under wall of the bulla becomes much smaller.

In the recent Equidæ the upper margin of the mesial wall of the bulla touches the periotic, so that a fissure is lacking.

The note of Palmer (1913*b*, p. 884), that in the fossil *Anoplotherium* the bulla projects freely under the petrosal, expresses that perhaps there was a cleft between the two.

In *Sus* the formerly described cleft between the bulla and the periotic is lacking, according to Van Kampen. In the recent *Hippopotamus* this cleft between the bulla and the periotic is present; in the young animal it is broader than in the adult.

In some Cervidæ (*Cariacus, Capreolus*) we find a fissure between the bulla and the periotic, though as a rule in the Cervidæ the bulla touches the periotic. Also, in the Bovidæ as a rule, the inner lip of the bulla touches the periotic; in *Ovis*, however, this is only the case in the caudal part, while rostrally in the neighborhood of the ostium tympanicum tubæ we find a cleft between the bulla and the petrosal.

(*b*).—In the Wall of the Recessus Meatus

Another kind of opening we find sometimes in the bony recessus. This is due to the development of the recessus, which in such cases begins as a tuberculum tympanicum anticum and posticum of the fore and hind

legs of the tympanic annulus. These tubercles when growing touch each other, not covering an opening, which later on closes. We find it often in *Erinaceus*, and in *Homo*. Also in *Galeopithecus*, the bony covering of the recessus is often not totally bony in the adult animal.

In the underwall of the recessus meatus of the Herpestinæ (Van Kamp.; Carlsson, 1910*b*, p. 566) we find a cleft or an aperture that is distally closed; this aperture can be closed so far that only a groove is present. We find these different stages in different genera and species, but sometimes also in different specimens of the same species and then evidently due to age or to other factors. In *Herpestes urva* and *Suricata* we find a cleft. Carlsson (1910*b*, p. 566) describes a groove in the end of the meatus auditorius externus in *Galidia* and *Hemigalidia*. In the Viverrinæ and in *Eupleres* this cleft, aperture, or groove, is lacking Van Kamp.; Carlsson, 1910*b*, p. 566). Also, in the Hyænidæ this cleft is lacking, though the cylindrical auditory meatus very much resembles that in the Herpestinæ.

In the recent Canidæ the oral under edge of the short external auditory meatus often shows an incision resembling that of the Herpestinæ, though not so distinct. Also *Putorius putorius* shows a fine cleft-like perforation in the under wall of the cylindrical auditory meatus in the neighborhood of the transition into the recessus meatus; in other species of the genus *Putorius* this aperture is absent as a rule.

Similar conditions to those in the Herpestinæ are found in the recent rodents. *Hydrochœrus*, *Dasyprocta* and *Dinomys* show a longitudinal cleft in the underwall of the auditory meatus from the transition of the recessus meatus and the cylindrical meatus to the margin of the porus acusticus externus. In *Myocastor coypus*, *Cavia* (Van Kamp.; Bondy, 1907, p. 346), *Lagostomus trichodactylus*, *Chinchilla* and *Lagidium*, both margins of the incision are connected in the distal part, thus forming an aperture. In the old *Cavia* this aperture has become a circular groove. Among the non-Hystricomorphæ these apertures are absent; in *Pteromys petaurista* only a short cleft is present. In *Lepus* sometimes a groove is found, resembling that of *Cavia*, but less distinct, and not circular but straight. According to Scott (1905, p. 392) the fossil *Neoreomys* shows an auditory tube with a ventral slit opening into the central hole in the outer wall of the bulla almost exactly as in *Dolichotis*. Also the fossil *Prolagostomus* (Scott, 1905, p. 451) shows a large opening into the bulla delow the auditory meatus.

Openings in the Bulla

Sometimes the bulla is partly open, as is mentioned above, and the same is the case with the opening in the external auditory meatus. Here we shall describe only the openings for the larger blood-vessels, nerves and so forth, lying in the bulla or between the bulla and the elements against which the bulla and the foramen magnum bullæ lie. We shall limit our interest to these openings and not mention the many openings in the neighborhood of the bulla, which Cope in his well-known article (1880*b*) found to be especially valuable in diagnosis.

In the cases where there is only a ring-like tympanic and in the cases where the ventral wall is partly uncovered, we do not find well-circumscribed openings. Only these kinds of apertures interest us here, but of these only the larger ones will be mentioned and not the small ones for very thin bloodvessels, nerves, and so forth. Thus the very thin chorda tympani nerve sometimes pierces the bulla (see Bondy, 1907, pp. 400, 306, *Talpa*).

It remains to be noted that larger openings for veins are lacking in the bulla or between the bulla and the elements against which the bulla lies.

Foramen Magnum Bullæ

The opening of the cup- or bowl-shaped bulla which is closed by the skull is called the foramen magnum bullæ. This opening is sometimes reduced as the upper margin bends around. For example, in *Tupaia* the forward prolongation of the tympanic cavity is dorsally covered in this way by the entotympanic, while this is lacking in the allied *Ptilocercus* which in this respect is more primitive.

In the modern Rodentia the mesial margin of the bulla is more or less turned inward, lying against the petrosal, with which it often fuses and with which it can form rostrally a short tuba ossea.

In the modern Ursidæ and Mustelidæ the margin of the bulla is bent inward and lies against the petrosal. In *Procyon lotor*, in which the front, mesial, and back margins of the bulla are turned inward, we find a similar condition. In *Felis* the bent upper margin of the bulla is well developed. Thus the foramen magnum is narrowed, a feature also mentioned by Dawkins (1878, p. 49) for *Felis spelæa*, where, according to this author, the entotympanic chamber of the bulla is closed on all sides except at the top, where there is a long fissure in which the promontorium of the petrosal lies. In *Felis domestica* not only the bent part of the mesial margin is well developed, but rostrally it extends even above the septum bullæ,

which it thus separates from the promontorium. In the Viverrinæ as well, very distinctly in *Paradoxurus* for instance, but not in *Herpestes*, this rostrally bent margin of the entotympanic extends between the tympanic and the promontorium into the outer chamber of the bulla.

In the modern Phocidæ the inwardly turned margin of the bulla lies closely against the petrosal, while its caudal margin partly covers the fenestra cochleæ.

In the Cetacea in general (Zittel, 1893, p. 163) the bulla is involute, the mesial wall being bent inward.

In the modern Delphinidæ the mesial lip of the bulla is a little reflected inward, which is also the case with the margin between the processus sigmoideus and the processus tubarius.

The long axis of the bulla of *Kogia* (Schulte, 1917, pp. 395, 396) is nearly transverse. Thus the rostral border is strongly rolled and turned toward the periotic. This comprises the two lips of the bulla. The caudal lip is heavy and strongly rolled, presenting near its middle a shallow concavity which lies opposite to but not in contact with the caudal pole of the pars cochlearis. The rostral lip is thinner and has a more complicated contour; from the annulus tympanicus it is directed mesad and is notched close to the processus sigmoideus, which, projecting rostrad, overhangs the interval between the lip of the bulla. Mesal to the attachment of the malleus the margin is prolonged into an uncinate process, which, strongly bent upon itself and with a globose enlargement of its deflected extremity, is received into a concavity of the periotic and firmly ankylosed with that bone.

In the fossil *Diochotichus vanbenedeni* (True, 1910, p. 27) the thickened and convoluted posterior portion of the inner lip occupies rather more than one-half its length.

In the Mystacoceti in general (Lydekker, 1887, p. 16; Hanke, 1914, p. 510) the superior portion of the inner wall of the bone is reflected and involuted. Already in the fœtal *Megaptera* (Ridewood, 1922, p. 242) the dorso-mesial edge of the bulla is involute. In *Balænoptera*, according to Lillie (1910, p. 779), the bulla is shaped like a cowrie, the upper edge of the inner surface rolled into the cavity of the bone.

In the young *Hippopotamus* the mesial surface of the bulla is bent inward. In *Camelus* and *Auchenia* the upper edge of the mesial surface is a little reflected and lies against the petrosal. In *Ovis* and other Bovidæ the upper margin of the mesial wall of the bulla is turned inward.

In the Prosimiæ and primates we have no proper foramen magnum bullæ, as the petrosal itself contributes to the bulla. Yet we can compare

the place occupied by the promontorium in the petrous roof of the tympanic cavity with the foramen magnum. Then we can add here the remarks on the petrous roof of the tympanic cavity in the monkeys. This roof takes part in the cerebral cavity, as is easily understood (Van Kamp.; Lorenz von Liburnau, 1905, p. 468, *Megaladapis;* Gregory, 1920, p. 210, *Lemur* and *Adapis*).

In *Lemur mongos* the promontorium lies nearly in the center of the roof of the tympanic cavity, which for a large part is formed by the bulla. The bulla is extended on the caudal, mesial and rostral side of the promontorium by excavation of the petrosal. In the fossil *Adapis* (Gregory, 1920, p. 210) the petrous roof of the hypo-tympanic sinus takes a greater part in the cerebral cavity than in *Lemur;* in both it takes a large share in the brain-cavity. In the fossil *Megaladapis edwardsi* (Lorenz von Liburnau, 1905, p. 468) the roof of the spacious tympanic cavity occupies an extensive surface on the mesial side of the cerebral facies of the os temporale.

In *Perodicticus potto* the cavity of the mesial chamber of the tympanic cavity is still more deeply excavated in the petrosal on the mesial and caudal side of the promontorium than is the case in *Lemur*.

In *Tarsius* the caudal portion of the bulla cavity shows a small caudal extension behind the promontorium; the mesial wall is but little excavated. The wall of the rostral chamber extends laterally and in the cerebral cavity.

In the modern Hapalidæ and Cebidæ the entire oral point of the periotic is filled with cellulæ. Thus we can say that the bulla participates in the wall of the brain-cavity. In the Cercopithecidæ as well we find cellulæ petrosæ in the wall of the cerebral cavity.

Fissura Glaseri

The fissura Glaseri is at first the aperture for the cartilage of Meckel, which disappears later in the development. Later on we find the chorda tympani nerve in it and often also the ramus inferior of the stapedial artery.

The fissura Glaseri lies between: (a) the sulcus malleolaris of the tympanic (that is, a groove turned toward the cartilage of Meckel and that lies in that part of the tympanic which develops first in ontogeny) and (b) the periotic, or (c) the margo fissuræ of the squamosal (that is, the rostral prolongation of the margo tympanicus of the squamosal); it lies alongside the tegmen tympani.

Often the fissura Glaseri is circular and does not have the shape of a groove as in *Homo*.

In Notoryctidæ the circular opening between the tympanic, the processus tympanicus ossis alisphenoidei and the processus entoglenoideus of the squamosal, is probably also the fissura Glaseri.

The fissura Glaseri in the modern Canidæ and Ursidæ lies between the bulla and the squamosal, while in the Felidæ it lies between the bulla and the alisphenoid.

In the Delphinidæ it is a small aperture between the tegmen tympani and that part of the margin of the bulla that lies between the processus tubarius and the processus sigmoideus.

In *Lemur mongos* and *Perodicticus potto* the small fissura Glaseri lies between the margo fissuræ of the squamosal and the bulla.

Ostium Tympanicum Tubæ and Orificium Tubæ

In the mammals the tympanic cavity communicates with the pharynx by means of a narrow Eustachian tube. The adult *Ornithorhynchus* forms the only exception; here we find a broad communication.

As a rule the tuba enters the tympanic cavity in the front, but sometimes, under the influence of other organs in the neighborhood, this place of entering, it is shifted backward. We find this in *Echidna* and in the Myrmecophagidæ (Van Kamp.; Winge, 1915, p. 240), where it really is present, though formerly denied.

In the cases where there is only a tympanic ring and in the cases where the ventral wall of the tympanic cavity is more or less membranous, there is no well-circumscribed opening for the Eustachian tube. This opening is called ostium tympanicum tubæ and in the cases where the Eustachian tube is partly covered by means of bone, i.e., by a so-called pars ossea tubæ, the opening is called the orificium tubæ.

In *Echidna*, according to Gaupp (1908, p. 663), the tuba passes between the tympanic and the pterygoid. According to Watson (1916, pp. 325, 354), during development it passes between the pars cochlearis and the posterior end of the Echidna-pterygoid, while in the adult *Echidna* the Eustachian tube passes through a notch between the Echidnapterygoid and the basisphenoid.

Among the marsupials, the ventral wall is nearly totally membranous in *Phascolomys* and therefore there is no ostium tympanicum tubæ in the dry skull. In the other marsupials (except that it lies between the tympanic and the periotic) it lies generally between the tympanic process of the alisphenoid and that of the periotic (Van Kamp.; Gregory, 1910, p.

223; Watson, 1916, p. 354) and in connection with the development of these two wings the opening is more or less well circumscribed, as can be seen in the Peramelidæ, in the Dasyuridæ and in *Phalanger ursinus*. Where the tympanic process of the periotic is lacking it lies behind the processus tympanicus alisphenoidei, as is the case in *Phascolarctus* and in practically all Phalangeridæ. In the Macropodidæ the ostium tympanicum tubæ lies between two parts of the tympanic wing of the alisphenoid, a condition totally different from what we have seen above, so that according to Van Kampen there is every reason to believe that the element that lies on the caudal side of the Eustachian tube is an entotympanic secondarily fused with the alisphenoid.

Among the insectivores the ventral wall is practically entirely membranous in the Soricidæ and therefore the dry skull does not show an ostium tympanicum tubæ. In many insectivores this aperture is an open groove between the tympanic process of the alisphenoid and that of the basisphenoid. In *Centetes*, where the prolongation of the tympanic cavity that lies in front of the tympanic and the periotic is very large in the adult skull, this groove is very long, and also in *Gymnura* (Erinaceidæ) it has the shape of a gutter, but in *Erinaceus*, where this forward prolongation of the tympanic cavity is very short, this groove is covered by the tympanic; we find the same in *Talpa* and in *Myogale* (Van Kamp.; Gregory, 1910, p. 264), while in *Hemicentetes* this groove is limited only on one side, as the tympanic process of the alisphenoid is hardly developed. In *Rhynchocyon* the ostium tympanicum tubæ, according to Van Kampen, lies between the two portions of the tympanic wing of the alisphenoid but according to my own investigations (1924) the so-called medial portion is the rostral entotympanic. In *Tupaia* the small opening for the Eustachian tube pierces the wall of the entotympanic bulla. In contrast with the conditions found in the marsupials, in the insectivores the periotic does not cover the ostium tympanicum tubæ, as this is brought forward together with the forward prolongation of the tympanic cavity.

In the Microchiroptera the ostium tympanicum tubæ lies between the tympanic, the entotympanic and the alisphenoid, but the latter lies sometimes at such a distance before the periotic that it does not lie in the wall of the ostium tympanicum tubæ. In the Megachiroptera the alisphenoid does lie in the wall of the ostium tympanicum tubæ.

In *Galeopithecus* the opening of the ostium tympanicum tubæ is totally surrounded by the bulla and not by the periotic.

Among the edentates an ostium tympanicum tubæ is missing in the

dry skull in *Orycteropus, Manis* and *Cholœpus,* as the ventral wall is more or less membranous and in *Tatusia novemcincta,* where the entotympanic is practically totally cartilaginous. In *Priodontes giganteus* the ostium tympanicum tubæ is large, as the entotympanic is not strongly developed; it lies between this element and the tympanic. Nor in *Tolypeutes tricinctus* is the ostium tympanicum tubæ distinct, as the entotympanic is slightly developed and does not or at least does not always reach the tympanic. In *Xenurus* (=*Lysiurus*) *unicinctus* the entotympanic is much better developed and lies closely against the tympanic, so that the ostium tympanicum tubæ, which lies between these two elements, is much better circumscribed. Also in *Dasypus* and *Zaëdyus* and, according to Van Kampen probably also in *Chlamydophorus,* the ostium tympanicum tubæ is small and totally surrounded by the bulla. In *Bradypus* the ostium lies in the fore part of the bulla between the tympanic and the entotympanic. In the Myrmecophagidæ the far-backwardly shifted ostium tympanicum tubæ lies between the tympanic and the processus tympanicus basioccipitalei or as in *Cycloturus* between the tympanic and the pterygoid.

It is Van Kampen's opinion that in the Gravigrada we have a similar condition as in *Cholœpus,* which means that there is a membranous portion between the tympanic and the entotympanic, and therefore he thinks that the ostium tympanicum tubæ lies in the fore part of this fissure. In nearly all the Gravigrada that I could investigate the tympanic and the entotympanic lie close together. The ostium tympanicum tubæ in *Hapalops* and allied genera, and in *Mylodon,* was a small opening between the entotympanic and the tympanic, the latter contributing to the ostium a curve in the form of half a circle. In other genera the tympanic was lacking in my material and this relation remained unknown. In *Lestodon,* where the ventral wall is for the larger part not closed by bone, the ostium tympanicum tubæ is of course lacking in the dry skull.

In the modern Rodentia the ostium tympanicum tubæ as a rule is small and lies in the antero-mesial corner of the bulla. As a rule it lies between the petrosal and the bulla, though this is often determined with difficulty by the fusion of these two. As a rule it is more or less covered by the bulla with its styliform process. Sometimes a tuba ossea is present, as we have seen. In *Castor fiber* and probably also in some Hystricomorphæ the ostium tympanicum tubæ does not lie between the bulla and the periotic, but perforates the wall of the bulla and the processus styliformis, in which the ventrally uncovered ostium lies.

In the modern Canidæ and Ursidæ the orificium tubæ lies between

the bulla and the alisphenoid. In the Procyonidæ the inclined bulla covers the ostium tympanicum tubæ. In *Procyon lotor* the ostium tympanicum tubæ is not a simple round aperture, but is lengthened to a fissure, which occupies the whole length of the reflected upper edge of the rostral wall of the bulla; this canal being dorsally closed by the alisphenoid. In the recent Mustelidæ the far forwardly extended bulla entirely covers the aperture for the Eustachian tube. In the modern Viverridæ the ostium tympanicum tubæ lies between the tympanic and the alisphenoid. In the Viverrinæ we find on its mesial side also the reflected upper margin of the entotympanic, which projects into the outer chamber of the bulla. In the modern Hyænidæ the aperture for the Eustachian tube is enclosed by the alisphenoid, the squamosal and the bulla; in *Proteles* as well by the tympanic only, not by the entotympanic. According to Pocock (1916*a*, p. 267) the opening for the Eustachian tube in the Felidæ lies at the antero-internal angle of the bulla. The orificium tubæ is covered by the alisphenoid and the bulla, i.e. for the larger part by the tympanic, but also to a small degree by that part of the entotympanic that turns inward and projects between the septum bullæ and the promontorium. As in other groups as well it not only transmits the tuba but also the musculus tensor veli. In *Felis spelæa* (Dawkins, 1878, p. 48) the Eustachian tube is transmitted by a large irregular cavity formed by the junction of the bulla, the posterior processes of the basi- and alisphenoids and the petrosal. In the fossil *Dinictis* (Riggs, 1896*b*, pp. 237, 238) the Eustachian canal is separated from the foramen lacerum medium by a thin plate of bone.

As a general character of the Fissipedia, Zittel (1893, p. 608) mentions that the Eustachian tube opens in a somewhat irregularly formed aperture.

The ostium tympanicum tubæ in the Phocidæ is a long fissure in the roof of the extension of the bulla in front of the petrosal and is dorsally closed by the squamosal.

The tuba passes through an opening between the inclined bulla, which covers the ostium tympanicum tubæ and the alisphenoid in *Phoca*, between the bulla and the squamosal in *Halichœrus*, while in the young *Cystophora* it passes between the bulla and the far backwardly extended pterygoid and palatinum. In the fossil seal described by Wyman (1850, p. 229) the imperfectly divided canal which lodges the Eustachian tube and the tensor tympani muscle is of remarkable dimensions, especially when compared with that of *Phoca grœnlandica*.

In the modern Otariidæ and Trichechidæ the orificium tubæ lies between the bulla and the alisphenoid.

In the Cetacea, according to Zittel (1893, p. 163), the inwardly reflected mesial surface of the bulla leaves a large irregular cleft open for the Eustachian tube. In the Odontoceti (Hanke, 1914, pp. 508, 509) the ostium tympanicum tubæ in the rostral wall of the bulla is a broad cleft, while in none of the Mystacoceti could Hanke find this cleft, because of the fact, according to this author, that the tuba does not reach the bulla, as it opens into the sinus pterygoideus, the air-sinus lying between the tympano-periotic and the processus digitiformis of the pterygoid.

In the modern Delphinidæ the rostral part of the fissura petrotympanica transmits the Eustachian tube. It causes a tube-like forward extension of the bulla. The orificium tubæ is extraordinarily wide and especially high, probably in relation to the presence of a rostral system of air-sacs, of which the central space, the vestibulum pneumaticum, communicates with the tuba or, by means of the orificium tubæ, with the tympanic cavity.

According to Turner (1913, p. 13) the Eustachian end of the tympanic cleft in *Balænoptera musculus* is less scooped out than in *Balænoptera sibbaldi.*

In *Tapirus* the ostium tympanicum tubæ occupies the rostral part of the cleft in the dry skull between the tympanic and the crest on the petrosal.

In the adult but not very old *Rhinoceros* the tuba probably passes through the most oral part of the cleft between the tympanic and the entotympanic. In old skulls it is more distinctly bounded and lies in the rostral corner of the bulla.

In *Equus* the orificium tubæ lies between the two parts of the bulla, which meet with a sharp angle.

In the modern Suidæ the ostium tympanicum tubæ lies between the bulla and the petrosal. As the vertical axis of the bulla inclines forward, the antero-superior wall of the bulla covers the ostium tympanicum tubæ.

In the fossil *Archæotherium clavus darbyi* (Troxell, 1920*b*, p. 369) the Eustachian foramen lies on the anterior end of the bulla.

In the modern Camelidæ the ostium tympanicum tubæ lies between the bulla and the petrosal.

In *Typotherium cristatum*, according to Van Kampen, the Eustachian foramen is indistinct, probably it lies between the bulla and the petrosal. The groove through which the tuba probably enters is very indistinct and lies on the lateral side of the pointed process which lies against the basi-

sphenoid. In *Hegetotherium* (Sinclair, 1909, p. 74) the Eustachian canal opens on the suture between the tympanic and the basisphenoid at the elongated anterior extremity of the bulla.

In *Toxodon platensis*, according to Van Kampen, the ostium tympanicum tubæ lies between the petrosal and the bulla; from this point the sulcus tubarius runs downward along the front wall of the bulla and on both sides of this bulla we find a sharp edge, of which the lateral one ends on the styliform process.

In *Procavia* (*Hyrax*) the ostium tympanicum tubæ does not lie between the bulla and the petrosal, but perforates the rostral wall of the bulla. The sulcus tubarius is short in consequence of the slight inflation of the bulla.

In *Lemur* the ostium tympanicum tubæ lies on the lateral side of the not-inflated anterior process of the bulla, made invisible in the ventral view by the bulla, which extends beneath it. In the fossil *Notharctus osborni*, according to Gregory (1920, p. 178), the anterior opening of the bony Eustachian canal is situated as in *Lemur*. In the fossil *Palæopropithecus* (Standing, 1908, p. 81; Gregory, 1920, p. 176) the orifice of the Eustachian duct lies at the posterior end of Standing's foramen lacerum medium (=Gregory's foramen ovale), with which it is more or less confluent in some skulls or from which it is distinct in other skulls.

In the young *Perodicticus potto* the ostium tympanicum tubæ lies between the petrosal, the petrous bulla, the tympanic and the alisphenoid, the latter on its dorsal side. In the adult *Perodicticus* this ostium is made invisible in the ventral view by the extended bulla. In *Necrolemur* (Gregory, 1920, p. 180) in front of the bulla and lateral to the anteromedial protuberance there is a foramen which may be the opening of the Eustachian tube, since it strongly resembles that opening in the Nycticebidæ.

In *Tarsius* the ostium tympanicum tubæ lies between the tympanic and the petrosal part of the bulla. This fissure continues in a longitudinal fissure in the wall of the bulla, which is, however, closed in the adult skull. The bulla extends still farther forward over the ostium tympanicum tubæ than is the case in other Prosimiæ. The inner margin of the ostium tympanicum tubæ is formed by the thickened outer margin of the septum in the bulla.

The so-called ostium tympanicum tubæ in the primates is properly not just the same as that in the Prosimiæ, as an anterior narrow part, the pars tubaria or canalis musculo-tubarius, is added to the tympanic cavity. The communication between this narrowed anterior portion and the

further tympanic cavity is the homologue of the ostium tympanicum tubæ of the Prosimiæ.

Foramen Stylomastoideum Primitivum and Definitivum and the Fissura Tympano-mastoidea

In the fœtal skull the facial nerve leaves the tympanic cavity and also the skull through the foramen stylomastoideum primitivum, lying at the end of the second part of the canalis facialis, which part is formed by the sulcus facialis. This foramen stylomastoideum primitivum is laterally limited by the tympanohyal, dorsally and medially by the mastoid and ventrally either by the hyoid, if this shows the opisthotrematic condition, or by the tympanic in all other cases. This condition remains in the adult monotremes (Van Kamp.; Gaupp, 1908, p. 687, *Echidna*), many insectivores, edentates, and others. In the Erinaceidæ, for example, it lies between the mastoid, the tympanohyal and a small process of the mastoid, the top of which sometimes lies against the top of the tympanohyal, so that the foramen stylomastoideum is closed. In *Sorex* this foramen is also closed, as the top of the tympanohyal lies against the petrosal, namely the processus tympanicus petrosi. In the Talpidæ also this foramen is closed all around as the tympanohyal touches the petrosum, and in *Chrysochloris* we have a similar condition.

Among the edentates, where a foramen stylomastoideum primitivum occurs in the adult skull, this aperture can be open on the under side or totally closed by the tympanohyal. This is the case if the top of the tympanohyal lies against the mastoid, so that the foramen stylomastoideum primitivum lies between the mastoid and the tympanohyal. Then it seems, especially if the two are fused, that the foramen stylomastoideum primitivum perforates the mastoid (Scott, 1903*b*, p. 123, *Propalæohoplophorus;* Sefve, 1915, p. 63, *Scelidotherium*).

In *Orycteropus* the foramen stylomastoideum primitivum is incompletely surrounded, as the top of the tympanohyal is free. This is not the case in *Manis*, as the tympanohyal is fused on both ends with the periotic, so that the tympanohyal limits the foramen stylomastoideum primitivum anteriorly. Among the Gravigrada (Van Kamp.; Sefve, 1915, p. 63, *Scelidotherium;* also my own investigations on *Hapalops* and allied genera and on *Scelidotherium*) the foramen stylomastoideum primitivum lies between the mastoid and the tympanohyal, which lies with its top closely against the mastoid and sometimes is fused with it. *Lestodon* (see my own investigations) forms an exception in this respect, so that the foramen stylomastoideum primitivum is not totally surrounded. Accord-

ing to Van Kampen, Leidy's double foramen stylomastoideum of the Gravigrada is the primitive stylomastoid foramen and probably a foramen mastoideum.

In *Tatusia*, *Priodontes*, *Xenurus* (=*Lysiurus*) and *Tolypeutes* the foramen stylomastoideum primitivum is totally closed, as the top of the tympanohyal lies against the mastoid. Also in the fossil *Stegotherium* (Scott, 1903*a*, p. 21) the stylomastoid foramen is large and distinct.

In the Glyptodontidæ (Van Kamp.; Scott, 1903*b*, p. 123, *Propalæohoplophorus*) the foramen stylomastoideum primitivum (according to Van Kampen the same as Burmeister's external auditory meatus with its external opening) lies between the mastoid and tympanohyal, whose top is fused with the mastoid everywhere where the tympanohyal is found in these fossils.

In many creodonts the stylomastoid foramen which is mentioned in literature must be a primitive one.

According to Wortman (1906, cited by Matthew, 1909, pp. 415, 416, 424, 436; Van Kamp.; Wortman, 1901, pp. 293, 294) the Creodonta and also the Pinnipedia are distinguished from true Carnivora by the opening of the stylomastoid foramen on the posterior surface of the skull. However, this foramen is not characteristic for these groups (Matthew, 1909, pp. 416, 424, 436), but has been identified by Osborn (1900, p. 274, cited by Matthew, 1909, p. 416) in *Mesonyx* and *Patriofelis* with the postmastoid, an identification which, according to Matthew (1909, pp. 416, 424, 436) is correct.

The stylomastoid foramen, according to Matthew (1909, p. 416), has its normal position in the seals and so far as he was able to judge it is perfectly normal in all Creodonta. According to this author (Matthew, 1909, p. 424) it appears to have the usual position, as in the Fissipedia and most other mammals, at the postero-external margin of the otic fossa. I should like to add the remark, that in these mammals the so-called stylomastoid foramen is the definitive one, while in those creodonts in which the bulla is absent, the primitive one is visible. At this postero-external margin of the otic fossa or at the posterior end of the mesotympanic fossa lies the stylomastoid foramen (Matthew, 1909, pp. 424, 425, 436) in *Limnocyon*, *Thinocyon*, *Sinopa*, *Vulpavus*, *Viverravus*, *Patriofelis*, *Uintacyon*, *Tritemnodon*. In *Limnocyon velox*, according to Wortman (1902*a*, p. 202), the stylomastoid foramen (postmastoid?) issues upon the inferior surface of the mastoid. In *Patriofelis*, Matthew (1909, p. 424) describes an inferior groove in the mastoid apparently continuous with the stylomastoid foramen. According to Matthew (1909, p. 451) in

Thinocyon velox, Vulpavus, Viverravus (Van Kamp.; Matthew, 1909, p. 358) and apparently in all the smaller Creodonta, the posttympanic process of the squamosal sends a small spur inward across the posterior end of the mesotympanic fossa, nearly reaching the petrosal and anteriorly defining the foramen stylomastoideum. In my opinion it is not at all impossible that this spur is formed by the tympanohyal, which as a rule anteriorly bounds the foramen stylomastoideum primitivum.

In *Cynodictis intermedius* (Carlsson, 1914, p. 228) the stylomastoid foramen, which in my opinion is probably the primitive one, as the bulla is not preserved, opens into a deep fossa formed by a portion of the mastoid.

In the Odontoceti (Hanke, 1914, p. 508) the facial nerve comes out of the fissura tympano-periotica, while in the Mystacoceti its foramen lies above this fissura, from which it is nearly entirely separate. In the modern Delphinidæ the stylomastoid foramen is surrounded by the petrosal only; it forms an extension of the caudal part of the fissura petro-tympanica.

In the modern Sirenia the foramen stylomastoideum primitivum is indistinctly bounded.

The stylomastoid foramen in *Notharctus* (Gregory, 1920, p. 161), which opens on the ventral surface of the mastoid behind the carotid foramen, is no doubt the foramen stylomastoideum primitivum. Perhaps also other remarks on the stylomastoid foramen concern this primitive one. This is perhaps the case in the notice that the stylomastoid foramen in *Notharctus* is located as in *Lemur* (Gregory, 1920, p. 178), that this foramen in *Adapis* is in the same position as in *Notharctus* (Gregory, 1920, p. 422), that this foramen in *Megaladapis edwardsi* (Lorenz von Liburnau, 1905, p. 463) is small and lies behind the canalis caroticus.

In other cases a so-called third part of the canalis facialis s. Fallopii is formed when the neighboring elements (the posttympanic process, the mastoid, the bulla, and others) grow downward (Van Kamp.; Gregory, 1910, p. 224). They enclose both the facial nerve and the cartilage of Reichert (=the hyoid) together, or each of them separately. The aperture of this canal through which the facial nerve runs is the foramen stylomastoideum definitivum or the foramen faciale Denker. It is surrounded as a rule (Van Kamp.; Gregory, 1910, p. 430) by the tympanic, the mastoid and the paroccipital process, sometimes also by the squamosal. Moreover, the tympanohyal or the hyoid can lie in its wall but this depends on whether the tympanohyal or the hyoid, if present,

lies in or outside the third part of the canalis facialis. If the facial nerve and the hyoid come out through the same aperture, we call this the fissura tympanomastoidea.

Sometimes the stylomastoid foramen is incompletely surrounded, as the bony auditory bulla is but little developed, as in the Didelphyidæ (Van Kamp.; Gregory, 1910, p. 224), Peramelidæ and *Phascolarctus*. In the Dasyuridæ there is a short third part of the canalis facialis, formed by the mastoid, posttympanic process of the squamosal and processus tympanicus petrosi, while in *Thylacynus* the processus tympanicus petrosi is small or absent, so that according to Gregory (1910, p. 224) the foramen stylomastoideum, which is probably the primitive one, lies at the bottom of a canal formed by the tympanic, the mastoid and the paroccipital. In the Notoryctidæ the foramen stylomastoideum is probably the small aperture between the tympanic and the mastoid that lies just behind the under margin of the external auditory meatus, in a location similar to that in the Macropodidæ and Phalangeridæ; this is due to the presence of an external auditory meatus. In the adult *Phascolomys* the tympanic and the mastoid form as a rule a complete foramen stylomastoideum, which is open sometimes, as we find also in young skulls. In the adult *Macropodidæ* as well the foramen stylomastoideum is surrounded by the tympanic and the mastoid. In the Phalangeridæ we have an aperture for the tympanohyal lying between the tympanic and the mastoid and separated from it a foramen stylomastoideum lying between the mastoid and the external auditory meatus, which are fused and form a third part of the canalis facialis. So in general we can say (Gregory, 1910, p. 224), that in diprotodonts it appears that the canal issues on the postero-external border of the skull between the tympanic and the mastoid.

In *Centetes* the foramen stylomastoideum is incompletely surrounded as it is not closed toward the inner side, while in *Microgale* and *Oryzoryctes* it is closed by the plate of the periotic. In *Erinaceus europæus* the foramen stylomastoideum is incompletely separated from the foramen caroticum posterius (Van Kamp.; Gregory, 1910, p. 171). In the Macroscelidæ the foramen stylomastoideum, lies between the external auditory meatus and the processus mastoideus, in *Tupaia* between the bulla and the mastoid.

In the Megachiroptera the foramen stylomastoideum is incompletely surrounded by bone; in the Microchiroptera it lies between the bulla and the mastoid.

In *Galeopithecus* we find it between the tympanic, the mastoid, and the posttympanic process.

In *Cholœpus* the foramen stylomastoideum definitivum lies between the tympanic, the mastoid and the tympanohyal; the latter is lacking in this wall in *Bradypus*, where, as we have seen above, the tympanohyal lies in a vagina processus hyoidei. In the Bradypodidæ the foramen stylomastoideum definitivum is often divided by a narrow bony bridge probably for a branch of the facial nerve. In *Myrmecophaga* we find a short third portion of the facial canal; the foramen stylomastoideum definitivum lies behind the external auditory meatus between the tympanic, mastoid and tympanohyal. In *Dasypus sexcinctus* the opening for the tympanohyal and the stylomastoid foramen are separated. The top of the tympanohyal lies in a little groove between the bulla and the mastoid, while the foramen stylomastoideum definitivum lies more laterally at some distance. In the young *Dasypus sexcinctus* there is only a foramen stylomastoideum primitivum lying between the tympanohyal, the mastoid and the tympanic. Later on the external auditory meatus develops and if the caudal wall of the auditory meatus is formed, we find a foramen stylomastoideum definitivum between the external auditory meatus and the processus mastoideus.

In the modern Rodentia the foramen stylomastoideum definitivum always lies between the mastoid and the bulla, behind the porus acusticus externus or behind the base of the external auditory meatus. In the newborn *Hydrochœrus capybara* it is small, according to Preller (1907, p. 379). In *Echinomys cajennensis* (Winge, 1888, p. 87) the far downwardly extended mastoid process can partly conceal this foramen.

According to Matthew (1909, p. 436) the foramen stylomastoideum definitivum in the Carnivora lies on the posterior border of the bulla, between the tympanic and mastoid. This is probably the place of this foramen in *Mesonyx* and *Harpagolestes*, where, according to Matthew (1909, p. 436), this foramen has the usual position.

In *Canis* the foramen stylomastoideum definitivum lies between the mastoid and the bulla behind the porus acusticus externus and in consequence of the slight backward extension of the bulla just in front of the paroccipital process and near the caudal end of the bulla.

In the modern Ursidæ this foramen lies in the fore part of the groove between the bulla and the mastoid, behind the porus acusticus externus. Also in the Procyonidæ it lies between the bulla and the mastoid; the foramen is single. According to Riggs (1898, p. 258) the stylomastoid foramen in *Pseudobassaris* (*Amphictis*) lies near the foramen lacerum posterius as in *Bassaris*.

In the modern Mustelidæ this foramen lies between the bulla and the

mastoid, according to Pocock (1921, pp. 476-478) typically on the inner side of the mastoid prominence; its position and its distance from the foramen lacerum posterius vary however in accordance with the inflation of the bulla. Often there are two foramina, one a little behind the other; in other species there is but one foramen, which in such cases is narrowed in the middle. Probably the rostral foramen or rostral half of the twinned foramen transmits the facial nerve, the posterior one the hyoid arch. According to Van Kampen (1907, p. 695) this is really the case in *Putorius putorius*, in which two separate foramina occur. In the fossil *Mustela palæattica* (Weithofer, 1888, p. 227) the stylomastoid foramen is almost kidney-shaped; it lies behind and beneath the external auditory meatus. In *Oligobunis darbyi* (Thorpe, 1921*a*, p. 481) the stylomastoid foramen is rather large.

In the modern Viverridæ the foramen stylomastoideum lies between the mastoid, tympanic, entotympanic and tympanohyal. Except in *Nandinia* the tympanohyal always lies in a groove in the entotympanic, which (Van Kamp.; Carlsson, 1910*b*, p. 568) nearly (*Arctictis* and *Paradoxurus*) or entirely (*Herpestes* and *Galidia*) can be separated from the stylomastoid foramen. In *Cryptoprocta ferox* (Carlsson, 1911, p. 425) the tympanohyal is attached in a groove behind the stylomastoid foramen. In *Suricata* this foramen does not lie behind the porus acusticus externus, but a little more mesialward, in consequence of the presence of a cylindrical external auditory meatus.

In *Hyæna* it lies behind the external auditory meatus, between the bulla and the mastoid.

In the modern Felidæ there is a short third part of the canalis Fallopii. The foramen stylomastoideum definitivum lies between the mastoid, tympanic, entotympanic and tympanohyal. Sometimes the groove in the side wall of the bulla is closed all around, in which case the tympanohyal is separated from the foramen stylomastoideum definitivum. According to Merriam (1909, p. 297) the stylomastoid foramen in the lion and tiger is situated relatively much farther from the median plane than in *Felis atrox* var. *bebbi*.

In the Pinnipedia the stylomastoid foramen lies between the mastoid and the bulla. In the modern Trichechidæ the third part of the canalis Fallopii is formed by the mastoid, tympanic and probably also by the tympanohyal. Between the mastoid and the bulla lies a narrow groove; in its rostral end lies the stylomastoid foramen, in its caudal end lies a second foramen probably for the hyoid arch. In the adult skull this separation is more distinct than in the pullus.

In the fossil *Theosodon* (Scott, 1910, p. 118) the stylomastoid foramen is deep-set, but large and conspicuous.

In the modern Tapiridæ the third part of the canalis Fallopii is very short; the stylomastoid foramen in the dry skull lies between the periotic, tympanic and tympanohyal.

In *Rhinoceros* the foramen stylomastoideum definitivum is enclosed by the tympanohyal, entotympanic and the base of the paroccipital process; as the latter in not very old skulls does not yet reach the bulla, the stylomastoid foramen in such specimens is incomplete.

In *Equus* the foramen stylomastoideum definitivum lies between the mastoid, the posterior wall of the vagina processus hyoidei and the wall of the bulla. According to Van Kampen the processus jugularis does not lie in the wall of the stylomastoid foramen, as was formerly described.

In the modern Suidæ the foramen stylomastoideum lies between the bulla, the processus posttympanicus and the paroccipital process, completely surrounding a vertical canal, except in *Dicotyles*, where the paroccipital process does not touch the bulla. The tympanohyal may lie in this canal or in a vagina of the bulla, which either more or less coheres with it or is separate from it.

In the recent Hippopotamidæ the tympanohyal lies in the third part of the canalis Fallopii; the stylomastoid foramen lies between the posterior wall of the bulla, the paroccipital and the posttympanic processes.

The cylindrical hollow on the tympanic for the attachment of the tympanohyal in the fossil *Anoplotherium* (Palmer, 1913*b*, p. 884) perhaps represents a vagina processus hyoidei; the stylomastoid foramen lies immediately behind this hollow. In my opinion this stylomastoid foramen is the primitive one, as it is described on that side of the skull where the bulla is absent.

In *Oreodon*, according to Leidy (1854, p. 32), the foramen stylomastoideum lies between the base of the paramastoid process and the pars petrosa and in advance of this lies the pit for the reception of the styloid process. In *Oreodon culbertsonii* Osborn and Wortman (1894, p. 216) describe the condition as follows: at the base of the paroccipital process, on the side looking toward the postglenoid, are seen two fossæ, separated from each other by a well-marked lamina of bone extending out from the paroccipital; in the anterior of these fossæ is found the point of articulation of the tympanohyal element of the hyoid arch, while in the posterior fossa is seen the external opening of the stylomastoid foramen. In *Oreodon gracilis* (Osborn and Wortman, 1894, p. 218) the double fossa at the base of the paroccipital is less distinct than in *Oreodon culbertsonii;*

in *Oreodon bullatus* (*loc. cit.*, p. 218) the posterior fossa at the base of the paroccipital is but faintly represented, the anterior being large and distinct, while in *Eporeodon major* (*loc. cit.*, p. 218) there is no posterior fossa at the base of the paroccipital.

In the modern Camelidæ the third part of the canalis Fallopii is rather long; it is formed by the tympanic and the posttympanic process. The tympanic separates the tympanohyal from the foramen stylomastoideum definitivum.

In the modern Tragulidæ the third part of the canalis Fallopii is short; it is formed by the tympanic, tympanohyal and mastoid. The tympanohyal separates the stylomastoid foramen from the bulla. Thus this foramen is surrounded by the tympanohyal and by the mastoid and for a very narrow part only by the external auditory meatus. The conditions found in the modern Cervidæ resemble that in *Tragulus*.

In the modern Giraffidæ the tympanohyal is enclosed in a vagina, and thus the foramen stylomastoideum lies between the tympanic, the posttympanic process and the exoccipital, which covers the mastoid.

In the modern Bovidæ the stylomastoid foramen lies between the mastoid, the bulla and the tympanohyal, the latter being excluded in the cases where it is enclosed in the bulla.

In *Typotherium cristatum*, according to Van Kampen, the foramen stylomastoideum definitivum lies between the tympanic and the posttympanic process. The cylindrical fossa or deep pit, in which the hyoid arch is inserted, and which lies on the outer posterior side of the bulla, external to the paroccipital process, and which Scott (1912, pp. 114, 292) mentions in some genera of the Typotheria, is probably not the stylomastoid foramen, but the vagina processus hyoidei only. The same remark concerns the notices of Sinclair (1909, pp. 74, 89) on the deep pit or fossa for the tip of the stylohyal in *Hegetotherium* and *Pachyrukhos*.

In the Toxodontidæ the foramen stylomastoideum definitivum lies between the paroccipital process and the vagina for the hyoid arch. In *Nesodon* (Scott, 1912, p. 140) it is of unusual size.

In *Elephas* the tympanohyal, which lies in a groove in the posterior wall of the bulla, with which it is fused except in young skulls, lies between the exoccipital, the squamosal and the bulla. On its lateral side lies the foramen stylomastoideum definitivum between the tympanohyal, the bulla and the processus posttympanicus. The more proximal portion of the third part of the canalis Fallopii is entirely surrounded by the wall of the bulla.

In the young *Procavia* (*Hyrax*) the foramen stylomastoideum

definitivum lies between the tympanic and the posttympanic process. In the elder specimen in consequence of the extension of the cylindrical auditory meatus the third part of the canalis Fallopii lengthens, receiving the paroccipital process for a small part in the wall of the foramen stylomastoideum definitivum.

In *Lemur* the stylomastoid foramen lies between the squamosal and the bulla, behind the porus acusticus externus. In *Notharctus* (Gregory, 1920, p. 178) it was located as in *Lemur*, but perhaps this concerns the foramen stylomastoideum primitivum. No doubt this is the foramen, called the stylomastoid foramen, which opens on the ventral surface of the mastoid behind the carotid foramen (Gregory, 1920, p. 161). Perhaps the foramen stylomastoideum definitivum in *Notharctus* (Gregory, 1915, p. 422) lies immediately external to the posterior carotid foramen. In *Adapis* (Gregory, 1915, p. 422) the stylomastoid foramen is in the same position as in *Notharctus*. In *Megaladapis edwardsi* (Lorenz von Liburnau, 1905, p. 463) the stylomastoid foramen is small; it lies behind the canalis caroticus.

In *Chiromys* the stylomastoid foramen lies behind the porus acusticus externus and just in front of the posttympanic process.

In the Lorisidæ and Galaginæ the foramen stylomastoideum definitivum lies on the boundary of the tympanic and the petrous portion of the bulla, between these two and the mastoid. In the species which possess a cylindrical auditory meatus, it lies a little mesially of the porus acusticus externus.

In the Tarsiidæ the small stylomastoid foramen lies in the groove between the bulla and the mastoid. In a similar groove lies this foramen in the Hapalidæ behind the porus acusticus externus. Also in *Ateles* it lies between the tympanic and the mastoid. In the Cercopithecidæ the foramen stylomastoideum definitivum lies between the mastoid and the base of the external auditory meatus. In the Hylobatidæ and Anthropomorphæ it lies on the same place. On the mesial side of it or a little more forward, a second foramen for the hyoid arch occurs.

Posterior Carotid Foramen, Canalis and Sulcus Caroticus

The posterior carotid foramen lies generally in the hinder part of the bulla, a little more on the medial side than the stylomastoid foramen. It is not always present, first, since there is not always a bulla, as in monotremes, in *Sorex*, *Orycteropus*, and others; secondly, since the ventral wall of the bulla is sometimes partly membranous. Even if there is a totally closed bony bulla, the entocarotid may remain outside the bulla and the

stapedial artery may be reduced. According to Van Kampen this is the case in the marsupials. Gregory (1910, p. 223) provisionally calls a foramen between the petrosal and the basioccipital the posterior carotid foramen, which probably transmits a posterior branch of the entocarotid and which he found in all the polyprotodonts examined, but which was not recognized in the diprotodonts. This opening, however, seems to lie outside the bulla. Owen (1859, p. 314) describes in *Dasyurus*, *Thylacinus* and *Thylacoleo* a posterior carotid foramen lodged in a fossa between the basioccipitosphenoid and the bulla.

In cases in which the bulla shows a posterior carotid foramen we can distinguish three different conditions. In the first, an exceptional condition, the stapedial artery enters through the foramen caroticum posterius; this is found in the Muridæ, where the stapedial artery branches off from the entocarotid artery outside the bulla. In the second condition the entocarotid itself enters the bulla through the posterior carotid foramen. This does not happen always in placentals (Van Kamp.; Gregory, 1920, p. 179; Matthew, 1909, p. 350). As the entocarotid runs along the ventral surface of the cochlea toward the foramen caroticum, much depends on the place where the upper margin of the medial part of the bulla touches the skull, whether the entocarotid lies inside or outside the bulla. If this margin is formed by a tympanic process of the basisphenoid or by the basioccipital, it is a matter of course that the entocarotid runs through the bulla. In other cases we find in this respect even in closely allied groups that the entocarotid runs through the bulla or remains on the medial side of it. A third condition is presented by the cases in which the posterior carotid foramen opens into a canalis caroticus or a sulcus caroticus, formed either by the inner upper margin of the bulla alone or by this together with the periotic and basioccipital. The entocarotid then does not lie inside the bulla.

In the Insectivora the entocarotid generally runs through the bulla, which agrees with the presence of a tympanic wing of the basisphenoid in many insectivores (Van Kamp.; Matthew, 1909, p. 437). Sometimes the posterior carotid foramen lies between the processus tympanicus ossis basisphenoidei, the periotic, and the tympanic, as in *Centetes*, where this foramen is not distinctly circumscribed. Often the posterior carotid foramen is a groove in the processus tympanicus petrosi, which is closed farther on by the tympanic. We find this in *Erinaceus*, in *Hylomys*, in *Myogale* (Van Kamp.; Gregory, 1910, p. 264). In *Erinaceus* this opening is incompletely separated from the stylomastoid foramen (Van Kamp.;

Gregory, 1915, p. 428; 1920, p. 171; Carlsson, 1922, p. 233). According to my own investigations (v. d. Klaauw, 1924), which partly contradicts the descriptions given by Van Kampen, also in the Macroscelididæ the entocarotid divides the tympanic wing of the periotic into two parts, which are here closed by the caudal entotympanic. According to Carlsson (1910*a*, pp. 353, 389) the foramen caroticus posterius in *Rhynchocyon* and in *Macroscelides typicus* lies in the suture between the petrosal and the entotympanic, while in *Petrodromus* and many other species of the genus *Macroscelides* this foramen lies in the petrosal. In *Talpa* the posterior carotid foramen is situated between the tympanic and that part of the periotic that lies behind the tympanic; in *Chrysochloris* it is found on the same place; in *Solenodon* (Gregory, 1910, p. 247) it lies probably in or near the deep circular notch between the petrosal and the mastoid. In *Tupaia* the entocarotid enters the tympanic cavity between the bulla and the periotic in the caudal lateral part of the bulla (Carlsson, 1922, p. 233). In the stem-form of the Menotyphla or the ancestral menotyphlan family the entocarotid, according to Gregory (1910, p. 285), entered the tympanic chamber from the rear.

In the Megachiroptera the entocarotid remains outside the tympanic cavity, but the entotympanic may form a groove for the entocarotid and also there may be a canal formed by the entotympanic and the petrosal. In the Microchiroptera there is a posterior carotid foramen lying between the periotic and the bulla.

In *Galeopithecus* the posterior carotid foramen is perhaps the aperture at the back of the bulla; this aperture opens in a canal which is perhaps a carotid canal and which is formed by the upper margin of the bulla, the periotic and the basioccipital.

In *Manis gigantea* and in this species alone the entotympanic covers the sulcus caroticus in the petrosal, so that a canalis caroticus is formed. In *Cholœpus* the entotympanic forms a sulcus caroticus, as I found, resembling that of the fossil *Scelidotherium* (see my own investigations), but the roof is not so well developed as in this fossil. Van Kampen does not mention this roof and perhaps this is individually variable. In *Bradypus* the medial side of the entotympanic shows a deep groove, often closed to a canal, by which the foramen lacerum anterius is covered. Among the Gravigrada I found a beautifully preserved sulcus caroticus in *Scelidotherium*, which partly differs from the description given by Van Kampen. It is a well developed saddle-shaped groove leading to the foramen lacerum anterius, which is open, just as the sulcus caroticus is open over its whole length. Probably a similar roof for the sulcus

caroticus is present in *Hapalops* and allied genera and in *Mylodon* (see my own investigations). In a few specimens of *Hapalops* I found that the rostral portion of this sulcus was transformed into a canal covering the foramen lacerum anterius. Perhaps this occurs in all specimens (being broken away in the so-called ill-preserved specimens); perhaps it is individually variable. Van Kampen describes for *Mylodon gracilis* a badly developed sulcus caroticus in the entotympanic and a strongly developed one in the basis cranii. My specimen of *Mylodon garmani* does not show this so distinctly, due to the matrix and the probably compressed state of the skull. In *Lestodon* (see Van Kampen's and my own investigations) the entotympanic does not show a sulcus caroticus. Van Kampen notices the same for *Nothrotherium*. Stock (1913, pp. 343, 347, 348) mentions an aperture in the median wall of the "tympanic bulla," but, as we shall see later on, this tympanic bulla is the hinder inflated part of the pterygoid and has nothing to do with the auditory bulla. Van Kampen concludes that according to the figures given by Leidy, in *Megalonyx* the entotympanic shows a sulcus caroticus and perhaps even a canalis caroticus.

Huxley (1865, p. 55) thinks, that in *Glyptodon* the carotid canal probably traversed the anterior part of the external wall of the bulla but, as we have already seen, his interpretation of the bulla is not correct and the auditory bulla is not yet known.

In the Myrmecophagidæ (Van Kamp.; Winge, 1915, p. 240) the entotympanic is reduced, which is the reason that the carotid enters the tympanic cavity. The foramen caroticum posterius lies in a deep groove (in which also the foramen jugulare opens), totally surrounded by the periotic, the basioccipital and laterally by that part of the bulla that is probably formed by the entotympanic. In *Cycloturus* (see Van Kampen, 1905, p. 489 not in edition 1904) we find a closed canalis caroticus separated from the tympanic cavity. This canal is formed by the periotic, basioccipital and entotympanic and therefore is not comparable with that of *Bradypus* and of the Dasypodidæ. A second canal situated medially of this canalis caroticus is probably for the arteria maxillaris interna; it lies between the basioccipital and the pterygoid (Van Kamp.; Winge, 1915, p. 240). The wall between the carotid canal and the tympanic cavity, which is probably formed by the entotympanic, shows an aperture in *Cycloturus* probably for the stapedial artery (see Van Kampen, 1905, pp. 489, 490; not in edition 1904).

In nearly all Dasypodidæ (Van Kamp.; Huxley, 1865, p. 55) the medial wall of the entotympanic shows a sulcus caroticus, which is gen-

erally rather deep and which can be closed to a canal, then the foramen lacerum anterius is covered just as in *Bradypus*. This is individually variable, left and right, even in the same skull.

In the modern adult Rodentia (Van Kamp.; Winge, 1895*a*, p. 38; Gregory, 1910, p. 329) the arteria carotis, if present, runs either along the mesial side of the bulla toward the foramen lacerum anterius (caroticum) or, as a rule, through a canal or a groove formed by the wall of the bulla. In the adult Sciuridæ the carotid is wanting and therefore also the canal or groove; the arteria stapedia enters through the foramen caroticum posterius, which lies just beneath the foramen lacerum posterius, at the posterior end of the mesial wall of the bulla. In *Lepus* (Van Kamp.; Gregory, 1910, p. 329) the foramen caroticum posterius is a round foramen in front of the foramen lacerum posterius, caudally it is a canal, rostrally a groove between the bulla and the petrosal. In *Pedetes caffer* there is a sulcus only. A similar conditions is found in *Castor*, in which it is closed by the basioccipital to a canal. In the Muridæ the rostral part of the bulla shows a sulcus, which is sometimes but little developed and which is sometimes closed to a canal by the basioccipital and the styliform process. Moreover, the Muridæ (Van Kamp.; Winge, 1895*a*, p. 38) show a foramen caroticum posterius for the arteria stapedia, which branches off outside the tympanic cavity; this foramen lies outside the foramen lacerum posterius at the posterior end of the bulla on the boundary of the bulla and the petrosal. A similar condition is found in *Dipus*. In many other genera the groove or canal in the bulla is wanting.

In the normal course of the carotid in such Creodonta as it has been determined (Matthew, 1909, p. 424) the entocarotid enters the otic fossa at a point a little anterior to the foramen lacerum posterius (Van Kamp.; Matthew, 1910*c*, pp. 297, 298) and more median, thence grooving the side of the basioccipital, forward to the foramen lacerum medium. According to Matthew (1909, p. 436) the more internal branch of the entocarotid, which is more or less certainly the principal branch, in *Patriofelis*, *Mesonyx*, *Sinopa*, *Viverravus*, *Vulpavus* and *Uintacyon*, does not enter the tympanic chamber but lies between the bulla and the basioccipital, passing forward over the margin of the latter bone at or in front of the foramen lacerum posterius, and grooving the side of the basioccipital forward to the foramen lacerum medium. In *Dromocyon vorax* according to Wortman (1901, p. 294) the foramen lacerum posterius is probably also the point of entrance of the internal carotid artery, although the author was unable to discover any very distinct canal, which answers to this foramen in the carnassident skull. In the Miacidæ

(Pohle, 1920, p. 57; Carlsson, 1921, p. 72) the carotid artery runs through a groove in the petrosal.

The ordinary place of the carotid artery in their ancestors among the insectivores may be changed in the Carnivora, according to Winge (1895*b*, pp. 45, 125).

According to Matthew (1909, pp. 436, 437; see also pp. 323, 350, 358, 381, 451, 477, etc.) in the primitive Insectivora-creodont ancestral type two main branches of the entocarotid besides the stapedial one are present, which also are retained in most or all of the Eocene Carnivora. In the Fissipedia, in the Arctoidea at least, the external of the two main branches became vestigial, while the internal, which is the principal or only branch, carried the principal blood supply (Matthew, 1909, pp. 436, 437).

In the recent Carnivora the carotis runs through a canal in the upper mesial border of the bulla, which border is either formed by the entotympanic or by the tympanic, while according to Matthew (1909, p. 477) a groove, which leads forward between the petrosal and the basioccipital, is the position normal to modern Carnivora. In the primitive and more generalized carnivorous skull (Scott, 1889, p. 234; Matthew, 1910*c*, p. 297) the foramen lacerum posterius and the carotid canal are distinct from each other. In the Fissipedia, according to Zittel (1893, p. 608), the foramen of the carotid canal lies on the mesial side of the bulla either immediately in front of the foramen lacerum posterius or at a short distance in front of it.

In the arctoid Carnivora, according to Matthew (1909, p. 424), in the normal course of the carotid the entocarotid enters the otic fossa at a point a little anterior to the foramen lacerum posterius (Van Kamp.; Teilhard de Chardin, 1914–1915, p. 53) and more median, thence grooving the side of the basioccipital forward to the foramen lacerum medium.

In the modern Canidæ (Van Kamp.; Zittel, 1893, pp. 620, 669; Pocock, 1916*a*, p. 261) the foramen caroticum posterius lies on the inner side and in front of the space that leads to the foramen lacerum posterius in which it lies concealed. According to Van Kampen (see also, Gregory, 1910, p. 430) the carotid canal is a groove in the mesial wall of the bulla, which posteriorly is closed by the basioccipital, anteriorly by the sphenoid, while according to Pocock (1916*a*, p. 262) in *Canis* posteriorly the canal lies between the bulla and the periotic, anteriorly being a tube in the bulla itself. In *Amphicyon* (Filhol, 1883, p. 82) the carotid canal is complete and has the same course as in *Canis*, also the foramen caroticum posterius lies inside the space of the foramen lacerum posterius. In

Pachycynodon (Teilhard de Chardin, 1914–1915, p. 40) the foramen caroticum posterius is distinct and lies a little in front of the foramen lacerum posterius. In *Temnocyon altigenis* as well (Thorpe, 1922*a*, p. 167) the external carotid foramen is separate. Also in *Plesiocyon* (Teilhard de Chardin, 1914–1915, p. 53) this large carotid foramen lies posteriorly in the margin of the bulla. In *Cynodictis gracilis* (Scott, 1889, p. 233) the carotid canal is not enclosed in the posterior lacerate foramen. In Matthew's (1907, p. 191) material of *Enhydrocyon crassidens* the carotid canal was not clearly recognizable.

In the modern Ursidæ according to Van Kampen the foramen caroticum posterius lies far backward as in the Canidæ. In the young specimens and in the adult specimens of one species this foramen remains uncovered, while in all other adults the raised borders of the basioccipital cover this foramen and entirely enclose it in the foramen lacerum posterius. According to Reynolds (1906, p. 10), however, the carotid foramen is large and placed on the inner margin of the bulla, usually near the middle but occasionally more posteriorly. The closed carotid canal is formed by the wall of the bulla.

In the modern Procyonidæ as well the closed carotid canal lies in the mesial wall of the bulla. The foramen caroticum posterius sometimes lies rather far forward or near the middle of the bulla, but as a rule it lies posteriorly. It is, however, never concealed in the foramen jugulare. In the fossil *Pseudobassaris riggsi* (Riggs, 1898, p. 258, *Amphictis;* Pohle, 1917, p. 408) the posterior carotid foramen lies just in front of the foramen lacerum posterius as in *Bassaris* and the canalis caroticus resembles that in *Jentinkia* (*Bassariscus*).

In the modern Mustelidæ the foramen caroticum posterius is always separate (Van Kamp.; Zittel, 1893, p. 645) and always lies far in front of the foramen jugulare (Van Kamp.; Owen, 1859, p. 314), as a rule near the middle of the mesial wall of the bulla, sometimes still more oralward, for example, at the level of the suture between the basioccipital and the basisphenoid. The wide posterior carotid foramen opens in the canalis caroticus, which is closed all around by the wall of the bulla, except in *Mydaus meliceps*, in which it is an open groove. In front of the foramen lacerum anterius the canal continues as a groove between the bulla and the sphenoid. Sometimes, as in *Enhydra*, the carotid canal is very wide, resembling that in the Pinnipedia. In the fossil *Proailurus* (Schlosser, 1890, p. 74; Zittel, 1893, p. 666) the canalis caroticus lies in the rostral part of the mesial side of the bulla. The position of the carotid foramen in *Plesictis robustus* and *lemanensis* according to Teilhard de Chardin

(1914–1915, p. 59) is more mustelid-like than viverrid-like. In *Megalictis ferox* (Matthew, 1907, pp. 198, 199) the carotid is large and situated close in front of the posterior lacerate foramen. In *Oligobunis darbyi* (Thorpe, 1921*a*, p. 481) the carotid canal is not clearly defined but it is located internally and about medially of the bulla. In *Amphictis* (Pohle, 1917, p. 404) the canalis caroticus runs between the petrosal and the basioccipital. In *Palæoprionodon*, according to Winge (1895*b*, p. 54), the canalis caroticus seems to run through the mesial margin of the bulla.

In the modern Viverridæ the foramen caroticum posterius which is large and distinct (Zittel, 1893, p. 660) is situated farther forward than in the Felidæ (Van Kamp.; Owen, 1859, p. 314), the bulla being more backwardly prolonged than in the modern Canidæ (Pocock, 1916*a*, p. 262; see also, Scott, 1889, p. 233). According to Pocock (1916*a*, pp. 267, 268) the posterior carotid foramen may be far forward and only a short distance behind the foramen lacerum medium (*Paguma, Diplogale*; see also *loc. cit.*, p. 263) or near the middle of the inner wall of the bulla, as in most of the genera (see also, p. 262, *Civettictis;* p. 263, *Arctictis;* p. 264, *Arctogalidia* and *Cryptoprocta;* p. 265, *Mungos ichneumon*) or set far back, only a little way in advance of the foramen lacerum posterius (*Cynictis;* see also, p. 265, *Mungos smithii* and *Nandinia*).

In the Viverrinæ the posterior carotid foramen lies between the entotympanic and the basioccipital, while in the Herpestinæ it lies in the suture between the tympanic and the entotympanic (Van Kamp.; Carlsson, 1910*b*, p. 566; on *Galidia*, p. 596). In *Cryptoprocta ferox* (Carlsson, 1911, p. 425) this foramen lies between the entotympanic and the basioccipital as in the Viverrinæ. In mongooses of other genera than of the genus *Mungos* the foramen caroticum posterius, according to Pocock (1916*a*, p. 265), apparently always pierces the bulla just behind the inner portion of the partition of the bulla and its position varies in accordance with the length of the two chambers. In *Cynodictis*, for example, where the posterior chamber is very short and the anterior very long, the orifice in question is only a little way in front of the foramen lacerum posterius, whereas in *Ichneumia albicauda*, where the anterior chamber is small and the posterior large, the posterior carotid foramen is set far forward (Pocock, 1916*a*, p. 265). In *Genetta* (Pocock, 1916*a*, p. 263) this foramen lies at about one-fourth of the distance from the anterior end of the posterior chamber of the bulla. In *Arctictis binturong*, according to Carlsson (1920, p. 341), the posterior carotid foramen lies near the point of the highest inflation. The carotid canal in the Viverridæ is much wider than that in the Felidæ. The length of the canalis varies, depending on

the position of the posterior carotid foramen. Thus it is long in *Cynictis* and short in *Ichneumia albicauda* (Pocock, 1916*a*, p. 265).

In relation to this position of the posterior carotid foramen the entotympanic does not participate in the wall of the carotid canal in the Herpestinæ, while in the Viverrinæ it does, as a rule (Van Kamp.; Carlsson, 1910*b*, p. 566; 1920, p. 341, *Arctictis binturong*).

The carotid canal in the Viverridæ, according to Pocock (1916*a*, p. 268), shows great differences. It may be a long, completely bony tube traversing the wall of the bulla (*Mungos* and allied genera; see also *op. cit.*, pp. 264, 265), or it may be a complete bony tube (formed by the bulla alone) only at its anterior end, and an open channel in the bulla posteriorly (*Genetta, Paguma;* see also *op. cit.*, p. 263 and *Arctogalidia* on p. 264) or it may be an incomplete tube or an open channel throughout its length in the bulla (*Civettictis, Viverricula, Viverra;* see also *op. cit.*, p. 262 and immature *Arctictis* on p. 263) or it may form a very distinct ridge running obliquely across the cavity of the bulla (*Cynogale;* see also *op. cit.*, p. 264). In *Paradoxurus niger* (Pocock, 1916*a*, p. 263) the carotid canal resembles that in *Paguma larvata* except that the anterior portion is not a complete bony tube in the tympanic.

In the Viverrinæ according to Van Kampen (Van Kamp.; Carlsson, 1910*b*, p. 566) the groove in the entotympanic is sometimes open (*Viverra civetta*, sometimes in *Paradoxurus, Eupleres*) but as a rule it is closed by the basioccipital, while in the Herpestinæ it is closed by the tympanic alone, the basioccipital being excluded. According to Carlsson (1910*b*, p. 566), however, the carotid canal in *Galidia* and *Hemigalidia* is caudally bridged over by the basioccipital, while rostrally it is surrounded by the tympanic, as in the Herpestinæ. In a young skull of *Eupleres* the carotid canal, according to Carlsson (1910*b*, p. 567), is surrounded by the tympanic, thus differing from the Viverrinæ. In *Genetta*, according to Pocock (1916*a*, p. 263), the groove, corresponding to that in the bulla, lies in the periotic. In *Diplogale* (Pocock, 1916*a*, pp. 263, 264) the short and simple carotid canal lies between adjacent portions of the tympanic, periotic basioccipital, while in a subadult *Arctogalidia* (Pocock, 1916*a*, p. 264) the groove in the tympanic is bordered on the admedian side by the basioccipital only.

In *Cryptoprocta* the carotid canal, according to Van Kampen is closed and formed by the entotympanic; according to Carlsson (1910*b*, p. 567) it runs as in the Viverrinæ in a groove between the basioccipital and the entotympanic, by which it is bridged over in the rostral part; while according to Pocock (1916*a*, p. 264) the carotid canal slants as a

groove on the tympanic, but where it dips beneath the surface it is converted into a complete cylindrical tube formed by the tympanic alone.

Thus, as a rule, the carotid canal lies in the rostral part of the mesial wall of the bulla (Van Kamp.; Schlosser, 1890, p. 74). In *Nandinia*, however, a groove on the bulla is absent. In *Nandinia* (Pocock, 1916*a*, p. 265; Pohle, 1920, p. 57; Carlsson, 1921, p. 72) the carotid runs over a groove on the periotic and not between the anterointernal portion of the tympanic bone and the basioccipital, as formerly has been described (see Pocock, 1916*a*, p. 266). According to Carlsson (1921, p. 72) *Viverra civetta* and *Fossa* agree with *Nandinia* in this respect.

In the modern Hyænidæ (Van Kamp.; Owen, 1859, p. 314) the foramen caroticum posterius lies in the mesial wall of the bulla; the course of the carotid resembling that in the modern Felidæ. In *Proteles* the posterior carotid foramen lies near the middle of the mesial wall of the bulla, on the boundary of the two chambers of the bulla and thus the carotid canal lies in the wall of the true tympanic chamber only. In *Hyæna* the posterior carotid foramen lies a little more backward. According to Zittel (1893, p. 660) the carotid foramen in the Hyænidæ is very small and indistinct.

In the modern Felidæ (Van Kamp.; Pocock, 1916*a*, pp. 266, 268), the foramen caroticum posterius sometimes lies just in front of the foramen lacerum posterius not infrequently even within the depression which leads to this lacerate foramen so as to open within the foramen lacerum posterius. Thus it is closely connected with the posterior lacerate foramen (Zittel, 1893, p. 664; Matthew, 1910*c*, pp. 297, 312) and the posterior carotid foramen may be called internal and not distinct (Cope, 1880*c*, p. 835). In *Felis*, according to Owen (1859, p. 314), the posterior carotid foramen lies at the fore part of the foramen jugulare, notching the bulla at the fore part of that foramen.

The carotid canal in the modern Felidæ is very narrow (Van Kamp.; Cope, 1880*c*, p. 834; Winge, 1895*b*, p. 54) in relation to the reduced state of the carotid artery in the adult animal. It runs forward to the reduced foramen lacerum anterius. This canal lies in the upper border of the mesial wall of the bulla (Van Kamp.; Winge, 1895*b*, p. 54). Exceptionally only the carotid canal is a closed bony tube in its posterior half (Pocock, 1916*a*, pp. 266, 268); as a rule it is an open channel, apparent as a short shallow groove notching the bulla close to the basioccipital (Van Kamp.; Pocock, 1916*a*, pp. 266, 268), by which it is closed to a canal.

These characters in the fossil Felidæ may principally differ from

those of the modern ones and agree with those in other modern Carnivora (Van Kamp.; Cope, 1880*c*, p. 834; Scott, 1889, p. 216). Thus in the so-called Nimravidæ the posterior carotid foramen is entirely distinct or well separated from the foramen lacerum posterius (Cope, 1880*c*, p. 835; Scott, 1889, p. 238). This character is found in *Archælurus* (Cope, 1880*c*, p. 834; Zittel, 1893, p. 672), *Nimravus* (Cope, 1880*c*, p. 834), *Dinictis* (Cope, 1880*c*, p. 834; Scott, 1889, p. 215; Matthew, 1910*c*, pp. 297, 309), *Hoplophoneus* (Cope, 1880*c*, p. 834; Matthew, 1910*c*, p. 297; Adams, 1896, p. 421). In *Smilodon* (Cope, 1880*c*, p. 835; Matthew, 1910*c*, p. 297), in *Machairodus* (Zittel, 1893, p. 673) and probably also in *Drepanodon* (Cope, 1880*c*, p. 835), however, the position of the posterior carotid foramen agrees with that in the modern Felidæ.

In *Dinælurus crassus* (Eaton, 1922, p. 446) the foramen caroticum posterius is a veritable foramen, completely enclosed by the thin lateral expansion of the basioccipital, and not merely an open notch in this lateral expansion, as is the case in various examples of *Nimravus*. According to Eaton, it is also the regular occurrence in *Dinictis* that the entrance to the carotid canal is apparently through an open notch in the lateral expansion of the basioccipital. According to Riggs (1896*b*, p. 238) this carotid foramen in *Dinictis* lies on the median side of the bulla and near it. Riggs (1896*b*, p. 238) calls this foramen in *Dinictis* small, Scott (1889, p. 215) calls it large, and Zittel (1893, p. 669) calls it distinctly developed.

In *Hoplophoneus occidentalis*, according to Riggs (1896*a*, p. 41), the carctid canal is represented by a groove alongside of the basioccipital within the bulla; it terminates just without the posterior end of a ridge bounding the median groove of the basioccipital.

The carotid canal in the "Nimravidæ" (Scott, 1889, p. 239; Schlosser, 1890, p. 37) is conspicuous. In *Machairodus*, according to Winge (1895*b*, p. 56), a carotid canal is not found.

In the modern Phocidæ the posterior carotid foramen lies behind the middle of the mesial wall of the bulla, thus a little more forward than in *Ursus* and agreeing more with the other Arctoidea. The carotid canal is formed entirely by the entotympanic. It is very wide in contrast to the Arctoidea, except *Enhydra*. Thus it is easily understood that in the fossil seal described by Wyman (1850, p. 229) the entrance of the carotid canal is seen in its full width, when the base of the skull is turned upward.

In the modern Otariidæ the foramen caroticum posterius lies far backward; it lies in the oral wall of the depression leading to the foramen lacerum posterius, while in other species it is separated from this forame n

The carotid canal is very wide. In the pullus it is not yet closed; soon, however, it is enclosed in the mesial wall of the bulla.

In the modern Trichechidæ as well the carotid canal is very wide. It lies in the entotympanic, resembling in its course that of the Otariidæ. The foramen caroticum posterius lies far backward in the bulla but still in front of and separate from the foramen jugulare.

In the Cetacea there is no sharply bounded foramen caroticum posterius in the dry skull; in the Delphinidæ, for example, the carotid artery enters through the caudal part of the fissura petro-tympanica.

In the fossil *Theosodon* (Scott, 1910, p. 118) no carotid canal is discoverable.

In the modern Tapiridæ, Rhinocerotidæ, Equidæ, Suidæ and Hippopotamidæ there is present neither a sulcus nor a canalis caroticus.

In the adult *Camelus* and *Lama* the mesial wall of the bulla shows a distinct sulcus caroticus, closed by the basioccipital to a canal, which nearly vertically leads to the foramen lacerum anterius. In the fossil *Poëbrotherium* (Scott, 1891*a*, p. 20) the carotid canal is distinct from the foramen lacerum posterius.

In the modern Tragulidæ the carotis forms a shallow groove in the mesial wall of the bulla; sometimes the sulcus is deeper. In *Tragulus* by exception, according to Van Kampen, the groove is closed all around to a canal.

In the fossil *Leptomeryx evansi* (Scott, 1891*b*, p. 349) the carotid canal does not groove the side of the bulla.

In the modern Cervidæ the posterior end of the mesial wall of the bulla shows a more or less deep groove, which leads the carotid to a foramen between the petrosal and the bulla. Through this foramen, which is related to the fissura petro-tympanica, the carotid artery enters the tympanic cavity.

The shallow groove posteriorly in the mesial wall of the bulla in the modern Giraffidæ is probably a sulcus caroticus. The bulla in the fossil *Protoceras* (Scott, 1895*a*, p. 320) is not channelled by the carotid canal.

In the modern Bovidæ the groove in the mesial wall of the bulla is sometimes distinct, and thence the carotid runs through the tympanic cavity to the foramen lacerum anterius. Just as in the Cervidæ this course through the tympanic cavity in *Ovis* is no primitive condition as in the insectivores, but is due to the presence of a fissura petrotympanica.

The Typotheria show different conditions. In the family Interatheriidæ (Sinclair, 1909, p. 2) the carotid canal and the foramen lacerum posterius are fused. It is mentioned for *Protypotherium* (Sinclair, 1909, pp.

22, 51, 74; Gregory, 1910, p. 363) and *Interatherium* (Sinclair, 1909, pp. 51, 74) though traces of a septum dividing the two foramina are observable in *Protypotherium* (*loc. cit.*, p. 22). Owing to the fusion of the bulla with the basioccipital the carotid foramen is shifted posteriorly at the base of the paroccipital process (Sinclair, 1909, p. 22). In the family Hegetotheriidæ (Sinclair, 1909, p. 3) the carotid canal and the foramen lacerum posterius are widely separated. In *Hegetotherium* (*loc. cit.*, p. 74) the carotid foramen perforates the suture between the basioccipital and the tympanic opposite the middle of the bulla, and is widely separated from the foramen lacerum posterius (Van Kamp.; Gregory, 1910, p. 363). In *Pachyrukhos* (Sinclair, 1909, p. 89; Gregory, 1910, p. 363) the internal carotid enters the skull between the basioccipital and the bulla near the suture between the basioccipital and the basisphenoid.

In *Typotherium cristatum* no carotid canal occurs, according to Van Kampen.

In *Toxodon platensis*, according to Van Kampen, the entrance of the canalis caroticus is probably represented by a groove, which lies about in the middle of the boundary between the under margin of the bulla and the basis cranii between these two. This groove is figured by Roth according to Van Kampen. Owen (1840, p. 22) describes the carotid canal in *Toxodon platensis* anterior to the petrous bone, i.e., according to Van Kampen, the bulla. In *Toxodon burmeisteri* it is mentioned by Burmeister (1867, p. 262). In *Nesodon*, according to Scott (1912, p. 140), there is no carotid canal on the inner side of the bulla, as also Van Kampen concluded from the figures given by Lydekker (1893).

In a young *Procavia* Van Kampen describes a distinct sulcus caroticus in the bulla, while in the adult skull no canalis or sulcus is present. According to Gregory (1910, p. 363) in the *Hyraces* the carotid canal is united with the foramen lacerum posterius, which in my opinion is not correct.

In young specimens of *Elephas* (Van Kamp.; Weithofer, 1890, p. 213) the mesial wall of the bulla shows a groove, while old specimens show in this place a vertical canalis caroticus, which is closed all around by the bulla itself. Such a condition among the ungulates is described by Van Kampen in *Elephas* and in *Tragulus* only. In *Mastodon arvernensis* Weithofer (1890, p. 114) describes a somewhat indistinct foramen, which mesially lies on the side of the sphenoid bone.

In the Sirenia (Van Kamp.; Dilg, 1909, pp. 100, 116, *Manatus*) there is of course no sulcus or canalis caroticus in the dry skull.

In most of the Lemuriformes (Van Kamp.; Gregory, 1915, p. 431)

the arteria promontorii, or main branch of the internal carotid, passes through the bulla. This is a primitive condition (Van Kamp.; Gregory, 1915, p. 431). The course of the entocarotid in these Lemuridæ and also in the Chiromyidæ (Van Kamp.; Gregory, 1910, p. 321; 1913*b*, p. 248) corresponds with that in the Tupaiidæ. According to Gregory (1915, p. 428) the characteristic arrangement of the carotid branches in the Lemuriformes is not as primitive as that in the recent insectivores, but on the other hand it is more primitive than that in the Tarsiiformes and the higher primates (Van Kamp.; Winge, 1895*a*, p. 16). In most of the modern true Lemuridæ, as well as in the fossil *Notharctus* and *Adapis*, according to Gregory (1920, pp. 178, 179), the main internal carotid (art. promontorii) is small and the cerebra received their supply chiefly from the vertebral arteries.

In *Lemur mongos* (Van Kamp.; Winge, 1895*a*, p. 37, *L. collaris*) the foramen caroticum posterius lies just in front of the stylomastoid foramen in the caudal wall of the bulla, in the immediate neighborhood of the place where the bulla without distinct boundary passes into the mastoid. Thus Van Kampen supposes that originally it arose on the boundary of the bulla and the mastoid. The same position is found in other modern Lemuridæ as in *Lepilemur*, in the Indrisinæ (Van Kamp.; Gregory, 1915, p. 440). Thus in typical lemurs (Gregory, 1915, p. 428; 1920, pp. 165, 174; Carlsson, 1922, p. 233) the main internal carotid enters the bulla on its postero-external border medial to and below (i. e., in front of) the foramen stylomastoideum. Wortman has erroneously located the posterior carotid foramen on the posterointernal border of the bulla in the region where it enters in many modern carnivores (see Gregory, 1915, pp. 428, 427; 1920, p. 174). Also in *Propithecus* (Gregory, 1920, p. 175) the posterior carotid foramen is situated on the postero-external corner of the bulla. A foramen at the posterior tip of the bulla in *Lichantos* (*Avahi*) according to Gregory (1920, p. 176), is apparently the posterior carotid foramen.

In *Microcebus furcifer* (Van Kamp.; Gregory, 1920, p. 179) the very small posterior carotid foramen lies a little more mesialward than in *Lemur* and more as in *Chiromys*. Thus it lies near the foramen lacerum posterius, on the supposed junction of the bulla and the mastoid.

In the Chirogaleinæ in general, however, the main branch of the internal carotid does not pass through the tympanic cavity at all but enters the braincase through the large foramen lacerum medium, a condition which is probably a secondary later specialization (Winge, 1895*a*, pp. 16, 37; Gregory, 1915, pp. 429, 430, 431, 432, 434; 1920, pp.

178, 179; Carlsson, 1922, p. 233). Not in all Chirogaleinæ, however, is the foramen lacerum medium open (Van Kamp.; Gregory, 1915, p. 434, *Myoxicebus*). In the Chirogaleinæ, where the foramen lacerum anterius is partly roofed over by the bulla, the arteria promontorii may have entered the bulla by the posterior carotid foramen (Van Kamp.; Gregory, 1920, p. 179).

In the fossil *Megaladapis edwardsi* (Lorenz von Liburnau, 1905, p. 463) the foramen of the very narrow canalis caroticus lies on the mesial side of the foramen stylomastoideum.

In the fossil *Palæopropithecus* (Gregory, 1920, p. 176) the posterior carotid foramen is not located; it seems highly probable that there is some inconspicuous foramen in the posterior part of the bulla, which has hitherto escaped notice.

In the fossil *Notharctus* the course of the internal carotid canal conforms to the lemuriform type (Gregory, 1915, p. 440; 1920, p. 169; see also, Gregory, 1913*b*, p. 251, on Wortman's opinion); the same is true of the position of the posterior carotid foramen (Gregory, 1915, p. 433), which thus is found at the postero-lateral corner of the bulla in front of the stylomastoid foramen (Gregory, 1915, p. 422; 1920, pp. 165, 183, 218).

In *Adapis* as well the course of the internal carotid artery is fundamentally similar to that in the typical lemurs (Winge, 1895*a*, p. 37; Gregory, 1915, p. 440; 1920, p. 211) and also the position of the posterior carotid foramen (Gregory, 1915, p. 433), which thus also lies at the postero-lateral angle of the bulla in front of the stylomastoid foramen (Gregory, 1920, pp. 165, 178, 183). In *Adapis* as well there is no carotid foramen on the under surface of the bulla as in *Tarsius* and in the monkeys (Winge, 1895*a*, p. 37).

In the ancestral protoadapine stock as well, according to Gregory (1920, p. 232), the posterior carotid foramen was situated as in *Notharctus*, at the postero-external angle of the bulla.

Aphanolemur gibbosus (Granger and Gregory, 1917, p. 857) agrees with *Notharctus* in the course of the internal artery.

In one skull of *Archæolemur edwardsi* Standing (1908, pp. 100, 101) describes a deep cylindrical channel between the roughened surface of attachment of the rectus anticus major muscle and the summit of the bulla. Perhaps this is formed by the carotid artery. According to Gregory (1920, p. 177) the posterior carotid foramen in *Archæolemur* lies at the posterior end of the bulla.

In the modern Chiromyidæ (Van Kamp.; Gregory, 1915, p. 435) the

course of the internal carotid is as that in the Lemuridæ and Indrisidæ. The posterior carotid foramen lies at the posterior end of the bulla, 3 mm. below the stylomastoid foramen (Gregory, 1920, p. 177). It lies more mesialward than it does in *Lemur* and more nearly as in *Microcebus furcifer*. It lies either in the bulla or on the boundary of the bulla and the mastoid, as to which opinions differ.

In the Lorisiformes in general (Winge, 1895*a*, p. 37; Gregory, 1915, pp. 430, 431, 436; Carlsson, 1922, p. 233) the main branch of the internal carotid artery does not pierce the bulla at all, but enters the braincase through the widely open foramen lacerum medium, a condition which is probably secondary. Besides this, Winge (1895*a*, p. 37) describes a very small posterior carotid foramen in the caudal wall of the bulla a little outside the foramen jugulare in *Nycticebus tardigradus*. A similar small foramen is found by Van Kampen in *Perodicticus*, *Nycticebus* and *Galago*, lying, according to him, on the same place as in *Microcebus*. In young specimens this foramen lies posteriorly in the bulla between the petrosal and the bulla. Gregory (1915, p. 430; 1920, p. 180) mentions as a general character of the Lorisidæ a reduced foramen caroticum posterius lying at the posterointernal region of the bulla immediately in front of the foramen lacerum posterius.

In *Tarsius* (Van Kamp.; Winge, 1895*a*, p. 38; Gregory, 1915, pp. 429, 431; 1920, p. 179) the arteria promontorii or true entocarotid is greatly enlarged and supplies the chief arterial supply for the cerebra. This artery pierces the bulla (Van Kamp.; Winge, 1895*a*, pp. 16, 38; Gregory, 1915, p. 431; 1920, p. 180) in the middle of its lower surface (Gregory, 1915, pp. 430, 431, 437). In the embryo *Tarsius* the entrance to the carotid canal is nothing else than a deep groove in the lateral margin of the petrous bulla, closed by the tympanic. The wall of the carotid canal is already ossified, before the septum in the bulla is ossified. In the adult *Tarsius* the carotid canal lies in the thickened lateral margin of this septum, and the posterior carotid foramen lies laterally on the boundary of the two parts of the bulla. Winge (1895*a*, p. 38) describes still another small foramen in the caudal wall of the bulla, which is not confirmed by Van Kampen (Van Kamp.; Gregory, 1920, p. 180).

The fossil *Necrolemur* (Gregory, 1915, pp. 430, 442) resembles *Tarsius* in the position of the posterior carotid foramen, which lies on the inner or medial surface of the bulla (Gregory, 1915, pp. 430, 431) immediately in front of the foramen lacerum posterius (Gregory, 1920, p. 180). Through this carotid foramen the main branch of the internal carotid apparently entered (Gregory, 1915, p. 431).

In the fossil "*Anaptomorphus*" (*Tetonius*) (Gregory, 1915, pp. 430, 431) the place of the posterior carotid foramen is unknown, but the internal carotid must surely have traversed the tympanic chamber, either as in *Necrolemur* or as in *Tarsius*.

In the New and Old World monkeys (Van Kamp.; Winge, 1895*a*, pp. 12, 53; Gregory, 1915, p. 429; 1920, p. 179) the internal carotid, which is supposed to be homologous with the arteria promontorii, is greatly enlarged and furnishes the chief arterial supply for the cerebra. Thus the development of the carotid canal is related to that of the brain (Winge, 1895*a*, pp. 11, 52). The posterior carotid foramen is more or less shifted forward, never so much as in *Tarsius* (Van Kamp.; Winge, 1895*a*, p. 38) and sometimes even not greatly different in position from the original place. It is shifted forward medially along the bulla. In relation to this the adult specimen still shows cellulæ of the bulla between the posterior carotid foramen and the tympanic, while in *Tarsius* they immediately join each other.

In the New World monkeys(Gregory, 1920, pp. 180, 218) the carotid foramen is shifted medially; it faces posterointernally and it is generally near the posterior border of the bulla.

According to Gregory (1920, p. 165) the opening of the carotid canal in the South American monkeys retains its old place behind the ring, but in these genera is also internal to it and presents inward or inward and backward rather than outward and backward. In the primitive Platyrrhinæ, according to Gregory (1916, p. 266) the internal carotid canal is frequently located on the posterior side of the periotic.

In the modern Hapalidæ the posterior carotid foramen lies in the posterior half of the mesial wall of the bulla, a little in front of the foramen lacerum posterius. It lies a little more anteriorly than in the Lemuridæ, but not so much as in *Tarsius*. Precisely, it does not lie in the bulla, but at the place where the wall of the tympanic cavity passes into the wall of the labyrinth and thus mesially from the wall of the bulla, an important difference from the condition found in *Tarsius*. The foramen caroticum posterius is little or no larger than that in the Lemuridæ and *Tarsius*. The canalis caroticus runs obliquely upward and forward through the septum, which separates the tympanic cavity from the cellulæ petrosæ. The carotid canal is entirely surrounded by bone. On the small canal between the bulla and the basioccipital in *Hapale* and others, see Gregory (1920, p. 181).

In some genera among the modern Cebidæ the foramen caroticum posterius is the same width, or only slightly wider than that in the

Hapalidæ; in other genera, however, it is much wider. As a rule it lies a little more backward than that in the Hapalidæ, sometimes rather far backward. The carotid canal runs upward and forward; cellulæ petrosæ partly surround it.

In the primitive Catarrhinæ, according to Gregory (1916, p. 266), the internal carotid canal pierces the periotic on its posteroventral surface.

In the modern Cercopithecidæ the foramen caroticum posterius is wide. In the new-born specimen this foramen lies between the bulla and the petrosal proper. In the adult it sometimes lies on the mesial side of a first indication of a crista petrosa. The position is the same as in the Cebidæ, with which the carotid canal also agrees. According to Gregory (1920, p. 181) the carotid pierces the bulla more posteriorly than in the Hylobatidæ and the Simiidæ.

In the Hylobatidæ and Anthropomorphæ the posterior carotid foramen has the normal position, and also the course of the carotid canal resembles that in the lower monkeys. The posterior carotid foramen in some genera faces backward, in others downward. In *Hylobates* it is much wider than that in the lower monkeys.

In *Homo* only, the carotid canal (Van Kamp.; Rouvière et Delmas, 1913) does not lie within the tympanic cavity but in front of it, a secondary condition in consequence of the reduction of the cellulæ petrosæ, which in the monkeys separate the carotid canal from the proper tympanic cavity. In man (Van Kamp.; Winge, 1895*a*, p. 28; Gregory, 1916, pp. 278, 280) the carotid canal is much larger than in all anthropoids in consequence of the enormous development of the brain.

Anterior Carotid Foramen

The entocarotid enters the skull through the foramen caroticum, which often coincides with the foramen lacerum anterius s. medium (Zittel, 1893, p. 16; 1923, p. 409, says that the "innere Kopfblutader," by which he probably means the entocarotid artery, enters through the posterior lacerate foramen and leaves through the anterior lacerate foramen; this of course is not correct). On a separate foramen caroticum remote from the foramen lacerum medium in the hyænas, see Pocock (1916*e*, p. 307).

In many cases, where the bulla is very large, the foramen lacerum medium lies inside the bulla, so that it is not necessary for the entocarotid which entered the tympanic chamber through the posterior carotid foramen to leave it again. In the cases however where the entocarotid enters

through a posterior carotid foramen and where the foramen caroticum lies outside the bulla, the artery has to pass out again. The opening through which it leaves is called the anterior carotid foramen.

The anterior carotid foramen in *Lepus* lies on the mesial side of the foramen for the Eustachian tube and is also covered by the bulla.

In *Canis* (Pocock, 1916*a*, p. 262) the foramen caroticum anterius lies at the anterointernal angle of the bulla on the admedian side of the adjacent orifice of the Eustachian tube and just above the foramen lacerum medium through which the artery enters the cranium.

In the modern Ursidæ the anterior carotid foramen lies at the rostral point of the bulla just mesially of the orificium tubæ.

In the modern Procyonidæ this carotid foramen lies in the rostral part of the bulla about beneath the anterior lacerate foramen.

In the modern Mustelidæ the rostral foramen of that part of the sulcus caroticus which lies in front of the foramen lacerum anterius is found on the mesial side of the orificium tubæ.

In the Viverridæ in general, according to Pocock (1916*a*, p. 262), the anterior carotid foramen opens into a space beneath the bulla common to it and the Eustachian tube. Also for *Cryptoprocta* and *Mungos* especially, Pocock (1916*a*, pp. 264, 265) mentions that the anterior carotid foramen lies alongside the Eustachian aperture.

In the Viverrinæ (Van Kamp.; Pocock, 1916*a*, p. 263, *Genetta*) this carotid foramen lies just above the foramen lacerum medium and is covered by the bulla. In the Herpestinæ, however, it lies a little behind the foramen lacerum anterius and it is not covered by the bulla. In *Cryptoprocta* the anterior carotid foramen is partly covered.

In *Felis spelæa*, according to Dawkins (1878, p. 48), the foramen caroticum anterius lies together with the Eustachian aperture in the large irregular cavity formed by the junction of the bulla, the basi- and alisphenoid and the petrosal.

In the modern Phocidæ the foramen caroticum anterius is concealed from view by the bulla. To this carotid foramen and to the foramen lacerum anterius leads either a wide entrance or a narrow canal, enclosed in the wall of the bulla, of which the rostral foramen lies far forward, thus resembling the conditions found in the Mustelidæ.

In the Otariidæ the foramen caroticum anterius is externally visible; it lies just beneath the foramen lacerum anterius and on the mesial side of the orificium tubæ.

In the modern Cetacea the carotid artery leaves the tympanic cavity through the rostral part of the fissura petrotympanica.

Separate Foramen for the Inferior Branch of the Stapedial Artery

Generally the inferior branch of the stapedial artery leaves the tympanic chamber through the fissura Glaseri, but sometimes through a distinct opening, which is found in some insectivores. In *Centetes* it is probably the very small opening in the tympanic process of the alisphenoid. In *Erinaceus* the opening lies in the tympanic process of the alisphenoid or in a groove in this process, which is closed by the tympanic (Van Kamp.; Gregory, 1910, pp. 247, 261; 1915, p. 428; 1920, p. 172). In *Myogale* it lies between the tympanic and the alisphenoid, external to the foramen ovale (Van Kamp.; Gregory, 1910, p. 264). In *Ericulus* and *Microgale* it lies just beneath the foramen ovale. In *Tupaia* (Gregory, 1915, p. 428; 1920, p. 174) the ramus inferior of the stapedial artery issues from the tympanic cavity anteriorly, as in *Erinaceus*.

Gregory (1915, pp. 428, 429; 1920, p. 182) emphasizes the total lack of this carotid foramen in all recent Lemuriformes, *Notharctus* and *Adapis*, notwithstanding their agreement in the course of the entocarotid with that of the Tupaiidæ (Van Kamp.; Gregory, 1910, p. 321; 1913*b*, p. 248).

Gregory (1920, p. 172) calls this carotid notch or foramen in *Erinaceus* "foramen caroticum alisphenoidei."

Internal Structure of the Bulla

Elements of the Bulla Partly or Entirely Covering Each Other

A remarkable feature is found in marsupials. In the Peramelidæ, Dasyuridæ, and only a little or not at all in the Notoryctidæ, the bulla alisphenoidea covers a larger or smaller part of the tympanic.

In Macropodidæ, on the other hand, the proximal part of the under surface of the meatus acusticus is curved downward, so that the under margin of the tympanic lies against the external surface of the alisphenoid bulla.

A still more extreme condition is found in the Tupaiidæ and in the lemurids of Madagascar. In the Tupaiidæ the narrow tympanic ring lies free in the auditory bulla, which is formed by the entotympanic, showing only a membranous connection with the inner wall of this bulla (Van Kamp.; Winge, 1893*a*, p. 43; Gregory, 1910, p. 274; Matthew, 1909, p. 504; the statement that we have the same condition in the Macroscelidæ is not right; Carlsson, 1910*a*, p. 352; 1922, pp. 230, 231). It is also proposed as a possibility, that the sulcus tympanicus, with the margo sulci tympanici s. crista tympanica, pushed more and more into the bulla and finally lost its contact with the rest of the tympanic, so

that the free ring in the bulla should be only a part of the tympanic (Winge, 1893*a*, p. 44; 1895*a*, p. 39). This is not probable, especially in relation to the ontogeny of the bulla in the lemurids, which teaches us that the annulus of the adult is not a secondarily detached part of the bulla (Van Kamp.; Gregory, 1920, p. 163). In the Tupaiidæ the free tympanic ring lies immediately against the inner wall of the bulla, in contrast with the condition in the lemurids. In the lemurids of Madagascar we find also a free tympanic ring in the bulla (Van Kamp.; Winge, 1893*a*, p. 43).

In all recent Prosimiæ from Madagascar and in these recent Prosimiæ only, we find a ring-like free tympanic lying within the auditory bulla, so as to be completely concealed by the wall of the bulla, as seen from below. It occurs among recent forms in the lemurs, *Chirogaleus*, *Propithecus* and allied genera (Van Kamp.; Winge, 1893*a*, pp. 43, 44; 1895*a*, pp. 17, 20, 39, 54; Gregory, 1915, pp. 422, 426, 434, 345, 440; 1916, p. 264; 1920, pp. 163, 164, 214, 221; Carlsson, 1922, p. 231; Zittel, 1923, p. 639), in the Chiromyidæ (Van Kamp.; Winge, 1893*a*, pp. 43, 44; Gregory, 1915, pp. 426, 435; 1920, p. 221; Carlsson, 1922, p. 231).

Among the fossils, the tympanic lies within the bulla in a similar way in *Notharctus* (Gregory, 1915, pp. 422, 426; 1920, pp. 164, 165, 194, 218, 220, 224, 227, 232) and in *Adapis* (Van Kamp.; Gregory, 1915, pp. 422, 426; 1920, pp. 164, 194, 213, 214, 220), so that it is given as a character for the Adapidæ in general (Gregory, 1915, pp. 433, 440; Zittel, 1923, p. 639) and also for the ancestral protoadapine stock (Gregory, 1920, p. 232). Farther on it is described in the fossil Megaladapinæ (Gregory, 1915, p. 426; Lorenz von Liburnau, 1905, p. 464, *Megaladapis edwardsi*), in the Pleistocene Lemuridæ (Gregory, 1920, p. 214), and in the Archæolemurinæ (Gregory, 1915, pp. 426, 435), as in *Nesopithecus* (Van Kamp.). Thus it is easily understood that this condition is given as a character of the Lemuriformes, to which larger group all or nearly all above-mentioned recent and fossil Prosimiæ are brought (Gregory, 1915, pp. 426, 432, 441; 1920, p. 183; Zittel, 1923, p. 638).

In *Lemur mongos*, according to Van Kampen, the ends of both legs of the tympanic lie against the inner wall of the lateral part of the bulla; the middle part of the ring, in contrast with that of *Tupaia*, is separated from the wall of the bulla by a rather broad space filled with membrane, which also occurs in other recent Prosimiæ from Madagascar (Van Kamp.; Winge, 1895*a*, pp. 17, 39; Gregory, 1920, p. 214). In the

Eocene Adapinæ as well, the tympanic ring was evidently separated from the inner wall of the bulla by membrane (Gregory, 1920, pp. 213, 214), while in the Pleistocene and recent Lemuridæ this membrane was reduced or absent (p. 214). An exception is formed by *Megaladapis edwardsi*, judging from the notes given by Lorenz von Liburnau (1905, p. 464) that the tympanic was coössified with the bulla. According to Van Kampen (1905, not in edition 1904) this condition probably signifies that the membrane connecting the tympanic with the inner wall of the bulla is ossified.

In *Palæopropithecus* (Gregory, 1915, pp. 434, 435) the bulla does not completely enclose the tympanic annulus. Also in the Eocene Adapidæ (Gregory, 1920, p. 212) the tympanic ring remains morphologically outside the bulla, except to a very limited extent. Thus Gregory's opinion (1920, p. 212) is that in a primitive lemur the tympanic ring should remain morphologically outside the bulla, and he gives (1920, p. 213) as a character of the hypothetical Palæocene protolemurines, that the hypotympanic sinus does not cover the tympanic ring.

According to Gregory (1915, p. 426; 1920, p. 220) the overlapping of the tympanic by the bulla in the Eocene and recent Lemuriformes is primitive for all primates, though it is not a primitive placental condition (p. 221). The alternative hypothesis, that the platyrrhine condition has been derived from a stage in which the bulla had not yet overlapped the tympanic ring, is not defended by Gregory (1920, p. 221). According to Gregory (1920, p. 220), in the ancestors of the Platyrrhinæ, probably the rapid transverse expansion of the brain initiated a secondary uncovering in the following manner. The tympanic ring, retaining its connections with the entoglenoid and posttympanic processes, shared in the general lateral displacement of this region, while the bulla itself remained fastened to the side of the basioccipital and to the postero-external corner of the basisphenoid. The ring was first exposed at the aperture of the bulla, then protruded from it and then began to overlap it, which is a generalized platyrrhine condition (Gregory, 1920, p. 218).

Sulcus Tympanicus and Crista Tympanica

The tympanic membrane is always attached to the tympanic even if this lies free in the bulla. As a rule it is attached in the groove or sulcus tympanicus, which the tympanic ring and also the broadened tympanic show on the inside. In a few cases, however, the sulcus tympanicus is lacking and the tympanic membrane is attached to the crista tympanica. According to Bondy (1907, p. 394) this is the case in Leporidæ (see also,

loc. cit., p. 322) and Caviidæ (see also, *loc. cit.*, pp. 346, 347). Also in *Talpa* (Bondy, 1907, p. 305) the tympanic membrane is attached to the crista, though a sulcus seems to be present.

In *Myoxus avellanarius* (*loc. cit.*, p. 329) and *Arvicola arvalis* (*loc. cit.*, p. 335) as well, the crista serves for the attachment of the tympanic membrane. In *Tolypeutes tricinctus* (Bondy, 1907, p. 349) the tympanic membrane is attached to the crista and to the true cavernous tissue that fills up the deep sulcus tympanicus. In *Canis familiaris* (Bondy, 1907, p. 353) the tympanic membrane is attached to the crista tympanica from the processus Folii toward the base of the cartilaginous "Chordafortsatz."

The margo sulci tympanici (Van Kampen) or the crista tympanica (Bondy, 1907, p. 394) is the bony ridge that lies on the medial side of the sulcus. It develops out of the bony margin on the medial side of the sulcus which the primitive tympanic ring shows, while the lateral margin disappears in the bony recessus meatus. Of course the tympanic membrane separates the tympanic cavity and the external auditory meatus, which often hardly can be separated externally, as the bony recessus meatus forms a part of the bulla. In the dry skull, where the tympanic membrane is lacking, Van Kampen takes the sulcus tympanicus as the limit between the tympanic cavity and recessus meatus. Bondy (1907, p. 394), however, takes the crista tympanica, as the sulcus is sometimes absent, as we have seen; also as there is often no well-marked transition between the sulcus and the inner wall of the bony recessus, and as the crista can be recognized much more easily.

Crista Tympanica and Sulcus Tympanicus Projecting into the Cavity of the Bulla

The crista tympanica (Bondy) or the margo sulci tympanici together with the sulcus tympanicus sometimes lie well within the inside of the bulla. This is due to the fact that the hypotympanic sinus extends so far laterally that it lies even on the lateral side of the most proximal part of the recessus meatus, which of course is especially distinct in the under part, more than in the rostral and caudal parts. We can thus say that the external auditory meatus projects into the cavity of the bulla.

This bony ridge in the bulla is sometimes called "annulus tympanicus" (Winge, 1893*a*, p. 44; Pocock, 1916*e*, pp. 303, 306; 1921, pp. 478, 484, 485), but this is not correct as it is only a part of the tympanic ring. We have spoken above of the improbability that the free ring in the bulla in Tupaiidæ and lemurids is nothing but this loosened

ridge of the inner wall of the bulla, (Winge, 1893*a*, p. 44; Van Kampen, 1904, p. 124; 1905, p. 448).

The feature that the margo sulci, together with the sulcus, lie far within the inside of the bulla is well known in Carnivora, Rodentia, and ungulates. This occurs also in many marsupials. We have seen that in some marsupials the tympanic is partly covered by the alisphenoid bulla but even in *Phascolarctus* and in the Phalangeridæ, where the alisphenoid does not cover the tympanic, the crista and the sulcus lie far within the inside of the bulla, while in *Phascolomys* the membranous ventral wall also reaches the tympanic at some distance on the lateral side of the sulcus tympanicus. In *Macroscelides* the crista and the sulcus also lie well within the inside of the bulla.

Among the rodents we find very different conditions in the various genera; the crista with the sulcus may lie within the inside of the bulla to different degrees, while in others this feature is not distinct.

This feature is also present in the modern Carnivora. Van Kampen mentions it for the Canidæ, Ursidæ, Mustelidæ (Van Kamp.; Bondy 1907, p. 361, *Mustela foina*), *Felis* and *Hyæna crocuta*, in which it is developed in different degrees. In *Phoca grœnlandica* it lies but a little way within the inside of the bulla. Dawkins (1878, p. 48) mentions in *Felis spelæus* in side the "meatus auditorius" in the true tympanic chamber, i.e., on the lateral side of the septum bullæ, a long septum or curtain partially dividing the chamber and forming a deep groove open downward, which passes under and in front of the "meatus." In the Felidæ and Viverridæ, according to Pocock (1916*e*, p. 303), the outer chamber of the bulla is itself partially divided from the external auditory meatus by a horseshoe-shaped ridge or crest. Pocock, (1921, pp. 478, 484, 485) mentions its differences in height in modern mustelids: in *Meles* and other genera it projects far into the cavity of the bulla, while in *Lutra*, *Grisonella*, *Pœcilogale*, it is less high and then closely applied to the roof of the bulla. According to Pocock (1916*e*, p. 306) it is the outer of the two laminæ of Mivart in *Hyæna*.

In *Equus* the proximal part of the external auditory meatus projects but slightly into the cavity of the bulla, as the hypotympanic sinus extends but little in the lateral direction. The same is the case in *Tragulus*, in the modern Cervidæ and Bovidæ; in the latter two groups it stands relatively far back on the inside of the bulla. In *Procavia*, however, in which the bulla is slightly developed, this feature is not present. In the modern Camelidæ the margo sulci and the sulcus stand but little back on the inside of the bulla, though the hypotympanic

extends far lateralward along the under wall of the external auditory meatus. This is caused by the fact that this lateral extension is filled with cancellous bone.

Sulcus Tympanicus

Sometimes a sulcus or groove is present on the lateral side of the crista tympanica but the tympanic membrane is not inserted in it, so that this groove must be called recessus meatus (Bondy, 1907, p. 322; *Lepus cuniculus;* p. 346, *Cavia cobaia*). In other rodents the tympanic membrane is inserted into the sulcus (Bondy, 1907, pp. 331, 332, *Cricetus frumentarius;* p. 336, *Mus decumanus*).

In *Vesperugo noctula* (Bondy, 1907, pp. 313, 314) we find a very broad sulcus tympanicus, which at the lateral margin of the bone is used for the attachment of the tympanic membrane, so that a bony recessus meatus is lacking; the sulcus is especially broad in the under part and filled with cavernous (?) tissue, as Bondy (1907, pp. 314, 316) found in all the Chiroptera examined.

The sulcus is as a rule broadest in the under part and diminishes in breadth and depth toward the extreme ends of the two legs of the tympanic ring (Bondy, 1907, p. 307, *Erinaceus*; p. 331, *Cricetus frumentarius;* p. 368, *Phoca vitulina;* p. 384, *Macacus nemestrinus;* Claudius, 1867, p. 8, *Rhytina*).

We do not find the sulcus along the whole length of the tympanic annulus as a rule. The reason is, that as a rule the pars tensa of the tympanic membrane is not attached to the extreme ends of the two legs of the tympanic ring, as we shall see later, describing the crista tympanica. In *Miniopterus schreibersi* (Bondy, 1907, p. 318), however, the sulcus is present on the entire circumference of the tympanic. In *Arvicola arvalis* (Bondy, 1907, p. 335) the sulcus is present except at the extremities of both horns of the tympanic. In *Mus musculus* (Bondy, 1907, pp. 338, 339) the well developed sulcus tympanicus occupies little more than half the ring. In *Rhytina* (Claudius, 1867, p. 8) the dorsal third part of the line of attachment of the tympanic membrane is lacking; the sulcus is very distinct behind and beneath and ends suddenly with the caudal horn of the tympanic; this groove continues on a projecting bony ridge on the rostral horn of the tympanic. The sulcus tympanicus in *Rhytina* (Claudius, 1867, p. 8) lies on the lateral side of the tympanic ring, so that the diameter of the tympanic membrane is larger than the lumen of the tympanic ring in relation to the form of the tympanic ring, which in transverse section is elliptical. In *Halicore* (Freund, 1908, p. 621,

the sulcus is distinct on the rostral leg, indistinct on the caudal leg of the tympanic.

The sulcus tympanicus is very differently developed. In *Phoca vitulina* (Bondy, 1907, p. 368) it is rather broad but little deep. In *Halitherium schinzi*, according to Lepsius (1882, p. 36), the sulcus is broad, its under margin is sharp, its upper margin plainly rounded, most sharp along the caudal horn. The sulcus is very distinct in *Rhytina* (Claudius, 1867, p. 8). It is less distinct in the modern Sirenia, especially in *Manatus*. Freund (1908, pp. 617, 619, 621) mentions that it becomes deeper during development in *Halicore*. In *Kogia* (Schulte, 1917, p. 396) the bulla is deeply incised, evidently serving for the attachment of the drum membrane. In *Phocæna communis* (Matthew, 1912, p. 594) a typical sulcus is wanting. In the Balænopteridæ the sulcus is sometimes distinct, in other cases absent, a feature which is perhaps related to age. In *Homo*, according to Bondy (1907, pp. 387, 388), the sulcus tympanicus as a rule is present, but often very poorly developed and practically never along the entire outline uniformly developed.

Even in fossils the sulcus tympanicus is sometimes distinct, as we have already seen. Owen (1840, p. 59) mentions for *Glossotherium* a groove, one line in breadth, along the concave margin of the tympanic for the attachment of the ear-drum.

Crista Tympanica or Margo Sulci Tympanici

The crista tympanica or margo sulci tympanici is highest in the under part of the tympanic and diminishes in height toward the two legs of the tympanic. In a few cases (Bondy, 1907, p. 394) the crista ends on the ventral side of the extreme ends of the two legs of the tympanic, Bondy's so-called "Tympanicumschenkel," which limit Bondy's so-called "Tympanicumdefekt" (*loc. cit.*, p. 300). We find this in *Talpa* (Bondy, 1907, p. 305).

As a rule, however, the crista ends with a spina tympanica anterior and posterior, which lie not at the tops of the extreme ends of the tympanic ring, but at a short distance before these tops (Bondy, 1907, p. 300). The development of these spinæ is very different. Often only one is developed (Bondy, 1907, p. 394). The length of the crista, and in connection with this the place of the spinæ, is also very different (Bondy, 1907, p. 395). These features are related to the development of the membrana Shrapnelli, whose under margin is the line that connects the two spinæ tympanicæ (Bondy, 1907, p. 395).

In *Erinaceus* the crista ends on the top of the very short rostral leg,

while on the caudal leg it does not reach the top (Bondy, 1907, pp. 307, 308). In *Sorex* it also ends at the top of the rostral leg, while on the caudal leg we find a spina tympanica posterior, which is absent in another species of this genus (Bondy, 1907, p. 310). In *Vesperugo noctula* the crista also ends on the rostral leg at the top and on the caudal leg in a small spina tympanica posterior (Bondy, 1907, p. 313). In *Vesperugo serotinus*, where the tympanic is very simple without processes, we also find the crista at the top, while on the caudal leg it is distinct only for a short distance (Bondy, 1907, p. 315). In *Vespertilio murinus* too the crista is found over the whole length of the rostral leg, while it is absent on the extreme end of the caudal leg (Bondy, 1907, p. 317). In *Plecotus auritus*, on the caudal leg of the tympanic the crista ends in a short spina tympanica posterior just behind the caudal end of the rostral leg (Bondy, 1907, p. 319). In *Rhinolophus ferrum equinum* the crista ends on the rostral leg at a very short distance before the top and on the caudal leg near the place of connection with the rostral leg (Bondy, 1907, pp. 319, 320). In *Miniopterus schreibersi*, where the tympanic does not show any processes, the line that separates the pars tensa of the tympanic membrane and the membrana Shrapnelli, Bondy's so-called "Grenzbogen," lies between the two pointed extreme ends of the two legs of the tympanic (Bondy, 1907, p. 318).

In *Tolypeutes tricinctus* (Bondy, 1907, p. 349) the crista tympanica is well developed and ends on the posterior leg of the tympanic before its end, on the anterior leg on the top; whether or not there is a spina tympanica anterior could not be decided.

As to the condition of the crista tympanica in the modern rodents we owe many remarks to Bondy (1907). In *Lepus cuniculus* (p. 321) the crista is ca. 1 mm. high, sharp and caudosuperiorly wanting on a distance of ca. 2 mm.; the spina posterior is distinct; the spina anterior is nothing else than a sharp point of the crista. Although the tympanic in *Sciurus vulgaris* (p. 325) is closed all around, the crista shows a small hiatus. In *Myoxus avellanarius* (p. 328) both spinæ are present, the spina posterior is better developed than the anterior; the crista is ventrally divided into two lips, between which the sulcus tympanicus is found. *Myoxus glis* (p. 330) shows a poorly developed spina tympanica anterior. In *Cricetus frumentarius* (pp. 331, 332), the crista is relatively high and sharp and shows at some distance from the extremity of the horn of the tympanic an indication of a spina tympanica anterior. In *Arvicola arvalis* (pp. 334, 335) the crista extends on the rostral leg of the tympanic as far as the place where this leg touches the tip of the caudal leg. In

Mus decumanus (p. 336) the crista reaches the free end of the caudal leg of the tympanic, but stops at a distance of 1 mm. from that of the rostral leg. In *Mus musculus* (p. 338) on the caudal leg the crista reaches the "Chordafortsatz," on the rostral horn of the tympanic, the sulcus malleolaris, but does not extend farther on this horn. The latter is also the case in *Mus silvaticus* (pp. 340, 341); on the caudal leg the crista finally diverges to the lateral surface of the tympanic. In *Mus minutus* (p. 342) the crista extends rostrally as far as the place of attachment of the Folian process, where it ends with a low, sharp spina tympanica anterior; the spina posterior is a little better developed. In Bondy's remarkable "Feldmaus" (p. 344) the crista is restricted to the corpus tympanici, being absent on the two horns; the spina tympanica posterior is pointed, while the spina anterior is absent. In *Cavia cobaia* (pp. 346, 347) the crista is well developed; it passes on the dorsal outline into a small bony plate, which also coheres with the petrosal and which forms the lateral wall of the epitympanic recess.

In *Canis familiaris* (Bondy, 1907, pp. 352, 353) the sharp crista tympanica extends rostrally to the Folian process, caudally to a small groove in which the cartilaginous "Chordafortsatz" is inserted. In *Fœtorius vulgaris* (p. 356) the crista tympanica is not found along the entire outline of the tympanic, which is closed all around; a small spina tympanica posterior is present. In *Fœtorius putorius* (p. 359) and in *Mustela foina* (p. 361) the crista occupies three-fourths of the entire outline only. In *Mustela foina* (p. 361) the crista reaches rostrally the sulcus malleolaris, caudally it gradually disappears. In *Fœtorius putorius* (p. 359) the spina anterior is poorly developed, and the spina posterior is fine and sharp. In *Viverra zibetha* (p. 363) the crista is present only in the ventral two-thirds of the ring; there are no distinct spinæ, which in *Herpestes fasciatus* (p. 364) are both indicated. In *Felis domestica* (p. 366) the crista tympanica gradually diminishes in height on the rostral leg of the tympanic; on the caudal leg it ends with a distinct spina posterior. In *Phoca vitulina* (p. 368) the spina anterior is indistinct and rudimentary; caudally the crista passes into the free margin of the lateral wall of the epitympanic recess.

In *Equus caballus* (Bondy, 1907, p. 369) the crista tympanica is well developed and ends with two blunt spinæ. In *Sus scrofa domestica* (p. 371) the crista is well developed; the spina tympanica posterior is distinct and there is no spina anterior. In *Cervus capreolus* (p. 376) the crista occupies but half the entire outline of the tympanic; it nearly reaches the end of the caudal leg, while on the rostral horn it extends to

the fissura Glaseri only. The latter also occurs in *Cervus elaphus* (p. 377), in which it reaches the root of the caudal horn of the tympanic. In *Capra hircus* (p. 380) the crista shows nearly the same extension as that in *Cervus elaphus*. In *Bos taurus*, according to Bondy (1907, p. 381), the crista agrees with that in *Cervus capreolus*.

In *Macacus rhesus* (Bondy, 1907, p. 385) a small spina tympanica posterior is present.

In *Homo*, according to Bondy (1907, pp. 387, 388), the crista tympanica as a rule is present, but often poorly developed and never uniformly developed along its entire outline. Both spinæ tympanicæ vary greatly in size; the anterior one is a little more constant; the posterior spina can be absent.

The projecting bony ridge on the tympanic in *Rhytina* (Claudius, 1867, p. 8) is perhaps a spina tympanica anterior, in my opinion. The sulcus tympanicus is prolonged along it, and thus the tympanic membrane probably is attached to it.

Septum Between the Recessus Meatus and the Bony Cylindrical External Auditory Meatus

In *Procavia* (*Hyrax*) there occurs a vertical septum between the recessus meatus and the bony cylindrical external auditory meatus. It seems as if the wall of the bulla (i.e., tympanic cavity and recessus meatus) continues in the lumen of the auditory meatus. It projects from the under and caudal wall about halfway in the lumen of the auditory meatus. In the very young animal no septum as yet is present. It develops secondarily, not as an outgrowth but by the widening of the lumen of the bony cylindrical external auditory meatus. The latter becomes relatively much wider, while the bulla retains about the same size.

In *Palæopropithecus* (Gregory, 1920, p. 176) a thick membrane that lies external to the tympanic annulus has become irregularly ossified, in such a manner as to obstruct the opening of the external meatus.

Processus Folii of the Malleus on the Inside of the Bulla

As we shall describe extensively later, the processus folii of the malleus is often connected with the tympanic. So it is a matter of course that we find it on the inside of the bulla, as is sometimes emphasized (Bondy, 1907, pp. 394, 402).

Bondy's "Chordafortsatz"

In a few cases we find another small process attached to the inner wall of the bulla, Bondy's so-called caudal "Chordafortsatz." This

element conducts the chorda tympani nerve from its entrance in the tympanic chamber toward the malleus. It is often bony, sometimes partly or totally cartilaginous and can be free or attached to the different elements in the hinder part of the tympanic chamber. So in a very few cases it is attached to the tympanic (Bondy, 1907, p. 401). Bondy describes this in *Vesperugo noctula* (*loc. cit.*, p. 315), where it lies just beneath the spina tympanica posterior, while in the allied *Vesperugo serotinus* the "Chordafortsatz" is a process of the basis of the processus hyoideus (*loc. cit.*, p 316).

Probably the "Chordafortsatz" is already described in some rodents by Hyrtl (cited by Van Kampen and by Bondy, 1907, p. 326, *Sciurus*) as the bony lamella of the tympanic, running from the upper periphery of the annulus tympanicus toward the promontorium, and behind which the incus and stapes are completely concealed. We owe many remarks on the "Chordafortsatz" in modern rodents to Bondy (1907). It is not always present. A bony "Chordafortsatz" is said to be absent in *Arvicola arvalis* (*loc. cit.*, p. 336), *Cavia cobaia* (p. 348) and *Dasyprocta aguti* (p. 349). In *Lepus cuniculus* (p. 323) it is a low bony ridge parallel to the tympanic membrane on the caudosuperior periphery of the tympanic. In *Sciurus vulgaris* (p. 326) the "Chordafortsatz" is a vertical bony plate evidently attached to the tympanic on the mesial side of its caudal leg. In *Myoxus glis* (p. 330) it is a mesialward-directed small bony plate on the caudal leg of the tympanic. In *Cricetus frumentarius* (p. 332) the strong bony "Chordafortsatz" lies on the caudal leg of the tympanic at some distance of its extremity; it is directed a little mesialward. In *Mus musculus* (p. 338) it is at right angles with the caudal leg of the tympanic, on whose root it originates, projecting into the tympanic cavity. In *Mus silvaticus* (pp. 340, 341) it is the extremity of the crista tympanica, which turns round the tympanic. In *Mus minutus* (p. 342) it originates on the mesial side of the caudal leg of the tympanic. In *Mus decumanus* (pp. 336, 337) the "Chordafortsatz" is the continuation of a process on the petrosal.

In *Canis familiaris*, according to Bondy (1907, pp. 353, 394), the plate which is probably homologous with the "Chordafortsatz" is cartilaginous and does not seem to ossify or at least to get a bony connection with the tympanic. Thus it is absent in the macerated skull. It is inserted in a little groove on the top of the hind leg of the tympanic. In *Fœtorius vulgaris* (p. 358) the bony "Chordafortsatz" originates on the mesial side of the crista tympanica, probably from the tympanic. In *Fœtorius putorius* (p. 361) it is rudimentary and attached to the bulla. In

Mustela foina (p. 362) it is attached to the tympanic, short and blunt. In *Viverra zibetha* (pp. 363, 364) the bony "Chordafortsatz" shows a cartilaginous tip; it is attached to the caudal leg of the tympanic above the crista tympanica, while in *Felis* it is free.

In *Equus caballus* (Bondy, 1907, p. 370) the "Chordafortsatz" is attached to the bulla. In Bondy's (1907, p. 375) material of *Sus scrofa domestica* the "Chordafortsatz" is cartilaginous but begins to ossify; caudally it is attached to the caudal leg of the tympanic, dorsally to the petrosal. In the young specimen of *Capra hircus* (Bondy, 1907, p. 380) the "Chordafortsatz" is still cartilaginous; it is attached to the caudal leg of the tympanic. In *Bos taurus* (p. 381) and in *Ovis aries* (pp. 382, 383) as well the cartilaginous "Chordafortsatz" is attached to the caudal leg of the tympanic.

In *Ateles paniscus*, according to Bondy (1907, p. 386), the rudimentary "Chordafortsatz" is a low, blunt bony ridge. In *Homo* (p. 392) it is bony and rudimentary; it belongs either to the tympanic or to the squamosal, but this point could not be decided in consequence of the early fusion of these elements. In *Macacus nemestrinus* (p. 385) and in *Hylobates leuciscus* (p. 387) there is no bony caudal "Chordafortsatz."

The rostral part of the cavity of the bulla rarely shows a special bony rostral "Chordafortsatz" (Bondy, 1907, p. 402).

Bondy (1907) describes this rostral "Chordafortsatz" in a few mammals. In *Sciurus vulgaris* (p. 327) it projects into the tympanic cavity from the tympanic in the neighborhood of the fissura Glaseri. In *Spermophilus citillus* (p. 328) it is very rudimentary. In *Ateles paniscus* (p. 386) the rostral bony "Chordafortsatz" no doubt belongs to the tympanic. In *Macacus nemestrinus* (p. 384) and *Macacus rhesus* (p. 385) it is a blunt bony ridge projecting into the cavity of the bulla. In *Hylobates leuciscus* (p. 387) it is lacking. In *Macacus nemestrinus*, according to Bondy (1907, p. 402), it seems to correspond with the rostral portion of the Folian process, which is detached from the malleus.

Septum Bullæ Formed by the Tympanic and the Entotympanic

A special kind of septum in the cavity of the bulla is that formed by the tympanic and the entotympanic. Where these two elements meet each other they can bend inward in the direction of the promontorium and thus divide the cavity of the bulla more or less into two chambers. These two laminæ of the septum may remain separate, but as a rule they fuse, leaving no trace of the double origin. This septum resembles very much the other septa which may occur in the auditory bulla. Though the

study of the ontogeny is the surest basis for determination whether or not the septum formed by the tympanic and the entotympanic is really present, even the position of the septum can give us much information. A septum which runs inward from the sulcus tympanicus can not be a septum bullæ formed by the tympanic and the entotympanic. Also a septum which runs all around the wall of the bulla can not be a septum bullæ, as the entotympanic is never closed all around and as the same is the case with the mesial margin of the tympanic. The septum bullæ always shows a free upper margin, the rostral, under, and caudal margins being attached to the bulla. Thus it is easily understood that it is often difficult to decide whether this special kind of septum is present or another kind which is found in different orders of mammals.

As to the creodonts, according to Schlosser (1890, p. 71), in *Hyænodon brachyrhynchus* and *Pterodon* a septum is absent. Probably also in the Miacidæ (Pohle, 1920, p. 57) the bulla is single-chambered. According to my own investigations, however, a septum bullæ, composed of the two laminæ, is present in *Hyænodon crucians* Leidy.

In the primitive carnivorous skull, according to Scott (1889, p. 234), the auditory bulla is almost certainly divided by a septum, as is still to some degree the case in *Canis*. This septum in the modern Canidæ, which is mentioned by many authors, is not formed however by the tympanic and the entotympanic but is quite another kind of septum, as we shall see in a later chapter. Also in some fossil Canidæ a septum in the bulla is described and often compared with that of *Canis;* it is of course impossible to say which of the two kinds of septa occurs in these forms. I shall mention them in a later chapter in which the septum in the recent *Canis* is described and discussed. On the other hand, the presence of a septum bullæ formed by the tympanic and the entotympanic is not excluded in such forms as *Daphænus* and *Pliocyon* (see my own investigations). In these genera a small true tympanic bulla is present and the presence of another entotympanic bulla is very probable. Now the true tympanic bulla is not open behind, but its under surface posteriorly bends upward in the direction of the petrosal and covers the true tympanic cavity behind and forms a septum bullæ. As the entotympanic was probably not fused with the tympanic (distinct break-lines are absent), this caudal wall of the true tympanic bulla forms the tympanic part of the septum bullæ only, the entotympanic lamina not being preserved.

In the modern Ursidæ there is no septum at all in the cavity of the bulla, which is undivided (see also: Cope, 1882, p. 472; 1883, p. 113;

Filhol, 1883, p. 85; Zittel, 1893, pp. 608, 639; Reynolds, 1906, p. 10; 1909, p. 11; Carlsson, 1921, p. 71). In the modern Procyonidæ as well there is no septum at all, the cavity of the bulla being undivided (see also: Zittel, 1893, p. 644; Carlsson, 1920, p. 372; 1921, pp. 71, 72). The cavity of the bulla in the fossil *Pseudobassaris riggsi* (Riggs, 1898, p. 258, *Amphictis;* Pohle, 1917, p. 408) also, is undivided.

In the modern Mustelidæ as a rule there is no septum at all in the bulla, which is thus single-chambered (see also: Scott, 1889, p. 231; Zittel, 1893, pp. 608, 645, 646; 1911, p. 392; 1923, p. 473; Scott, 1913, p. 550; Carlsson, 1921, p. 171). Sometimes a septum is found, which we shall mention in a next chapter, but this does not seem to be homologous with the septum bullæ formed by the tympanic and the entotympanic. Also in a number of fossil mustelid genera a septum in the cavity of the bulla has been described. Perhaps they are homologous with the septa just mentioned, which occur in a few modern mustelids, although their nature as septa bullæ formed by the tympanic and the entotympanic is not excluded. I shall return to these fossils in a later chapter in which the septa in the modern mustelids are mentioned and discussed. Probably that part of the septum bullæ which is formed by the tympanic is present in the fossil *Palæoprionodon,* in which, according to Teilhard de Chardin (1914–1915, p. 78), the true tympanic bulla hermetically covers the anterior chamber of the bulla. According to Winge (1895*b*, p. 53) a poorly developed rudiment of the septum bullæ is present in *Amphictis.*

In the Æluroidea (see also: Cope, 1882, p. 472; 1883, p. 113) the septum is generally large. This septum is formed by the inwardly-bent margins with which the tympanic and the entotympanic touch each other (Van Kamp.; Winge, 1895*b*, pp. 60, 95) and is thus a true septum bullæ.

In the modern Viverridæ the cavity of the bulla is divided by a septum (Cope, 1882, p. 474; 1883, p. 115; Zittel, 1893, pp. 608, 655, 656, 660; 1911, p. 395; 1923, p. 476; Pohle, 1920, p. 57; Carlsson, 1921, p. 74). This septum is formed by the tympanic and the entotympanic (Van Kamp.; Winge, 1895*b*, p. 56). In *Nandinia,* however, there is no partition, either cartilaginous, membranous or osseous in the bulla (Van Kamp.; Pocock, 1916*a*, p. 266; Pohle, 1920, p. 57; Carlsson, 1921, p. 74). This lack of the septum in *Nandinia,* according to Van Kampen, is a primitive character. Winge (1895*b*, p. 53) mentions a poorly developed rudiment of a septum in *Nandinia.* In *Paradoxurus* the septum bullæ is double, as the tympanic and the entotympanic do not fuse. Especially in the Herpestinæ the septum runs transversely, as the two chambers for the larger part lie one behind the other. The septum very much re-

sembles that in *Felis*. According to Pocock (1916*e*, p. 303) in the Felidæ and in the Viverridæ the free edge of the partition always reaches, or is situated close to, the same portion of the periotic, namely the portion which is pierced by the fenestra rotunda of the inner ear, and it is always just at this point that there is a passage or orifice between the two chambers. This partition, which rises from the floor of the bulla, may arise just below the lower rim of the external auditory meatus, or it may arise far away from that point. In the modern Felidæ the fenestra cochleæ may look out more or less into both chambers; in the Viverridæ, however, according to Van Kampen, this character is very different. Farther on, the fissure or foramen through which the two chambers in the Viverridæ communicate is differently developed (Van Kamp.; Gray, 1913, pp. 403, 407, *Herpestes*) and its place strongly depends also on the mutual position of the two chambers.

In the fossil *Ictitherium* the internal structure of the bulla, though not known, probably resembles that in *Hyæna*, according to Winge (1895*b*, p. 59).

In *Hyæna* (Schlosser, 1890, p. 28; Reynolds, 1902, p. 7) or in the Hyænidæ in general (Cope, 1882, pp. 472, 474; 1883, pp. 113, 115; Scott, 1889, p. 231; Zittel, 1893, pp. 608, 660; Winge, 1895*b*, p. 94; Zittel, 1911, p. 396; 1923, p. 477) the bulla is said to be simple, undivided by a septum. Later a septum bullæ has been described in the Hyænidæ (Van Kamp.; Winge, 1895*b*, pp. 59, 94; Pocock, 1916*e*, p. 303; Pohle, 1920, p. 57). According to Winge (1895*b*, pp. 59, 94) it lies far backward near the processus jugularis, varying in distance in *Hyæna crocuta* and *H. striata* and *brunnea*. Also according to Pocock (1916*e*, p. 303) this partition lies far backward. In *Proteles* (Van Kamp.; Schlosser, 1890, p. 28), the septum is transverse. In two immature skulls of *Proteles*, Pocock (1916*e*, p. 306) describes the septum bullæ as a vertical, thin, imperfectly ossified or fenestrated partition. In *Hyæna crocuta* this septum is transverse, not vertical as in *Proteles* and the Herpestinæ, but inclines, the under margin lying more caudally. It runs from the foramen caroticum posterius toward the foramen stylomastoideum. The foramen, through which the two chambers communicate, lies more mesially than laterally in the tympanic cavity, as both chambers are strongly bagged out lateralward. In all Hyænidæ the fenestra cochleæ looks into the posterior chamber; all other essential parts of the middle ear lie in the anterior chamber. According to Pocock (1916*e*, p. 306) it is not certain that this septum in the hyænas is the exact homologue of that of the cats. It is possible that in *Hyæna* this septum bullæ has been replaced by a

secondary partition of stronger growth. As we shall see in a later chapter, such a secondary partition is present in *Proteles* and occupies the position of the so-called septum bullæ in *Hyæna*, where it rises from the bulla near the paroccipital (Pocock, 1916*e*, p. 306).

In the modern Felidæ the bony septum bullæ, formed by the tympanic and the entotympanic, is well developed (see also: Cope, 1880*c*, p. 834; 1882, p. 474; 1883, p. 115; Zittel, 1893, pp. 608, 663, 664; 1911, p. 397; 1923, p. 478; Winge, 1895*b*, p. 53; Reynolds, 1902, p. 7; Scott, 1913, p. 544; Pohle, 1920, p. 57). This bony septum bullæ, which is well known in *Felis domestica*, corresponds with the groove on the outer surface of the bulla; it runs from a point on the mesial side of the ostium tympanicum tubæ toward just behind the porus acusticus externus. Thus it is nearly parallel to the mesial wall of the bulla. It is nearly vertical and is on its lateral side a little concave (Van Kamp.; Pocock, 1916*c*, p. 310, *Uncia uncia*). Its under, rostral, and caudal wall are fused with the wall of the bulla; the upper margin is free. A fissure is found between the upper margin of this septum and either the promontorium or the rostral bent margin of the bulla; backward from the promontorium this septum projects freely in the cavity of the bulla. According to Pocock (1916*c*, p. 311) the septum bullæ in *Felis leo, tigris, pardus* and *onca* is low. Pocock (1916*d*, pp. 326, 334) uses not only the position but also the size of this septum in the system of the existing species of Felidæ. Ontogony teaches us that this septum is formed by the tympanic and the entotympanic; the margins with which they touch each other bend inward in the direction of the promontorium; later on the two laminæ fuse so that no trace of the original double origin is left (Van Kamp.; Dawkins, 1878, p. 48). Pocock (1916*c*, and *d*) uses the height of the septum bullæ as a systematic character by which existing Felidæ can be distinguished.

According to Zittel (1893, p. 664) this septum bullæ is also present in the Pleistocene Felidæ. Cope (1880*c*, pp. 834, 835; 1881*a*, p. 166) could not demonstrate that the otic bulla is divided in the fossil *Archælurus, Nimravus, Dinictis, Pogonodon* and *Hoplophoneus*. Later on (Cope, 1882, p. 474; 1883, p. 115) a septum is mentioned for the bulla of the Nimravidæ. According to Scott (1889, p. 238) there is probably an almost complete bony septum between the chambers of the bulla in the Nimravidæ.

In *Dinictis felina*, according to Scott (1889, p. 214), the bulla is almost certainly divided by an internal septum into two chambers, though whether the chambers are situated one behind the other or one

internal to the other could not be determined from the material available.

In *Smilodon*, according to Scott (1913, p. 533), the bulla is divided by a septum into two chambers.

In the recent Pinnipedia the cavity of the bulla is undivided.

Septum Between the True Tympanic Cavity and the Hypotympanic Sinus

This septum will be described and discussed in the next chapter together with other septa in the bulla. We need only mention here Van Kampen's general conclusions (cited by Gregory, 1920, p. 212). We can start from a condition in which a septum lies between the true tympanic cavity and the hypotympanic sinus. Such a septum with a small distinctly bounded foramen pneumaticum occurs in the monkeys, *Canis jubatus* and *Tragulus*. By the enlargement of this foramen pneumaticum this septum is reduced, so that finally only vestiges of it remain (*Tupaia*, Lemuridæ, most Canidæ) or it vanishes entirely (Rodentia, many ungulates, Carnivora, and others).

Other Septa and Cellulæ

In addition to the septum bullæ formed by the tympanic and the entotympanic and the septum between the primary tympanic cavity and the hypotympanic sinus, there may also be another kind of septa or osteophytes in the bulla. If there are many of these septa the bulla shows the so-called cellular structure. If there are only a few septa, they often run radially from the tympanic membrane.

This cellular structure may be limited to a very small portion of the tympanic cavity and it may be formed by different elements of the bulla; moreover it may be present or absent in allied animals.

In *Talpa europæa*, for example, the basisphenoid as well as its tympanic process in the ventral wall, and the roof of the most rostral part of the tympanic cavity, show a spongy structure, but this does not fill up the whole tympanic chamber. In other Talpidæ, including *Myogale*, *Scalops*, *Condylura* and *Urotrichus*, we do not find this cellular structure. They show only a few larger ridges, as does *Urotrichus*, or thin bony bridges pass through a small part of the tympanic cavity, as is the case in *Scalops* and *Condylura*. *Chrysochloris* shows similar thin bony bridges in a small part of the tympanic cavity and also the spongy structure on the inside of the tympanic process of the basisphenoid, though not to such an extent as in *Talpa*. *Tupaia javanica* shows two bony ridges, which bound the forward prolongation of the tympanic cavity and of

which the larger one was already known by Winge (1893*a*, p. 44). In the allied *Ptilocercus* we find no septa and it seems to be more primitive in this respect (Van Kamp.; Gregory, 1910, p. 272).

In the Chiroptera (Van Kamp.; Gray, 1913, pp. 407, 409, *Plecotus auritus*) no septa occur.

In *Metacheiromys marshi* (Wortman, 1903, p. 348) the bulla is more or less filled with cancellous tissue. This is an exception among edentates.

In most of the modern Rodentia the internal surface of the bulla is smooth and the bulla itself is undivided (Van Kamp.; Winge, 1888, pp. 114, 191, *Palæolagus, Lepus;* pp. 130, 135, 193, Capromyini, Dasyproctini, Eriomyini; pp. 136, 137, 194, Castorini; p. 128, Hystricini; Zittel, 1893, p. 544, Caviidæ; Preller, 1907, pp. 378, 387, Caviidæ; p. 387, *Hydrochœrus capybara;* see also, Gray, 1913, pp. 400, 401, 403, 407, *Lepus cuniculus*). In *Lepus* the canalis caroticus forms only a slightly developed protuberance on the internal surface of the bulla. In other modern Rodentia there occurs one or a few low ridges, which partly radiate from the tympanic membrane; moreover scattered osteophytes are found here and there. In the Sciuridæ (Van Kamp.; Winge, 1888, pp. 136, 137, 194) and in a few others (Van Kamp.; Winge, 1888, p. 117, *Anomalurus;* p. 123, *Graphiurus*), these radiate septa are better developed; they do or do not reach the sulcus; there are three to five of them, which may be different in height. In the Octodontidæ (Van Kamp.; Winge, 1888, pp. 130, 134, 135, 193, p. 134, *Habrocoma;* Zittel, 1893, p. 542) we find different conditions: here only radiate septa occur, or there are also others which cross the former, so that a network with wide meshes results. In other modern rodents the interior of the bulla is described as finely cellular. Winge (1888, pp. 113, 114, 191) calls the bulla in *Lagomys* spongy. According to Bondy (1907, pp. 333, 334) the wall of the bulla in *Arvicola arvalis* contains two thin scales of compact bone, between which scattered little spongiosa-bars are found; as the internal scale of compact bone is defective to a high degree, a system of air-filled cavities communicating with the tympanic cavity results.

Thus in the cavity of the bulla in the modern Rodentia the same conditions are present as in the sinus epitympanicus, but the same conditions in both cavities are not always found together.

In the creodonts *Hyænodon brachyrhynchus* and *Pterodon* there is no septum, according to Schlosser (1890, p. 71).

In the modern Arctoidea, according to Winge (1895*b*, p. 60), sometimes there is a more or less complete septum in the tympanic cavity, re-

sembling that in the Herpestoidea, but that in the Arctoidea seems to develop as an ossification in a fold of mucous membrane which covers the internal surface of the bulla.

Flower and other authors (Van Kamp.; Cope, 1882, p. 472; 1883, p. 113; Filhol, 1883, p. 85; Scott, 1889, p. 234; Zittel, 1893, p. 620; Reynolds, 1909, p. 11) have described in *Canis* a very rudimentary septum with exactly the same situation as in the Felidæ. According to Winge (1895*b*, p. 94) the position of this septum in *Canis* does not agree with the septum bullæ in the Felidæ. According to this author (*loc. cit.*, p. 94) it does not run in *Canis* parallel to the annulus tympanicus, but arises transversely from it. Thus it seems to agree with the processes, ridges and crests, which are often found in Carnivora on the internal wall of the tympanic cavity, which develop as ossifications in folds of the mucous membrane and which often radiate from the annulus tympanicus (*loc. cit.*, pp. 94, 95). Thus the development is quite different from that of the septum bullæ in the Herpestoidea (*loc. cit.*, p. 95). According to Van Kampen, however, this septum, which is very distinct in *Canis jubatus*, runs transversely to the direction that these mucous folds would show. This septum runs all around the internal wall of the bulla itself and thus, according to Van Kampen, differs as well from the septum bullæ in *Felis*, which shows a free upper margin. In *Canis jubatus* the foramen pneumaticum is surrounded completely by the septum itself, and appears as a perforation of this septum. A similar septum is found in *Tragulus*, as we shall see. From this foramen pneumaticum in *Canis jubatus* a low bony ridge runs forward and backward on the septum toward the wall of the bulla: the part of this septum on the lateral side of this bony ridge is also present in the Herpestoidea, that on the mesial side, however, is absent.

According to Winge (1895*b*, p. 94) this septum in *Canis* is very rudimentary indeed. Occasionally it is such an inconsiderable ridge that it is hardly visible and in nothing different from other ridges on the internal surface of the bulla. According to Van Kampen it is largely developed in *Canis jubatus*, the septum is very high and the foramen pneumaticum between the two portions of the tympanic cavity rather small. In other species, however, the foramen pneumaticum is larger as the septum is reduced. It remains broadest in the rostral part (which is no doubt the cause of Flower's error) where sometimes also a groove on the outer surface of the bulla is visible. Of the rest the mesial part is best preserved, while of the other parts traces only are left. Sometimes this septum is so poorly developed that it does not differ from other

bony ridges on the internal wall of the bulla, which Flower and Winge (1895*b*, p. 94) mention. According to Van Kampen, the wall of that part of the cavity of the bulla which lies behind this septum is either smooth or shows radiate ridges. This septum in the Canidæ does not show a relation to the fenestra cochleæ and all essential parts of the tympanic cavity lie outside. Probably in connection with the reduced state of the septum and ridges, Zittel (1893, pp. 608, 620) and Scott (1913, p. 520) call the bulla in the Canidæ hollow and undivided.

In the fossil *Cynodesmus thoöides* (Scott, 1895*b*, p. 66) the bulla appears to be divided by a septum in very much the same manner as in *Canis*, into two widely communicating chambers, of which the posterointernal is much the larger. Also in *Cynodictis*, Scott (1898, cited by Van Kampen; see also, Scott, 1889, p. 233) supposes the presence of a septum as in *Canis*. According to Filhol (1883, p. 85) there is no septum in *Cynodictis*. In *Amphicyon*, according to Filhol (1883, p. 85), the septum, if present, is very rudimentary and less developed than in *Canis*. In the fossil *Enhydrocyon crassidens* (Matthew, 1907, p. 191) the septum of the bulla is little developed. The possibility of the presence of a septum bullæ, homologous with that in *Felis*, however is not excluded.

In the modern Ursidæ there is no distinct septum, as we have already mentioned in a preceding chapter. There are a few low and thin ridges of bone only. One of them perhaps agrees with the septum in the modern Canidæ, the others radiate from the tympanic membrane.

In the modern Procyonidæ, as well, there is no distinct septum at all (see preceding chapter). The internal wall of the bulla is smooth or shows a few very low radiate ridges other than the inwardly projecting wall of the canalis caroticus. Also in the fossil *Pseudobassaris* (Riggs, 1898, p. 258, *Amphictis;* Pohle, 1917, p. 408) the tympanic cavity is a single cavity.

In the modern Mustelidæ as a rule, as we have already mentioned, there is no distinct septum in the cavity of the bulla. In *Helictis*, Winge (1895*b*, pp. 68, 95) describes a considerable septum, which is larger than that found in any dog with which he compares it. It issues from the annulus tympanicus and runs nearly transversely through the bulla. According to Winge (1895*b*, p. 95) it is homologous with one of the crests which in other mustelids can originate from the annulus. These septa occur in many mustelids and show a higher development than in other Carnivora and parallel the conditions found in the ungulates. There are often a few or more ridges which radiate from the annulus tympanicus (Van Kamp.; Winge, 1895*b*, pp. 67; 66, *Martes;* p. 68, *Meles*), which are

more or less developed and which can show differences in height in the same bulla. Even species of the same genus (Winge, 1895*b*, pp. 39, 40, 121, 122, *Galictis*) can show either a cellular surface or a smooth surface. In still other modern mustelids (Van Kamp.; Winge, 1895*b*, p. 77, *Mustela;* Bondy, 1907, p. 356, *Fœtorius vulgaris;* pp. 358, 359, *Fœtorius putorius*) the number of radiate septa has increased; they are close together and connected by transverse rods and ridges so that the surface is cellular or spongy. Sometimes however the radiate structure is still very distinct. By this large development of the spongy wall in *Mustela* the proper cavity of the bulla is much narrowed (Winge, 1895*b*, pp. 70, 128), while it is spacious in *Galictis, Lyncodon, Mellivora, Ictidonyx,* and *Pœcilogale,* in which the internal surface of the bulla is not at all or only slightly spongy (Winge, 1895*b*, pp. 69, 127). According to Winge (1895*b*, pp. 39, 121) such a partial division into chambers is found in many other mammals, which "parcourent des galeries étroites."

We owe very extensive information on the internal structure of the bulla in the mustelids to Pocock (1921). According to this author (*loc. cit.*, pp. 473, 480) in *Helictis* one of the rafters, which rises low down on the tympanic ring behind, divides the bulla as completely into two subequal chambers as the septum bullæ does in the Felidæ. Also in *Grison, Gulo, Mellivora* and other genera (Pocock, 1921, p. 473) there is a very distinct partition, although it is not so complete as in the typical Æluroidea. In *Taxidea* and *Grisonella* (*loc. cit.*, p. 482) as well a posterior rafter, which is continuous with the posterior edge of the tympanic ring, cuts off a posterior chamber almost as completely as in some Æluroids. Moreover, Pocock (1921, pp. 478–486) describes the conditions in a great many genera of mustelids and uses these characters in a systematic list for determination of the genera (*loc. cit.*, pp. 484, 485). He mentions the complete or incomplete partition into two subequal chambers running from the posterior end of the tympanic ring or passing transversely from the posterior portion of the tympanic ring; he mentions the absence of this partition; he describes the rafters, plates, septa, trabeculæ, anastomosing ridges, pockets, septa, bony ridges, the thick bony walls composed of spongy bone permeated with air cells; he mentions the presence of air-cells everywhere and the absence of noticeable air-cells in different species.

In the fossil *Stenoplesictis cayluxi* (Scott, 1889, p. 232) the bulla is divided by a septum, which, according to Scott, cited by Zittel (1893, p. 656), is found in *Stenoplesictis, Palæoprionodon, Haplogale, Stenogale* and *Plesictis.* Perhaps this septum is homologous with that in *Helictis*

and its allies, perhaps it is a septum bullæ formed by the tympanic and the entotympanic.

In the modern Viverridæ no osteophytes occur. Sometimes the wall is smooth with the exception of a few ridges. Sometimes one of these is formed by the inwardly projecting sulcus caroticus; also the other ridges may be folds. In other Viverridæ, however, there occur a few true, not hollow, radiate ridges. In *Cynogale*, according to Pocock (1916*a*, pp. 264, 267, 268), the carotid canal forms a very distinct ridge or crest, which runs obliquely across the posterior chamber of the bulla to the septum and periotic and forms a low partition of that chamber. In *Nandinia* (Van Kamp.; Pocock, 1916*a*, p. 266; Pohle, 1920, p. 57; Carlsson, 1921, p. 74) there is no partition in the bulla. In *Herpestes griseus*, according to Gray (1913, p. 403), the internal surface of the entotympanic chamber is smoothly lobulated.

In *Hyæna* the small caudal chamber shows a number of irregular bony crests. The rostral chamber is either smooth or shows in front two ridges or laminæ, which have nothing to do with the septum bullæ (Van Kamp.; Pocock, 1916*e*, p. 306); the outer of these two laminæ is the tympanic ring, i.e., the inwardly projecting sulcus and crista tympanica. In *Proteles* the caudal chamber shows either a bony spear or bony walls. Pocock (1916*e*, p. 306) describes in two immature skulls of *Proteles*, on the inner wall of the posterior chamber of the bulla, a crest curving round the back of the chamber. As this crest in *Proteles*, which is present in addition to the normal vertical partition, occupies the position of the partition where it rises from the bulla in *Hyæna*, it is, according to Pocock (1916*e*, p. 306), possible that in *Hyæna* the normal partition has been replaced by a secondary partition of stronger growth, and thence it is not certain that the partition in hyænas is the exact homologue of that of the cats.

According to Pocock (1916*e*, p. 306) the inner wall of the posterior chamber of the bulla in Æluroidea is often strengthened by bony crests or ridges of varying height.

In the modern Felidæ the inner wall of the bulla is smooth, except for a few slightly developed ridges that radiate from the promontorium, which are mentioned for a few species, while in others septa occur, and still others, show strongly developed osteophytes. According to Pocock (1916*a*, p. 267) the carotid canal in the Felidæ frequently shows on the inside of the bulla as an upstanding ridge, resembling that in the viverrid *Cynogale*, but relatively smaller.

Also in the Phocidæ the carotid canal causes a longitudinal rounded prominence on the inside of the bulla, which for the rest is smooth.

The bulla in the Cetacea is hollow (see also, Zittel, 1893, p. 163).

In *Equus* a number of ridges project from the wall of the bulla, which they incompletely divide into "cells." These ridges radiate from the inwardly projecting sulcus and crista or proximal portion of the external auditory meatus.

In the modern Suidæ (see also: Scott, 1890, pp. 377, 390; Zittel, 1893, pp. 349, 367; Scott, 1899, p. 28; Winge, 1906, p. 137, *Sus;* p. 138, Dicotylini) the bulla is filled with cancellous tissue. The "cells" communicate by means of numerous openings with the tympanic cavity. Accerding to Matthew (1907, p. 216) in all upper Miocene, Pliocene, Pleistocene, and recent species the bullæ are filled with cancellous tissue; this character is common to *Dicotyles, Platygonus, Mylohyus* and *Prosthennops.* Also in *Desmathyus* and in "*Thinohyus*" *siouxensis* the bulla is filled with cancellous tissue (Matthew, 1907, p. 217). In the typical *Thinohyus* (Matthew, 1907, p. 217) this is not the case however. Also in *Perchœrus* (Scott, 1899, p. 28; Matthew, 1907, pp. 216, 217) the bulla is hollow and free from cancelli. Probably the cancellous structure has been independently acquired by the Suidæ (Scott, 1899, p. 28).

The bulla in *Elotherium* (Scott, 1898, cited by Van Kampen) is hollow. Winge (1906, p. 141) gives this as a character of the Entelodontini.

In the modern Hippopotamidæ irregular cellulæ communicate by means of an opening with the small part which is not filled with cancelli.

In the fossil *Ancodus* (*Hyopotamus*) according to Scott (1895, cited by Van Kampen), the cavity, of the bulla is free from cancellated tissue.

In the Anoplotheriidæ (see also, Zittel, 1893, pp. 349, 367) the bulla is filled with spongy tissue.

In *Cænotherium* (see my own investigations) the bone of the bulla is cancellous.

In *Agriochœrus* (Wortman, 1895, p. 147) the bulla is not filled with cancellous tissue. The bullæ in all Oreodontidæ are hollow and free from cancellous tissue (Scott, 1890, p. 377; Zittel, 1893, p. 349). A low ridge may occur, as the natural casts of the bullæ of an *Eporeodon occidentalis* specimen (Thorpe, 1921*b*, p. 96; see also my own investigations) seem to show; they are divided into anterior and posterior hemispheres.

In the modern Camelidæ (Van Kamp.; Scott, 1890, pp. 377, 390; 1891*a*, p. 15; 1899, p. 28; Zittel, 1893, p. 349; Winge, 1906, p. 98; Loomis, 1910, pp. 302, 322) the bulla is filled with cancellous tissue. It resembles that in the Suidæ and it does not resemble the radiate struc-

ture in *Equus*. The inflated wall of the cylindrical external auditory meatus also is filled with cancelli. In *Lama*, a thin wall with only a few foramina separates the true tympanic cavity from the cancelli. This wall connects the tympanic membrane with the petrosal; it is a little concave and bears a few low ridges, radiating from the tympanic membrane. Also in the fossil *Stenomylus* (Loomis, 1910, pp. 302, 321, 322) the bulla is filled with canceolated tissue. In *Poëbrotherium* (Scott, 1891*a*, p. 15; 1899, p. 28; Matthew, 1910*a*, p. 36; Loomis, 1910, p. 321) the bulla is filled with cancellcus bony tissue. In *Eotylopus reedsi* (Matthew, 1910*a*, p. 36) as well, the bulla is filled with cancellous tissues. In *Protylopus* (Scott, 1899, pp. 28, 44, 113, 117, 118), however, the bulla is hollow and free from cancellous tissue. According to Scott (1899, pp. 28, 116, 118) in the main tylopodan series the cancelli were developed after the series had become well established as such.

In the modern Tragulidæ (Van Kamp.; Scott, 1890, pp. 377, 390; 1891*b*, p. 358; 1899, p. 28; Zittel, 1893, pp. 349, 382, 384; Winge, 1906, pp. 107, 108) the bulla is filled with cancellous tissue. In *Tragulus javanicus*, according to Van Kampen, occurs a cancellous type similar to that in the Camelidæ. Also in *Tragulus meminna* a cancellous bulla occurs: in one skull, however, Van Kampen found a hollow bulla separated superiorly from the proper tympanic cavity by a thin bony septum with one small cleft-like opening. Though Scott (1899, p. 28) as yet had no information concerning the traguline series, there is, according to this author, no reason to doubt that the chevrotains acquired the cancellous structure of the bulla within the limits of the family after it had begun its separate existence.

In the fossil *Leptomeryx* (Scott, 1891*b*, pp. 346, 359; 1895*a*, p. 313; 1899, pp. 16, 112; Zittel, 1893, p. 389; Matthew, 1902*c*, p. 313; Winge, 1906, p. 108) the auditory bullæ are not filled with cancellated tissue, but are hollow.

In the modern Cervidæ the bulla is hollow. In a few species osteophytes are mentioned.

In the modern Giraffidæ as well the bulla is hollow, but contains osteophytes of a remarkable form. In the fossil *Protoceras* (Scott, 1895*a*, p. 313; 1899, p. 20; Winge, 1906, p. 106) the bulla is hollow and not filled with cancellous tissue.

In the fossil *Hypisodus* (Matthew, 1893–1903, p. 440; Winge, 1906, p. 108; Loomis, 1910, p. 321; Troxell, 1920*a*, p. 393) the bullæ are empty, not filled with cancellous tissue.

In the true Ruminantia (Scott, 1890, p. 377) and in the existing

Pecora generally (Scott, 1895*a*, p. 313; 1899, p. 28) the bulla is hollow and not filled with cancellous tissue. *Bos* (Van Kamp.; Bondy, 1907, p. 381), however, shows cancellous tissue in the bulla. This also is the case in *Anoa* (Winge, 1906, p. 125) and according to Van Kampen in *Tragelaphus* and probably in other large antilopes as well. In these Bovidæ with cancellous tissue the cavity of the bulla is much wider than that in the other Artiodactyla, which show a spongy bulla. In *Tragelaphus* the communication with the proper tympanic cavity is accomplished by means of one narrow opening, in *Bos taurus* more openings occur. In *Bos* the bony plates which form the "cells" radiate toward the proper tympanic cavity. This radiate arrangement also shows the higher or lower ridges or septa, which sometimes in the Bovidæ rise from the wall of the bulla, which for the rest is hollow (Van Kamp.; Gray, 1913, p. 407, (*Ovis aries*). Sometimes one or more septa occur, dividing the bulla in two or three chambers which communicate with each other. Osteophytes have been described in *Capra*.

In *Protypotherium* (Sinclair, 1909, p. 22), in *Hegetotherium* (Sinclair, 1909, p. 74) and probably also in *Typotherium cristatum* (Van Kampen) the bullæ are hollow.

In the Toxodonta, according to Scott (1912, p. 292), the bulla is hollow, free from cancellous bone, which Scott (1912, p. 137) emphasizes for the genus *Nesodon*. In a young skull of *Toxodon platensis* Van Kampen describes a few low, irregular ridges in the bulla, which for the rest is hollow.

In the Entelonychia, according to Scott (1912, p. 266), the interior of the bulla is hollow and free from cancellous tissue.

In *Procavia* we find a ridge parallel to the sulcus tympanicus. This ridge separates the mesial, thick-walled, probably entotympanic portion of the bulla from the lateral, thin-walled, probably tympanic portion. This latter portion shows a groove-like excavation lying within the margo sulci. This excavation, which is the rudiment of a hypotympanic sinus, shows a few irregular, low ridges at right angles with the sulcus or more regular ridges, which resemble that in *Equus*.

In *Elephas* the bulla shows one large cavity and many plates on its walls, which cross each other so that many irregular "cells" are formed. Their cavities are much wider than those in the Suidæ and more as in the Bovidæ, and also occur in the under wall of the true cylindrical external auditory meatus. In *Dinotherium giganteum*, according to Claudius (1865, cited by Van Kampen), the tympanic cavity shows cancelli.

In the higher ungulata, in contrast to the most primitive ones

according to Winge (1906, p. 66), the interior of the bulla may be partly filled with spongy bone. We have already seen that Scott (1899, p. 28) defends the independent development of the cancellous structure in different groups of the Artiodactyla.

According to Van Kampen, the primitive condition of the spongy bulla is perhaps that in which ridges or septa rise up from the wall of the bulla and radiate from the tympanic membrane. Such a condition is found among the ungulates in *Procavia*, in *Equus* and in some Bovidæ. Together with the larger inflation of the bulla, the septa become higher and connected by transverse bridges. The radiate structure remains as a rule more or less distinct. Often a nearly complete compact wall is present between the part of the tympanic cavity which is filled with cancelli and the proper tympanic cavity. In this wall one or a few small foramina are present, as we have seen. In other cases (*Sus*, *Bos*, *Elephas*) this wall has disappeared and the communication happens by means of a great many openings. In the case of total resorption of the bony bars the bulla becomes hollow. In *Tragulus* the original separating wall may remain as a septum which resembles that in *Canis jubatus*.

In *Lemur mongos* the bulla is hollow and its internal surface is smooth, with the exception of one low septum. This septum runs from the lateral margin of the promontorium forward as far as the rostral wall of the bulla. It remains on the mesial side of the tympanic. It lies between two bulging parts of the tympanic cavity, namely, that in the prolongation along the basisphenoid and that beneath the tuba auditiva. Backward in the cavity of the bulla a ridge of the promontorium, which runs toward the hind wall of the bulla, forms the lateral boundary of a caudal bagging-out part of the tympanic cavity. This ridge and this septum, both in the upper wall of the tympanic cavity, together with the promontorium, incompletely divide the upper half of the tympanic cavity into a larger mesial and a smaller lateral portion. The latter contains all essential parts of the middle ear and forms the true tympanic cavity. Also, Gregory (1920, p. 174) mentions an oblique septum in *Lemur*, which incompletely separates the hypotympanic from the true tympanic cavity. Moreover, in the fossil *Notharctus* (Gregory, 1920, p. 178) the cavity of the bulla is divided into external and medial parts by an incomplete septum running along the cochlea, the outer chamber being the true tympanic cavity, the inner being the hypotympanic sinus. Stehlin (1912, cited by Gregory, 1920, pp. 166, 211) mentions in *Adapis* an ossified tympanic membrane, which according to Gregory (1920, pp. 166, 211), however, represents a fold of the hypotympanic region of the

bulla surrounding the pneumatic foramen; where it has grown over the tympanic ring, the wall of the hypotympanic sinus forms an infolded part, a thin sheet of bone, which more or less enwraps the tympanic ring in its ventral half. It is differently developed in *Adapis parisiensis* and *Adapis magnus* (Stehlin, cited by Gregory, 1920, p. 211). According to Gregory (1920, p. 211) the modern *Lemur* represents a further advance in the direction of simplification, as the enlargement of the pneumatic foramen (Van Kamp.; *loc. cit.*, p. 164) and concomitant withdrawal or resorption of the osseous folds surrounding this foramen, according to Gregory (1920, pp. 211, 212), is secondary. The hypotympanic sinus in *Notharctus* (Gregory, 1920, p. 218) is empty.

In *Magaladapis edwardsi*, according to Lorenz von Liburnau (1905, p. 464), a ridge runs from the rostral margin of the annulus tympanicus toward the foramen for the tuba auditiva: this ridge divides the cavity into a mesial and a lateral half.

In the modern Chiromyidæ (Van Kamp.; Gregory, 1920, p. 177) the septum, which divides the cavity of the bulla incompletely into medial and lateral moieties, is perhaps a little lower than in *Lemur* and the lateral of the two moieties is relatively smaller than in *Lemur*.

In *Perodicticus potto* the cavity of the bulla is completely divided into two chambers by a septum. We can imagine this septum developed out of the enlarged septum in the rostral part of the tympanic cavity in *Lemur*. It is also attached to the rostral margin of the bulla; its upper margin runs along the ventral part of the promontorium, its under margin runs along the oral and under wall of the bulla and is connected with the bulla along the sulcus tympanicus. This septum toward the lateral side is slightly concave; it is not perfectly vertical, but the under margin lies a little more lateralward than the upper margin. Its caudal end bends lateralward and covers the proper tympanic cavity behind. The caudal narrow half of the mesial chamber shows a number of bony rods and ridges, which for the greater part radiate from the promontorium and from the septum. This is different from the conditions found in *Lemur*. Another difference from *Lemur* is that in *Perodicticus* both rostral bulgings of the tympanic cavity lie on the mesial side of the septum; the caudal bulging as well lies in the mesial chamber. The lateral chamber, which contains all essential parts of the middle ear, is thus completely separated from the mesial chamber; they communicate via the epitympanic recess and the epitympanic sinus, the latter communicates with the mesial chamber. In the young skull this septum has not yet developed.

In the modern Tarsiidæ (Van Kamp.; Winge, 1895*a*, p. 13) a bony septum corresponds with the two portions of the bulla, which can be distinguished externally. This septum stands on the petrosal transversely on the length axis of the bulla. This septum is not complete, but shows laterally a small foramen by which the two portions communicate. The thickened lateral margin surrounds the carotid canal and forms the inner margin of the ostium tympanicum tubæ. The internal surface of the rostral chamber is smooth, except for a few low ridges. The rostral chamber is an accessory cavity as the caudal one contains all essential parts.

In the fossil *Tetonius* (*"Anaptomorphus"*) *homunculus*, according to Gregory (1915, p. 431; 1920, p. 180), a remnant of a long septum is attached to the small cochlea; it separates the true tympanic cavity from the hypotympanic cavity; very possibly the carotid ran in this septum.

In the ancestors of the Platyrrhinæ, according to Gregory (1920, p. 220), the cavity of the bulla itself diminishes, and it retains the cancellous condition which usually precedes the resorption of its tissue, while the tympanic becomes cancellous.

In the generalized Platyrrhine, according to Gregory (1920, p. 218), the hypotympanic sinus was cancellous.

The cellulæ petrosæ in the primates are always fine in contrast to those in the Prosimiæ.

In *Midas rosalia*, one of the Hapalidæ, a nearly complete bony septum bounds rostrally the true tympanic cavity, which lies in the caudal part of the bulla. This true tympanic cavity is hollow; its inner wall bears a few low ridges only, rising up into the tympanic cavity. In this septum, just within the ostium tubæ, lies the foramen pneumaticum. It opens into the cellulæ petrosæ, which lie in the rostral part of the bulla, through which pass irregular bony rods and septa which cross each other. These cellulæ occur rostrally even in the point of the bulla, backward within and even beneath the tympanic cavity to the foramen caroticum posterius, which they enclose mesially as well as laterally.

In the modern Cebidæ as well, cellulæ petrosæ occur (Van Kamp.; Winge, 1895*a*, p. 21). The foramen pneumaticum, through which the cellulæ petrosæ communicate with the true tympanic cavity, is large; it lies quite near the ostium tympanicum tubæ. The very small and narrow true tympanic cavity bears on its mesial wall a poorly developed longitudinal ridge, which ends behind in a processus cochleariformis. The cellulæ petrosæ fill up the whole bulla and extend farther backward than in *Midas* and enclose the foramen caroticum on all sides.

In the modern Cercopithecidæ the bulla is entirely filled with cellulæ, except the true tympanic cavity, which in form resembles that in the Cebidæ, being only a little more flattened laterally. These cellulæ as a rule are much smaller than those in the Platyrrhinæ, but here also show variations in size in different genera. The cellulæ petrosæ extend backward mesially and laterally from the foramen caroticum; they occur in the styliform process, and elsewhere. The cellulæ petrosæ communicate with the true tympanic bulla through a few small foramina in the mesial wall of the tympanic cavity just in front of the carotid canal. Their position entirely agrees with the one larger foramen in *Ateles*.

In the new-born Cercopithecidæ the foramen pneumaticum is still simple and actually it is so in the adult as well, but projecting bony plates of the cellulæ petrosæ divide it in a few smaller foramina.

In *Gorilla* (Van Kamp.; Gray, 1913, p. 397) the true tympanic cavity resembles in its form and in the condition of its walls that in the Cercopithecidæ and that in man. The cellulæ extend in the under wall of the petrosal to within the point of the pyramid; the cellulæ surround the tuba ossea, the carotid canal, etc. The cellulæ petrosæ and the cellulæ mastoideæ are no longer separate. This is probably a secondary condition in consequence of the great extension, and probably they develop outward from two centers as in the lower monkeys. A communication of the cellulæ with the tympanic cavity occurs still in the same place as in the lower monkeys, though in the gorilla this happens via some foramina. In the orang-utan the cellulæ petrosæ are less developed than in the *Gorilla*.

In *Homo* (Van Kamp.; Gray, 1913, pp. 397, 398, 399) the true tympanic cavity is represented by a minute diverticulum. In the monkeys as well it is really no more than the flattened primary tympanic cavity.

In relation to the strong reduction of the bulla in man the cellulæ petrosæ are very limited and probably represented by the "cellulæ tubariæ" only, which still partly surround the carotid canal. In consequence of the enormous development of the carotid artery and thus of the carotid canal, the foramen pneumaticum in the monkeys is limited to a small foramen. In man the carotid canal is still wider and the foramen pneumaticum thereby still more reduced than in the monkeys. In consequence of the reduction of the cellulæ petrosæ the carotid in *Homo* lies in front of the bulla and not within the bulla.

Development of the Septa and Cellulæ

We have already mentioned the nature of the development of the septum bullæ, formed by the tympanic and the entotympanic.

Septa may develop as a secondary ossification of mucous folds. According to Van Kampen however, this is probably an exceptional condition. The osteophytes, which occur in many mammals, probably develop in this way. Also the septum in the Tarsiidæ probably is an ossification of a mucous fold running from the inner wall of the bulla around the probably already ossified carotid canal.

As a rule the septa and bony rods seem to develop in the same way as those in other cavities of the skull, that is, they are saved from resorption. Thus in *Sus*, according to Van Kampen (Van Kamp.; Bondy, 1908, pp. 597, 598, 599) the septa in the bulla do not develop secondarily, but are already present from the very first beginning of the inflation of the bulla. They develop in the same manner as those in spongy bone. The sinus hypotympanicus therefore must be considered as a diploëtic cavity, which is pneumatized out of the tympanic cavity. This pneumatization may happen through one or a few foramina in the wall which separates the true tympanic cavity from the hypotympanic sinus. As we have already seen, this wall may be absent and the cancelli left, while in other cases this wall is left and the cellulæ are partly or entirely resorbed. In the rodents probably the septa develop in the same way as those in the ungulates. The septum in *Canis* according to Van Kampen, is, not an ossification in a mucous fold but probably a part of the original flat wall present before the inflation takes place. The rest of this original wall becomes concave by bone-apposition on the outside and simultaneous resorption on the inner side.

The septum in the Nycticebidæ, which completely separates the mesial portion of the tympanic cavity from the lateral one, has quite another development. The cavity in the mastoid extends forward in the hind part of the petrous plate of the bulla, which it inflates and makes hollow, splitting the inner wall of the bulla. Thus the original inner wall of the bulla mesially forms the definitive mesial wall of the bulla and laterally the septum.

Different Skeletal Elements Forming the Bulla

Use of Proportions in Systematics of the Smaller Groups

We have met and we shall still meet many peculiarities in the bulla that can be and are used to distinguish smaller groups, as the inflation of the bulla, the internal structure, the length and other characters of the external auditory meatus, the expansion of the epitympanic sinus and so forth. The proportions of the different elements forming the bulla also are used for this purpose. That they can be used in questions of affinity is

shown by the remarks on the auditory bulla in different lipotyphlous insectivores, which Gregory (1910, pp. 264, 266, 267) makes; he ends his remarks with this sentence (p. 267): "Although the same elements contribute to the complex bulla, and thereby reveal the subordinal relationship of the families, yet the proportions of the several elements are very different." Previously Winge used the proportions of the elements to determine relationships. Concerning the shape of the tympanic, it is Winge's opinion (1893*a*, pp. 41, 86) that the Chiroptera are derived from lower insectivores with a ring-like tympanic and *Galeopithecus* from more highly developed insectivores with an expanded tympanic. In *Cholœpus* and *Bradypus* the same elements, viz. the tympanic and the entotympanic, constitute the bulla, yet they have an absolutely different aspect, an important reason being that the proportions of the two elements are different.

The bulla of the hyænas and the allied Herpestoidea, according to Winge (1895*b*, pp. 47, 59, 94, 126), differ in the mutual relative size of the tympanic and the entotympanic, in the hyænas the latter being relatively smaller. Among the Hyænidæ as well this relative size of the entotympanic shows differences. According to Winge (*loc. cit.*) the entotympanic is very considerable in *Hyæna crocuta*, while in *Hyæna striata* and *brunnea* it is noticeably narrowed and occupies but a small corner between the processus jugularis and the processus mastoideus.

In the Felidæ and the Viverridæ, according to Pocock (1916*e*, p. 303), the septum bullæ, which rises from the floor of the bulla and marks the boundary of the tympanic and the entotympanic, may arise just below the lower rim of the external auditory meatus, or it may arise far away from that point. In the former case the antero-external chamber is small; in the latter it is large as compared with the postero-internal or posterior chamber.

Pocock (1916*c*, pp. 310, 311, 312, 316; 1916*a*, pp. 326, 334) describes the position of the septum bullæ in various recent Felidæ and thus also the relative size of the tympanic and entotympanic. The posterior end of this line is a fixed point situated just in front of the stylomastoid foramen, but the position of this line and its anterior termination vary considerably in different species (*loc. cit.*, p. 326). In *Uncia uncia* (*loc. cit.*, p. 310) the anterior termination lies behind the basioccipital suture, while in *Felis leo*, *tigris*, *pardus* and *onca* (*loc. cit.*, p. 311) it lies on the anterior face of the bulla. These variations in the position of this line and its anterior termination have a profound effect upon the relative sizes of the tympanic and the entotympanic. When this line lies a long way

below the auditory meatus, the tympanic is comparatively very large. Conversely, when this line lies tolerably close to the auditory meatus, the entotympanic is much larger than the tympanic. In his summary Pocock (1916*d*, p. 334) concludes that within the limits of the species, or genera of Felidæ, intergradation exists in the position of this line and thus also in the relative size of the tympanic and the entotympanic.

According to Pocock (1916*a*, p. 265) the entotympanic in *Cynictis* is very short and the tympanic very long; in *Ichneumia* the tympanic is small and the entotympanic is large. As to differences in the relative size of the tympanic and the entotympanic in other Viverridæ and especially those between the Viverrinæ and the Herpestinæ I refer to the chapter on the entotympanic, where much information is given. I do the same for the differences in the broadening of the tympanic and its relation to the relative size of the petrosal plate of the bulla in the Prosimiæ and the primates.

Use of the Presence of Different Elements in Systematics of the Larger Groups

All these characters, however, are too variable to distinguish larger groups. For that purpose the different skeletal elements that form the bulla give better characters.

In this respect we have to mention here Flower's classical investigation, but still it was neglected till Van Kampen added (1904, 1905) many new features illustrating the importance of the knowledge of the elements forming the bulla to determine the group of mammals to which the animal belongs and also in some questions of the phylogeny of the groups. Therefore it is hard to understand why Scott (1913, p. 67), who describes those parts which are needful to work out the history and descent of the various groups of mammals, in this respect does not mention a word as to the different elements forming the bulla.

Van Kampen's paper (Van Kamp.; Gregory, 1910, p. 426), contains numerous illustrations of this kind, but we will pick out only a few characteristic examples and add others given by other authors.

The marsupial skull is characterized by an alisphenoid bulla. A tympanic process of the basisphenoid is present only in insectivores. Though this wing is not present in all insectivores, its diagnostic value cannot be better illustrated than by the notice of Gregory (1910, p. 261) that it is perhaps surprising that in the fossil *Ictops* the tympanic process of the basisphenoid is absent, while this fossil is related to the erinaceids and while the allied Miocene *Cayloxotherium* (*Neurogymnurus*) had this

tympanic wing highly developed. The conditions in the auditory region in *Notoryctes* and *Chrysochloris* are radically different, and Gregory (1910, p. 257) says that there could be cited no better example of the importance of the auditory region in the study of ordinal relationships and of "palæotelic" characters of this kind as compared with "cænotelic" or adaptive resemblances. On the other hand the many points of agreement between the marsupials and the insectivores are often emphasized (see also: Matthew, 1909, p. 506; Gregory, 1910, p. 269), but according to Van Kampen this is perhaps more the consequence of convergence than of affinity. It is a matter of course that similar characters can be attained in different groups, as often is seen after they have sprung out of a common stem (Gregory, 1910, p. 286). In *Palæoryctes puercensis*, a fossil zalambdodont insectivore, we find no indication of marsupial affinities; the basicranial structure appears to be more primitive even than the most primitive recent insectivore and is more nearly in accord with that of the early creodonts, while the construction of the otic bulla is comparable with that in the more primitive Centetidæ and with *Solenodon*. So this genus is best interpreted as a central type from which the several modern specializations have arisen, with which view the considerable approach to the creodonts is in accord (Matthew, 1913, pp. 310, 311, 313). Unfortunately many Eocene mammals, the primates alone excepted, show no ossified bulla (Matthew, 1909, p. 510). In my opinion this is due to the fact that the tympanic ring or the bulla is loosely attached to the skull, but this is a general primitive character which is not limited to one order.

Van Kampen emphasizes that the construction of the bulla in the Insectivora agrees with the division of this group into Menotyphla and Lipotyphla and not with Trouessart's division in Arctogeæ and Notogeæ, in which the Talpidæ and Chrysochloridæ are separated (Van Kamp.; Gregory, 1910, p. 266). *Tupaia* and the allied *Ptilocercus*, which amid many differences in the skulls reveal their family relationship, especially in their close agreement in the character of the base of the skull (Gregory, 1910, pp. 273, 274), in the characters of the bulla differ widely from the Lipotyphla and approach the lemuoird type (Gregory, 1910, pp. 272, 274). Also the Macroscelidæ are entirely unlike any lipotyphlous insectivore, but resemble the Tupaiidæ in the mode of formation of the bulla (Gregory, 1910, pp. 281, 284), though there are, as we shall see later, great differences (see also, Winge, 1893*a*, p. 44). Probably the difference in the bulla between the lipotyphlous and the menotyphlous insectivores is not one of kind, but rather of degree, as it is not impossible that

the tympanic process of the petrosal in the lipotyphlous insectivores is an entotympanic that has secondarily lost its independence (Gregory, 1910 gives the reverse of Van Kampen's opinion in this respect, apparently erroneously). At any rate the difference, as it now stands, is a great one and implies a relatively long period of separation between the Menotyphla and Lipotyphla (Gregory, 1910, p. 274).

So the remarks of Schlosser (1887) on the bulla of the insectivores, in which he notices the greater or less completeness of the bulla, and so forth, without saying a word of the elements forming the bulla, are not what we need to determine the relationships of the families.

The Chiroptera do not show a remarkable resemblance to any other group of the mammals; most of all they resemble the menotyphlous insectivores because of the presence of an entotympanic and the absence of a tympanic process of the sphenoid. How easily an incomplete knowledge of the bulla can give false conclusions is shown by the Chiroptera. Formerly the Megachiroptera were said to have a tympanic ring and the Microchiroptera a closed bulla, but Van Kampen's thorough research showed that in the Megachiroptera the tympanic also is sometimes expanded and that the entotympanic also is present but, in contrast with that of the Microchiroptera, is cartilaginous and therefore is lacking in the dry skull. So the complete bulla shows that the difference is one of degree.

Also Winge uses the construction of the auditory bulla to determine relationships of groups. Winge (1893*a*, pp. 87, 88, 43, 44) already showed that the bullæ of the Tupaiidæ and of *Galeopithecus* have a great external resemblance and show a much higher development than the Chiroptera, whose ancestors they therefore cannot be, but that an investigation of the interior teaches that the two are different in principle, though Winge himself does not decide whether the free ring in the bulla of the Tupaiidæ is the whole tympanic or only the loosened crista tympanica with the sulcus tympanicus.

The possiblity of relationship of the Pholidota with the Xenarthra, according to Gregory (1910, pp. 338, 339), is indicated not only by the lack of a sinus hypotympanicus and the large size of the sinus epitympanicus, but especially by the presence of a reduced entotympanic. In possessing a well-developed entotympanic the Xenarthra recall the Menotyphla and Carnivora (Gregory, 1910, p. 341). Though the same elements constitute the bulla in *Manis* and in the Xenarthra, there are great differences between the two and also within the order Xenarthra.

Therefore, Matthew's note (Matthew and Granger, 1918, p. 648) that the tympanic region in *Palæanodon* agrees with the general loricate type but also with *Manis*, can give in this respect an agreement only in a very general sense.

According to Gregory (1910, p. 329) the raised and more or less excavated lateral margins of the basisphenoid in the rodent skull for the very large inflated bulla tend to indicate that in the case of *Microgale* and other insectivores the functional participation of the ali- and basisphenoid in the bulla is no indication of relationship to the marsupials but a result of the pressure exerted by the expanding bulla upon the borders of the adjacent bones. In my opinion criticism seems to be allowed. The basisphenoid in the wall of the tympanic cavity is present in the Insectivora only and not in the marsupials. The so-called tympanic wing of the alisphenoid in insectivores is a rostral entotympanic. The processus tympanicus alisphenoidei and basisphenoidei are probably remnants of structures in the lower vertebrates, as we shall see. The bulla in these lower mammals does not show such an enormous inflation. Examples are lacking to indicate that other elements of the bulla are covered by these wings of the adjacent bones.

The presence of an entotympanic does not indicate close relationship, (Carlsson, 1910*a*, p. 394; 1922, p. 267) as it is found in many mammal orders. The entotympanic is remarkable in that it is very distinct in the adult bulla of all genera of a certain group, and seems to be absent in another allied group, judging from the adult skull. I mention in this respect the Arctoidea and the Herpestoidea among the modern Fissipedia, the Menotyphla, and the Lipotyphla insectivores. In many other orders, however, the adult skull shows an entotympanic in a very few genera only. This fact, and also that of the total absence of the entympanic in the adult skull of all species of an allied order (Rodentia) is very remarkable from the point of relationship. The investigation on the development of the auditory bulla has shown an entotympanic in many cases in which the adult bulla does not show it. The conditions in this respect are not a little complicated by the discovery of two different entotympanics, a rostral and a caudal one. Investigations on the development of the bulla in a larger number of mammals may throw more light on the distribution of either of them in the mammals and thus perhaps on their relationship.

Division of Elements According to Eustachian Foramen, False and True Bulla

Only two elements necessarily lie in the wall of the tympanic cavity, the tympanic and the periotic, for the reason that the tympanic bears the tympanic membrane and the periotic bears the fenestræ ovalis and rotunda. Yet we do not always find them as elements constituting the bulla. Only in a relatively small number of the mammals does the periotic form a so-called tympanic wing in the bulla, while the tympanic is nearly always found in the bulla, if there is a bulla and not a mere tympanic ring; only the Tupaiidæ and the lemurids of Madagascar form the exception; here the tympanic forms a free ring in the interior of the bulla.

The elements that can be found constituting the bulla are (Winge, 1893*b*, pp. 67, 142; Van Kampen; Bondy, 1907, p. 401): (ecto) tympanic, periotic, squamosal, alisphenoid, basisphenoid, entotympanic, basioccipital, exoccipital, pterygoid, processus Folii of the malleus with the ossiculum accessorium malleoli, tympanohyal, Bondy's caudal "Chordafortsatz" (skeletal element of Spence).

A division can be made according to the ostium tympanicum tubæ. On the rostral or oral side of this opening lie almost exclusively the alisphenoid and the squamosal, also the Folian process with the ossiculum accessorium malleoli and the pterygoid. On the caudal side of this ostium lie the periotic, basisphenoid, entotympanic, tympanohyal and Bondy's caudal "Chordafortsatz." The tympanic can lie rostrally as well as caudally of the opening for the Eustachian tube.

Another division is sometimes made between true tympanic and false bulla (see Scott, 1913, p. 628; Matthew 1909, p. 504). Matthew gives as examples of a true tympanic bulla the Carnivora, Rodentia and primates, but among the Carnivora the entotympanic often occurs, and the primates show a well-developed tympanic process of the periotic; Matthew calls this entotympanic an outgrowth from the petrosal, and accordingly the outgrowth either from the alisphenoid or from the basisphenoid is called a false bulla. Though the indication that an animal possesses a false bulla is very important, it is still much more important to know what element or elements constitute this false bulla.

Indistinct Compound Structure of the Bulla

Many examples show that the course of the sutures in the bulla can hardly be determined except in the late-fœtal and new-born stages which show that the bulla is complex, while the dry skulls, even of

very young specimens, do not show a suture at all. This is also a reason to avoid the term "true tympanic bulla." To give a few examples: Van Kampen mentions that the course of the sutures could hardly or not at all be determined among his material in: *Notoryctes* (i.e., the elements in the marsupial bulla are not always connected by sutures, as a notice in Zittel, 1893, p. 88, suggests), *Talpa europæa, Chrysochloris, Rhynchocyon* (in the suture between the tympanic and the caudal entotympanic), and also in *Plecotus auritus.* This last example shows that even if there is no distinct suture, still the different elements can be seen, as the entotympanic is thin and transparent, while the tympanic is thick and not transparent (Van Kamp.; Revilliod, 1917, p. 21, Chiroptera in general, fossil Palæophyllophora Sanctæ-Nebouleæ). Also in the modern Viverridæ as a rule the entotympanic is thinner than the tympanic. The same occurs in the modern Felidæ, although different in various species. This difference in thickness makes a difference in transparency.

In the adult *Bradypus* the tympanic is fused with the entotympanic, which is not yet the case in the young skull; the adult skull sometimes shows an irregular bony ridge which indicates the suture. In the dry skull of an adult *Dasypus, Zaëdyus* and *Chlamydophorus,* no suture in the bulla is visible; that it must be a complex bulla can be concluded from the conditions found in the other modern Dasypodidæ. Exceptionally in the bulla of *Dasypus* a suture is found, and the development of the auditory bulla shows a well developed entotympanic (Van der Klaauw, 1924*b*). Therefore we have every reason to believe that the bulla of *Prozaëdius* (Scott, 1903*a*, p. 71) and *Peltephilus* (Scott, 1903*a*, p. 90), which are said to be formed by the tympanic, also contain an entotympanic. Perhaps the deep notch in the bulla of *Prozaëdius* (Scott, 1903*a*, p. 71) is an indication of this complexity.

In *Tapirus* Van Kampen supposes that the entotympanic is indistinguishably fused with the petrosal. In *Sus* the entotympanic, if present, is fused with the tympanic without a trace of a suture. In *Procavia* (*Hyrax*) as well, very soon after birth the entotympanic is fused with the tympanic without leaving a trace of a suture. The boundary between these two elements in *Procavia* corresponds, in my opinion, perhaps with the boundary on the internal surface of the bulla, which runs parallel to the sulcus tympanicus along the margin of greatest height of the bulla and which separates the thin excavated tympanic from the thicker entotympanic.

In the adult Nycticebidæ there is no distinct suture or boundary

between the tympanic and the processus tympanicus petrosi, which in younger stages is present. In the adult Hapalidæ there is no trace of the compound structure of the bulla, which, however, from analogy may be considered to be present, as in other monkeys both the tympanic and the petrosal plate are distinct (see Van Kampen, fœtal *Cebus;* Bondy, 1907, p. 383, *Macacus nemestrinus*, only partly separated, for the rest no distinct boundary; Bondy, 1907, p. 386, *Ateles paniscus* tympanic nowhere reaches the mesial wall of the tympanic cavity). In a new-born *Macacus* the tympanic and the petrosal plate in the bulla are indistinguishably fused.

The different elements of the bulla may sometimes be identified from the difference in the surface of the elements. For example, in *Hapalops* and allied genera (see my own investigations) the under surface of the entotympanic is rough and that of the tympanic is smooth. In these genera and also in *Mylodon* (see my own investigations) the tympanic and the entotympanic show a different curvature, and where the two elements lie close together there is not a gradual but a rather sharp transition in surface.

Processus Folii of the Malleus and Ossiculum Accessorium Malleoli

The Folian process of the malleus and the ossiculum accessorium malleoli may form a part of the bulla, though it is a small part.

The Folian process lies in the sulcus malleolaris of the tympanic and often coössifies with the tympanic (see Gregory, 1910, pp. 266, 282, marsupials and insectivores, etc.), a feature that is easily understood in connection with the view that both are homologues of elements of the lower jaw of the lower vertebrates.

The ossiculum accessorium malleoli also may form a very small part of the bulla, but its importance lies in its possible homology with a third element of the lower jaw of the lower vertebrates (Van Kampen, 1904, p. 366; 1905, p. 707; (Van Kamp.; Watson, 1916, pp. 345, 361, 365; Ridewood, 1922, p. 242). I refer to the literature cited in my article on the auditory ossicles (1924*a*, pp. 609, 610), to which I now add: Broom (1911, p. 922), Wortman (1921), Ridewood (1922, pp. 242, 243), Böhm-Tiateje (1921), Voit (1923), v. d. Klaauw (1924*c*, *Cholœpus*). Perhaps also the far forwardly-extended prolongation of the processus longus mallei described in *Halicore* by Lepsius (1882, p. 45) represents an ossiculum accessorium malleoli. Lepsius considers it as a further ossification of the cartilage of Meckel.

This ossiculum accessorium malleoli, which according to Böhm and

Voit is nothing but an outgrowth of the Folian process of the malleus, is also sometimes fused with the tympanic.

In *Cholœpus*, probably also in *Bradypus* and in some Gravigrada, Van Kampen found in the cranial wall of the rostral part of the tympanic cavity an element which he homologizes with the ossiculum accessorium malleoli. According to my own investigations in *Cholœpus* (v. d. Klaauw, 1924*c*) it is not formed by this auditory ossicle, but by a peculiarly formed processus perioticus superior. Probably also in the Gravigrada (see also the figures of my own investigations on *Scelidotherium* and *Hapalops*) it is therefore not an ossiculum accessorium malleoli but a processus perioticus superior.

Skeletal Element of Spence (Bondy's Caudal "Chordafortsatz")

Bondy's caudal "Chordafortsatz" can be formed by the so-called skeletal element of Spence. It is a very small element, but its importance lies in its possible homology with a part of the extra-columella of the lower vertebrates in mammals. For further information I refer to my article 1923.

Pterygoid

In *Echidna* (see also: Gaupp, 1908, pp. 662, 663, 756, 759; Watson, 1916, pp. 353, 354) we find the pterygoid in the wall of the tympanic cavity; it lies in the ventral wall between the tympanic and the periotic on the oral side of the Eustachian tube forming the front of the tympanic cavity. During development the pterygoid grows in the caudal direction on the ventral surface of the pars cochlearis and gets a connection with the tympanic by its strong broadening, but it remains separate from the capsula cochlearis by the mesial portion of the tympanic groove. It shows a rather deep excavation, the so-called recessus medialis cavi tympani. It is probably the result of the extreme backward prolongation of the palate with the consequent posterolateral displacement of the pterygoids and of the Eustachian tubes (Van Kamp.; Gregory, 1910, p. 151) and does not seem to be a primitive condition, which could be judged to be a support for the view that the tympanic is homologous with the quadrate of the lower vertebrates, a view that for other reasons as well is not probable (Gregory, 1910, p. 151).

The homologization of the "Echidna pterygoid" has been a matter of divergent opinions, of which I will mention only the following. Watson (1916, p. 364; see also: Van Kampen, 1922, pp. 56, 57; Gregory and Noble, 1924, pp. 457, 458) derives the "Echidna pterygoid" from the

posterior or quadrate ramus of the epipterygoid of a cynognathid and thus compares it with the processus tympanicus alisphenoidei.

Also for *Erinaceus* the presence of the pterygoid in the wall of the tympanic cavity has been described, but according to Van Kampen this element is not the pterygoid but the alisphenoid.

The presence of the pterygoid in the ventral wall of the tympanic cavity in *Myrmecophaga* is confirmed by later investigations (see Van Kampen, 1905, p. 488; not in edition 1904; Winge, 1915, p. 240). Next to the accessory cavity in the basioccipital a second accessory cavity lying in the rostral part of the tympanic cavity occurs in the Myrmecophagidæ. This cavity lies in the alisphenoid and in the pterygoid. According to Winge (1915, pp. 242, 243, 244) this accessory cavity in the pterygoid is not at all or only very feebly developed in *Cycloturus*, and is well developed in *Myrmecophaga* and *Tamandua*.

The inflated hinder parts of the pterygoid are erroneously described as "tympanic bullæ," formerly by Gervais (cited by Van Kampen) and even later by Stock (1913, pp. 343, 347, 348). That they have nothing to do with the auditory bullæ has been emphasized by Reinhardt (1878, p. 277), by Van Kampen (1904, 1905) and Hay (1917, pp. 116, 118, 119).

In the Delphinidæ the pterygoid shows a concavity in which is found a portion of the cavities of the rostral system of air-sacs, which cohere either with the auditory tube or directly with the tympanic cavity itself. A similar concavity for the same purpose has been described in *Balænoptera*.

Occipital

The hypotympanic sinus in a very few cases is expanded into the exoccipital. We find this in *Phascolomys* and in *Elephas*. In *Phascolomys* the exoccipital shows on the rostral side a small concavity. In *Elephas* the exoccipital shows a large cancellous space with a wide aperture, corresponding with a similar aperture between the bulla and the periotic. According to a notice in literature the tympanic cavity in *Elephas* communicates as well with the other diploëtic cavities of the skull.

Winge (1893*b*, p. 95) describes the processus jugularis of the occipital in the wall of the tympanic cavity in *Macrotis* or in the Peramelidæ in general. According to Winge (1895*b*, p. 49) the base of the processus jugularis of the occipital in *Stypolophus* seems to conform a little with the tympanic cavity. In *Amphictis* (*loc. cit.*, p. 52) the same occurs as in *Stypolophus*, but to a less degree. One would suppose, however, according

to Winge's remark (1895*b*, p. 52) that the processus jugularis in the recent *Nandinia* resembles that in *Amphictis*, that the form of the paroccipital process is not influenced by the tympanic cavity but by the bulla.

In the modern Delphinidæ the processus paroccipitalis shows a concavity containing a portion of the caudal system of air-sacs, the so-called sinus pneumaticus paroccipitalis. This cavity communicates with the tympanic cavity either via the apertura posterior in the connecting part of the processus petrosus and the processus tympanicus, or, in the cases where this aperture is wanting, via the sinus pneumaticus peripetrosus, of which it then forms an appendix.

The so-called exoccipital in the wall of the tympanic cavity in the Notoryctidæ, according to Van Kampen, is not the exoccipital but the mastoid. Also the presence of the exoccipital in the wall of the tympanic cavity in the Talpidæ, according to Van Kampen, is not correct.

A tympanic process of the basioccipital is found only in *Myrmecophaga*. This peculiar feature can easily be understood in relation to the very reduced condition of the entotympanic. Also, in *Cholœpus* the basioccipital shows a similar erected lateral crest, which is here excluded from the tympanic cavity by the well developed entotympanic. If we imagine this element to be very much reduced, we have a condition such as is found in *Myrmecophaga*. In *Cycloturus* (Van Kampen, 1905, pp. 488, 489, not in edition 1904) the basioccipital, which is covered by the pterygoid, is excluded from the tympanic cavity, as the entotympanic is much better developed. In *Myrmecophaga* the basioccipital is slightly excavated and forms a small accessory cavity.

According to Winge (1915, p. 113) the lateral margin of the basioccipital does not show a trace of the tympanic cavity in *Hoplophorus euphractus* and *Propalæohoplophorus australis*, but in *Lomatophorus ornatus* this margin is excavated, without doubt by an extension of the tympanic cavity. Among these Glyptodontidæ we have probably analogous cases to those in the Myrmecophagidæ in respect to the development of the entotympanic.

Accessory cavities in the diploë of the occipital communicating with the tympanic cavity have been described for *Talpa* and *Chrysochloris*.

Formerly the entotympanic in the Bradypodidæ, not yet recognized as a separate element, has been described as a lamella of the basioccipital, which of course is not correct.

Tympanohyal

The tympanohyal is the most cranial element of the hyoid bar, which in general, especially in many of the lower mammals, forms a little process on the hinder part of the crista facialis petrosi, where it is connected with the periotic and forms the so-called processus hyoideus. In the few cases where we have a coössified tympano- and stylohyal, we have the so-called processus styloideus. It is important to give these different names to morphologically different processes. Also the processus styliformis is sometimes called processus styloideus (Zittel, 1893, pp. 16, 20; 1923, p. 409), but to avoid confusion it is better to call this process, processus styliformis.

Scott's abnormal attachment of the hyoid to the anterior part of the bulla in Toxodontia (Scott, 1912, p. 114, etc.) may be mentioned here, but is discussed in the chapter on the processus styliformis.

According to Scott (1912, p. 114) the point of attachment of the hyoid arch in the Santa Cruz Typotheria is very exceptional; the junction of the paroccipital process with the tympanic leaves no room for the hyoid in its usual position and it is displaced to the external side of the bulla, near the posterior end, where a cylindrical fossa may be seen in some of the genera.

In exceptional cases the tympanohyal is well developed and forms a distinct bony process on the periotic with a freely projecting top.

Sometimes there is no bony tympanohyal, as in Didelphyidæ, Peramelidæ, Dasyuridæ, Notoryctidæ, *Phascolarctus* and *Phascolomys*, thus in the majority of the marsupials. In *Phalanger* only there often seems to be a tympanohyal, and it differs in this respect from all the other marsupials. Perhaps it is absent also in *Chrysochloris* and *Tupaia*. Van Kampen could not find a tympanohyal in his skull material of Delphinidæ, though it has formerly been described in literature.

For the Chiromyidæ Van Kampen supposes the possibility of the absence of a bony tympanohyal, if it is not indistinguishably fused with the neighborhood. In the Tarsiidæ as well, no bony tympanohyal is found. In the Hylobatidæ and Anthropomorphæ, except in the orang-utan, the top of the tympanohyal is not visible in the aperture which it normally occupies, and thus the tympanohyal is either not ossified, or which seems more probable, is very short.

The notice of Pocock (1916*b*, p. 222) that in typical members of the Felidæ the tympanohyal remains generally, if not always, cartilaginous through life up to its point of attachment with the bulla is probably related to the tympanostyloid cartilage.

Another cause of the absence of a bony tympanohyal in the dry skull may be the exceptional condition which is found in some species of *Erinaceus*, in which the tympanohyal is cartilaginous at both ends, while in all other cases it is coössified with the petrosal. The tympanohyal in *Orycteropus* also is said to ossify independently.

Often the tympanohyal can not be detected because it is so thin and fragile that it has disappeared, as Van Kampen observes for Megachiroptera. In the modern Suidæ as well, the tympanohyal is easily broken off and is often absent in dry skulls. In the Santa Cruz Typotheria, according to Scott (1912, p. 114), the hyoid is loosely connected with the skull and very rarely is found in position. In the material of *Typotherium cristatum* investigated by Van Kampen, the tympanohyal was not visible. The same is the case in his material of *Toxodon platensis*. The little cylindrical bone described by Burmeister (1867, p. 262) in *Toxodon burmeisteri*, and which according to Van Kampen is the tympanohyal, was also preserved only on one side of the skull. In the specimen of *Anchitherium bairdii* described by Leidy (1854, p. 69) the base of the styloid process alone remained.

Another reason that it is not visible is that it is covered. Thus the bony meatus acusticus externus covers it in the Macroscelidæ. In many cases it lies for the greater part in the bulla and is difficult to see, as is perhaps the case in the Hylobatidæ and Anthropomorphæ. An exception in this respect is the tympanohyal in *Centetes*, in which it lies for the greater part outside the tympanic cavity.

Another reason that the tympanohyal is not visible is that it is enclosed in a vagina processus hyoidei or styloidei. In the chapter on the vagina processus hyoidei s. styloidei many examples are given of the covering of the tympanohyal.

Another reason for the indistinctness of the tympanohyal is its fusion with the surrounding elements. Together with examples of this cause of its indistinctness I shall remark on the fusion of the tympanohyal in general, especially that on the fusion of its distal top with the mastoid or periotic. A few notes of cases in which it nearly touches skeletal elements in its neighborhood may precede as introduction.

In *Sorex* and *Myogale* the top of the tympanohyal lies against the periotic and in *Erinaceus* against the tympanic.

In the modern *Procavia* (*Hyrax*) the thin, rather long tympanohyal is in contrast to that in the other modern ungulates, directed more backward, so that its top reaches the mastoid.

Perhaps the spur from the posttympanic process of the squamosal,

which runs inward across and bridges the posterior end of the mesotympanic fossa, nearly reaching the petrosal, and which anteriorly defines the foramen stylomastoideum primitivum in *Vulpavus*, *Viverravus* and *Thinocyon*, and apparently in all the smaller Creodonta (Matthew, 1909, pp. 358, 451), is the tympanohyal. In *Dromocyon vorax*, on the other hand, no plug-like tympanohyal is present, according to Wortman (1901, p. 293); there is rather a deep recess, which probably marks the point of attachment of the hyoid arch.

In a few cases the tympanohyal does not form a process, as it is connected at both ends with the mastoid. This is found in *Echidna* (see also: Gaupp, 1908, pp. 645, 733, 734; Gregory, 1910, p. 157) and perhaps also in *Galeopithecus*.

In the Macropodidæ we find also a bony bridge connected with both ends with the mastoid, but it does not seem to be formed by the tympanohyal.

In *Manis* the tympanohyal is fused at both ends with the periotic and forms a horizontal bony bridge, distinct in varying degrees in different species. In *Cholœpus* we find it in the caudal part of the fissure between the tympanic and the entotympanic, lying against the mastoid, and forming, together with the mastoid and the paroccipital process, the articular surface for the stylohyal (Van Kamp.; Turner, 1851, p. 206). In the Gravigrada (see also my own investigations on *Hapalops* and allied genera, *Scelidotherium* and *Mylodon*) the top of the rather thick, distinct tympanohyal lies against the mastoid and is often fused with it; it forms the rostral part of the sometimes enormously developed surface for the articulation of the stylohyal; as to the latter feature, perhaps *Scelidotherium* and *Nothrotherium* form an exception, according to Van Kampen.

Also in the Glyptodontidæ, according to Van Kampen, the tympanohyal is present and probably fused at its top with the mastoid, though often it seems to be broken off, as Van Kampen found in his own material.

In the adult *Myrmecophaga* the thin tympanohyal is fused with the neighborhood. Also in *Dasypus sexcinctus* the thin tympanohyal is fused with the neighborhood, the top being visible between the bulla and the mastoid; this opening lies at some distance from the stylomastoid foramen. In *Tatusia*, *Priodontes*, *Xenurus* (=*Lysiurus*) and *Tolypeutes* the top of the distinct tympanohyal lies against the mastoid. Thus the statement that the tympanohyal is present only in *Orycteropus* among the Edentates, is not correct (Gregory, 1910, p. 335).

In the modern Rodentia the tympanohyal is never distinct; no

doubt, however, it is always present, but mostly small and indistinguishably fused with the neighborhood; in many rodents we find the opisthotrematic condition. Van Kampen found a distinct tympanohyal in a few rodents; in *Castor fiber* it is well developed.

In *Canis* the small bony tympanohyal is fused with the neighborhood; the top is often visible within the stylomastoid foramen in a small groove of the bulla. In *Otocyon*, in relation to the strongly inflated bulla, the hyoid has become opisthotrematic and touches the paroccipital process.

In the modern Mustelidæ the tympanohyal seems to be indistinguishably fused with the tympanic; in *Galictis* only, Van Kampen found a tympanohyal. According to Van Kampen (1907, p. 695) the short tympanohyal in *Putorius putorius*, as well, is not distinctly separated from the neighborhood.

In *Felis* as a rule the tympanohyal is indistinct, as it is often fused with the groove in the wall of the bulla in which it lies. In the modern Viverridæ, on the other hand, the short tympanohyal as a rule is distinct as usually it is not fused with the bulla.

In the adult Otariidæ the tympanohyal is fused with the bulla, the top being separate from the foramen stylomastoideum; in the pullus the thin tympanohyal lies in the groove of the bulla. In the adult Trichechidæ as well the tympanohyal is not distinct, while in the pullus it is a thin rod between the tympanic and the mastoid.

In the modern Camelidæ the tympanohyal, at least its proximal portion in adult skulls, is fused with the bulla. In *Procavia* (*Hyrax*) as well the tympanohyal is fused with the bulla.

In the Lemuridæ the tympanohyal is not distinctly visible; probably it is fused with the neighborhood.

In the fossil *Palæopropithecus maximus*, according to Standing (1908, p. 75), the paroccipital process on its outer edge is fused with the styloid process. The tympanohyal in the Chiromyidæ, if not absent, is indistinguishably fused with the neighborhood. In the Nycticebidæ in general, as well, the tympanohyal is probably fused with the neighborhood. In the Hapalidæ the tympanohyal is not distinctly visible; probably it is fused with the bulla and the tympanic; Van Kampen could not find the formerly described processus styloideus. Also in *Ateles* the tympanohyal probably is entirely fused with the neighborhood.

In *Cercocebus collaris* the top of the tympanohyal is fused with the wall of the tympanic cavity, the rest of the very distinct, thin, curved tympanohyal runs freely through the tympanic cavity, within which it is

situated. In *Macacus cynomolgus* the tympanohyal is fused over its whole length with the caudal wall of the tympanic cavity and thus does not project freely. Sometimes, not constantly however, a short stylohyal freely projects; it is fused with the skull and anteriorly is appressed to the bulla.

In most cases the tympanohyal is a thin slender process. Sometimes it shows an aberrant form. It can be plate-like, as in *Sorex,* In *Priodontes, Xenurus* (=*Lysiurus*) and *Tolypeutes* the distal portion of the tympanohyal is broadened to a small leaflike expansion and for this reason it reaches or nearly reaches the entotympanic. In *Priodontes* this expansion also reaches the exoccipital and encloses in this way a second aperture behind the stylomastoid foramen; it lies between the tympanohyal, the mastoid and the exoccipital.

In *Orycteropus* the tympanohyal is short, hook-like and its top is free (see also, Gregory, 1910, p. 335).

In *Castor fiber,* as an exception among the modern Rodentia, the tympanohyal is distinct, rather long and thick and resembles very much that in *Sus;* it is protrematic (in many other Rodentia it is opisthotrematic), the top of the tympanohyal is free and visible between the bulla and the mastoid. As in the artiodactyls, the tympanohyal in *Castor* is entirely excluded from the boundary of the tympanic cavity.

In the modern *Hyæna,* as an exception among the Carnivora, the tympanohyal is distinct and long. In the Phocidæ the tympanohyal is rather large and curved; in the Otariidæ and Trichechidæ it is thin.

In the Delphinidæ a short bony tympanohyal has been described, which Van Kampen could not affirm.

In the Balænopteridæ and Balænidæ the tympanohyal is a large conical bony mass.

In the "Protungulata," according to Van Kampen, the tympanohyal is probably little developed and more or less directed backward, as is still found in the recent *Procavia.* In the other modern ungulates the tympanohyal is distinct and mostly even very large. This large size is especially caused by the fact that the tympanohyal extends farther forward than is generally the case. This fact explains the feature that the distal part of the tympanohyal as a rule curves forward, thus differing from that in all other mammals.

In the fossil *Theosodon* (Scott, 1910, p. 118) the tympanohyal is relatively long, slender, cylindrical and outwardly curved; it is not attached to the tympanic bone, but to the posttympanic process of the squamosal.

In the modern *Rhinoceros* the tympanohyal is rather long and extraordinarily thick, attached in the usual way to the petrosal, and directed downward and a little forward; the tympanic excludes it from the boundary of the tympanic cavity. In the recent Tapiridæ the tympanohyal is shorter and thinner than in *Rhinoceros*. In *Equus* it is about as long as that in *Rhinoceros*, but it is thinner.

In the modern Suidæ the tympanohyal is long, and in comparison with that in the majority of the ungulates, thin, so that it is easily broken off and often is wanting in the dry skull; it is free over its whole length except at the point of attachment to the periotic. In a similar manner the thick and long tympanohyal in *Hippopotamus* is entirely free, lying partly in a groove of the bulla, partly in a groove of the exoccipital. In the fossil *Mesoreodon chelonyx* (Scott, 1895*b*, p. 130) the tympanohyal is a short, stout, cylindrical bar. In the modern Ruminantia the tympanohyal is well developed and long; in the Bovinæ especially it is very thick.

In *Elephas* the tympanohyal is short and thick.

In *Manatus* and *Halicore* the tympanohyal is distinct, short and thick; the stylohyal is connected with it and also with the exoccipital (opisthotrematic condition). In *Halitherium*, according to Lepsius (1882, p. 36), the processus styloideus is a distinct large rough excavation. Also in *Rhytina* Claudius (1867, p. 8) describes a rough excavation for the attachment of the stylohyal, lying behind the place of fusion of the caudal leg of the tympanic with the skull.

Squamosal

Besides the periotic and the tympanic the squamosal is the element that we find most of all in the wall of the tympanic cavity. We find it very often in the lateral wall of the recessus epitympanicus, but also in many cases we find the squamosal in the fore and upper wall of the tympanic cavity. Then the pars entoglenoidea squamosi lies in the wall of the tympanic chamber; in a few cases it forms a high ridge or process, the so-called processus entoglenoideus, which forms a part of the wall of the tympanic cavity.

In *Echidna* we find the squamosal just in the fore wall of the tympanic cavity, while in *Ornithorhynchus* it is totally excluded (thus no epitympanic recess).

In the Diprotodontia the pars entoglenoidea squamosi is strongly broadened and lies in the roof and the fore wall of the tympanic cavity. On the lateral side it is continued in a processus entoglenoideus, which is visible externally. In the Phalangeridæ, except in *Trichosurus*, the

processus entoglenoideus is badly developed (Van Kamp.; Winge, 1893*b*, pp. 98, 99, on *Phascolomys*). A postglenoid ridge of the squamosal is also present in the fossil *Ictops*, as in the zalambdodonts (Gregory, 1910, p. 261). In the Notoryctidæ there is also a processus entoglenoideus, which also perhaps lies in the wall of the tympanic cavity. How far the ridge on the posttympanic process of the squamosal in different didelphyids (Winge, 1893*b*, pp. 20, 36, 59) forms a part of the tympanic chamber. I cannot say.

Also in the insectivores we find a processus entoglenoideus in the lateral wall of that part of the tympanic cavity which lies in front of the periotic and tympanic, as in Centetidæ, *Solenodon* and *Potamogale*. In *Rhynchocyon* there is also a processus entoglenoideus that forms no part or only a little of the tympanic chamber. It is absent in *Erinaceus* (Van Kamp.; Gregory, 1910, p. 261) and in *Sorex*, where the squamosal only forms the lateral wall of the epitympanic recess; likewise it is absent in *Myogale*.

In *Manis* we find the squamosal in the upper fore wall of the tympanic cavity, in the place where we should expect the alisphenoid.

In the Xenarthra the processus entoglenoideus is strongly developed but lies outside the tympanic cavity.

In the modern Rodentia, Cetacea and *Manatus* the squamosal is entirely absent in the wall of the tympanic cavity.

In *Lemur mongos* the squamosal perhaps occurs in the cranial wall of the tympanic cavity. In a young specimen of *Perodicticus potto* the inner margin of the squamosal lies together with the alisphenoid in the roof of the tympanic cavity in front of the tegmen tympani.

Basisphenoid

The insectivores are the only order in which the basisphenoid lies in the wall of the tympanic cavity. Although we find this in most of the families (Van Kamp.; Matthew, 1909, p. 504; Carlsson, 1922, p. 231, Erinaceidæ), there are a few families and forms that do not show a tympanic wing of the basisphenoid. There is considerable evidence that the ancestral insectivore was not distinguished by large tympanic flanges on the basisphenoid (Gregory, 1910, p. 291). According to Van Kampen the processus tympanicus basisphenoidei is absent in *Solenodon* (see also, Gregory, 1910, pp. 245, 255, 268), in *Sorex* (see also, Gregory, 1910, p. 265) and in *Tupaia* (Van Kampen, 1904, pp. 124; 1905, p. 449; according to Gregory, 1910, p. 274, slight or absent) and among the Macroscelidæ absent or nearly absent (Van Kampen, 1904, pp. 121, 123; 1905,

p. 445, 447; Gregory, 1910, p. 281). It also seems to be lacking in the fossil family Hyopsodontidæ (Matthew, 1909, pp. 507, 510, 514) and in the fossil *Ictops* (Gregory, 1910, pp. 261, 268). In *Geogale* the margins (rims) are a little erected, but not so much that they form a part of the wall of the tympanic cavity (Van Kampen, 1904, p. 102; 1905, p. 425). A well-developed tympanic wing of the basisphenoid we find in the Centetidæ, Potamogalidæ, Erinaceidæ, Talpidæ, Chrysochloridæ and among the fossils in Leptictidæ (Matthew, 1909, p. 534) and in *Cayluxotherium* (*Neurogymnurus*) where it is highly developed (Gregory, 1910, pp. 261, 263). There are differences in the development of the tympanic wing. Among the Centetidæ it is higher in *Centetes* and *Ericulus* than in *Hemicentetes* (in the latter genera the tympanic ring lies in a more horizontal plane); in *Erinaceus* it is but moderately developed (Gregory, 1910, p. 266), it is higher but shorter than in *Centetes*, according to Van Kampen, while in *Gymnura* it is larger than in *Erinaceus* and more expanded laterally (this is probably the reason why the tympanic is more erected). In Talpidæ the wing is very large (Gregory, 1910, p. 267), in *Talpa europæa*, according to Van Kampen, it is not high, but long; in *Chrysochloris* it is much higher than in *Talpa* and in one of the other Talpidæ, *Myogale*, it is greatly expanded (Gregory, 1910, p. 264).

Concerning the presence of the basisphenoid in the wall of the tympanic cavity, this cavity is prolonged forward along the alisphenoid (Van Kampen, 1904, pp. 126, 127; 1905, pp. 451, 452). Therefore we find the basisphenoid usually in the foremost part of the tympanic cavity, namely, in that part that lies in front of the periotic and the tympanic. In *Centetes* we find it medially and partly ventral to this part; in *Erinaceus*, where this part is much shorter, it lies in the medial wall of the cavity. More caudally we find it between the tympanic and the periotic (Van Kampen, 1904, pp. 99, 100, 104, 105, 113; 1905, pp. 422, 423, 428, 436) where it separates the petrosal from the basioccipital (Gregory, 1910, p. 246), while in forms where this tympanic wing of the basisphenoid is lacking, the petrosal is closely appressed to the side of the basioccipital (Gregory, 1910, pp. 246, 261).

Sometimes the wing of the basisphenoid also forms the roof of the rostralward prolonged part of the tympanic cavity, where we should expect the alisphenoid (Van Kampen, 1904, pp. 113, 115; 1905, pp. 436, 437, 439).

A deeply excavated tympanic wing of the basisphenoid has been described for *Centetes* and *Myogale*. In *Chrysochloris* the flat part of the basisphenoid between the two wings is said to contain a sinus which by

means of a pair of apertures establishes a communication between the two tympanic cavities (Van Kampen, 1904, p. 118; 1905, p. 442).

In other cases the basisphenoid does not show a flat part between the two tympanic wings, and then the latter touch each other in the sagittal plane, as in *Myogale*, or nearly touch, as is the case in *Hemicentetes* and *Microgale*.

There remains to be mentioned that perhaps the tympanic process of the basisphenoid has originally nothing to do with the basisphenoid, but that it is secondarily connected with it (for further information see: Van Kampen, 1904, pp. 126, 127; 1905, pp. 451, 452). Van Kampen (1922, pp. 55, 56, 57) considers the processus tympanicus basisphenoidei as homologous with the basitemporale, though the separate development of this process is not known and is not even probable.

Alisphenoid

The presence of an alisphenoid bulla is a generally known feature of the marsupial skull, yet it is not restricted to the marsupials, in so far as the alisphenoid is present in the wall of the tympanic cavity. On the other hand, an alisphenoid bulla is not always found in marsupials. It is said to be absent in *Phascolomys* (Van Kampen, 1904, p. 87; 1905, p. 406; but see also, Winge, 1893*b*, p. 98) and among the fossils in *Ptilodus* (Broom, 1914, p. 123; but see also, Gidley, 1909, p. 619) and in some of the so-called Sparassodonta (Sinclair, 1906, p. 336) as in *Prothylacinus* (*loc. cit.*, pp. 340, 364, 349) and in *Borhyæna* (*loc. cit.*, pp. 340, 349).

We find the alisphenoid in the tympanic chamber in all recent marsupial families, except the Phascolomyidæ. (Owen, 1859, p. 313; Zittel, 1893, p. 88; 1923, p. 428; Wortman, 1901, p. 294; 1902*b*, p. 439; Matthew, 1906, pp. 212, 213, 215; Sinclair, 1906, p. 336; Scott, 1913, p. 628; Watson, 1916, pp. 354, 364; Van Kampen, 1922, p. 56; Gregory and Noble, 1924, p. 451). As to the fossils, it has been described for *Ptilodus* (Gidley, 1909, p. 619; but see also, Broom, 1914, p. 123), *Thylacoleo* (Owen, 1859, p. 314; 1866, p. 76), *Microbiotherium* (Sinclair, 1906, p. 410), and for some genera of the so-called Sparassodonta (Sinclair, 1906, p. 336) as *Cladosictis* (*loc. cit.*, pp. 339, 379) and *Amphiproviverra* (*loc. cit.*, pp. 339, 397).

The development of the alisphenoid in the tympanic chamber shows different stages (Van Kamp.; Gregory, 1910, p. 227; Watson, 1916, p. 354) It can be a mere depression in the hinder border of the glenoid region for the reception of the anterior wall of the membranous tympanic cavity, more or less developed (Gregory, *loc. cit.*, see also,

Zittel, 1893, p. 88) as we find it in the Didelphyidæ (Van Kamp.; Gregory, 1910, p. 220, who considers it to be here a primitive stage). Often it grows backward, finally embracing the tympanic annulus, as in the Phascolarctidæ (see also: Winge, 1893*b*, p. 88; the condition in *Thylacoleo* resembles that in *Phascolarctus* in some respects, see *loc. cit.*, p. 97; Owen 1859, p. 314, compares *Thylacoleo* in this respect with the Dasyuridæ, where according to Van Kampen the tympanic wing of the alisphenoid is differently developed). Much of the same condition as in *Phascolarctus* obtained, according to Van Kampen, also in one specimen of *Phalanger* that he examined. In the Phalangistidæ as a rule (Van Kamp.; Winge, 1893*b*, pp. 89, 100) and always in Macropodidæ the tympanic wing of the alisphenoid is united with the paroccipital process; in the latter family it turns upward, reaches the petrosal and excludes the exoccipital from the tympanic cavity, and thus differs in these characters from the Polyprotodontia and gives rise to a situation which is morphologically derived from that in the primitive Didelphids and not vice versa (Gregory, 1910, p. 227). So the development of the tympanic wing of the alisphenoid is very different and is often used in characterizing families and genera. Going more into details, after the general information given above, and setting apart *Phascolomys* and the Didelphyidæ in general (see also above), we notice first Winge's descriptions of the development of the tympanic wing of the alisphenoid in different genera and species (1893*b*, pp. 14, 20, 28, 31, *Grymæomys;* p. 35, *Philander;* pp. 37, 41, *Didelphys;* p. 59, *Hemiurus*). In the Peramelidæ it is sometimes as much developed, as a rule more strongly developed than in Didelphidæ, and not only in different genera but even in the genus *Perameles* itself we find differences in the size and form of the alisphenoid bulla (Van Kamp.; Lydekker, 1887, p. 256; Winge, 1893*b*, p. 95). In the Dasyuridæ also the well-developed bulla alisphenoidea is larger or smaller and more or less inflated in different genera (Van Kamp.; Winge, 1893*b*, p. 93; *Thylacoleo* is compared with the Dasyuri by Owen, 1859, p. 314; see also, Owen, 1866, p. 76; *Microbiotherium*, idem, by Sinclair, 1906, p. 410). In Notoryctidæ the alisphenoid bulla is strongly inflated and forms the anterior third of the bulla (Van Kamp.; Scott, 1905, p. 370; Gregory, 1910, p. 257); in the Phalangeridæ it is also well developed (Van Kamp.; Lydekker, 1887, p. 188). In *Phascolarctus* the development in general is the same, large and inflated (Van Kamp.; Winge, 1893*b*, pp. 97, 100) and still separated from the paroccipital process (see above; Van Kamp., 1904, pp. 83–84; 1905, p. 406). In the Phalangistidæ and especially in the Macropodidæ we have the extreme development, as we have seen

above (Van Kamp.; Lydekker, 1887, p. 205, on the non-inflated bulla of *Æpyprymnus*).

The alisphenoid bulla helps to form the ostium tympanicum tubæ. In connection with the situation of the alisphenoid, it remains as a rule on the lateral side of the Eustachian tube, and so we find it on the lateral side of the ostium tympanicum tubæ. As an exception to this rule we find that in the Macropodidæ it also forms the hinder border of the ostium tympanicum tubæ. This exceptional condition is an indication that this hinder part is perhaps another element, secondarily connected with the alisphenoid (Van Kampen, 1904, pp. 91, 92; 1905, pp. 414, 415).

The alisphenoid bulla is said to be also an insectivore character (Wortman, 1902*b*, p. 439; Matthew, 1906, pp. 212, 213, 215; 1909, p. 525; Sinclair, 1906, p. 336; Watson, 1916, pp. 354, 364; Van Kampen, 1922, p. 56). As already noted above, the tympanic cavity is prolonged forward in connection with the presence of the basisphenoid in the wall of the tympanic chamber, and therefore this cavity also lies alongside the alisphenoid and the latter forms its dorsal and often also its rostral wall; but even in the cases in which we can speak of a tympanic process of the alisphenoid, it is much reduced in comparison with that of the marsupials (Van Kampen, 1904, p. 127; 1905, p. 451). Only in *Ptilocercus* and the embryo *Rhynchocyon* (Van Kamp.; Carlsson, 1910*a*, p. 352) does it at all approach the characteristic marsupial condition and form a concave shell; in the Lipotyphla it primitively forms merely a straight ridge separating the tympanic fossa from the glenoid region (Gregory, 1910, p. 286; also pp. 272, 274, 281, 283). According to Gregory (1910, pp. 272, 274, *Ptilocercus* compared with *Tupaia*) the marsupial-like developed wing is more primitive than the smaller one. This point now appears in another light, since I found (Van der Klaauw, 1924*b*) that an important part of the alisphenoid bulla in Macroscelididæ, namely the part on the medial side of the Eustachian tube, is not formed by the alisphenoid but is a rostral entotympanic. In the marsupials, however, according to Watson (1916, p. 354), it is not preformed in cartilage, but must be entirely a membrane ossification.

Yet we do not find the alisphenoid in the tympanic chamber in all insectivores (Van Kamp.; Matthew, 1909, p. 504). Thus the alisphenoid in the tympanic chamber is lacking in the Soricidæ for although the forward prolongation of the tympanic cavity is largely developed, the enormously developed foramen lacerum anterius s. medium excludes the alisphenoid from the tympanic chamber (Van Kamp.; Gregory, 1910, p. 265); it is absent also in *Talpa europæa*, as an exception among the Talpidæ.

An alisphenoid bulla or a tympanic wing of the alisphenoid is lacking in some or in all Leptictidæ (Matthew and Granger, 1918, p. 607; Van Kamp.; Matthew, 1909, pp. 507, 534) and also in the Hyopsodontidæ (Matthew, 1909, pp. 507, 510, 514) and in *Palæoryctes* (Matthew, 1913, pp. 310, 313). Yet it is possible that the alisphenoid still forms a part of the wall of the tympanic cavity, but does not form a real wing. That is perhaps the case in *Palæoryctes*, where we have an alisphenoid ridge which does not take part in the bulla (Matthew, 1913, p. 310).

A wing of the alisphenoid has been described for the fossil Leptictidæ (see above) and also for *Pantolestes* (Matthew, 1909, p. 525) and *Ictops* (Gregory, 1910, p. 261), where, as in the zalambdodonts, it is continuous with the postglenoid ridge of the squamosal, which is a primitive insectivore character (*loc. cit.*, p. 254).

As to the development of the part of the alisphenoid that lies in the tympanic chamber, we find the forward prolongation of the tympanic cavity large in *Centetes*, smaller in *Hemicentetes* (where the tympanic wing is scarcely indicated), *Ericulus* and *Microgale* (Van Kamp.; Matthew, 1913, p. 313), and still shorter in *Erinaceus*, (where the tympanic process is only a low transverse ridge, Van Kamp.; Gregory, 1910, pp. 261, 266, while in some other Erinaceidæ it is strongly developed and inflated). Here we find the alisphenoid in the rostral and dorsal, in *Centetes* also in the lateral wall of the forward prolongation of the tympanic cavity. In *Myogale* the alisphenoid is strongly excavated (Van Kamp.; Gregory, 1910, p. 264), and also in many other Talpidæ we find a cavity in the alisphenoid communicating with the tympanic cavity, while in *Talpa europæa* the spongiosa in the inflated alisphenoid does not communicate with the tympanic cavity, although in the dry skull it seems that there might have been a connection.

In the Macroscelididæ (Van Kamp.; Gregory, 1910, p. 281) we find the alisphenoid in the anterior wall of the tympanic cavity, sometimes well inflated (on the so-called tympanic wing on the medial side of the Eustachian tube, see above). In the Tupaiidæ we find it as a very small part of the cranial wall of the tympanic cavity; a processus tympanicus is lacking (Van Kamp.; Carlsson, 1910*a*, p. 352; 1922, pp. 230, 231; but see also, Gregory, 1910, pp. 274, 279). In the Chrysochloridæ we find also a tympanic wing of the alisphenoid (Gregory, 1910, p. 267); in *Solenodon* this tympanic wing is lacking or shows only a remnant of it (Gregory, 1910, pp. 253, 254; Matthew, 1913, p. 313).

In *Myogale* the two alisphenoid bullæ touch each other in the sagittal plane.

In the other orders of the mammals we do not find the alisphenoid bulla that we found in marsupials and insectivores. Sometimes this is emphasized, for instance for the (hypothetical) Mesozoic ancestors of the Carnivora (Gregory, 1910, pp. 307, 308: if present, not forming a hollow shell for the tympanic cavity), for the immediately ancestral family of the creodonts (*loc. cit.*, p. 300: little or no "alisphenoid bulla") and for the creodonts (*loc. cit.*, pp. 302, 303; Matthew, 1909, p. 525). In *Mesonyx*, according to Winge (1895*b*, p. 50), a large portion of the wall of the tympanic cavity seems to be formed either by proper ossifications (entotympanic) or by outgrowths of the bones which adjoin it. As to the latter condition, perhaps the possibility of the presence of an outgrowth of the alisphenoid is meant. According to Matthew (1906, p. 230), however, no false (alisphenoid) bulla is a primitive carnivore feature. The absence of an alisphenoid process contributing to the formation of an otic bulla is emphasized for *Sinopa* (Wortman, 1902*b*, p. 439; Matthew, 1906, pp. 213, 215) and *Dromocyon vorax* (Wortman, 1901, p. 294).

In Megachiroptera the alisphenoid covers the foremost part of the tympanic cavity dorsally and we find it anteriorly also in *Galeopithecus* (see also, Gregory, 1910, p. 317).

In the fossil *Palæophyllophora*, according to Revilliod (1917, p. 37), the anterior wall of the tympanic cavity is formed by the lacuna in the alisphenoid (Van Kamp.; *loc. cit.*, p. 45, on *Pseudorhinolophus*).

In the monotremes, on the other hand, we do not find the alisphenoid in the boundary of the tympanic cavity; perhaps it is a primitive character, but Van Kampen (1904, pp. 73, 74; 1905, p. 396) feels inclined to consider it as an independent deviation.

In *Orycteropus* the alisphenoid lies in the upper fore wall of the tympanic cavity between the tympanic and the periotic; according to Van Kampen it does not contain a part of the epitympanic sinus, as is formerly described.

In *Myrmecophaga* (Van Kampen, 1905, p. 488; not in edition 1904) the alisphenoid probably forms the dorsal and medial wall of the rostral accessory cavity, while the pterygoid forms the ventral wall; formerly this cavity is described in the pterygoid and even in the palatinum. This accessory cavity is very much reduced or even lacking in *Cycloturus*. This cavity in the alisphenoid in the Myrmecophagidæ is an analogy with that in the marsupials obtained by convergence.

The note of Stock (1913, p. 348), that in *Nothrotherium* the alisphenoid forms the roof of the auditory capsule, is worthless, as this

"auditory capsule" has nothing to do with the auditory bulla, since it is the inflated hind portion of the pterygoid.

In *Manis* we do not find the alisphenoid in the wall of the tympanic cavity; in the place where we should expect it we find, in contrast to most lower mammals, the squamosal.

In none of the adult rodents, according to Winge (1888, pp. 103, 184), is the alisphenoid present in the external surface of the tympanic cavity.

In the modern Canidæ the alisphenoid projects a little in the tympanic cavity and forms the tuba ossea together with the bulla. In the modern Ursidæ as well the alisphenoid lies in the superior wall of the tympanic cavity and with the bulla surrounds the Eustachian foramen. In *Lutra* and *Putorius* at least, among the modern Mustelidæ, the alisphenoid does not lie in the wall of the tympanic cavity. In the modern Viverridæ the alisphenoid forms the roof of the orificium tubæ and thus is visible in the tympanic cavity. In the modern Hyænidæ it extends rather far in the rostral chamber of the tympanic cavity and partly forms the wall of the tuba ossea. In the modern Felidæ the alisphenoid lies in the rostro-superior wall of the bulla; it extends above the tuba in the tympanic cavity and reaches the tegmen tympani; between the alisphenoid and the bulla lies the orificium tubæ and the fissura Glaseri.

In *Lemur mongos* the alisphenoid probably is present in the cranial wall of the tympanic cavity. In the young *Perodicticus potto* the alisphenoid lies in the roof of the tympanic cavity in front of the tegmen tympani, while in the adult skull it is indistinguishably fused with the petrosal.

In *Midas rosalia* the alisphenoid is excluded from the tympanic cavity. In the primates in general the alisphenoid does not lie in the wall of the tympanic cavity, the tegmen tympani occupying its place.

The tympanic wing of the alisphenoid in marsupials and insectivores (see above) according to Watson (1916, pp. 354, 364. See also: Van Kampen, 1922, p. 57; Gregory and Noble, 1924, p. 451) is an essential feature of the primitive mammalian bone, and agrees with the Echidna-pterygoid and with the posterior ramus of the epipterygoid of cynognathids, of which various relations to the neighborhood are exactly those of the tympanic wing of the alisphenoid. According to Van Kampen (1922, p. 56) the tympanic processes of the alisphenoid perhaps have the same origin as those of the basisphenoid, and in this case would be homologous with the basitemporalia.

Tympanic

We have already described many features in relation to the (ecto) tympanic. We have discussed its ontogeny, its change in place, when the ventral wall is formed, where and how it is connected with the skull, where it is closed dorsally, and so on. We have seen that it is in many cases a primitive and sometimes a slightly broadened ring, and also we have seen cases where it forms a cylindrical tube of the meatus acusticus externus. There remains only to be described where and how it forms a part or the whole of the auditory bulla, as well in the ventral wall of the tympanic cavity, as in the covering of the recessus meatus acustici externi. Of course this is not the case where we have a primitive ring, and we find it only to a small degree where there is a broadened tympanic ring. These two expansions of the tympanic that we shall now describe form an inflated surface, as can easily be understood. The lateral expansion bends upward and the fore and hind walls are curved in the caudal and rostral direction, covering the recessus meatus acustici externi (therefore Zittel, 1923, p. 409, is not correct in saying that it lengthens in a horizontal direction; perhaps he means the cylindrical tube, but this is not directly formed by the tympanic ring, as the recessus is intercalated).

The expansion of the tympanic on the medial and lateral side is a more specialized condition than the primitive ring-like tympanic (Van Kamp.; Stromer von Reichenbach, 1912, pp. 151, 161; Zittel, 1893, p. 22; 1911, p. 334; 1923, p. 412). Especially if there is but a small general expansion it is impossible to determine by an external investigation whether this is an expansion in the ventral wall or whether it is a bony recessus meatus, as only the situation of the sulcus tympanicus or the margo sulci tympanici (= crista tympanica) can give the solution.

Sometimes we have a tympanic expanded to the lateral side but not in the ventral wall, and there is good reason to believe that this is a primitive condition, and that the lateral expansion is phylogenetically older than that in the ventral wall (Van Kamp.; Steinmann and Döderlein, 1890, p. 686). This is the case among the marsupials in the Peramelidæ, in the Dasyuridæ, except *Thylacynus*, probably also in the Notoryctidæ (Van Kamp.; Gregory, 1910, p. 257), in *Phascolarctus* and in *Phascolomys*, all of which, except *Phascolomys*, show only a lateral expansion of the tympanic covering the recessus meatus acustici externi and no more, while *Phascolomys* shows also a bony cylindrical meatus. In *Thylacinus* there is a process of the tympanic in the ventral wall of the tympanic cavity behind the alisphenoid bulla. Van Kampen found

a similar condition in a specimen of *Phalanger*, but it is not impossible that this is an entotympanic secondarily fused with the tympanic. In the Macropodidæ there seems to be an expansion in the ventral wall, but a more thorough investigation shows that it lies against the external surface of the alisphenoid bulla. In no case does the tympanic cover the entire ventral wall of the tympanic cavity (Van Kamp.; Matthew, 1906, pp. 212, 213). Also in the bony recessus meatus acustici externi the marsupials show differences. In the Peramelidæ it is short (longer in *Peragale* than in *Perameles*) and wide, and shows only a fore and an under wall, and narrows toward the lateral side. Among the Dasyuridæ it is longer in *Thylacynus* than in other genera, and in this family also, as in the Peramelidæ, wider rather than narrower than in the diprotodonts, and nearly absolutely horizontal. Though in the Notoryctidæ there is also only a bony recessus and no cylindrical meatus, it is more in agreement with the diprotodonts, as the external opening is very small, due to the fact that the under wall curves upward and the fore wall to the caudal side. In *Phascolomys*, in the Phalangeridæ and in the Macropodidæ there is a bony recessus as well as a cylindrical meatus, but the two are not always clearly distinguishable. So in *Phascolomys* the two parts can not be distinguished externally as the under and fore wall are strongly thickened, and in some of the Macropodidæ at an advanced age the recessus disappears as the under wall of the proximal part of the meatus thickens.

As a primitive Eutherian character common to nearly all Eocene mammals, Matthew (1910*b*, p. 65) mentions the imperfectly ossified bulla in which the tympanic is never very much broadened in the ventral wall of the tympanic cavity.

Among the insectivores also we find a tympanic which is not expanded in the ventral wall, though it shows a bony recessus meatus acustici externi. We find this in *Centetes*, *Erinaceus* (Van Kamp.; Bondy, 1907, p. 307), *Sorex* (Van Kamp.; Bondy, 1907, p. 310) and *Talpa*. So in the insectivores the tympanic does not lie in the ventral wall, at least not to a considerable amount (Van Kamp.; Matthew, 1906, pp. 212, 213; 1909, p 504), but this does seem to have been the case in the fossil *Ictops* (Matthew and Granger, 1918, p. 607). This is perhaps also the case in *Necrolestes* (Scott, 1905, p. 368) though the notice that the tympanic bulla is ossified is very incomplete. Also in the insectivores the lateral expansion is developed to a very different degree. In *Sorex*, where according to the common opinion there is only a narrow ring, Bondy (1907, p. 310) describes on the ventral side a very small bony

plate in the recessus. Also *Centetes* shows the very first beginning of a bony recessus, in some Centetidæ a little better developed than in others, and in this respect more like *Erinaceus* (Van Kamp.; Bondy, 1907, p. 307), that also shows, especially on its under margin, a lateral expansion. In the Talpidæ (Van Kamp.; Gregory, 1910, p. 267) the bony recessus is very differently developed, sometimes as in *Erinaceus* but sometimes even less, and perhaps in a few cases it is absent. In *Talpa* it runs up a little to the lateral side, becoming narrower and narrower, but in the Chrysochloridæ it runs up much more, as the inclination of the tympanic membrane is much greater and also it is more convex than in *Talpa*. In the Macroscelidæ (Van Kamp.; Carlsson, 1910*a*, p. 352; Van der Klaauw, 1924*b*) the tympanic forms not only a bony recessus but also a cylindrical meatus. In *Tupaia*, on the other hand, the tympanic has nothing to do with the bulla.

A very small expansion in the ventral wall is found in *Cynonycteris* (Pteropodidæ) and in *Roussettus* (Van der Klaauw, 1922) and also in the Microchiroptera, differently developed in different species. *Cynonycteris* also shows, differing in this respect from *Pteropus*, a bony recessus meatus and even a short cylindrical meatus. In *Roussettus* I also found a bony recessus meatus. In the Microchiroptera there is only a rudiment of a bony recessus, and even this is sometimes lacking, as in *Vespertilio murinus* and also in *Vesperugo noctula* (Bondy, 1907, p. 313). The figures of *Phyllonycteris* and *Monophyllus* (Anthony, 1917, Pl. LVI, figs. 4 and 8) show a broadened tympanic.

A greatly broadened tympanic occurs in *Galeopithecus*, where the totally closed ventral wall is not wholly formed by the broadened tympanic, as the adult dry skull seems to show (Van Kamp.; Winge, 1893*a*, pp. 41, 43, 86, 87, 88; Gregory, 1910, p. 317); because a very small part is covered by the entotympanic (see Van der Klaauw, 1922). Moreover, the tympanic covers the recessus meatus and also forms a well-developed cylindrical meatus.

In *Manis* both horns of the tympanic are narrow, but the remaining principal portion is broadened, as well in the recessus as in the ventral wall, though in the latter feebly.

In *Cholœpus* the tympanic is narrow and horseshoe-like; only at the place of the transition of the fore leg in the middle portion, the medial margin shows a small forwardly-directed bony process, lying in the lateral boundary of the tuba auditiva. In *Bradypus* (see also, Turner, 1851, p. 207, who did not yet know the entotympanic) the tympanic is broadened toward both sides, in the recessus meatus as well as in the

ventral wall, where it reaches the entotympanic. According to Turner (*loc. cit.*, p. 208) the tympanic in "*Arctopithecus*" is well developed and inflated.

In the Gravigrada the tympanic as a rule is a narrow incomplete ring, as we have seen. The external auditory meatus described by Burmeister (cited by Van Kampen) according to Van Kampen is nothing but the narrow portion on the lateral side of the sulcus tympanicus. A local broadening on the lower margin of the tympanic is described by Owen (1840, p. 59) for *Glossotherium* as "a rugged process half an inch long." A broadened tympanic occurs in *Lestodon* (see Van Kampen's and my own investigations), where the ventral wall is partly covered by the tympanic. This broadening is also visible in a figure of *Pseudolestodon debilis* by Burmeister (see Van Kampen). Van Kampen fixes our attention upon a figure of *Megalonyx* given by Leidy (1855), where the tympanic is perhaps a little broader than is the rule in Gravigrada. According to Van Kampen, in *Megatherium* also the tympanic is probably broadened, as well in the ventral wall as in the recessus. The external auditory meatus described for *Megatherium americanum* by Owen (1856, p. 573) cannot be this meatus, as it is formed by the mastoid and petrosal (it is probably the entotympanic). According to Turner (1851, p. 209) the tympanic in *Megatherium* is small and not inflated; the process, which may probably belong to the tympanic, according to Van Kampen is probably an entotympanic. Thus the tympanic in the Megatheriidæ is not always a narrow tympanic ring as Reinhardt (1878, p. 277) notices. In *Grypotherium listai* Woodward (1900, p. 66) describes the tympanic as an irregular curved plate only slightly bullate, but forming a complete floor for the tympanic cavity, not produced into an auditory meatus. That this floor cannot be complete, we shall see later on; also that an entotympanic is present. In *Nothrotherium texanum* Hay (1917, p. 118) describes the tympanic as inflated below into a bulla of moderate size, whose external surface is rough, but probably this inflation is not formed by the tympanic but by an entotympanic.

As the tympanic in the Glyptodontidæ is not yet known, it is impossible to say whether it is broadened or not. Huxley's part of the tympanic element (1865, p. 55; the same as the petromastoid below the digastric depression in Owen's Catalogue) according to Van Kampen is a part of the mastoid.

In the Myrmecophagidæ the tympanic is very broad in its under portion, diminishing toward the two horns. This broadening lies as well in the ventral wall as in the recessus. The under surface of the tympanic

runs up mediolaterally or is nearly horizontal, different in the genera *Myrmecophaga, Tamandua,* and *Cycloturus.* In *Myrmecophaga* the broadening in the ventral wall lessens in the ventral direction and forms a triangular process of the under margin of the tympanic.

Among the Dasypodidæ a cylindrical external auditory meatus is said to be present only in *Dasypus, Zaëdyus* and *Chlamydophorus,* as we have seen above; which is partly false; this means that it is formed by the ossified meatus auditorius externus cartilagineus. These three genera show a bony recessus meatus and perhaps the tympanic is also broadened in the ventral wall. In *Tolypeutes tricinctus* (Bondy, 1907, p. 349) the tympanic is not broadened in the ventral wall and also shows in its most ventral part a feebly developed recessus meatus. The auditory bulla of the adult *Dasypus, Zaëdyus* and *Chlamydophorus* does not show any suture, while in other recent Dasypodidæ the auditory bulla is distinctly complex. Exceptionally there occurs a suture in the bulla of *Dasypus,* and the development of the auditory bulla in *Dasypus* shows that not a tympanic but also a well-developed entotympanic participates in the bulla. Thus there is good reason to believe that in *Zaëdyus* and *Chlamydophorus* also the bulla is complex. How much the tympanic is broadened in the ventral wall further investigations must decide. At all events we know sufficient to consider critically the notes that the auditory bulla in these three recent genera is formed by the inflation of a well-developed tympanic (Turner, 1851, p. 214, *Dasypus;* Osborn, 1904, p. 164, *Dasypus;* Winge, 1915, pp. 8, 17, 229, *Euphractus sexcinctus;* p. 231, *Chlamydophorus;* Matthew and Granger, 1918, p. 625, *Dasypus*). And no doubt we have to consider these notes for fossil Dasypodidæ in a similar way. Sometimes they are compared even with the recent *Dasypus* and *Zaëdyus* (Scott, 1903*a*, p. 71), though according to Winge (1915, p. 229) *Euphractus* is more highly developed in respect to the completeness of the bulla than is *Prozaëdius.* Such an auditory bulla, formed by the inflation of a well-developed tympanic, has been described for the fossil *Prozaëdius* (Scott, 1903*a*, p. 71; see also my own investigations), *Peltephilus* (Scott, 1903*a*, p. 90; Winge, 1915, p. 232) and *Metacheiromys* (Wortman, 1903, p. 348; Osborn, 1904, p. 164; Matthew and Granger, 1918, p. 625; see also my own investigations). In a fossil *Eutatus* as well, I could not find a distinct complex bulla. In *Palæanodon* according to Matthew and Granger (1918, pp. 624, 625), the tympanic, is expanded into an incomplete bulla, without any ossified meatus; it is nearest to *Cabassous,* but the anterior portion of the tympanic is more expanded.

In the modern Rodentia (see also, Matthew, 1910*b*, p. 65) the tym-

panic, and this element only, forms the bulla, to which a bony recessus meatus always belongs. And according to Winge (1888, pp. 103, 184) no adult rodent is known in which the tympanic is ring-like. Among the fossils, however, quite different conditions have been described. In the earlier Eocene genera of the Ischyromyidæ (Matthew, 1910*b*, pp. 44, 61, 65) in contrast with the genus *Ischyromys* itself, the bulla is incompletely ossified. In *Paramys* (Matthew, 1910*b*, p. 47) as well the bulla is probably incomplete. In *Sciuravus* (Matthew, 1910*b*, p. 60), in which the bulla is also incompletely ossified, the ossification comprises little besides the tympanic ring.

In the creodonts according to Gregory (1910, p. 303), only a true tympanic bulla is found. Wortman (1901, pp. 288, 294) mentions that the auditory bullæ in *Harpagolestes macrocephalus* and *Dromocyon vorax* are apparently developed exclusively from the tympanic. Matthew (1909, p. 486) could not determine whether or not the tympanic in *Harpagolestes* was expanded into a complete bulla. According to Matthew (1909, pp. 486, 487) the tympanic ring is expanded into a small simple bulla in *Mesonyx* and *Synoplotherium* and into a thin-walled bulla in *Dissacus navajovius*, *Pachyæna ossifraga* and *P. intermedia*, *Synoplotherium* and *Mesonyx*. Yet a little doubt seems to be justified. First, Matthew (1909, p. 414) says that in the later Mesonychidæ a substantially similar bulla is present as in the seals, Ursidæ and Mustelidæ, and (*loc. cit.*, p. 504) that the Carnivora, Rodentia and Primates show a true tympanic bulla. We shall see, however, that the bulla in many of these groups is not formed exclusively by the tympanic. Secondly, the presence of an entotympanic in one of the Creodonta (see my own investigations, *Hyænodon*) warns us to be prudent, as we can expect it in other creodonts. The same is indicated, though the entotympanic is not necessarily present in all cases, where an incompletely ossified bulla is present. Now in the creodonts the bulla seems to be completely ossified only exceptionally. To the above given examples we may add the following. According to Matthew (1909, pp. 326, 327, 414, 465) it is completely ossified in the Mesonychidæ and in certain species of *Hyænodon*, and according to Scott (1913, p. 559) in *Mesonyx* and *Dromocyon*. As a rule, however (Matthew, 1909, p. 326, 327), the bulla in the creodonts is not completely ossified, though usually it is in the Hyænodontidæ, e.g., (Matthew, 1909, pp. 414, 465). In contrast with the thin-walled bulla in allied species, the tympanic ring in *Dissacus saurognathus*, *Pachyæna gigantea* and *Harpagolestes*, according to Matthew (1909, p. 487), is extended as a thick, irregular mass. This seems to include an incompletely ossified

bulla, though this does not seem to be necessary (Van Kamp.; Matthew, 1909, p. 486, *Harpagolestes*). In *Triisodon heilprinianus*, *Arctocyon* and *Mesonyx*, according to Matthew (1901, p. 30), the bulla, if not absent, is rudimentary, which according to this author is a primitive character that will probably be found in nearly all Basal Eocene placentals. Perhaps this character "rudimentary" means in a part of the cases incompletely ossified, i.e., a rather narrow tympanic which does not cover the entire ventral wall of the tympanic cavity. According to Winge (1895*b*, pp. 46, 126) the tympanic in the Palæonictidæ is more or less ring-like and does not constitute the entire ventral wall of the tympanic cavity. According to Pohle (1917, p. 407) the tympanic in the Creodonta is ring-like, which seems to mean that it does not form the entire ventral wall of the tympanic cavity.

In the ancestor of the Carnivora among the Insectivora, according to Winge (1895*b*, p. 43) the tympanic was ring-like. According to Van Kampen, however, in the original Carnivora the tympanic was broadened, showing a bony wall in the recessus meatus and in the ventral wall resembling that in *Paradoxurus*.

According to Matthew (1909, p. 315) the bulla in the later Carnivora is formed either by expansion of the tympanic ring or from a distinct ossification of the os bullæ, the tympanic remaining ring-shaped. To what extent this is true will be shown in the next pages.

In the modern Canidæ the tympanic forms a part of the bony ventral wall, the rest being formed by the entotympanic, which, however, is indistinct in the adult skull, in which the bulla seems to be formed by one element as the entotympanic ossifies out from the tympanic. Thus it is easy to understand why it has been described as being formed by the tympanic only (Van Kamp.; Winge, 1895*b*, pp. 47, 126). There is a small recessus meatus, which is partly covered by the bony ventral wall as the hypotympanic sinus extends laterally. In *Fennecus zerda* the porus acusticus externus is enormously large, which agrees with the shortness or absence of the external auditory meatus.

Knowing the complete fusion of the tympanic and the entotympanic in the modern Canidæ, it is probable that also in the fossil Canidæ with a completely ossified simple bulla the tympanic does not constitute the entire bulla. I mention in this respect the Cynodontinæ (Teilhard de Chardin, 1914–1915, p. 36; Zittel, 1923, p. 469). These two elements are no doubt separated in *Daphænus*, where the true tympanic portion of the bulla only is left as the so-called small bulla (Van Kamp.; Leidy, 1853, p. 393; Zittel, 1893, p. 625; Scott, 1895*b*, p. 73; 1898, cited by Van

Kampen; Matthew, 1906, p. 214; Scott, 1913, p. 526; Teilhard de Chardin, 1914–1915, p. 78). The same is the case in *Pliocyon medius* (Matthew, 1918, p. 194; my own investigations) and perhaps also in *Daphænodon* (Scott, 1913, p. 525; Matthew, 1918, p. 194). Zittel (1923, p. 467) even gives this small bulla as a character of most of the Amphicyoninæ. According to Scott (cited by Van Kampen) there is no tubular auditory meatus in *Daphænus*, the external opening into the bulla being a mere hole, but the anterior lip of this opening is drawn out into a short process, somewhat as in existing dogs.

In the modern Ursidæ (Van Kamp.; Winge, 1895*b*, pp. 47, 60, 126) the tympanic is scale-like and covers the entire wall of the tympanic cavity. The same is the case in the modern Procyonidæ and Mustelidæ (Van Kamp.; Winge, 1895*b*, pp. 47, 60, 126). The same is found in the fossil *Pseudobassaris riggsi* (Pohle, 1917, pp. 405, 407, 408) and in many fossil mustelids. Yet it is possible that this bulla is constituted not only by the tympanic but also by the entotympanic, which are so completely fused that no trace of the original double structure is left. In this respect I mention the presence of a small entotympanic in the modern *Meles taxus* (Van der Klaauw, 1924*b*) and the incompletely ossified bullæ in the fossil *Palæoprionodon* (Teilhard de Chardin, 1914–1915, p. 78; Zittel, 1923, p. 473) in which the anterior chamber only is covered by bone, the petrosal remaining almost totally uncovered. Also in the Amphictidæ, according to Winge (1895*b*, pp. 46, 59, 60, 126), the tympanic is relatively small, more or less ring-shaped, and does not constitute the entire ventral wall of the tympanic cavity.

In the modern Viverridæ, Hyænidæ and Felidæ the tympanic only partly covers the ventral wall of the tympanic cavity (Van Kamp.; Winge, 1895*b*, pp. 46, 59, 60, 126; Pohle, 1917, p. 407) though it is variously large (Van Kamp.; Winge, 1895*b*, pp. 47, 53, 56, 59, 126); in the Hyænidæ it covers a much greater part than in the Felidæ and Viverridæ.

In the modern Viverridæ the tympanic is a broadened incomplete ring (Van Kamp.; Winge, 1895*b*, p. 56; Gray, 1913, p. 403; Teilhard de Chardin, 1914–1915, p. 78; Pohle, 1920, p. 56; Carlsson, 1920, p. 341). The broadened tympanic forms a bony recessus meatus and, in addition, in the Herepestinæ, but not in the Viverrinæ and in *Cryptoprocta*, forms a cylindrical external auditory meatus. *Arctictis* shows a lip-like broadening of the rostral wall resembling that in the Felidæ.

In the modern Hyænidæ as we have already seen, the tympanic covers a very large part of the ventral wall of the tympanic cavity.

According to Winge (1895*b*, p. 53) even in the lowest Felidæ the tympanic is ring-shaped and forms only a part of the ventral wall of the tympanic cavity. In *Felis* the tympanic is broadened in the ventral wall of the tympanic cavity and forms a recessus meatus and also a lip on the rostral wall, which is the rudiment of a cylindrical external auditory meatus. In the fossil *Nimravus debilis* Eaton (1922, p. 449) describes a delicate tympanic ring, which in my opinion is either a primitive ring which is out of place, or a part of the bulla, or even of a septum. In *Dinælurus crassus*, according to Eaton (1922, p. 447), the bullæ, although incomplete, are much more fully developed than in *Nimravus*, a considerable portion of the thin wall of the bulla on each side being preserved in extension of the thickened tympanic ring, and traces of the median walls of the bullæ being visible, closely pressed against the lateral expansions of the basioccipital. In this respect it shows a decided advance beyond the stage reached by *Nimravus* and is a further development toward the recent Felidæ.

In the Otariidæ and Phocidæ, according to Winge (1895*b*, pp. 47, 60, 126) the tympanic forms the entire covering of the ventral wall of the tympanic cavity. Later on, however, as we shall see, a well developed entotympanic is found in species of these groups and also in the Trichechidæ, so that probably the tympanic only partly covers the ventral wall.

In the Cetacea (Van Kamp.; Ridewood, 1922, p. 242) the bulla is formed by the tympanic only. The bulla shows a strong extension in the ventral wall, but also a bony recessus meatus.

The wall of the recessus meatus in the Delphinidæ is very irregular. Its rostral lip is formed by the processus sigmoideus, which is separated by a deep groove from the processus conicus posterior s. processus medius, by a deep groove from the processus conicus posterior s. processus medius, which lies in the under lip. The short caudal wall of the recessus meatus is formed by the handle of the processus posterior tympanici. *Phocæna* in this respect forms an exception as this process does not project outside the tympanic membrane, and thus the wall of the recessus meatus shows a defect in this place. The upper wall of the recessus meatus in the Delphinidæ is short; it is a horizontal ridge which projects forward either from the processus posterior or from the mastoid and which is separated by a narrow fissure only from the processus sigmoideus.

The bulla in the Odontoceti and in the Mystacoceti can be described, according to Hanke (1914, p. 505), as a body with two processes. According to Schulte (1917, p. 394) the tympanic in *Kogia* consists of an ental portion or bulla and a much larger lateral portion.

As to the processes of the tympanic, we refer to the chapter on its connection with the other skeletal elements of the skull, in addition to which we make the following remarks.

The sigmoid process probably represents the anterior extremity of the annulus tympanicus and in the early development lies rostrally; later on the anterior part of the tympanic grows very considerably in comparison with the caudal part, so that the sigmoid process now comes to occupy the middle of the total length (Ridewood, 1922, pp. 241, 242). In the Delphinidæ the under half of the wall of the processus sigmoideus, which is turned toward the tympanic cavity, is excavated; it forms an excavation of the external auditory meatus as it lies outside the sulcus tympanicus. In the Balænopteridæ the sigmoid process is not excavated. In *Kogia*, according to Schulte (1917, p. 395), the processus sigmoideus is large, almost egg-shaped, with the smaller end ventrad; from its poles two ridges run mesad, bounding a depressed area. In the porpoise, according to Ridewood (1922, p. 240), the sigmoid process is relatively longer and narrower and more S-shaped than in the mystacocetes. In *Balænoptera sibbaldi* Turner (1913, p. 16) describes a lip-like mallear process, which ascends toward but does not touch the under surface of the petrosal, and ends in a free rounded edge. Lillie (1910, p. 779) mentions in *Balænoptera* a ridge, the inner edge of which is continuous with the processus longus of the malleus; this ridge lies on the irregular extended lip formed by the upper edge of the outer side of the bulla; it lies immediately behind the anterior pedicle and at right angles to it; this ridge projects upward and nearly touches the periotic. In the fossil *Diochotichus vanbenedeni* (True, 1910, p. 26) the sigmoid process is thick, crescentic and but slightly inclined backward.

The processus conicus posterior s. processus medius bullæ in the Delphinidæ is short and knob-like. According to Van Kampen it is nothing else than the lateralwardly extended hypotympanic sinus. In the Delphinidæ this process is hollow, while in the Balænopteridæ this is not the case. In *Kogia*, according to Schulte (1917, p. 395), the processus conicus posterior s. lateralis is obscure. In the fœtal *Megaptera* (Ridewood, 1922, p. 242) this process is merely a lip, but it projects much more in the adult.

The anterior process of the tympanic which is fused with the periotic is called the processus tubarius s. conicus anterior. It forms together with the processus sigmoideus the processus anterior ossis tympanici (Boenninghaus). This processus tubarius is perhaps Schulte's (1917, p. 396) uncinate process on the rostral lip of the bulla. According to

Schulte (1917, p. 395), however, the processus conicus anterior is probably represented by a small elevation which forms the mesial limit of the depressed area on the sigmoid process. The processus anterior bullæ in the Mystacoceti (Hanke, 1914, p. 505) is narrow and very thin, thus differing from the Odontoceti. In *Balænoptera rostrata* Turner (1913, p. 16) emphasizes its thinness, which means that this plate of bone is very easily fractured. In *Balænoptera sibbaldi* (Turner, 1913, p. 16) this anterior pedicle is broad, in *Balænoptera* (Lillie, 1910, pp. 778, 781) it is longitudinally flattened and thin. In *Balæna physalus* the processus conicus anterior is shorter than in *B. rostrata* (Hanke, 1914, p. 510).

The processus petrosus s. posterior of the tympanic in the Delphinidæ is broad and massive, connected with the bulla by a narrow portion; this connecting part is often, not always, perforated by the apertura posterior for the sinus pneumaticus paroccipitalis. This process bears a groove for the facial nerve (Van Kamp.; Hanke, 1914, p. 508). In *Globiocephalus* the posterior process is not broad, but long and pointed, resembling that in the Physeteridæ. In *Platanista* it is better developed than in the Delphinidæ. In the Physeteridæ this posterior process, which has been described erroneously as "mastoid," morphologically is the abnormally situated hind lip of the external auditory meatus. An outgrowth of the processus posterior perhaps forms a part of a short cylindrical external auditory meatus. In *Hyperoodon*, and perhaps in other Physeteridæ as well, the apertura posterior is absent. In *Kogia*, according to Schulte (1917, p. 394), a rectangular facet of dense bone corresponds to the processus petrosus ossis tympanici of *Phocæna* which it resembles also in having a cavity in its interior which communicates with the tympanum; but the bone of *Kogia* is remarkable for the enormous expansion of this element into the "tympanomastoid", for the description of which I refer to Schulte (*loc. cit.*, pp. 394, 395). This processus petrosus in *Kogia* (*loc. cit.*, p. 395) is reduced to a plate of but moderate thickness at the mesal extremity of which the bulla is attached by a slender pedicle (*loc. cit.*, p. 396).

In the fossil *Diochotichus vanbenedeni* (True, 1910, p. 27) the posterior process of the bulla is nearly vertical, but curved inward toward the extremity; it is narrow and convex externally.

In the Mystacoceti, in contrast with the Odontoceti, the processus posterior tympanici projects like a spur in the ventral view; it is much larger in the Mystacoceti (Hanke, 1914, p. 508). Its proximal end forms a part of the wall of the external auditory meatus. The processus posterior in the Mystacoceti shows a groove for the facial nerve (Van Kamp.;

Hanke, 1914, p. 507). In *Balænoptera* it does not show an apertura posterior. In *Balæna physalus*, according to Hanke (1914, p. 510), this processus posterior is shorter than that in *B. rostrata*. The posterior pedicle in *Balænoptera rostrata* (Turner, 1913, p. 16) is a thin plate of bone and is very easily fractured. In *Balænoptera sibbaldi* (Turner, 1913, pp. 14, 15) the anterior surface of the broad posterior pedicle is hollowed and directed toward the tympanic cavity and the meatus. In *Balænoptera*, according to Lillie (1910, p. 779), the posterior pedicle is flattened in the direction of its length and is at right angles to the anterior pedicle.

In the very primitive ungulates the tympanic is ring-like, according to Winge (1906, p. 158). According to Van Kampen the tympanic in the "Protoungulata" probably formed the lateral wall of the bulla and a cylindrical external auditory meatus.

In a part of the Condylarthra at least, according to Van Kampen, the tympanic resembled that in *Tapirus* and *Rhinoceros*. In *Periptychus* according to Matthew (1901, p. 30), it is rudimentary, if not absent.

In *Tapirus americanus* the tympanic forms a bony recessus meatus and even a cylindrical lateral auditory meatus, but the extension in the ventral wall is little developed. It is an irregular outgrowth of the tympanic annulus in the radial direction, chiefly of the rostral leg. According to Winge (1906, p. 158) *Tapirus* shows a ring-like tympanic, which in my opinion means a broadened ring.

The tympanic in the modern *Rhinoceros* forms a small recessus meatus and also a cylindrical external auditory meatus. The tympanic is only the posterior and outer portion of Huxley's tympanic. In an adult, though not old, *Rhinoceros sumatrensis* Van Kampen describes the extension of the tympanic in the ventral wall as a downwardly and forwardly directed, irregularly triangular, plate-like process, lying in the prolongation of the tympanic membrane; it forms the lateral wall of the bulla.

In the modern Equidæ (Van Kamp.; Winge, 1906, p. 147) the tympanic apparently forms the entire bulla, though it is not impossible that an entotympanic, which is invisible in the adult, participates in it.

In the fossil *Eomoropus armarorum* the tympanic is broadened in the ventral wall of the tympanic cavity (Van Kamp.; Cope, 1881*c*, p. 390; Osborn, 1913, p. 268; my own investigations), but does not seem to cover the entire tympanic cavity.

In the Suidæ the tympanic seems to constitute the whole bulla, but perhaps an entotympanic participates in it as well. In the Hippopotamidæ as well the presence of an entotympanic is very doubtful; the

tympanic seems to form the entire bulla and the cylindrical bony external auditory meatus.

In all other modern artiodactyls the tympanic apparently forms the entire bulla and the cylindrical external auditory meatus, so far as can be judged from the dry skull. In the Oreodontidæ a similar condition occurs.

In the Typotheria and Toxodontidæ as well the bulla seems to be formed by the tympanic only. Owen's (1840, p. 22) petrous bone in *Toxodon*, according to Van Kampen, is the mesial portion of the bulla, i.e. the portion that lies on the mesial side of the sulcus tubarius and the vagina processus hyoidei.

In *Elephas* the tympanic seems to form the entire bulla, but this is not the case in *Hyrax* (*Procavia*) in which the tympanic only partly covers the ventral wall of the tympanic cavity, which for the rest is covered by an entotympanic.

According to Winge (1906, p. 66) the tympanic in the higher ungulates is scale-like.

In the modern Lemuridæ the ring-like tympanic lies inside the bulla and does not form a part of its wall. In *Adapis*, according to Winge (1895*a*, p. 37), the tympanic probably lies in the wall of the bulla as in *Tarsius*, and not inside the bulla as in *Lemur*. Later investigations, however, have shown, as we have seen, that Winge's supposition is not right. As to *Megaladapis edwardsi* (Lorenz von Liburnau, 1905) Van Kampen supposes that it is possible that the long bony external auditory meatus is formed by the tympanic, which is entirely fused with the rest of the bulla.

In the modern Chiromyidæ the tympanic ring lies freely within the bulla.

In the modern Nycticebidæ or Lorisidæ (Van Kamp.; Winge, 1895*a*, pp. 17, 20, 54; p. 37, *Otolicnus;* Gregory, 1915, pp. 427, 436, 441) the tympanic lies outside the petrosal bulla, forming its outer margin; it is not broadened in the ventral wall of the tympanic cavity but in the wall of the recessus meatus only. Gregory (1915, p. 441) inclines to the opinion that the exposure of the ectotympanic has occurred independently in the Lorisiformes and Tarsiiformes.

In *Tarsius* (Van Kamp.; Winge, 1895*a*, pp. 17, 37; Gregory, 1915, p. 426) as well, the tympanic forms the wall of the recessus meatus and the bony cylindrical auditory meatus, but it does not lie in the ventral wall of the tympanic cavity. Also in the fossil *Anaptomorphus*, *Hemiacodon*, *Necrolemur* and *Microchœrus* the tympanic is not hidden beneath the bulla, but forms its external portion (Gregory, 1915, p. 426; 1916, p.

264, *Necrolemur*). Thus it is given as a general character of the Tarsiiformes that the tympanic is enlarged and forms the outer margin of the bulla (Gregory, 1915, pp. 426, 437, 441; Zittel, 1923, p. 644).

In the Primates as well, the tympanic is exposed (Van Kamp.; Gregory, 1920, p. 227) and never ring-like but always broadened (Van Kamp.; Winge, 1895*a*, pp. 12, 53). In contrast to the conditions found in the Prosimiæ the tympanic in the Primates is broadened in the ventral wall of the tympanic cavity as well (Van Kamp.; Gregory, 1920, p. 218, generalized Platyrrhinæ).

In the primitive Platyrrhinæ, according to Gregory (1916, p. 266), the tympanics form widely open, swollen zones adherent to the bullæ. In comparison with *Notharctus*, according to Gregory (1920, p. 165), the tympanic in the South American monkeys is displaced outward and thus is drawn to the outer side of the bulla, increasing greatly in size.

In the Hapalidæ the tympanic forms a short and wide recessus meatus, its margin being very narrow, rostrally only slightly broader. Probably the tympanic is also broadened mesialward, but only along the under rostral margin. Thus the portion of the bulla that lies between the tympanic membrane and the ostium tympanicum tubæ and that ends in the processus styliformis is formed by the tympanic, as in *Homo*. The cellulæ petrosæ extend into this portion.

In the modern Cebidæ the tympanic forms a very short external auditory meatus, which is nothing more than the slightly broadened margin of the annulus tympanicus. In some genera, in very old specimens, this margin shows small bony processes and tubercles. Probably the rostral margin of the tympanic is also broadened in the ventral wall of the tympanic cavity.

In the primitive Catarrhinæ, according to Gregory (1916, p. 266), the tympanic was elongate tubular. In the modern Hylobatidæ and Anthropomorphæ the tympanic forms the bony cylindrical external auditory meatus and probably a part of the lateral rostral wall of the bulla, which ends in the processus styliformis.

Entotympanic

Under this name we take together all the skeletal elements, bony or cartilaginous, that lie in the ventral wall of the tympanic cavity and are ontogenetically primarily independent of the other elements in the auditory bulla, except perhaps the tympanohyal and the cartilage of the Eustachian tube. These elements bear also the names metatympanic (Wincza) or os bullæ (Parker). It often loses its independence very early

in ontogeny, so that only the very young or even the fœtal skull shows it (see my own investigations on the development of the entotympanic). This is the reason that for many years the entotympanic was known only in a few mammals. Investigations, especially those of Van Kampen, have shown it in a great many mammals. My own researches on newborn and late-fœtal material have added a few examples, and also have shown that we must distinguish at least two different elements: a caudal entotympanic, which often is connected very early in life with the tympanohyal and grows from behind forward, and a rostral entotympanic, which very early in ontogeny is connected with the cartilage of the Eustachian tube and grows from this region in the caudal direction.

In a great many cases the presence of an entotympanic is very doubtful. In many fossils the bulla is imperfectly ossified (see chapter on membranous ventral wall) and according to Matthew (1910*b*, p. 65) is a primitive Eutherian character common to nearly all Eocene mammals, generally lost in the modern forms. This condition may be due to the presence of an entotympanic. In *Echidna*, for instance, there is found a small piece of cartilage that could perhaps be an entotympanic. In marsupials we have a little more certain knowledge. Here in exceptional cases is found a suture in the tympanic process of the petrosal as in *Perameles*, or there is found a distinct element as in *Phascolomys*, and Parker often mentions an "os bullæ" in marsupials. Winge (1893*b*, p. 129) and also Van Kampen could not find an entotympanic in their marsupial material. Still Van Kampen suggests that it is present in many marsupials and that perhaps we must look for it in the tympanic process of the petrosal in Didelphyidæ, Peramelidæ, Dasyuridæ and Phalangeridæ, or in the peculiarly situated hinder portion of the alisphenoid bulla in Macropodidæ. Perhaps also the tympanic process of the petrosal in the fossil *Microbiotherium* (Sinclair, 1906, p. 410) is an entotympanic.

So, also, in many insectivores the entotympanic is perhaps an element secondarily fused with one of the other elements. Perhaps it is the tympanic process of the basisphenoid, as Parker suggests, or according to Van Kampen (1904, p. 127; 1905, pp. 451, 452) it is more probably the tympanic process of the petrosal (Van Kamp.; Gregory, 1910, pp. 246, 257, 264). But this is not necessary and even the structure of the bulla in *Rhynchocyon*, where we find both entotympanics and also the tympanic process of the petrosal, warns us to be careful in comparing every tympanic process of the petrosal with the entotympanic. Of course it is possible that the entotympanic secondarily looses its independence

and coössifies with the periotic very early in ontogeny, or even develops as if it were a tympanic process of this bone. Gregory (1910, pp. 274, 279; Van Kamp.; Matthew, 1909, p. 504) incorrectly interprets the idea of Van Kampen, as given above, saying that the entotympanic is merely the expanded and secondarily independent tympanic wing of the petrosal (see my criticism on this point in my articles, 1922*a*, p. 4; 1922*b*, p. 138, footnote).

The entotympanic without doubt is present in the Menotyphla, absent in other modern Insectivora (Van Kamp.; Carlsson, 1910*a*, p. 352; 1922, p. 231). In *Tupaia* the whole bulla with the recessus meatus acustici externi and the short cylindrical bony meatus (the last absent in *Ptilocercus*) is formed by the entotympanic; the tympanic lying in the bulla as a free ring (Van Kamp.; Gregory, 1910, pp. 274, 279, 280, 317, 322; 1913*b*, p. 248; Matthew, 1909, p. 504; Carlsson, 1910*a*, pp. 352, 394; 1922, pp. 230, 267). Perhaps we have the same condition in *Ictops* (Matthew, 1909, p. 504). In *Rhynchocyon* and in the Macroscelidæ in general, we have also a well-developed (caudal) entotympanic, though it forms only a part of the bulla (Van Kamp.; Gregory, 1910, pp. 281, 284, 317; Carlsson, 1910*a*, pp. 352, 394; 1922, p. 267) and seems to develop in bone (Van der Klaauw, 1924*b*) and not in cartilage (see Matthew, 1909, p. 504); moreover, it is independent of the petrosal. Beyond this entotympanic, according to my investigations (Van der Klaauw, 1924*b*), there is also a rostral one, developed in cartilage and described as that part of the tympanic wing of the alisphenoid that lies medial of the Eustachian tube and that is well-developed in *Rhynchocyon* and very small in *Petrodromus*. An entotympanic seems to be absent in the Hyopsodontidæ (Matthew, 1909, pp. 507, 510, 514), although in this and analogous cases it is not unlikely that it was a loosely attached element that easily falls out.

A well-developed entotympanic is found in the Chiroptera. In general it is very large, as often the tympanic is not much expanded in the ventral wall of the tympanic cavity and as these two features are in direct relation to each other. In many cases it is cartilaginous and falls out in the dry skull, in which the ventral wall seems to be membranous (see Winge, 1893*a*, p. 43). It is not impossible that this cartilage ossifies in very old age. In *Pteropus* it ossifies to a very slight extent in some species; this ossified portion can be concave, forming a sulcus or a part of a canal for the carotid artery. It can be free or attached to one of the neighboring skeletal elements. In general the entotympanic in Chiroptera seems to be a reduced element. In other Microchiroptera, on the

other hand, it is bony and connected with the tympanic (Van Kamp.; Gregory, 1910, p. 319).

Many figures of skulls of Chiroptera show these two elements in the bulla (see e.g., Anthony, 1917, Pl. LVI, figs. 4 and 8; Miller, 1907), although perhaps it is not superfluous to give warning against the confusion of the entotympanic bulla with the promontorium, as a study of the literature shows. Revilliod (1917, p. 21) mentions an entotympanic in the fossil *Palæophyllophora sanctæ-Neboulex* and in the fossil *Pseudorhinolophus schlosseri* (*loc. cit.*, Pl. I, fig. 8), in which in my opinion, judging from this figure, the entotympanic if present is very narrow.

In *Manis tricuspis*, and still better developed in *Manis gigantea* (Van Kamp.; Gregory, 1910, pp. 338, 339) we find a small free bony entotympanic. It lies caudally behind the tuba auditiva, touching the tympanic and the periotic, lying between these two elements and reaching in *Manis gigantea* the basioccipital and the basisphenoid. It lies on the lateral side of the carotid artery and in *Manis gigantea*, as in *Pteropus*, forms a canalis caroticus, together with the sulcus caroticus in the periotic. It is not yet known in other Manidæ, but possibly it has fallen out in the dry skull, being a very small reduced free element.

In *Orycteropus* no bony entotympanic is found (Van Kamp.; Gregory, 1910, p. 335).

In the Xenarthra the entotympanic is as a rule well developed (Van Kamp.; Gregory, 1910, p. 338). Here it is most highly developed among mammals, except in Carnivora, but it is never inflated, except perhaps in *Chlamydophorus*. The entotympanic in Xenarthra, if not reduced, is a flat plate, lying caudally from the tuba auditiva on the periotic; it shows on the medial wall a sulcus or canalis caroticus. No doubt this form of the entotympanic is the most primitive one that we know. It develops as cartilage (Van Kampen's investigations on *Tatusia*, 1915; see my own investigations in *Tatusia* and *Dasypus*, 1922, 1924*b*). Perhaps in *Bradypus* it develops as bone (see Van der Klaauw, 1922). Though formerly already figured and sometimes also described, it was more completely described by Van Kampen, who was the first to homologize it with the entotympanic.

In *Cholœpus* the entotympanic is a vertical plate on the periotic, and covers the greater part of the ventral wall; on the rostral side it reaches the pterygoid, and on the caudal side the paroccipital process and as a rule is fused with the tympanohyal. In young skulls it is a free element. In *Cholœpus hoffmanni* it is a short, forwardly directed process of the tympanohyal.

In the adult *Bradypus* the entotympanic is fused with the tympanic; if it develops as cartilage, it ossifies very early, but perhaps it develops as bone. The entotympanic in the Bradypodidæ has been described previously as a lamella of the basioccipital.

In the Gravigrada the entotympanic is often very distinct. Notwithstanding this and the fact that it is often figured, it is very seldom described either as an entotympanic or as any other feature. Burmeister (1886, cited by Van Kampen), who describes it as a part of the mastoid, mentions that it is often loosely attached, so that this may be the reason that it is often lost. Many other figures, on the other hand, as well as Van Kampen's and my own investigations, show that it is often very well preserved. The entotympanic in the Gravigrada resembles very much that in *Cholœpus*. It is as a rule a vertical plate on the periotic, sometimes directed from a nearly mediodorsal to a lateroventral plane, thus forming not only an inner wall but also an under wall of the tympanic cavity. Very often it reaches the pterygoid on the rostral side and on the caudal side the paroccipital process and the tympanohyal, with which according to Van Kampen it is often fused. Sometimes it shows very distinct sutures (for example *Scelidotherium*, according to Van Kampen's and my own investigations), while in other cases these have disappeared. The latter case, which rather often occurs, is the reason that the entotympanic is described as a part of one of the neighboring elements. This vertical plate shows on the medial side a roof for the carotid canal, which is very distinct in *Scelidotherium* (see my own investigations which, in this respect, are partly in contrast with those of Van Kampen, who mentions that the entotympanic is thickened halfway its length and reaches the basis cranii, so that the entrance to the foramen lacerum posterius and anterius are sharply separated, which is not the case in my specimen; perhaps this is due to a less well preserved specimen or to specific differences). Probably the entotympanic is meant by Owen's (1858, p. 102, Pl. IX) "rough bifid under surface of the petrosal, that divides the carotid canal from the auditory cavity" in *Scelidotherium leptocephalum*. Also the figure of *Scelidotherium* given by Sefve (1915, Pl. X, fig. 1) shows a distinct entotympanic.

A similar condition to that described for *Scelidotherium* by Van Kampen occurs, according to this author, in *Glossotherium darwini* (see also, Burmeister, cited by Van Kampen). Perhaps the entotympanic is meant in *Glossotherium* by Owen's (1840, p. 61) "small rugged portion of the os petrosum, that separates the jugular from the carotid canal"; at all events, Pl. XVI, fig. 2 shows a distinct entotympanic. A distinct,

long, narrow, plate-like entotympanic is shown in the figure of *Grypotherium* given by Woodward (1900, Pl. v, fig. 1*a*).

In *Nothrotherium* (=*Cœlodon*) *escrivanense* (Van Kamp.; Reinhardt, 1878, T. I., fig. 2) according to Van Kampen the entotympanic shows the ordinary shape; it is plate-like; it reaches the pterygoid, but the sulcus caroticus is lacking. Perhaps the entotympanic is a part of the tympanic, described by Hay (1917, p. 118) in *Nothrotherium texanum*, where the tympanic is inflated below into a bulla of moderate size, whose external surface is rough. Perhaps it is the vertical plate in *Nothrotherium graciliceps*, which according to Stock (1913, p. 348) extends anterior to the stylohyal process and which abuts upon the posterior wall of the "bulla" (that is, the inflated hinder portion of the pterygoid).

In *Mylodon gracilis* Van Kampen describes a high but short entotympanic, reaching neither the paroccipital process nor the basis cranii, and containing a poorly developed sulcus caroticus, while the sulcus caroticus in the basis cranii is much better developed. In the specimen of *Mylodon garmani* that I investigated, the entotympanic does reach the paroccipital process; even a suture is lacking between the two; on the rostral side it reaches the pterygoid and the basisphenoid; it lies against the tympanohyal; the roof of the sulcus caroticus is probably present, but not so well developed or preserved as in *Scelidotherium*. These differences may be due partly to the compression of this skull, partly to specific differences. This specimen of *Mylodon garmani* is figured by Allen (1913), where on Plate I and especially on Plate II the entotympanic is visible, which is probably described by Allen (1913, p. 323) as that part of the petrosal with which the tympanic is fused solidly. In the figure of *Mylodon harlani tenuiceps* given by Stock (1917, Pl. IV) the entotympanic is also a long narrow plate. In the figures after Lydekker of *Mylodon robustus* reproduced in Abel (1912, fig. 404) and in Abel (1919, fig. 584) there seems also to be an entotympanic. Perhaps an entotympanic is designated by Owen (1842, pp. 25, 26) in his description of *Mylodon robustus* as: (*a*) "the rugged cubical process" of the petrotemporal that bounds, together with the mastoid, the tympanic cavity posteriorly, and bounds the jugular foramen anteriorly; (*b*) the smoother conical process of the petrosotemporal that bounds the tympanic cavity internally, and that forms the innermost portion of the petrous bone and that is a subcompressed conical protuberance, the blunt apex of which projects downward into the lateral emargination of the basisphenoid and forms the outer and posterior boundary of the canalis caroticus or (*c*) perhaps even the rough protuberance of the

sphenoid; the Plate IV does not show this so well that it can be determined. Probably in *Paramylodon nebrascensis* the entotympanic is that part of the petrous bone, that according to Brown (1903, p. 574) forms its inner portion and is a subcompressed, conical protuberance uniting with the basisphenoid in a straight line, forming the outer and posterior margin of the carotid canal (in *Mylodon* the basisphenoid is distinctly emarginated for its reception). Perhaps also a part of the entotympanic is formed by the rugged process of the petrosotemporal that lies on the outside and posterior to the above-mentioned conical process; this rugged process forms the anterior boundary of the jugular foramen and the depressions for the stylohyal; in front it bounds the posterior part of the tympanic cavity.

In *Lestodon armatus* Van Kampen describes the entotympanic as a small element; it is shorter and lower than is the rule in the Gravigrada; therefore it reaches neither the pterygoid nor the paroccipital process, from which it is separated by the foramen lacerum posterius; it does not show a sulcus caroticus. My own investigations on *Lestodon myloides* agree with this description, except that the fore part is not broadened and does not reach the basis cranii, as is the case in *Lestodon armatus*. It is fused with the mastoid and does not reach the tympanohyal in my specimen.

In *Megalonyx jeffersonii*, according to Van Kampen, Leidy's (1855, p. 10) "offset from the auditory process" (the auditory process = the tympanic), which is "a rough ridge" that separates the carotid foramen from the "deep infundibular pit constituting the osseous continuation of the tympanic tube," is an entotympanic, which according to Van Kampen shows a sulcus or even a canalis caroticus and reaches the tympanic, from which it is separated by a distinct suture. Perhaps the rough ridge that separates the jugular from the carotid foramen is also a part of the entotympanic.

In *Megatherium* probably an entotympanic is present as well, though Van Kampen could not derive an exact description from his material. According to Van Kampen it is probably Leidy's (1855, p. 52) external auditory meatus and Owen's (1856, p. 573) mastoid and petrosal elements, which combine to form his so-called meatus auditorius externus and Turner's (1851, p. 209) "strong process, which may probably belong to the tympanic bone and forms a portion of a vaginal process and lies immediately in front of the circular facet for the stylohyal bone."

Perhaps an entotympanic is meant in *Planops magnus* by Scott's (1904, p. 324) "the exposed portion of the periotic, which is a narrow

vertical ridge with a groove on each side of it and which ends ventrally in a roughened process."

I found a distinct well-developed entotympanic in many specimens of the genera *Hapalops*, *Schismotherium*, *Megalonychotherium*, *Analcimorphus* and *Pelecyodon*. The general characteristic form of the entotympanic in these genera is a vertical plate on the periotic, reaching the pterygoid and the basis cranii on the rostral side and the paroccipital and mastoid processes and the tympanohyal on the caudal side. On its medial side it shows a roof for the sulcus caroticus, which sometimes in its fore part is closed to a canalis caroticus, but perhaps this is individually variable as in other edentates or it is due to the state of preservation. This entotympanic is figured for many of these small Gravigrada in Scott's Reports, to which I refer. These figures are not always correct, as I found by comparing the specimens with their figures in Scott. This is partly due to the fact that the entotympanic was not studied and described and the importance of the knowledge of its details was not known or appreciated. The last-mentioned reason and the often poor state of preservation are the reasons that in so many figures in various papers the entotympanic is badly figured, though drawn true to the specimen, as I found in a few cases. Therefore I will not try to derive a description of the entotympanic from these figures. Thus I refer without further notes to many figures not only in Scott's Reports, but also in Ameghino (1889, Pls. XLII, XLIV, XLVII, XLVIII). Scott does not mention the name entotympanic but perhaps this element is meant by his "narrow strip of the periotic, which is exposed on the surface of the skull" (1903*b*, p. 216, *Hapalops brachycephalus;* 1904, p. 298, *Schismotherium fractum*). Scott's note (1904, p. 285) that in *Analcimorphus giganteus* the foramen lacerum posterius is chiefly, if not entirely, enclosed in the basioccipital, is not correct, as the entotympanic lies in its lateral wall.

In *Myrmecophaga* the entotympanic is very much reduced: probably the bony plate in the hinder wall of the tympanic cavity between the periotic, basioccipital, exoccipital and tympanic is an entotympanic, but it is not separated from the tympanic and mastoid by distinct sutures. The consequence of this reduction is that the basisphenoid lies in the wall of the tympanic cavity. In *Cycloturus* (Van Kampen, 1905, pp. 488, 489; not in edition 1904) the entotympanic is better developed, so that the basioccipital is excluded from the tympanic cavity; this entotympanic reaches the basioccipital with its under margin; it forms the lateral wall of the carotid canal and bears an aperture which probably encloses the stapedial artery.

In the Glyptodontidæ the entotympanic is not yet known but, as we have seen above, perhaps cases occur analogous to those in the Myrmecophagidæ.

In all recent Dasypodidæ probably a large entotympanic occurs though it is not always distinct. As a rule it shows a sulcus or canalis caroticus. A well-developed bony entotympanic occurs in *Xenurus* (=*Lysiurus*) *unicinctus;* it touches the narrow tympanic ring, separated from it by a distinct suture; it is well developed in the other directions as well; in old skulls it is fused with the tympanohyal; the outer surface is convex, the surface in the tympanic cavity itself is flat. In *Priodontes giganteus* the entotympanic is less completely developed; it still touches the tympanic, but it does not extend so far in the other directions as it does in *Xenurus.* In *Tolypeutes tricinctus* the bony entotympanic is also more poorly developed than in *Xenurus* and it does not reach, or does not always reach, the tympanic. In the adult *Xenurus duodecimcinctus* Winge (1915, p. 37) describes some little bony plates in the incompletely ossified ventral wall. In *Tatusia novemcincta* (Van Kamp.; Winge, 1915, p. 67) the entotympanic is almost totally cartilaginous, lying between the tympanic and the periotic; only the upper margin shows one or more small ossifications, which are not firmly fused with one of the neighboring bony elements. Thus the entotympanic is totally absent in the dry skull, which therefore does not give us the right idea of the structure of the auditory bulla (see Matthew and Granger, 1918, p. 625).

In *Dasypus* (Van Kamp.; Scott, 1903*a*, p. 71; Osborn, 1904, p. 164; Winge, 1915, pp. 8, 17, 229, *Euphractus sexcinctus;* Matthew and Granger, 1918, p. 625), in *Zaëdyus* (Van Kamp.; Scott, 1903*a*, p. 71) and in *Chlamydophorus* (Van Kamp.; Winge, 1915, p. 231) the adult skull shows a bulla without suture and therefore seems to be formed only by the tympanic. The conditions found in the other recent Dasypodidæ make it very probable that also in these three genera the bulla is complex and that the suture between the tympanic and the entotympanic has disappeared. Important in this respect are the facts that sometimes in *Dasypus* a suture in the bulla is found (see Van Kampen) and that the development of the auditory region of *Dasypus sexcinctus* shows a well-developed cartilaginous entotympanic (Van der Klaauw, 1924*b*), and that in the young skull some thin bony plates lie in the not yet further ossified ventral wall (Winge, 1915, p. 37, *Euphractus sexcinctus*).

We find similar notes for fossil Dasypodidæ, but here also there is every reason to believe that the bulla is complex and contains a tympanic and an entotympanic and that the suture has disappeared. Thus

these also seem to be formed only by the tympanic. This is the case in *Peltephilus* (Winge, 1915, p. 232; Scott, 1903*a*, p. 90), in *Eutatus* (see my own investigations), in *Prozaëdius* (Scott, 1903*a*, p. 71; Winge, 1915, pp. 228, 229, though the tympanic cavity is not so completely covered as in *Euphractus;* see also my own investigations), in *Stenotatus* (Winge, 1915, p. 228) and in *Metacheiromys* (Wortman, 1903*a*, p. 348; Osborn, 1904, p. 164; see also my own investigations). Perhaps there is sometimes a suture in these often broken bullæ, but this is very difficult to determine. Perhaps, also, the fact that in *Prozaëdius* the bulla is so incomplete that it is deeply notched from behind in a very peculiar and characteristic manner (Scott, 1903*a*. p. 71; see also my own investigations) indicates that the bulla is complex.

In *Stegotherium* perhaps an entotympanic is referred to by Scott's (1903*a*, p. 16) "a part of the auditory or petrosal portion of the periotic, which is quite large and very superficial in position and which is not entirely concealed from view by the tympanic." In the specimen that I investigated the entotympanic was lacking; thus it was probably cartilaginous or a loosely attached bone.

In *Palæanodon* a distinct bony entotympanic seems to be present. It is described by Matthew and Granger (1918, p. 625, fig. 39) as "ossifications arising from the petrosal, which apparently support the bulla on the posterior and internal side." This position on the posterior side of the tympanic is important in respect to my own opinion on the primitive position of the caudal entotympanic (see Van der Klaauw, 1922) and its possible phylogenetic origin from the hyoid bar (Van Kampen, 1915). Of course this position is under great influence of the space between the condyles and the fossa glenoidea, and therefore it is important that Matthew and Granger (1918, p. 624) mention that in *Palæanodon* the space between the condyles and the otic region is considerably greater than in modern armadillos.

In the modern Rodentia no entotympanic is known and the bulla seems to be formed by the tympanic only. Perhaps an investigation on microscopical serial sections may show its presence. In a few fossil rodents the entotympanic is present perhaps as a separate element, cartilaginous or bony, that is, in the cases where the bulla is said to be incompletely ossified. Of course this place is not necessarily occupied by a skeletal element, as this part of the ventral wall of the tympanic cavity also may have been membranous. An incompletely ossified bulla has been described by Matthew (1910*b*, pp. 44, 60, 65) in the earlier genera of the Ischyromyidæ, in *Sciuravus* and probably in *Paramys*.

Probably in many creodonts an entotympanic occurred. There are

many indications for this supposition. Sometimes the bulla is said to be incompletely ossified. In all Eocene Creodonta, according to Matthew (1910*c*, p. 298), the bulla is never completely ossified. According to Matthew (1909, p. 326) the bulla is not completely ossified except in a few of the creodonts. In the Hyænodontidæ (Matthew, 1906, p. 217; 1909, p. 465; Zittel, 1911, p. 379; 1923, p. 459) the bulla is ossified to a varying degree; usually it is incompletely ossified but in certain species the bulla is complete. In such a complete bulla in *Hyænodon*, according to my own investigation, a well developed bony entotympanic participates. Thus in the creodonts the presence of a bony entotympanic even in a completely ossified bulla is not unlikely. Such a completely ossified bulla, which is not present in all creodonts as Schlosser (1887, pp. 164, 213) mentions and which is present for example in *Proviverra Ruetimeyeri* (Schlosser, 1887, p. 213), seems to be an exceptional condition in the Creodonta. According to Pohle (1917, p. 407), however, this part of the ventral wall of the tympanic cavity is usually cartilaginous. Winge (1895*b*, p. 50) supposes that a large portion of the wall of the tympanic cavity in *Mesonyx* is formed either by outgrowths of the surrounding bones or by proper ossifications, i.e., the entotympanic. In this respect Van Kampen refers to a figure of *Mesonyx* given by Cope (1884). Van Kampen supposes that the entotympanic is present in many Creodonta and that it is inflated as in the modern Carnivora and not plate-like as in the Xenarthra. In *Hyænodon* (see my own investigations) the entotympanic does not lie behind but on the mesial side of the tympanic, a feature which is probably related to the pushing backward of the glenoid articulation to a position opposite the occipital condyles (Matthew, 1906, p. 217).

In the insectivores, from which the Carnivora are derived, the ventral wall of the tympanic cavity is membranous, according to Winge (1895*b*, pp. 43, 45, 123, 125). In the more generalized or primitive Carnivora, according to Matthew (1910*c*, p. 297), the bulla is never completely ossified, which according to Scott (1913, pp. 539, 540) is a primitive feature. According to Van Kampen, however, the ancestral Carnivora showed a bony entotympanic, as a bony entotympanic occurs in various groups and is present as early as in the insectivores. Probably the entotympanic in the ancestral Carnivora resembled that in *Nandinia*, in which the entotympanic shows various primitive characters: it is relatively small and it does not form a septum bullæ. The entotympanic in the ancestral Carnivora according to Van Kampen, however, was bony, in this respect resembling more that of *Paradoxurus* than that of

Nandinia. Van Kampen supposes that the entotympanic in the ancestral Carnivora was not plate-like as that in the Xenarthra, but inflated, the latter condition already being found in the Insectivora as well.

In the later Carnivora, according to Matthew (1909, p. 315), the bulla ossifies after two distinct plans; the chamber is formed either by expansion of the tympanic ring or from a distinct ossification of the os bullæ, the tympanic remaining ring-shaped. This rule no doubt in general is true. Of course it is possible that in the first-mentioned plan the study of the development of the bulla might show that in the bulla an entotympanic participates as well, but that is not visible in the dry skull. The ossification of the cartilaginous entotympanic is not necessarily distinct as we shall see later (*Canis*) and also the entotympanic may remain cartilaginous throughout life (*Nandinia*). As a rule, however, the entotympanic and thus also the bulla in the modern Carnivora is ossified (Van Kamp.; Schlosser, 1887, p. 213; Zittel, 1893, p. 608; 1911, p. 384; 1923, p. 464; Matthew, 1909, p. 355; Stromer von Reichenbach, 1912, p. 180).

In the Arctoidea, according to Winge (1895*b*, p. 60), an indication of an os bullæ may be found as a proper ossification center in the caudal part of the outer wall of the tympanic cavity, but it does not gain much independence and soon is completely fused with the tympanic. According to Van Kampen this remark probably bears upon the Pinnipedia.

In the true Arctoidea, i.e., the Canidæ, Procyonidæ, Ursidæ, and Mustelidæ, no distinct ossification of the entotympanic is known in the modern forms. Thus the bulla in these forms is simple (Matthew, 1909, p. 355).

In the modern *Canis* the entotympanic develops in cartilage (Van Kamp.; Van der Klaauw, 1922). Perhaps it is Owen's (1859, p. 313) inflated petrosal in the bulla of the dog. This cartilaginous entotympanic seems to ossify out from the tympanic, a proper ossification center being absent. Thus the bulla is simple and seems to be formed by the tympanic only (Van Kamp.; Scott, 1913, p. 520).

In the fossil *Cynodesmus thoöides* (Scott, 1895*b*, p. 73) the enlarged bulla is fully ossified and the posterior chamber is indistinguishably fused with the anterior. A simple bulla is mentioned by Teilhard de Chardin (1914–1915, pp. 29, 40, 53) for the American *Cynodictis*, for *Pachycynodon* and *Plesiocyon*. In the "formes cynodontiennées," according to Teilhard de Chardin (1914–1915, p. 89), the ossified bulla is simple, while among the "formes cynodictiennes" (*loc. cit.*, p. 88) there exist species with a double bulla. In *Cynodictis*, according to Scott (1889,

p. 233; 1898, cited by Van Kampen) the entotympanic is bony and fused with the tympanic, showing a distinct boundary, which appears as an external constriction of the bulla as in most of the Viverridæ, thus connecting the dogs and the viverrines. The conditions in the recent *Canis* warn us to be prudent concerning lines and other marks on the surface of the bulla. In *Canis* this surface sometimes shows an indistinct line running from the mesial margin of the orificium tubæ obliquely backward and lateralward. It resembles very much the line in *Felis* between the tympanic and the entotympanic but it has nothing to do with it, as it corresponds with the septum in the bulla, which is not homologous with the septum bullæ in *Felis*. The rostral part of the course of these lines is, however, almost identical, the caudal part being very different.

In other fossil Canidæ the presence of an entotympanic cannot be denied. In *Daphænus* (Scott, 1895, p. 73; 1898, cited by Van Kampen) the posterior chamber is lost in all the skulls which Scott had the opportunity of examining, exposing the periotic from below; the entotympanic remains cartilaginous or, at all events, was separate from the tympanic and less probably it was a loosely attached bony capsule, resembling that in *Paradoxurus*. Scott (cited by Van Kampen) considers this condition more as a primitive than as a degenerate one. Also in *Pliocyon* (Matthew, 1918, fig. on p. 191; see also my own investigations) an entotympanic is present.

In the modern Ursidæ no entotympanic is known; the surface of the bulla does not show an indication of a compound condition. I do not know what to think about the remark of Owen (1859, p. 313) that the bulla in the bear is formed by the tympanic and the inflated petrosal, which in other examples given means the entotympanic.

Also in the Procyonidæ an entotympanic is not known.

In the modern Mustelidæ the bulla is simple and never shows an indication of a compound structure. The development of the bulla in *Meles taxus* (Van der Klaauw, 1924*b*) shows the presence of a slightly developed entotympanic. Perhaps its ossification occurs as in *Canis*, or they fuse indistinguishably in an early period. I do not know what to think about the remark of Owen (1859, p. 313) that the bulla in the otter is formed by the tympanic and the inflated petrosal, which in other examples given means the entotympanic.

A simple bulla is mentioned by Teilhard de Chardin (1914–1915, pp. 59, 74, 89) for *Plesictis*, *Palæogale felina* and *minuta*, and *Bunailurus lagophagus*, in which the bullæ resemble that in *Mustela*. In these fossils the bulla seems to be fully ossified (Teilhard de Chardin, 1914–1915, p. 59, *Plesictis robustus*).

In the fossil *Stenoplesictis cayluxi* (Scott, 1889, p. 232) an external constriction of the bulla plainly indicates the separation into two chambers. This illustrates the fact that the presence of a simple or a compound bulla characteristic for the different groups of the modern Carnivora is not always characteristic for the allied fossils (Van Kamp.; Scott, 1889, p. 232). In other fossil Mustelidæ the entotympanic no doubt was present as a separate element, not fused with the tympanic, but the entotympanic has not been preserved, the tympanic chamber only being left. This is the case in *Palæoprionodon* (Van Kamp.; Winge, 1895*b*, p. 54; Teilhard de Chardin, 1914–1915, pp. 78, 89; Zittel, 1923, p. 473) and in *Amphictis* (Van Kamp.; Winge, 1895*b*, p. 59; Pohle, 1917, pp. 404, 405; 1920, p. 50). The entotympanic in *Amphictis* according to Pohle (*loc. cit*) is cartilaginous, while Winge (1895*b*, p. 59) supposes that the ventral wall of the tympanic cavity in the Amphictidæ is membranous-cartilaginous. Teilhard de Chardin (1914–1915, p. 78) supposes that the entotympanic in *Palæoprionodon*, as well, was cartilaginous.

In the Æluroidea (Van Kamp.; Matthew, 1909, p. 355; Gregory, 1910, p. 315; Pohle, 1917, p. 407) or Herpestoidea (Van Kamp.; Winge, 1895*b*, p. 60) the bulla is compound and partly formed by the entotympanic. Owen's (1895, p. 313) inflated petrosal, which participates in the bulla of the cat, hyæna and civet, no doubt is the entotympanic.

In the modern Viverridæ (Van Kamp.; Winge, 1895*b*, p. 56; Carlsson, 1921, p. 74) the entotympanic as a rule is bony (Van Kamp.; Teilhard de Chardin, 1914–1915, p. 80, *Prionodon*). In *Nandinia* only it remains cartilaginous (Van Kamp.; Pocock, 1916*a*, p. 265; Carlsson, 1921, pp. 71, 74). Van Kampen found a small bony center in the cartilaginous entotympanic of *Nandinia binotata*. This cartilaginous condition in *Nandinia* according to Van Kampen, is not a primitive one, but secondarily it remains in a younger developmental stage.

In most of the Viverridæ, according to Scott (1889, p. 233), the bulla is marked by an external constriction. In species of the genera *Paradoxurus* and *Cynogale* the entotympanic is free from the tympanic, while in all other modern Viverridæ they are fused. As a rule, however, the boundary between the two elements remains distinct. Exceptions in this respect are *Cryptoprocta ferox* (Van Kamp.; Carlsson, 1910*b*, p. 567; 1911, p. 425) and *Arctictis binturong* (Van Kamp.; Carlsson, 1920, p. 341; differently distinct in various skulls), in which the boundary between the entotympanic and tympanic is not much more distinct than in the Felidæ. According to Carlsson (1911, p. 425), however, the external boundary between these two elements is more distinct than in the Felidæ.

The entotympanic in the Viverridæ is relatively large (Van Kamp.; Gray, 1913, p. 403, on *Herpestes griseus*) and large in comparison to that in the Hyænidæ (Van Kamp.; Winge, 1895*b*, pp. 47, 59, 126). The size may be very different as is illustrated by the following remark of Pocock (1916*a*, p. 265): in mongooses of different genera the length of the two chambers varies; for example, in *Cynictis* the posterior chamber is very short and the anterior very long; in *Ichneumia* the anterior chamber is small and the posterior large. In *Arctictis binturong* (Carlsson, 1920, p. 341) the mesial portion of the bulla is relatively little developed; the entotympanic is much more inflated than the tympanic, which forms a characteristic feature of the Viverrinæ. In the young *Eupleres* (Carlsson, 1910*b*, p. 567) the tympanic is strongly developed and reaches the height of that of the entotympanic, and in this respect resembles the Herpestinæ.

The entotympanic in the Viverridæ covers the caudal portion of the tympanic cavity (Van Kamp.; Scott, 1889, p. 214; Winge, 1895*b*, p. 56) but the forward extension is different. In the Herpestinæ as a rule (Van Kamp.; Carlsson, 1910*b*, pp. 565, 567, 596, *Galidia*, *Hemigalidia*, *Galidictis*, Herpestinæ in general; Carlsson, 1911, p. 425) the small entotympanic chamber lies behind the tympanic chamber and the groove between the two runs transversely; the mesial margin of the bulla is formed by the tympanic and the entotympanic (Van Kamp.; Carlsson, 1910*b*, p. 566). In the genus *Herpestes* the lateral portion of the entotympanic extends a little more rostralward than the mesial one and thus the entotympanic lies a little lateralward from the caudal part of the true tympanic chamber. In the genus *Rhynchogale* the tympanic chamber is much smaller than the entotympanic chamber and thus resembles the Viverrinæ. In the Viverrinæ (Van Kamp.; Carlsson, 1910*b*, pp. 565, 566, 567; 1911, p. 425) the entotympanic extends forward on the mesial side of the tympanic, so that the mesial wall of the bulla is entirely or nearly entirely formed by the entotympanic (Van Kamp.; Carlsson, 1910*b*, p. 566). This feature is very distinct in *Arctictis binturong*, where the entotympanic chamber partly covers the true tympanic chamber. In *Paradoxurus* and *Viverra* this rostral extension of the entotympanic is less developed than in *Arctitis* but still distinct in comparison with the condition found in the Herpestinæ. In *Nandinia* also the entotympanic extends a little forward on the mesial side of the tympanic. The bulla in *Fossa* (Carlsson, 1910*b*, pp. 566, 567) is developed as that in the Viverrinæ. Also in *Eupleres* (Van Kamp.; Carlsson, 1910*b*, p. 567) the bulla resembles that in the Viverrinæ: the entotympanic extends forward on the mesial side of the tympanic. In *Cryptoprocta ferox* Van

Kampen mentions the same character, but according to Carlsson (1910*b*, p. 567; 1911, p. 425), however, the entotympanic does not lie on the mesial side of the tympanic but on or near its caudal side. According to Carlsson (1911, p. 425) the rostral tympanic portion in *Cryptoprocta ferox* shows as small a size as that in the Viverrinæ.

In the fossil *Ictitherium*, according to Winge (1895*b*, p. 59), the bulla no doubt is constituted as that in *Hyæna*.

In the modern Hyænidæ the external surface of the bulla does not show the compound structure, as is evident from the study of the internal structure of the bulla (see chapter on septum bullæ). In *Proteles* the entotympanic chamber lies entirely behind the true tympanic chamber and is much larger than the anterior chamber. In the hyænas (Van Kamp.; Winge, 1895*b*, pp. 47, 59, 94, 126; Pocock, 1916*e*, pp. 303, 306) the entotympanic is relatively small, the posterior chamber being smaller than the anterior tympanic chamber. In *Hyæna crocuta* according to Winge (1895*b*, p. 94) the entotympanic is still very considerable; *Hyæna striata* and *brunnea*, however, in this respect are less primitive than *Hyæna crocuta;* their entotympanics are strongly narrowed and occupy only a small corner between the processus jugularis and the pars mastoidea (Van Kamp.; Winge, 1895*b*, p. 59). While Winge (1895*b*, pp. 47, 126) emphasizes the small size of the entotympanic in the Hyænidæ in comparison with that in the Viverridæ, Pocock (1916*e*, p. 306) notices that the partition lies much farther back than in Felidæ, but, however, that it is not much farther back than in *Cynictis*.

Even in the lowest Felidæ, according to Winge (1895*b*, p. 53), the bulla shows an "os bullæ," reaching with its lateral margin the mesial margin of the tympanic. It is always strongly inflated (Van Kamp.; Winge, 1895*b*, p. 54) and never plate-like as in the Xenarthra and fused with the tympanic (Van Kamp.; Winge, 1895*b*, p. 54). The entotympanic covers the greater part of the ventral wall of the tympanic cavity (Van Kamp.; Winge, 1895*b*, p. 59). The strongest inflation of the bulla lies in its mesial larger portion. The entotympanic which in the adult is bony (Van Kamp.; Matthew, 1910*c*, pp. 297, 312) develops as a free cartilage, behind and mesially from the tympanic. In the adult skull it extends far forward and lies for the larger part on the mesial side of the tympanic (Van Kamp.; Scott, 1889, p. 214) although the bulla is strongly extended backward, which can be judged from the position of the porus acusticus externus in the rostral half of the bulla. The suture between the tympanic and the entotympanic in the adult recent Felidæ is very indistinct; it is a poorly developed groove or "rough line" running from

the stylomastoid foramen toward the orificium tubæ. According to Pocock (1916*d*, p. 326) the line of the origin of the partition (septum bullæ) is generally marked on the outer surface of the bulla by a shallow groove (Van Kamp.; Pocock, 1916*c*, p. 310, *Uncia uncia*). The posterior end of this groove is a fixed point in front of the stylomastoid foramen, but its position and anterior termination vary considerably in different species (Pocock, 1916*d*, p. 326). These variations have a profound effect upon the relative sizes of the two chambers and are used by Pocock to distinguish different species of the recent Felidæ (see chapter on the use of the size of the different elements of the bulla in systematics).

In the fossil *Felis atrox* var. *bebbi*, according to Merriam (1909, p. 296), the tympanic is quite distinctly set off from the entotympanic. The anterior spine of the tympanic extends farther forward than the anterior extension of the entotympanic, a feature which in my opinion is probably related to the fact that the space between the mastoid and the postglenoid processes and opposite the external auditory meatus is somewhat wider than in the lion (Merriam, *loc. cit.*).

An indication, though no certainty, of the presence of an entotympanic is given by the descriptions of an incompletely ossified bulla. Such an incompletely ossified bulla is present in *Dinictis* (Matthew, 1910*c*, pp. 297, 309; Zittel, 1911, p. 398; 1923, p. 479; Scott, 1913, pp. 539, 540) and in *Hoplophoneus* (Matthew, 1910*c*, pp. 297, 312; Zittel, 1911, p. 397; 1923, p. 478; Scott, 1913, p. 537). In my opinion the ventral wall of the tympanic cavity in such cases is not necessarily membranous or cartilaginous, but a free or very loosely attached bony entotympanic may have been present. Noteworthy in this respect is the remark of Adams (1896, p. 421) on *Hoplophoneus primævus*, that the bullæ, judging from a cast, were moderately inflated, which in my opinion probably implies that the tympanic cavity was entirely covered by skeletal elements. Riggs (1896*b*, p. 237) remarks also that the bulla in *Dinictis* is well inflated. Scott (1889, p. 214) could not determine whether the chambers of the bulla in *Dinictis felina* are situated one behind the other or one internal to the other; in my opinion the latter was probably the case, as Scott (*loc. cit.*) mentions that the shape of the bulla is feline and that the mastoid process occupies an anterior position.

In the Nimravidæ (Scott, 1889, p. 238) the bulla shows no external sign of division; the entotympanic, which is probably present, is bony. A completely ossified bulla is also present in the fossil *Machairodus* (Matthew, 1910*c*, p. 314; Zittel, 1911, p. 397; 1923, p. 478) and *Smilodon* (Matthew, 1910*c*, pp. 297, 315). The entotympanic, if present, is bony

in these genera. The presence of a septum, which can be homologized with the septum bullæ in *Felis*, gives us information on the presence of an entotympanic in completely ossified bullæ (see chapter on septum bullæ). However, in a completely ossified bulla, in the cases where no septum is present (see the chapter on the septum bullæ) or where the septum can not be homologized with certainty with the septum bullæ, it is not possible to determine the presence of an entotympanic if boundaries, sutures or grooves on the surface are absent as well.

In the Pinnipedia (Van Kamp.; Gregory, 1910, p. 315) a distinct entotympanic may be present. We have already mentioned that the remark of Winge (1895*b*, p. 60), that the os bullæ is present in the Arctoidea, probably bears upon the condition of this region in the Pinnipedia, according to Van Kampen. Van Kampen describes in a fœtus of *Cystophora cristata* a free bony element; older specimens of this species show a completely ossified bulla with a distinct groove, which is probably the boundary between the tympanic and the entotympanic. This groove runs about from the orificium tubæ toward the stylomastoid foramen, so that the greater part of the bulla is formed by the entotympanic. In other Phocidæ a similar groove, but a less distinct one, is found. This entotympanic develops in cartilage (Van der Klaauw, 1924*b*).

In a pullus of a modern Otariid Van Kampen found a suture in the bulla running from the orificium tubæ toward the stylomastoid foramen; in a skull which is a little older this suture has disappeared. The entotympanic lies on the mesial side of the tympanic.

In a pullus of a modern Trichechid as well Van Kampen describes a distinct suture between the tympanic and the entotympanic, showing the same course as that in *Otaria*, i.e., from the Eustachian foramen toward the vagina for the tympanohyal. In adult skulls as well a groove occurs, which, however, runs transversely from the tuba toward a point a little behind the stylomastoid foramen and which thus has changed its course.

In the most primitive ungulates, according to Winge (1906, p. 66), as in many other primitive mammals, the tympanic is ring-like and the greater part of the outer surface of the tympanic cavity is membranous or cartilaginous. According to Van Kampen the bulla of the Protungulata probably showed a loose entotympanic in its inner and under wall.

In the Litopterna, according to Scott (1910, p. 3), the bulla is imperfectly ossified and thus, as in all these cases, it is possible that a cartilaginous or bony entotympanic was present.

In the modern rhinoceros a bony entotympanic is present and

was described by Huxley as the anterior and inner portion of the tympanic. They touch each other caudally. In an adult, though not old, *Rhinoceros sumatrensis* Van Kampen describes it as a high vertical plate, whose upper margin lies against and is fused with the pars petrosa; a suture between the two is present. The entotympanic runs in the sagittal direction, thus forming the mesial wall of the bulla, but rostrally and caudally it bends lateralward. This caudally bent portion is dorsally separated from the petrosal by an open space. The rostrally bent portion inclines and thus forms the upper rostral wall of the tympanic cavity. In this region it is fused with the tegmen tympani, no suture being visible. In the fossil Rhinoceridæ an entotympanic was probably also present. Perhaps it is, though very indistinctly, figured by Pavlow (1893, Pl. IV, fig. 1*a*) and by Cope and Matthew (1915, Pl. CXXVII) for *Aphelops*, in which the bulla seems to be a complicated structure. Toula (1902, p. 74) mentions for *Rhinoceros* (*Ceratorhinus*) *hundsheimensis* a complexly formed bony mass, which probably relates to the entotvmpanic though this element is not distinctly figured (see *loc. cit.*, Pl. III).

In *Tapirus indicus*, Parker (1882, p. 776) describes a flat, somewhat curved fibro-cartilage which lies between the tympanic and the periotic on the lower side, passing posteriorly into a mass of fibrous tissue, in which is imbedded a very definite os bullæ which thus remains in a rudimentary condition. Van Kampen, not knowing of this observation of Parker, says that it is improbable that a loose entotympanic lies in the fissure in the dry skull between the tympanic and the crest on the petrosal. According to Van Kampen it seems more probable that the entotympanic is fused with the petrosal and represents the crest on the under surface of the petrosal, which in form and position agrees with the entotympanic in *Rhinoceros*. A boundary is absent, however, a shallow groove only being present.

In *Equus*, no separate entotympanic is visible, though its presence remains possible.

In *Eomoropus armarorum* an entotympanic is perhaps present (see my own investigations). It is that part described by Cope (1881*c*, p. 390) as the inner longitudinal ridge of the inferior surface of the petrous bone, which is less prominent and is in close contact with the basioccipital.

In *Sus* Parker has described a few "os bullæ" which are said to develop as bone. Van Kampen could not find them. If present, they apparently fuse early with the tympanic. In this respect I mention a few figures in which a line is drawn over the surface of the bulla. This

line might be the suture between the tympanic and the entotympanic. These figures are given by Miller (1906, Pl. LVII, fig. 2) on *Sus peninsularis* and by Deninger (1909. Taf. III, fig. 1*a*) on a young *Babirusa babirusa*. In none of the skulls at hand could I find a similar line or suture.

A very doubtful case of an entotympanic in a fœtal hippopotamus exists in literature.

In *Procavia* (*Hyrax*) a well-developed entotympanic exists, which develops in cartilage (Van Kamp.; Van der Klaauw, 1922*a*, *b*), but which soon is indistinguishably fused with the tympanic. In very young skulls, however, the compound structure of the bulla is still distinct, as I found in specimens in the museums of Berlin and Washington.

In the Lemuridæ the bulla very much resembles that found in the Tupaiidæ, so that it seems probable that the bulla is formed by the entotympanic. Winge (1895*a*, p. 39) speaks of an "os bullæ" in *Lemur collaris* and Gregory (1910, p. 322; 1913*b*, p. 248; 1920, p. 227) of an entotympanic in the Lemuridæ, in the non-Malagasy lemuroids and in *Notharctus*. So far as ontogenetical data are known this bulla develops as an outgrowth of the petrosal or of the mastoid, as I shall describe in the next chapter. Moreover in the adult skull no suture is visible between the bulla and the periotic. Perhaps later investigations may show the independent development of the bulla from the periotic, but probably it develops as an outgrowth of the periotic, the entotympanic having lost its independence. Indications that the petrosal plate of the bulla in the Prosimiæ and the Primates is homologous with the entotympanic, according to Van Kampen, are the great resemblance in form of the bulla in the Lemuridæ with that in *Tupaia*, the presence of cartilage-cells in the already ossified bulla of *Tarsius* and the course of the main carotid branch, which runs either through the tympanic cavity or on the mesial side of the bulla. As to the latter indication, the value of it depends on the homologization of this main carotid branch in the various groups.

Periotic

The periotic forms the whole or, at least, the greater part of the medial wall of the tympanic cavity. It is beyond our special interest to describe this part of the periotic.

That we find the crista facialis petrosi in the lateral wall of the recessus epitympanicus, as in *Ornithorhynchus*, is an exception.

The mastoid is sometimes found in the hinder wall of the tympanic cavity, as in monotremes (Gregory, 1910, p. 151, *vide infra*), in Didelphyi-

dæ (Van Kamp.; Winge, 1893*b*, p. 20, *Grymæomys;* p. 36, *Philander;* p. 59, *Hemiurus;* Van Kamp.), in Notoryctidæ (where the mastoid has a cavity) and also in the other polyprotodonts (Van Kamp.; Zittel, 1923, p. 428). Burmeister (cited by Van Kampen) has described the entotympanic in the Gravigrada as a part of the mastoid. In the modern Trichechidæ the caudal wall of the tympanic cavity is formed by the pars mastoidea, which shifts between the pars petrosa and the tympanic. In *Lemur collaris*, according to Winge (1895*a*, p. 39), the bulla seems to be formed by an outgrowth of the pars mastoidea, which in the new-born specimen is separated from all other neighboring bones. According to other investigations, however, as we shall see, the bulla is formed by the ventral surface of the pars petrosa.

Of special interest to us are the cases in which we find a tympanic process of the periotic in the wall of the tympanic chamber.

Already in the monotremes we find a bony ridge that forms a low hinder wall of the tympanic cavity or we find a thin bony plate (Van Kamp.; Gregory, 1910, p. 151).

In the Didelphyidæ the under surface of the periotic forms a small horizontal process, directed laterally in the ventral wall of the tympanic cavity; it is of different development in different species; it touches the tympanic annulus, the alisphenoid and the mastoid, or does not touch them (Van Kamp.; Winge, 1893*b*, p. 20, *Grymæomys;* p. 35, *Philander;* p. 59, *Hemiurus*). In the Peramelidæ it is as a rule larger than in Didelphyidæ, but is absent in a few species; it touches the tympanic ring (in as much as the alisphenoid does not separate them), and sometimes it touches the mastoid, with which it is not connected, but it does not touch the alisphenoid, from which it is separated at least by the ostium tympanicum tubæ. In *Perameles* it is an uninflated concave plate, in *Peragale* it is inflated (Van Kamp.; Lydekker, 1887, p. 256 and Winge, 1893*b*, p. 95 on *Macrotis*); these two conditions are sometimes characterized as a "simple" and a "double bulla," as the tympanic wing of the alisphenoid is also inflated in both genera. In *Acrobates* we find a structure like that in *Peragale*. In *Thylacinus* the petrosal plate is small, not connected with the mastoid, and covers only a small portion of the ventral wall (Van Kamp.; Winge, 1893*b*, p. 91). In the other Dasyuridæ it covers the whole ventral wall and is connected with the mastoid; it forms a concave, rather thin plate, which in some species is inflated (Van Kamp.; Winge, 1893*b*, p. 91). Also the Notoryctidæ seem to have this tympanic process, which is a small vertical unexcavated plate (Van Kamp.; Gregory, 1910, p. 257). A tympanic process of the petrosal has been described also for the fossil *Microbiotherium* (Sinclair, 1906, p. 410).

It is not impossible that this tympanic wing of the petrosal is also an entotympanic, as Van Kampen suggestively notices it many times.

It is said to be absent in a few of the Peramelidæ, in *Phascolarctus*, in *Phascolomys*, in *Macropus*, and in the fossil *Cladosictis* (Sinclair, 1906, p. 379), and perhaps also in *Amphiproviverra* (*loc. cit.*, p. 397).

A tympanic process of the petrosal is also very common among insectivores (Van Kamp.; Gregory, 1920, p. 162). Sometimes the promontorium itself lies in the hinder wall of the tympanic cavity, without the formation of a tympanic wing. This is the case in *Talpa europæa;* the suggestion of Van Kampen that we had perhaps the same in *Rhynchocyon*, is not correct (Van der Klaauw, 1924*b*).

A real processus tympanicus petrosi is present in most of the families of the insectivores and forms the posterior wall of the tympanic chamber. We find it in *Solenodon* (Van Kamp.; Gregory, 1910, pp. 246, 255; Matthew, 1913, p. 313) occasionally articulating with the tympanic in the family Centetidæ in *Microgale* (Van Kamp.; Gregory, 1910, p. 246) and *Oryzoryctes* (Matthew, 1913, p. 313; Van Kampen, 1905, p. 425) forming a thin plate, that separates the foramen caroticum posterius from the foramen stylomastoideum. In *Macroscelides* (Van Kamp.; Carlsson, 1910*a*, p. 352) there is a distinct ridge, but not to the same degree as in lipotyphlous insectivores (Van Kamp.; Gregory, 1910, p. 281); in *Crocidura* the ridge covers the whole breadth of the periotic until the basioccipital, while in *Sorex* it is very low and narrow (Van Kamp.; Bondy, 1907, p. 310). Even in the genus *Erinaceus* (Van Kamp.; Carlsson, 1922, p. 231) the tympanic process of the petrosal is differently developed in the two groups of species into which they can be divided in relation to the structure of the tympanic region. Also in *Gymnura* and *Hylomys* and in *Myogale* (Van Kamp.; Gregory, 1910, p. 264) it is well developed. In *Rhynchocyon* (Van der Klaauw, 1924*b*) the carotis divides the tympanic wing into two processes on the petrosal, as in *Erinaceus europæus*. In *Rhynchocyon*, according to Van Kampen, it touches the exoccipital and the mastoid, the (caudal) entotympanic, and anteriorly the so-called tympanic wing of the alisphenoid, (the latter, according to my investigations, is the rostral entotympanic). In *Erinaceus* it touches anteriorly the tympanic wing of the basisphenoid and the same close connection is present in *Chrysochloris* (Van Kamp.; Gregory, 1910, p. 267).

According to Gregory (1910, p. 285) the tympanic process of the petrosal in the stem-form of the Menotyphla or in the ancestral menotyphlan family might have been scarcely larger than it is in *Solenodon*.

Perhaps there is reason for homologizing this tympanic process with the entotympanic, but not in all cases, for we have seen that in *Rhynchocyon* both entotympanics are present and also the tympanic process of the petrosal.

Its absence has been noticed in *Centetes* among the insectivores and also in the Tupaiidæ (Van Kamp.; Carlsson, 1910*a*, p. 352).

In *Palæoryctes* a short ridge has been described, into which the anterior end of the auditory prominence is prolonged; but this crest is not extended to take any considerable part of the bulla (Matthew, 1913, pp. 310, 313). This ridge has a position quite different from that of the ridges described above, which lie in the posterior wall of the tympanic chamber.

In *Orycteropus* the inner wall of the tympanic cavity is formed by a high sharp crest of the promontorium, which does not have the value of a processus tympanicus petrosi. The posterior crest on the petrosal in *Manis*, described by Matthew and Granger (1918, p. 625), is not mentioned by Van Kampen.

The petrosal and mastoid elements, which have coalesced with the base of the zygoma in *Megatherium americanum* (Owen, 1856, p. 573) and which, according to Van Kampen, form the wall of the tympanic cavity and not the external auditory meatus, as Owen thinks, are probably an entotympanic. Also the ossifications from the petrosal, which apparently support the bulla on the posterior and internal side in *Palæanodon* (Matthew and Granger, 1918, p. 625; fig. 39) are probably an entotympanic.

In *Oxyænodon*, according to Matthew (1909, p. 414), an incipient petrosal bulla is present. In *Limnocyon* (Matthew, 1909, pp. 434, 435) the petrosal prominence is low-crested; the auditory prominence projects above the basicranial surface with a strong oblique crest.

The notice of Owen (1859, p. 313) on the presence of an inflated petrosal which forms the bulla, and with which the true tympanic bone has coalesced in the cat, dog, hyæna, civet, otter, and bear, is not correct. We can imagine that in a part of these examples, but not in all, the entotympanic is meant, this element being absent or indistinct in the other part of these mammals.

In *Tapirus* the ventral surface of the promontorium shows a high thick crest which, according to Van Kampen, is probably the entotympanic, which is fused with the petrosal.

In the Prosimiæ and the Primates (Van Kamp.; Gregory, 1915, p. 426) the bulla or a large part of the auditory bulla is formed as an ex-

panded shell of the petrosal. The investigations of Forsyth Major (Van Kamp.; Gregory, 1920, p. 163) on different Prosimiæ (on the genera *Chiromys, Lepidolemur, Lemur* and *Avahis*) show the different stages of the development of the plate on the ventral margin of the pars petrosa. In the recent Lemuridæ this petrosal plate forms the entire bulla and the same is very probably also the case in the Chiromyidæ. In the fossil *Notharctus* and *Adapis* (Gregory, 1915, p. 422; 1920, pp. 162, 194, 224; Zittel, 1923, p. 639) and in the ancestral protoadapine stock (Gregory, 1920, p. 232) the general plan of construction is that common to the existing Malagasy lemurs: the bulla consists of a bubble or shell of bone; this bony shell apparently does not arise from a separate center like the entotympanic, but is derived solely from the periotic and represents perhaps what was once merely a rim of the periotic overlapping the membranous hypotympanic cavity.

In the modern Nycticebidæ this bony shell of the petrosal covers the ventral wall of the tympanic cavity, but not more, and is fused with the tympanic, which forms the lateral portion of the bulla. No suture is found between the bulla and the petrosal.

In the modern Tarsiidæ as well the bony covering of the ventral wall of the tympanic cavity and of this wall only is formed by a plate on the petrosal, which is not suturally separated from it. A shallow groove separates its caudal, narrow and smaller portion from its rostral, broad and more inflated part. This rostral prolongation is already present in the Nycticebidæ, but in its extreme condition it is characteristic for *Tarsius*, in which it extends far in front of the annulus tympanicus.

In the modern Hapalidæ the larger part of the tympanic cavity is probably also covered by a processus tympanicus periotici, but the development of the bulla is not yet known.

A fœtal *Cebus* shows a distinct plate on the petrosal, which almost certainly covers the entire ventral wall of the tympanic cavity in the adult skull.

In the higher monkeys, in the adult stage, the wall of the bulla is not as distinctly separated from the proper pars petrosa as is the case in the Prosimiæ. The early development, however, agrees. It is not correct to speak merely of an inflated petrosal without further explanation.

Influence of the Environment on the Bulla

Sometimes an abnormal structure and form of the bulla or place of the openings in the bulla is due to an influence of the environment on the bulla.

The brachycephaly or the dolichocephaly of the skull has a strong influence on the bulla (Osborn, 1902*a*, pp. 79, 82, 83). In the brachycephalic condition the postglenoid and posttympanic processes are approximated, especially below, enclosing the external auditory meatus; in the dolichocephalic condition, on the other hand, the external auditory meatus is not closed below. In the brachycephalic condition the auditory bulla is thrust inward and in the dolichocephalic condition it is exposed laterally.

In various genera of the Oreodontidæ the distance between the postglenoid and the posttympanic process differs in relation to the length of the occipital region. In *Agriochœrus*, however, this distance is narrower than in others, although the occipital region is long.

The shortening of the occiput in the modern Felidæ in general, according to Schlosser (1890, p. 37), causes the close bordering of the paroccipitals against the bullæ.

The changes in the bulla in *Elephas* during the development is caused by the progressive brachycephaly of the skull (Gregory, 1903, p. 389).

In the small bulla and consequently in the posterior position of the glenoid cavity, according to Owen (1840, p. 24), there is a close resemblance between *Toxodon* and the hippopotamus, tapir and rhinoceros.

In *Chrysochloris* the stylomastoid foramen lies a little more internally in relation to the external auditory meatus than in *Talpa*, which is the result of the shortening and broadening of the skull in *Chrysochloris*.

In my opinion the dolichocephalic or brachycephalic condition of the skull, especially the length of the occipital region, has an influence on the mutual position of the tympanic and the entotympanic.

In the modern Mustelidæ the bulla is extended far forward, which perhaps is related to the relatively far forward position of the fossa glenoidea; this makes a great horizontal extension possible and a vertical inflation superfluous. In relation to this far forward position of the processus postglenoideus, this process as a rule is free from the bulla.

Among the Ungulata, according to Winge (1906, p. 55), the fossa glenoidea may touch the tympanic, especially the external auditory meatus, and give it a peculiar form.

The proportions of the skull (Osborn, 1902*a*, p. 79) involve the mastoid among other elements around the auditory meatus. The development of the mastoid process (Matthew, 1910*c*, p. 296) is directly dependent upon the greater or smaller size of the cleidomastoid muscle,

which originates at the tip of the mastoid process, and of the sternomastoid muscle. According to Winge (1906, p. 66) the form of the tympanic in the higher ungulates can be strongly influenced by its neighborhood under the influence of the neck and masticatory muscles.

In the Glyptodontidæ the mastoid with the mastoid process lies far forward, on the lateral side of and not behind the pars petrosa. This is the reason that we find the foramen stylomastoideum far forward, and this perhaps explains why Burmeister (cited by Van Kampen) thought that this aperture was the external auditory meatus.

In the modern Mustelidæ the mastoid process is directed obliquely downward and forward and this seems to be the reason why the external auditory meatus as a rule runs forward. In the modern Procyonidæ, however, the mastoid process shows a similar position and form, but the cylindrical external auditory meatus is not at all or but little forwardly directed.

The strong development of the mastoid in the Phocidæ is perhaps the cause of the fact that the caudal leg of the tympanic is situated far forward and thus the tympanic membrane shows a large declination angle, and also of the fact that the bulla as a whole lies far rostralward at the level of the basisphenoid and even touches the pterygoid and the palatinum.

That the strong development of the postglenoid and mastoid process should prevent the development of the lateral part of the bulla and result in the cylindrical bony external auditory meatus, as formerly was thought for *Galeopithecus*, of course is not correct (Van Kamp.; Winge, 1893*a*, p. 43).

In *Echidna* we find as a specialized or aberrant character (Van Kamp.; Gregory, 1910, p. 156) an extreme backward prolongation of the palate, which is the reason that the ostium tympanicum tubæ lies far backward in the tympanic cavity (Van Kamp.; Winge, 1893*b*, p. 85), that the bony plate on the periotic is only developed in a transverse direction, and that the pterygoid lies in the wall of the tympanic cavity so that it touches the tympanic (Van Kamp.; Gregory, 1910, p. 151).

In *Manis* the pterygoid goes far backward, with these consequences: the tuba auditiva is displaced backward, the ostium tympanicum tubæ lies in the hind part of the tympanic cavity, the place for the entotympanic is diminished and probably also the entotympanic itself is reduced.

In the Myrmecophagidæ, except *Cycloturus*, the palate is prolonged far backward, as in *Echidna* so that not only the pterygoid lies in the

ventral wall of the tympanic cavity, but also the ostium tympanicum tubæ lies far backward and the entotympanic is reduced. This is the reason that the basioccipital lies in the ventral wall of the tympanic cavity and that the carotid runs through the tympanic cavity (Van Kamp.; Winge, 1915, p. 240).

The bulla is also dependent upon the structure of the brain (Matthew, 1909, p. 315). According to Gregory (1920, p. 165) in the South American monkeys the great widening of the brain-case, as compared with that of *Notharctus*, has evidently caused a relative displacement outward of the bony auditory meatus and of the attached ring, and inward of the bulla itself.

The enlargement of the brain causes the enlargement of the carotid. Because of this latter fact the foramen pneumaticum in the bulla of the Primates diminishes in size and the tympanic cavity is nearly completely separated into cellulæ petrosæ and proper tympanic cavity.

The forward shifting of the foramen magnum of the occipital has a strong influence on the bulla. In *Tarsius* it is affected by the enlargement of the orbitæ and by the erect position of the body. This rostral position of the foramen magnum in *Tarsius* causes the rostral displacement of the most inflated portion of the bulla, as the position of the foramen magnum between the caudal portions of the bullæ made the inflation of the latter impossible. Together with the foramen magnum the columna vertebralis cervicalis is displaced forward and thus also the carotid artery. This causes the rostral displacement of the foramen caroticum posterius in comparison with the position found in *Lemur*. This displacement in *Tarsius* must have taken place along the boundary of the tympanic and the petrous bulla, as young specimens indicate.

In the higher monkeys as well this rostral displacement of the foramen caroticum posterius in consequence of the forward shifting of the foramen magnum of the occipital is present save in a few genera, but does not attain the degree of that in *Tarsius*. This forward displacement in the higher monkeys, however, does not take place along the lateral side of the bulla but on its mesial side, i.e., between the bulla and the pars petrosa. This feature is related to the position of the foramen caroticum posterius in young specimens. In adult specimens it is less distinct and is evident only by the fact that the cellulæ of the bulla separate this foramen caroticum from the tympanic, while in *Tarsius* they lie close together. Thus there are points of agreement with *Tarsius*, but they have risen independently from equal causes.

The erect position of the body in man causes a stronger develop-

ment of the neck muscles and thus the origin of the mastoid process. In this mastoid process cellulæ mastoideæ could develop and therefore the cellulæ petrosæ could shrink and thus the bulla diminish in size. By this reduction of the bulla the foramen lacerum anterius becomes free and this explains why in *Homo*, as an exception, the cranial aperture of the carotid canal is visible externally.

ORIGINAL INVESTIGATIONS

HAPALOPS

1. *Hapalops* sp. Princeton No. 15112; Lower Santa Cruz Beds, 10 miles So. of Coy Inlet; O. A. Peterson; Sept. 23, 1896.
2. *Hapalops.* Princeton No. 15355; Lower Santa Cruz Beds; Killik Aike; J. B. Hatcher and O. A. Peterson; June 5, 1896.
3. *Hapalops?* sp. Princeton No. 15569; Lower Santa Cruz, Killik Aike, Patagonia; J. B. Hatcher; 1896.
4. *Hapalops robustus?* AMEGHINO. Princeton No. 15025; Lower Santa Cruz, 10 miles So. of Coy Inlet, Patagonia; J. B. Hatcher; Sept. 19, 1896.
5. *Hapalops robustus?* AMEGHINO. Princeton No. 15308; Lower Santa Cruz Beds, 10 miles So. of Coy Inlet; O. A. Peterson (?); Oct. 7, 1896. Described by Scott, Princ. Exp. Patag., V, p. 212, etc., Pl. XLII, fig. 1.
6. *Hapalops elongatus* AMEGHINO. Princeton No. 15011; Lower Santa Cruz, 10 miles So. of Coy Inlet, Patagonia; O. A. Peterson; Sept. 23, 1896. Described by Scott, Princ. Exp. Patag., V, p. 217, etc., Pls. XXXVII–XXXIX.
7. *Hapalops elongatus* AMEGHINO. Princeton No. 15160; Lower Santa Cruz, 10 miles So. of Coy Inlet, Patagonia; J. B. Hatcher; Sept. 1, 1896. Described by Scott, Princ. Exp. Patag., V, p. 217, etc., Pls. XXXVII–XXXIX, XLI.
8. *Hapalops elongatus* AMEGHINO. Princeton No. 15545; Lower Santa Cruz, Killik Aike, Patagonia; J. B. Hatcher; June 3, 1896. Described by Scott, Princ. Exp. Patag., V, p. 217, etc., Pls. XXXVII–XXXIX, XLI.
9. *Hapalops elongatus* AMEGHINO. Princeton No. 15597; Lower Santa Cruz, Killik Aike, Rio Sollegos, Patagonia; J. B. Hatcher; June 12, 1896. Described by Scott, Princ. Exp. Patag., V, p. 217, etc., Pls. XXXVII–XL.
10. *Hapalops angustipalatus* AMEGHINO. Princeton No. 15562; Lower Santa Cruz, 10 miles So. of Coy Inlet, Patagonia; J. B. Hatcher; Sept. 30, 1896. Described by Scott, Princ. Exp. Patag., V, p. 232, etc., Pl. XLIII.
11. *?Hapalops ponderosus* SCOTT. Princeton No. 15520, type; Lower Santa Cruz, 10 miles So. of Coy Inlet, Patagonia; J. B. Hatcher and O. A. Peterson; 1896. Described by Scott, Princ. Exp. Patag., V, p. 236, etc., Pl. LIV.
12. *Hapalops gracilidens* AMEGHINO. Princeton No. 15529; Lower Santa Cruz, Killik Aike, Patagonia; J. B. Hatcher; June 1, 1896. Described by Scott, Princ. Exp. Patag., V, p. 249, etc., Pl. XLIV.
13. *Hapalops vulpiceps* SCOTT. Princeton No. 15595, type; Middle Vertebrate Beds, Lake Pueyrredon, Patagonia; J. B. Hatcher; March, 1899. Described by Scott, Princ. Exp. Patag., V, p. 253, etc., Pl. XLIV.

14. *Hapalops platycephalus?* SCOTT. Princeton No. 15522; Middle Vertebrate Beds, Lake Pueyrredon, Patagonia; S. B. Hatcher; March, 1899. Described by Scott, Princ. Exp. Patag., V, p. 255, etc., Pls. XLII, XLV.
15. *Hapalops platycephalus* SCOTT. Princeton No. 15564, type; Middle Vertebrate Beds, Lake Pueyrredon, Patagonia; S. B. Hatcher; March, 1899. Described by Scott, Princ. Exp. Patag., V, p. 255, etc., Pl. XLV.
16. *Hapalops ruetimeyeri* AMEGHINO. Amer. Mus. Nat. Hist., No. 9293; Miocene, Santa Cruz Formation, Halliday Estancia, Santa Cruz, Patagonia; Amer. Mus. Exp., 1899. Fig. by Scott, Princ. Exp. Patag., V, Pl. XXXVII.
17. *Hapalops brachycephalus* AMEGHINO. Amer. Mus. Nat. Hist. No. 9176; Miocene Epoch, Santa Cruz Form. 7 miles So. of Monte Leon, Santa Cruz, Patagonia; Amer. Mus. Exp., 1899. Fig. by Scott, Princ. Exp. Patag., V, Pl. XXXVI.

TYMPANIC.—The angle between the tympanic ring and the horizontal and vertical plane is about 45°; at all events it does not lie nearly vertically as Van Kampen notices for the Gravigrada that he investigated. The tympanic is a rather narrow ring. There is neither a distinct mesial extension (forming a bony covering of a part of the "ventral wall" of the tympanic cavity) nor a lateral one (forming a bony external auditory meatus). Still the diameter of the lateral opening of the tympanic ring is smaller than the mesial one. The mesial side of the rostral part of the tympanic shows a curve in the form of a half circle for the auditory tube. The tympanic forms more than a half circle as the lateral view of the skull shows very clearly. Probably the tympanic was not free, as generally occurs in the Gravigrada, but the extremities of the two horns of the tympanic are fused with the skull, showing no distinct suture. In some of the skulls the tympanic is absent except for these two extremities, thus demonstrating their fusion with the skull. The tympanic does not seem to be fused with the entotympanic, to which it is closely applied. There is no partly membranous ventral wall.

In many cases the tympanic is absent or does not show the characters very well, but we have reason to believe that it is as described here. The same is the case with the entotympanic and still more so, because here we have many characters in a very fragile element, so that in many cases it does not show one or more of them. We shall not mention which specimen shows a described character and which not, except in a few cases where only a very few specimens or only one specimen show this character. So we shall give a general description, which we believe gives the right condition.

ENTOTYMPANIC.—The general form of the entotympanic is a vertical bony plate on the periotic. Its ventral or under margin lies close against the mesial side of the middle or most ventral part of the tympanic ring.

On the mesial side, on a more dorsal level, this entotympanic plate forms the roof of a groove between the vertical plate of the entotympanic and the basioccipital. After this general form-description we shall pass on to a more detailed one.

VENTRAL SURFACE OF THE ENTOTYMPANIC PLATE.—First of all we shall describe the ventral or under surface of the vertical plate, which we see if we examine the skull from the ventral side.

This ventral edge is nearly straight and rather narrow. Rostrally it reaches the caudal edge of the pterygoid and this part of the ventral edge of the entotympanic is broadened a little: first to the mesial side, (so reaching the basis cranii) and then still more so in front; also laterally,

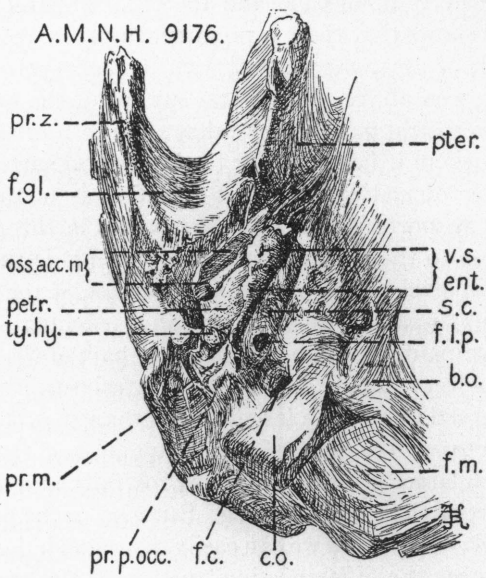

Fig. 1. *Hapalops brachycephalus* Ameghino A. M. N. H. No. 9176. Ventral and a little obliquely caudal view. Natural size.

touching the pterygoid rostrally. In the caudal part of the ventral edge it continues without a suture in the paroccipital process, whose ventral surface lies on the same level as that of the mastoid and the surface of the top of the tympanohyal, which lies closely against the mastoid. They apparently form together an articulating surface for the stylohyal. A suture between the paroccipital process and the mastoid is distinct only in a very few specimens. Just medially from the ventral surface of the

tympanohyal the ventral border of the entotympanic is a little narrower. Rostrally it curves around the ventral surface of the tympanohyal, forming a small bony angle between this and the tympanic ring. Caudally of the ventral surface of the tympanohyal as well it curves around it, though we are not sure here about the sutures between the entotympanic and the paroccipital process and between this process and the mastoid. On the ventral surface the entotympanic is not fused with the tympanohyal. If there is a connection between these two, as we may expect in accordance with the conditions in allied recent mammals, it must be on a more dorsal level but this cannot be traced in our specimens. Specimen Princeton No. 15569, where the tympanic ring fails, shows a distinct suture between the tympanohyal and the entotympanic seen from the rostral side, and shows that there is no direct fusion or connection on the rostromedial side of the tympanohyal with the entotympanic.

As we have seen above, the ventral surface of the entotympanic is broadened in the rostral part, which takes about a fourth part. Also in the caudal part where it lies medially to the ventral surface of the tympanohyal it is broadened a little—not so much as in the rostral part. Between these two parts it is rather narrow and in this part it lies just mesially and close to the ventral part of the tympanic ring. There is a little difference in level between the under surface of the entotympanic and that of the tympanic, the entotympanic reaching a more ventral level than the tympanic. In the most ventral part of the tympanic ring this difference is very small, but as the ventral surface of the entotympanic is a curved line with a larger radius than that of the tympanic, the difference between the level of the tympanic and that of the entotympanic is much larger in the places lying rostrally and caudally of this most ventral part of the tympanic ring. But also in the parts where the difference in level is very small we can easily distinguish the two elements. Not only can we see the difference in structure of the two surfaces, the tympanic being smooth and the ventral surface of the entotympanic rather rough, but also we can always see a distinct line between the two elements. As we have said above, the diameter of the mesial plane of the tympanic is larger than the lateral one, but still there is no imperceptible change toward the ventral surface of the entotympanic. There is always a more or less distinct groove between the two elements and in the roof of this groove we find the line mentioned above.

In the middle of the ventral surface of the entotympanic, half-way between its rostral and caudal end, this surface lies a few millimeters on a more ventral level than the unswollen lateral sides of the basis cranii.

In relation with the curving of this ventral surface this difference in level is smaller rostrally and finally disappears. The broadened rostral part of the ventral surface of the entotympanic is also curved in the direction lateralward to mesialward.

THE LATERAL SURFACE OF THE ENTOTYMPANIC PLATE.—As we have said above, the entotympanic is a vertical plate, standing vertically on the periotic. The lateral surface of this plate can be studied well only in the cases in which the tympanic fails, because where it is present the bulla nearly always is partly filled with matrix, covering the lateral plane of the entotympanic. The height of the vertical plate is about 3 to 4 mm. in general. The dorsal margin of the plate reaches the periotic; if there has been a fissure it must have been a very narrow one, but it seems more probable that there was a close connection, as in the recent *Cholœpus*. Except in the rostral part, as we shall see later, the lateral surface of the vertical plate is flat; perhaps dorsally it is a little more excavated and a little retreated from the lateral plane of the more ventral part, but this is not very distinct.

In the rostral part the condition is slightly different. Here the entotympanic plate has a greater height, as the under margin of the periotic is rounded in the plane of the entotympanic, and here also the dorsal margin of the entotympanic keeps its close contact with the periotic Moreover, the rostrodorsal part of the lateral surface of the plate extends in a more lateral direction. In this rostral part there is a more gradual transition from the ventral surface into the lateral one than we find in the more caudal part. This dorsolateral extension of the rostral part of the entotympanic lies between the pterygoid (on its rostral side), the periotic (on its dorsal and caudal side) and the tympanic (on its caudal and lateral side). This part of the entotympanic forms the mesial side of the bony opening for the Eustachian tube. In the rostral part of the auditory bulla we see that the tympanic and the entotympanic, which are connected for a long distance, are diverged. On its mesial side the tympanic shows a curve in the form of half a circle. In front of this half circle, tympanic and entotympanic once more touch each other, but in this case only in one point, in this way leaving an opening for the Eustachian tube. In this way also the tympanic forms a small bony process in the lateral wall of the Eustachian tube. As in many other cases, this opening for the Eustachian tube lies between the tympanic and the entotympanic. On the mesial and mesiorostral side of this opening we still find the entotympanic at a height of a few millimeters. This condition of the opening of the Eustachian tube is only very distinct

in Princeton No. 15545 (left side); unfortunately in many cases the tympanic ring is absent and consequently this opening also is missing.

THE MEDIAL SURFACE OF THE ENTOTYMPANIC PLATE.—As we have seen above, the ventral surface of the entotympanic is broadened in its rostral fourth part and connected with the basioccipital. In the more caudal part, however, the ventral surface of the entotympanic plate is narrower and in most cases is separated by a groove from the basioccipital. This groove is nearly always filled with matrix, but since, as we have seen, there is a difference in level between the ventral surface of the entotympanic plate and the lateral sides of the basioccipital, in most

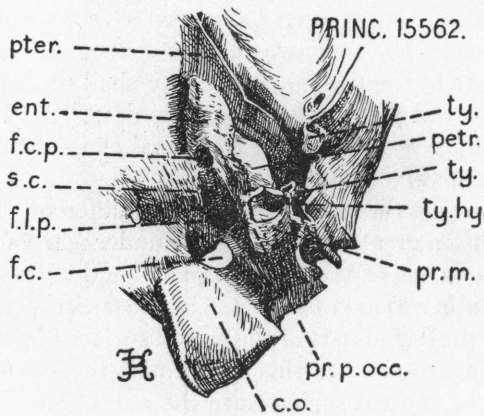

Fig. 2. *Hapalops elongatus* Ameghino. Princeton No. 15545. Ventral and a little obliquely caudal view. Natural size.

cases we find bone in the lateral wall (forming the ventral part of the mesial surface of the entotympanic plate) at a height of a few millimeters and then disappearing in the matrix which fills up the groove.

Probably this groove is the bony sulcus caroticus if we bring the conditions in connection with those in allied forms. In this case we have to expect here, on a more dorsal level, a bony roof for this sulcus caroticus, but in none of the specimens is this distinct. Only Princeton specimen No. 15562 shows this bony roof on the left side lying just behind the broadened rostral part of the ventral surface of the entotympanic on about the same level as the "basis cranii," but more caudally inclining dorsally into the foramen lacerum posterius. Its inclination is slight and thus this roof of the carotid sulcus is not saddle-shaped. In

the more rostral part of the bulla this groove is covered ventrally by the described broadened rostral fourth part of the ventral surface of the entotympanic, which touches the lateral side of the basioccipital. Princeton No. 15562 (left side) shows this condition very distinctly. Here we find a definite opening for the carotid, but this posterior carotid foramen is also visible in a few other specimens. In the other specimens there is no distinct posterior carotid foramen. Perhaps the bone surrounding it is broken away, perhaps it never has been present. Some recent edentates

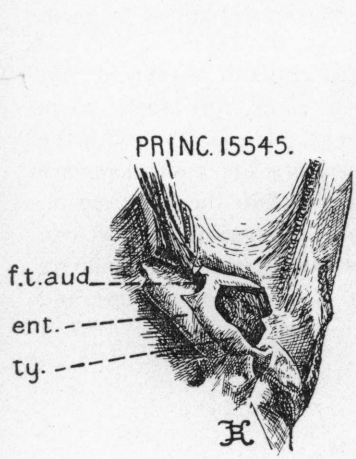

Fig. 3

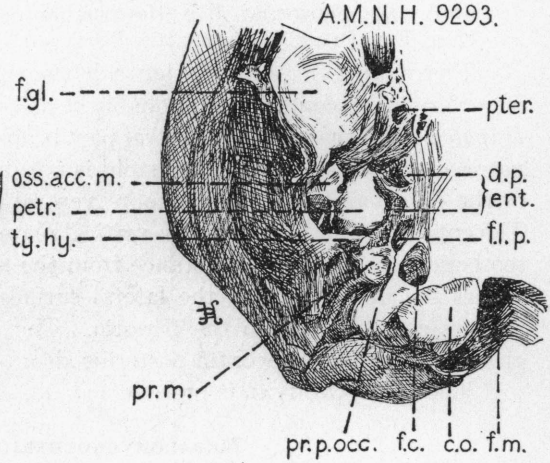

Fig. 4

Fig. 3. *Hapalops an gustipalatus* Ameghino. Princeton No. 15562. Ventral view. Natural size.

Fig. 4. *Hapalops ruetimeyeri* Ameghino. A. M. N. H. No. 9293. Ventral and a little obliquely lateral view. Natural size.

show us that this feature may be individually variable. Caudally the sulcus opens into the large foramen lacerum posterius, which is also filled up with matrix.

As we have already said, in many cases the entotympanic has been partly broken away so that most of the described details can be seen only in one or a few specimens. The figures illustrate this as well, for instance, specimen 15545 of Princeton shows the opening for the Eustachian tube very well, but for the rest the entotympanic is in a very bad condition. Sometimes the entotympanic has so far disappeared that only the most dorsal part still remains as a rather thin layer of bone covering the periotic. These specimens are worth mentioning as they show the bony

roof of the sulcus caroticus, caudally inclining dorsalward into the foramen lacerum posterius. Laterally of this bony roof we find the dorsal part of the abrupt vertical plate of the entotympanic still in connection with the paroccipital process. These specimens (Princeton No. 15569, A. M. N. H. Nos. 9176, 9293) also indicate that the dorsal surface of the entotympanic is in close connection with the under surface of the periotic.

SCHISMOTHERIUM

1. *Schismotherium fractum* AMEGHINO. Princeton No. 15524; Santa Cruz (Lower), Killik Aike, Patagonia; J. B. Hatcher; May 20, 1896. Described by Scott, Princ. Exp. Patag., V, p. 296, etc., Pls. L, LIII.

ENTOTYMPANIC.—On the left side the entotympanic is present, but in a very poor condition. Probably it had the same appearance as in *Hapalops*. In that case the rostral part is absent. The contact with the paroccipital process and the mastoid is not distinct. The ventral surface of the entotympanic lies on a more ventral level than the basis cranii. The entotympanic seems to be a vertical plate on the periotic, but we can see bone only for a short distance from the ventral surface; the matrix covers the dorsal part of the lateral surface of the entotympanic and also its connection with the periotic. The matrix fills up the carotid groove and foramen lacerum posterius also.

The TYMPANOHYAL is present.

MEGALONYCHOTHERIUM

1. *Megalonychotherium atavus* SCOTT. Princeton No. 15593, type; Santa Cruz (Upper), 5 miles So. of Coy Inlet, Patagonia; O. A. Peterson; Nov. 4, 1896. Described by W. B. Scott, Princ. Exp. Patag., V, p. 279, etc., Pl. XLVI.

TYMPANIC.—Absent in this specimen.

ENTOTYMPANIC.—Present on both sides, but in a rather poor condition. It is in contact with the paroccipital process. A suture between the two is not distinct; perhaps there is one visible on the left side. Nor is the suture distinct between the entotympanic and the pterygoid. As in *Hapalops*, the entotympanic is here a vertical bony plate on the periotic. The ventral surface lies on a little more ventral level than the basis cranii and is curved in the sagittal plane. There is no distinct broadening of the rostral part of the ventral surface of the entotympanic toward the mesial side and there is no broad contact with the basis cranii of this rostral part. The lateral surface of the entotympanic is flat and shows no distinct excavation in the dorsal part; the matrix partially covers this part and covers also the contact with the periotic. The dorsorostral portion extends in a more lateral direction, and the

height of the entotympanic plate is larger than in the more caudal parts. The matrix fills the foramen lacerum posterius and the sulcus caroticus, and covers its roof.

The TYMPANOHYAL is not very distinct.

ANALCIMORPHUS

1. *Analcimorphus giganteus leptocephalus* AMEGHINO. Princeton No. 15561; Santa Cruz (Lower), 15 miles So. of Coy Inlet, Patagonia; O. A. Peterson; 1896. Described by W. B. Scott, Princ. Pat. Exp., V, p. 283, etc., Pls. XLVIII, XLIX.
2. *Analcimorphus giganteus* AMEGHINO. Princeton No. 15163; Santa Cruz (Lower), 20 miles So. of Coy Inlet, Patagonia; O. A. Peterson. Described by W. B. Scott, Princ. Pat. Exp., V, p. 283, etc., Pl. XLVII.

TYMPANIC.—Present in specimen 15163 on both sides and in specimen 15561 on the right side. The angle between the tympanic and the horizontal and vertical plane is about 45°, at all events the tympanic is not nearly vertical. The tympanic is broader in its ventral part of the ring than in *Hapalops*, for instance; probably we have here a case of extension of the tympanic ring in the medial direction, forming a part of the bony covering of the ventral wall of the tympanic cavity. The porus acusticus externus is a large aperture. The tympanic has the form of a half ring. The curve in the tympanic forming a half circle represents the opening for the Eustachian tube. Here also a very small bony process lies in the lateral wall of the foramen for the auditory tube. The sutures between the horns of the tympanic ring and the squamosal are partly indistinct.

ENTOTYMPANIC.—The entotympanic is present in both specimens on both sides. If we might expect the same conditions here as in *Hapalops*, the entotympanics are in a bad condition. For the rest the matrix makes many details invisible, as I shall mention later for some features. Here also the ventral surface of the entotympanic is on a little more ventral level than the ventral part of the tympanic ring.[1] Rostrally this level of the ventral surface of the entotympanic and that of the basis cranii approach each other. Caudally the entotympanic reaches the paroccipital process, although there is no distinct suture between the two elements; in specimen 15163 there is a rather wide space between the two, where the bone probably has been broken away. Also in specimen 15163 there is rather a wide space between the rostral point of the ventral surface of the entotympanic and the pterygoid; here also the bone probably is broken away. For the rest it seems to show the same conditions

[1]The line in Scott's Plate XLVII, fig. 3, left side, is not the suture between the tympanic and the entotympanic but seems to be the center of the rounded ventral surface of the entotympanic plate.

as in *Hapalops*. It is a vertical bony plate on the periotic with a flat vertical lateral surface, as specimen 15561 shows, but here the dorsolateral extension of the rostral part of the entotympanic fails. The mesial surface is visible only for a short distance, the carotid sulcus being filled with matrix. The rostral part of the ventral surface, so far as present, is broadened, touching the basis cranii with its mesial side. The specimen is in too bad a condition to show the opening for the carotid artery. Behind this broadening the mesial side of the entotympanic plate forms the dorsolateral roof of the sulcus caroticus.

The TYMPANOHYAL is distinct in specimen 15561 on the right side in the place where we should expect it.

PELECYODON

1. *Pelecyodon cristatus* AMEGHINO. Princeton No. 15627; Santa Cruz (Lower), 20 miles So. of Coy Inlet, Patagonia; O. A. Peterson; Oct. 22, 1896. Described by W. B. Scott, Princ. Exp. Patag., V, p. 309, etc., Pl. LII.
2. *Pelecyodon cristatus* AMEGHINO. Princeton No. 15049; Santa Cruz (Lower), 10 miles So. of Coy Inlet, Patagonia, J. B. Hatcher; Sept. 19, 1896. Described by W. B. Scott, Princ. Exp. Patag., V, p. 309,etc., Pl. LII.

TYMPANIC.—A horseshoe-like narrow bone, resembling that in *Hapalops*. Not all tympanics are preserved, as they were probably loosely attached.

ENTOTYMPANIC.—In general the same as in *Hapalops*. The ventral surface is caudally in connection with the paroccipital process, although there is no distinct suture between the two elements. There is rather a wide space between the rostral point of the entotympanic and the pterygoid and perhaps here the bone is broken away. The rostral part, so far as it is present, is not broadened as in *Hapalops*, but is about as narrow as the more caudal parts. This rostral portion is directed to the medial side and also touches the basis cranii. Behind this rostral part the lateral side of the ventral surface of the entotympanic lies for some distance close against the tympanic. The ventral surface of the entotympanic is also a curved line, whose radius is much longer than that of the tympanic, so that the ventral surface of the entotympanic rostrally and caudally is on a much more ventral level than is the tympanic. In the middle we find only a very slight difference in level. But on the other hand, the ventral surface of the entotympanic does not lie on a more ventral level than the lateral sides of the basis cranii, which in this genus are swollen; it is possible that the deformed condition of specimen 15049 is partly to blame in this matter. The lateral surface of the entotympanic is flat, lies with its dorsal margin closely against the petrosal and shows in

the rostral part a dorsolateral extension. Behind the point where the ventral surface of the entotympanic touches the basis cranii, we should expect the sulcus caroticus, but this part is very indistinct.

MYLODON

1. *Mylodon garmani.* Museum of Comparative Zoölogy, Harvard University, Cambridge (Mass.); No. 8429, type. Described by G. M. Allen, 'A new *Mylodon.*' Memoirs of the Mus. of Comp. Zoöl. at Harvard College, XL, No. 7.

TYMPANIC.—The tympanic is present on both sides. Apparently it is not loosely attached to the skull but seems to be fused, as Allen already described for this specimen, taking Allen's periotic for the entotympanic. There are no distinct sutures where the horns are attached to the skull. It is a narrow, horseshoe-like, incomplete ring. The middle or most ventral portion of the tympanic is about 6 mm. broad, and so it shows neither a distinct medial extension (forming a bony covering of the so-called ventral wall of the tympanic cavity) nor a distinct lateral extension (forming a bony recessus meatus). The plane of the tympanic is nearly vertical, being only a little inclined from dorsolateral toward ventromedial. I do not know whether this is the natural condition or perhaps is partly due to compression of the skull. The same is the case with the very close connection of a large part of the tympanic ring with the lateral surface of the entotympanic plate. On the rostral side we find that the two elements diverge, forming the opening for the Eustachian tube. The tympanic and the entotympanic do not distinctly touch each other again in front of the Eustachian foramen. The curve in the form of half a circle for the Eustachian foramen and the small bony process in the lateral wall of the Eustachian tube are less distinct than in *Hapalops.*

ENTOTYMPANIC.—Also the entotympanic is present on both sides. I am not quite sure that this specimen shows the entotympanic in its natural condition. It gives the impression that it is compressed and partly broken and thus perhaps the following description does not give the natural condition.

The caudal extension of the entotympanic cannot be determined with certainty, as there is no distinct suture between the entotympanic and the paroccipital process. Also the rostral extension is very indistinct. On the right side the entotympanic seems to be a thin bony plate which comes into contact with the basisphenoid and the pterygoid; on the left side this rostral portion is absent with the exception of some small remains. The ventral surface of the entotympanic plate does not show the rather broad ridge as in *Hapalops* but in the central part, where it comes

in contact with the tympanic, it is a very thin plate, only about 2 mm. broad. Perhaps the under margin is broken away; in many places it has this appearance, and seen from the lateral side the under margin is about straight and not a curved line as in *Hapalops*. In the rostral and in the more caudal part the ventral surface is a little broader. Just mesially from the ventral surface of the tympanohyal the ventral surface of the entotympanic plate seems to be a little narrower than it is rostrally and caudally of this spot. The tympanohyal lies in a very compressed condition against the lateral surface of the entotympanic just behind the

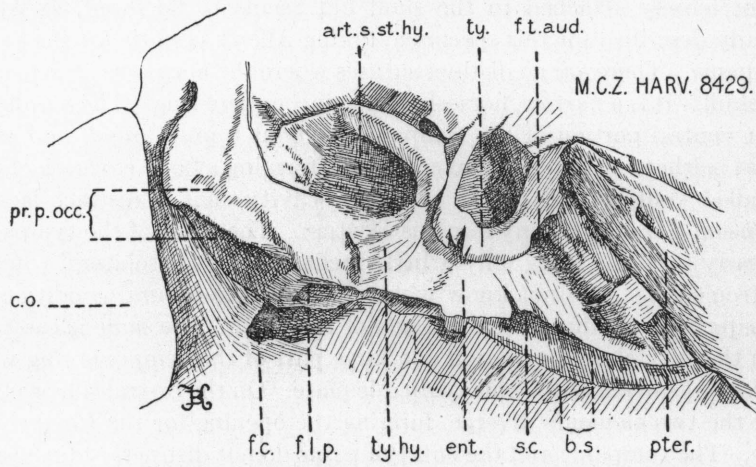

Fig. 5. *Mylodon garmani*. Mus. Comp. Zoöl., Harvard, No. 8429. Obliquely lateroventral view. Four-fifth natural size.

tympanic. Its sutures against the other elements and its form are very indistinct, which are of course not natural conditions. The ventral surface of the entotympanic or the paroccipital process (the suture between the two is not visible) and the ventral surface of the tympanohyal do not lie at the same level. We found in *Hapalops* that the ventral surfaces of the paroccipital process and that of the mastoid process lie on the same level and so close together that a suture between the two elements was distinct only in a few specimens. Unlike this we find in *Mylodon* that the ventral surface of the mastoid process, with the articular surface for the stylohyal, lies on a more dorsal level.

The lateral surface of the entotympanic is a flat plane, nearly vertical, and only a little inclined from dorsolateral toward ventromedial. The tympanic lies against this lateral surface from the posterior side of

the opening for the Eustachian tube to a short distance in front of the tympanohyal. In the central or most ventral part of the tympanic the level of the ventral surface of the entotympanic is about 10 mm. beneath that of the tympanic and this distance is still larger in the more rostral and caudal parts, as the tympanic ring has a rather small radius and the ventral surface of the entotympanic is nearly uncurved. Although there is no distinct suture between the tympanic and the entotympanic, yet there is no gradual transition of the surface of the tympanic into that of the entotympanic. The transverse section of the tympanic ring shows ventrally an angle, and consequently a rather deep groove occurs between the lateral surface of the entotympanic and the medioventral outer surface of the tympanic ring. As the tympanic is present on both sides, the dorsal part of the lateral surface of the entotympanic is not very distinct. The rostral part of this lateral surface shows on the right side (on the left side it is not preserved) the large dorsal extension, which also forms the mesial side of the opening for the Eustachian tube, thus resembling the conditions in *Hapalops*, with this difference only, that this dorsal extension is not inclined so much laterally as in *Hapalops*.

All that lies medially of the ventral surface of the entotympanic plate is in a very poor state of preservation, broken off, crushed, filled up with matrix, and so forth, and the sutures are very indistinct. In the rostral and middle portion of the entotympanic the ventral surface lies on about the same level as the swollen lateral sides of the basis cranii. In the more caudal parts, where we find the foramen lacerum posterius lying caudally from the ventral surface of the tympanohyal, the lateral sides of the basis cranii are not so much swollen up. In the middle part of the entotympanic, that is, in the place where the tympanic lies against it, between the very thin entotympanic and the basis cranii we find a deep groove. In the lateral wall of this groove at a height of a few millimeters we find the bone of the entotympanic, but the rest, and probably also the roof of the sulcus caroticus, is covered by matrix. In front of and behind this groove the entotympanic is in close connection with the basis cranii. How much influence the compression of the skull has had in these conditions I cannot tell. Perhaps this explains the differences between this *Mylodon* and *Mylodon gracilis* described by Van Kampen; perhaps they are due to specific characters.

SCELIDOTHERIUM

1. *Scelidotherium leptocephalum* OWEN. Mus. Comp. Zoöl., Harvard Univ., Cambridge(Mass.), No. 8812; Argentina, Buenos Ayres, Pampus Formation. This specimen has never been described, according to information by Dr. G. M. Allen.

TYMPANIC.—Absent on both sides in this specimen, and probably loosely attached.

ENTOTYMPANIC.—Present on both sides and in a very good condition. Especially the bony roof of the sulcus caroticus is in such a well-preserved condition that the general characterization of the entotympanic as a vertical plate on the periotic in this specimen appears to give only an incomplete idea of the form in general. Here we would characterize the

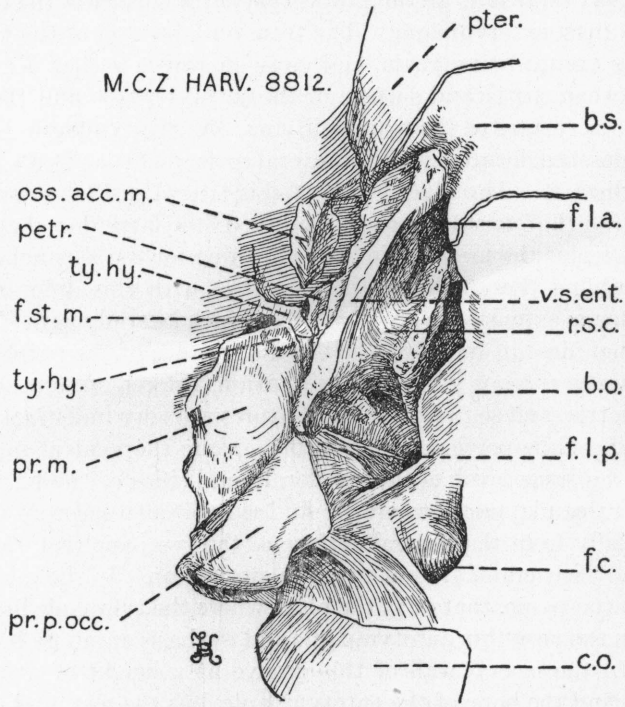

Fig. 6. *Scelidotherium leptocephalum* Owen. Mus. Comp. Zoöl., Harvard, No. 8812. Ventral view. Natural size.

entotympanic as a vertical plate on the periotic, bearing on its mesial side, on a more dorsal level, a bony roof for the sulcus caroticus, which has the shape of a broad saddle if seen from the ventral side.

THE VENTRAL SURFACE OF THE VERTICAL PLATE OF THE ENTOTYMPANIC.—This reaches the paroccipital process caudally. Here we find, unlike what I have as yet described in the other fossil edentates, a very distinct suture between the entotympanic and the paroccipital

process. This suture lies at rather a long distance behind the ventral surface of the tympanohyal and near the hinder margin of the ventral surface of the mastoid process (the ventral surface of this process lies on a more dorsal level than that of the paroccipital process). On the left side we find this suture dorsally only, as that caudal end of the entotympanic has broken off ventrally. The tympanohyal is partly enclosed in the mastoid process and the suture between these two fused elements is not always distinct, as the distal part of the tympanohyal is fused with the mastoid, proximally diverging and surrounding the foramen stylomastoideum primitivum. Nor is it possible to find a continuous suture between the caudal part of the entotympanic and the mastoid process. Between the tympanohyal and the entotympanic there is no connection superficially, but perhaps there is one on a deeper layer.

The rostral side of the ventral surface of the vertical entotympanic plate extends far forward but as the form and boundary of the caudal part of the pterygoid is very indistinct, the relation of the entotympanic to the pterygoid is indeterminable. The rostral part of the vertical entotympanic plate is broadened, and extending medialward; touches the basisphenoid just in front of the suture between the basioccipital and the basisphenoid, as the right side shows; in the left side of the skull we find a space between the two elements, but this does not seem to be the natural condition.

The ventral surface of the vertical entotympanic plate is very narrow in the central part and broadened a little in front of the tympanohyal, but it has a narrow surface again just mesially and behind the tympanohyal. Without doubt this ventral surface is not the real one, especially not in the central part, and it has the appearance of being crumbled off. This probably explains also the aberrant form of the ventral surface of the entotympanic plate seen from the lateral side, which shows that its center is concave instead of convex, as in *Hapalops* and allied genera.

The Lateral Surface of the Vertical Entotympanic Plate.—This is very peculiar. The smaller ventral part is a flat, nearly vertical plane, which alters with a rather sharp line into the distinct excavation that is shown by the larger dorsal part of the lateral surface of the entotympanic. This part is hollow in two directions, ventrodorsally as well as rostrocaudally. Rostrally and caudally the transition of the hollow dorsal and flat ventral portion is a more gradual one. As the tympanic fails, it is impossible to determine the relationship between the sharp line of transition in the middle part of the lateral surface of the entotympanic and the line of connection of the entotympanic with the tympanic. The

dorsal part of the lateral surface of the entotympanic makes a right angle with the ventral surface of the periotic. There is only a very narrow space between these two elements, although there does not seem to be a fusion. This lateral surface of the entotympanic does not form a horizontal extension over the ventral surface of the periotic. The rostral part of the entotympanic plate shows here also a dorsal extension, which is directed a little laterally. Without doubt this lateral surface also forms the mesial part of the opening for the Eustachian tube, but, as the tympanics are absent, the place cannot be determined with certainty.

THE MEDIAL SURFACE OF THE VERTICAL ENTOTYMPANIC PLATE.—The importance of this specimen of *Scelidotherium* lies principally in the wonderful preservation of the part of the entotympanic that lies mesially of the ventral surface of the plate-like part of the entotympanic. This mesial part was never so well preserved in all the other fossil edentates I examined. I infer therefore that this is the natural conditon and that the condition found by Van Kampen is due to a less excellent preservation, unless these differences are due to specific characters. Moreover, I suppose that the other fossil edentates, already described, would show nearly the same conditions as I shall describe here. Seen from the ventral side, on the mesial side of the ventral surface of the entotympanic plate is a saddle-shaped, bony structure on a morphologically somewhat more dorsal level. This saddle-shaped structure has on its mesial side as well a bony ridge nearly parallel with the ventral surface of the plate-like part of the entotympanic, but not quite as long as the latter and not reaching down to the same ventral level as the latter, and not down to the ventral level of the external sides of the basis cranii. There remains a deep groove between this mesial bony ridge and the lateral sides of the basis cranii; on the right side only the rostral point is nearly in contact with the basis cranii. In the lateral wall of this deep groove between this mesial bony ridge and the lateral sides of the basis cranii we see for a short distance the bony medial surface of the entotympanic, the surface of which is nearly vertical, only a little directed from ventromedial toward dorsolateral. The more dorsal features of the skeletal elements enclosing this narrow, deep groove cannot be determined. The center of this saddle-shaped structure of course lies on the most ventral level, the roof of this carotid sulcus inclining dorsally to both sides, rostrally as well as caudally. Rostrally it leads toward the foramen lacerum anterius. The rostral margin of the entotympanic sulcus in its mesial half runs in a dorsolateral-ventromesial and slightly caudal direction. In its lateral half the rostral margin of the entotym-

panic groove cannot be described so easily; it runs in general in a rostro-caudal direction. Caudally the groove leads toward the foramen lacerum posterius; going backward it proceeds first very steeply dorsally, and then still more caudally, less so. The caudal margin of the entotympanic in this part lies nearly in the same transverse plane as the suture between the plate-like part of the entotympanic and the paroccipital process.

LESTODON

1. *Lestodon myloides.* Young specimen, A. M. N. H. No. 11270; Cope Pampean Collection.

TYMPANIC.—The tympanic is present on both sides but does not show the same position, so it must have been loosely attached to the skull. The place where the caudal horn of the incomplete ring is attached to the skull is not the same on both sides, and for that reason the place where the tympanic is in contact with the entotympanic is different. There is also a little difference in the angle which both tympanic rings form with the horizontal and vertical plane and therefore also in the height of the so-called ventral wall of the tympanic cavity. Probably the left tympanic is out of place and the right one shows the natural position.

The angle of the plane of the external (ventrolateral) surface of the tympanic ring with the vertical plane is a little less than 45° and with the horizontal plane a little more than 45°. The plane of the external surfaces of the tympanic meet each other at a short distance in front of the middle of the ventral side of the skull. The rostral horn of the tympanic is attached a little more mesially to the skull than the caudal horn. The two horns are rather narrow but the central portion is rather broad. Though the matrix covers the inner side of the tympanic ring and makes the sulcus membranæ tympani invisible, there is much reason to believe that the broadening to the lateral side is not as a bony recessus meatus, but that for the greater part on the mesial side the covering is a part of the so-called ventral wall of the tympanic cavity. There is no curve in the form of half a circle for the Eustachian tube and no bony process in the lateral wall of the Eustachian tube.

ENTOTYMPANIC.—The entotympanic is very short as compared with that in the other edentates we have described above. In position it is the caudal part of the entotympanic in these genera, and its rostral point remains at a rather great distance from the pterygoid and basisphenoid. The rostral point of the entotympanic reaches about the center of the tympanic ring. There is also a great distance between the caudal part

of the entotympanic and the paroccipital process, the two being separated by the enormously developed transverse foramen lacerum posterius. The entotympanic lies on the mesiocaudal side of the tympanic, mesially of the tympanohyal, and on the rostromesial side of the articulation surface of the mastoid for the stylohyal, and on the rostrolateral side of the foramen lacerum posterius. There is no distinct suture between this knobby bone, which I think must be the entotympanic, and the mastoid process, nor is there a suture in the rostrolateral bony wall of the foramen lacerum posterius, as far as can be seen. Nor is there a connection with

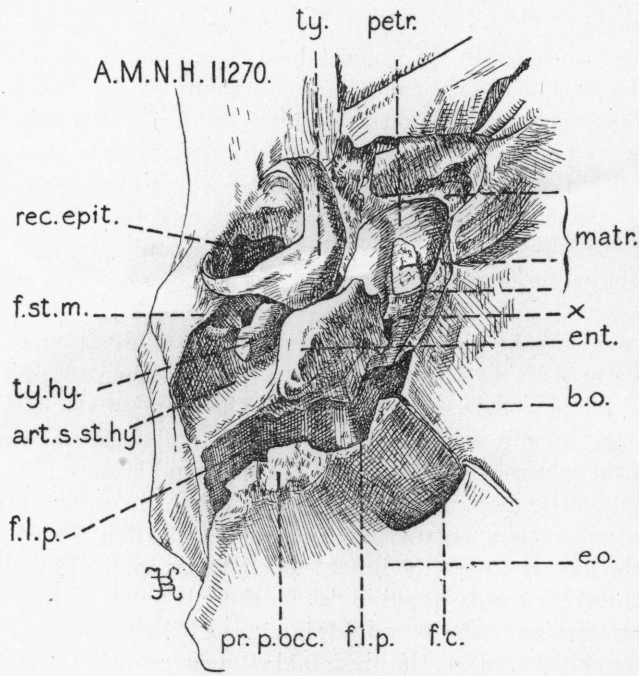

Fig. 7. *Lestodon myloides*, young specimen. A. M. N. H. No. 11270. Ventral and a little obliquely caudal view. Natural size.

the tympanohyal, whose distal top is not fused with the mastoid. Seen from the ventral side the entotympanic is nearly triangular, with nearly vertical walls. There is a lateral vertical wall just medially of the distal top of the tympanohyal, bending rostrally in a rostrolateral or nearly rostral transverse wall. A short distance medially of this angle it touches the tympanic in a narrow place (on the right side, where I think we have

the natural position). The third wall is a mesiocaudal one. This latter wall and the rostrolateral wall meet each other rostrally in rather an acute angle. The thin rostral part thus formed, seen from the mesial side, is pointed in two small points, a dorsal and a ventral one, the former only being preserved on the left side. Between this "dorsal point" and the ventral surface of the periotic lies a small bone, about 15 mm. long, 8 mm. broad and 3 mm. high. This small bone lies close to the periotic, but all around there is a groove between the two elements, and also between this small bone and the entotympanic. Perhaps it is a distinctly separated element, perhaps only a part of the periotic. On the right side the rostral portion of this small bone is partly absent. Between the lateral side of the basioccipital, which is not swollen in this region, and

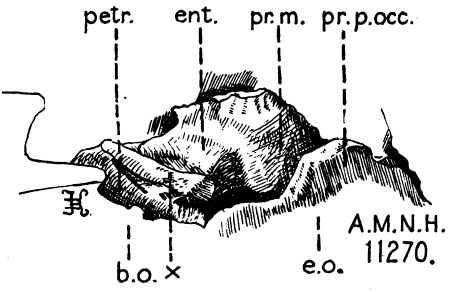

Fig. 8. *Lestodon myloides*, young specimen. A. M. N. H. No. 11270. Tympanic a. s. o. is not figured. Skull upside down. Obliquely ventro-caudo-mesial view. Natural size.

the periotic with the just described small bone on its ventral surface, we find a deep groove of a few millimeters breadth (on the right side filled with matrix or perhaps with plaster) and therefore the entotympanic does not reach the lateral side of the basis cranii, as Van Kampen mentions for his specimen, and lies on a more ventral level than the basioccipital. There is no distinct bony wall of a sulcus caroticus. Thus, I differ with Van Kampen's description of *Lestodon armatus* in the form of the entotympanic, but these are perhaps only specific differences.

As can be concluded from the short rostral development of the entotympanic and the narrow place of contact of the tympanic and the entotympanic, there must have been an extensive membranous or cartilaginous ventral wall. This explains the absence of an ostium tympanicum tubæ in this skull. The rostrolateral wall of the entotympanic is not

exactly vertical but is a little inclined, so that the tympanic cavity is enlarged in its dorsal portion.

On the right side there is a distinct cavity, which is probably the recessus epitympanicus; on the left side matrix covers this part.

Dasypodidæ

1. *Stegotherium tesselatum* AMEGHINO. Princeton No. 15566; Santa Cruz (Lower), Coy Inlet, Patagonia; J. B. Hatcher; June 3, 1896. Described by W. B. Scott, Patag. Princ. Exp., V, p. 37, etc., Pls. II, III, IV.
2. *Metacheiromys dasypus* OSBORN. A. M. N. H. No. 11718; Mus. Exp. 1903; Eocene Bridger Formation. Described by H. F. Osborn, 1904, Bull. A. M. N. H., XX, Art. 12, p. 163.
3. *Eutatus brevis*. Type; A. M. N. H. No. 11231; Cope Pampean, Buenos Aires. Described by Ameghino, 1881, Antiq. del Homb. en La Plata, II, p. 310.
4. *Prozaëdius proximus* AMEGHINO. Princeton No. 15567; Santa Cruz, Coy Inlet, Patagonia; J. B. Hatcher and O. A. Peterson; 1896–1899. Described by W. B. Scott, Princ. Exp. Patag., V, p. 78, etc., Pl. VI.
5. *Prozaëdius exilis* AMEGHINO. Princeton No. 15579; Santa Cruz (Lower), Killik Aike, Patagonia; J. B. Hatcher; 1896. Described by W. B. Scott, Princ. Exp. Patag., V, p. 76, etc., Pl. VI.

DESCRIPTION OF THE BULLÆ.—In *Stegotherium* there is preserved only an incomplete tympanic ring, which is a little broadened. In this specimen the malleus is still attached to the tympanic and together they describe more than 360° (see Scott's figure). The plane of the tympanic ring makes a smaller angle with the vertical than with the horizontal plane. Thus there is rather a wide space between the tympanic and the lateral border of the basis cranii, wider than we could expect from the figure Scott shows. This space was not occupied by an entotympanic. Perhaps the entotympanic was cartilaginous, or perhaps bony and then loosely attached to the skull. In my opinion there is no reason to suppose that the ventral wall was membranous, judging from the characters of the entotympanic in the recent Dasypodidæ.

In the specimen of *Eutatus* there is an inflated bulla which does not show a distinct suture in the bulla. Probably tympanic and entotympanic are fused together.

In the specimen of *Metacheiromys* we find a large flat bulla with a well-developed cylindrical external auditory tube. Perhaps this flatness is not the natural condition; as may be indicated by the cracks. There is such a crack on both sides, which could be a suture between the tympanic and the entotympanic but it is impossible to be certain in this question.

The bulla in the two specimens of *Prozaëdius* as well is very much broken up into pieces. Here also it is impossible to say whether one of

these breaklines corresponds with the suture between the tympanic and the entotympanic. An indication may perhaps be seen in the fact that a breakline in a similar place is found in all the four bullæ. An indication of the compound structure of the bulla is perhaps given by the fact that the bulla "is deeply notched from behind in a very peculiar and characteristic manner." This could lie between the tympanic and the entotympanic; that this, however, is not necessarily the case is shown by the young *Bradypus*, in which the tympanic bears a large aperture between the tympanohyal and the bulla, opening into the cavity of the bulla. There seems to be an opening in the rostromesial part of the bulla, but it is

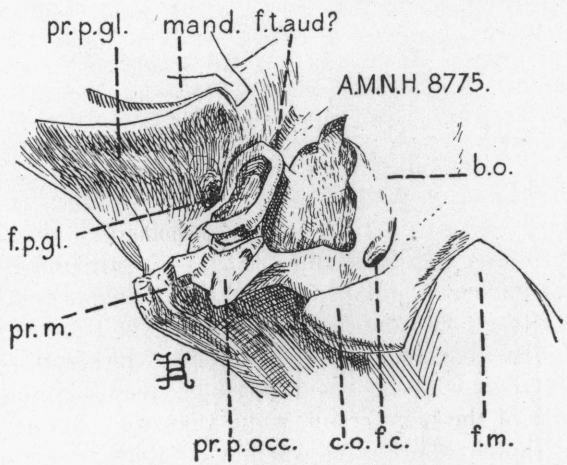

Fig. 9. *Hyænodon cruentus* Leidy. A. M. N. H. No. 8775. Ventral and obliquely caudal view. Natural size.

also difficult to be sure in this respect. If there is an opening, it is probably the foramen caroticum posterius.

I have not tried to give a full description of the bulla and its neighborhood. In the short time of my residence I have paid special attention to the entotympanic.

Hyænodon

1. *Hyænodon cruentus* Leidy. A. M. N. H. No. 8775; Oligocene, White River Formation, Cedar Creek Beds, Cedar Creek, Colorado.
2. *Hyænodon crucians* Leidy. A. M. N. H. No. 1372; Oligocene, White River Formation, Middle *Oreodon* Beds, Big Badlands, Cheyenne R., S. Dakota; Amer. Mus. Exped., 1894.

3. *Hyænodon cruentus* LEIDY. Princeton No. 12580; Oligocene, White River Formation, Turtle-*Oreodon* layer, L. *Oreodon* Beds, Expedition 1920. Will soon be described by Prof. W. J. Sinclair (Princeton) in: 'The Faunas of the Concretionary Zones of the *Oreodon* Beds.'

TYMPANIC.—The tympanic is present in the specimens 1 and 3 (left side) and absent in specimen 2, where we find only a part of the septum bullæ formed by the tympanic, as I shall describe below. What is present in the specimens 1 and 3 forms an incomplete bony ring. The ring is incomplete dorsally, leaving a rather large space which is closed

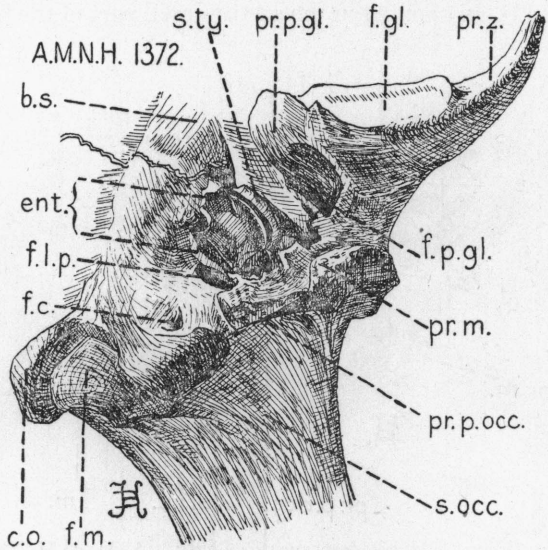

Fig. 10. *Hyænodon crucians* Leidy. A. M. N. H. No. 1372. Ventral and a little obliquely caudolateral view. Natural size.

by the squamosal. The ends of the two horns are not very distinct, especially that of the rostral one; in specimen 3, however, it is better seen than in specimen 1. The ring is narrow, about 2 mm. broad. There is no trace of an external auditory meatus and no extension of the mesial side, and there are no distinct traces that they are broken away. Yet I think probably there has been a mesial extension also in this species, as there is a part of the septum bullæ formed by the tympanic in the other species (specimen 2). Moreover, in specimen 1 the tympanic ring shows on the mesial side in the rostroventral part of the ring, a small bony triangle dorsally directed, which is perhaps the remainder of the septum bullæ.

If the conditions agree with those in the other species (specimen 2) the extension of the mesial side must have been very small. In specimen 1 the plane of the tympanic ring is directed from mediorostral to laterocaudal and forms an angle of 45° with the general plane of the under surface of the skull. In specimen 3, where the tympanic ring was found by Prof. Sinclair before I found it in specimen 1, the plane of the tympanic ring is a much more horizontal one. Thus seen from the lateral side, specimen 1 shows the tympanic ring more than specimen 3. I think that specimen 1, although the skull is a little crushed, shows the more

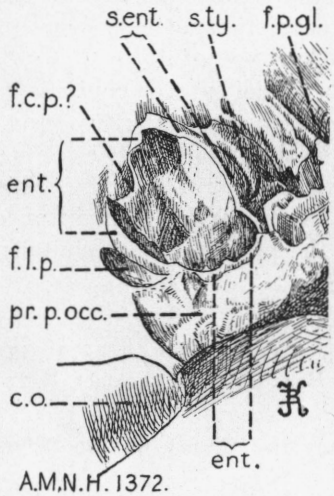

Fig. 11

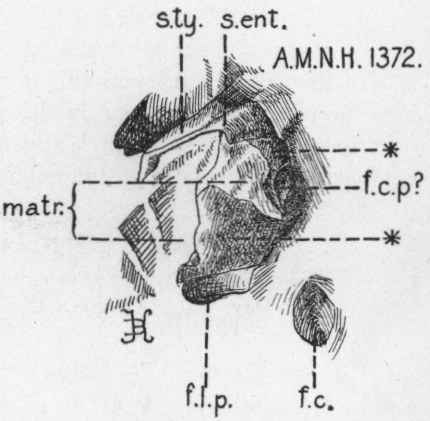

Fig. 12

Fig. 11. *Hyænodon crucians* Leidy. A. M. N. H. No. 1372. Nearly ventral view of the left bulla. 2× natural size.

Fig. 12. *Hyænodon crucians* Leidy. A. M. N. H. No. 1372. Nearly ventral view of the right bulla. 2× natural size.

natural condition, also if we take into account the height of the entotympanic bulla in the other species (specimen 2).

ENTOTYMPANIC.—There is no trace of an entotympanic in specimens 1 and 3. Specimen 2 shows on the left side, as well as on the right; the remains of an entotympanic bulla. The tympanic ring is absent and there is only a part of the septum bullæ left. The space for this ring is present. This entotympanic bulla lies on the mesial side of the tympanic ring, a feature which is probably related to the shortening of the occipital region of the skull. On the other hand, the paroccipital and mastoid processes do not seem to be expanded like a leaf over the caudal or

laterocaudal surface of the bulla. The ventral surface of the entotympanic bulla has been broken away and shows clearly that it is not the periotic (we have to expect the petrosal on a much more dorsal level). In a very dorsal level we find all around a bony wall, just the same as we find in the entotympanic chamber of the bulla of the cats. The laterorostral wall is the entotympanic part of the septum bullæ. On both sides, rather more distinct on the left side than on the right, close to this laterorostral wall of the entotympanic bulla, we find another bony plate, which I interpret as the dorsal part of the tympanic septum bullæ. In respect to the apertures in the neighborhood of the bulla, I refer to the figures. The center of the mesial side of the entotympanic bulla shows an aperture, which is perhaps the foramen caroticum posterius.

In all probability this entotympanic is a caudal entotympanic, as in *Felis*. *Hyænodon* cannot decide upon the question of the primitive situation of the caudal entotympanic in relation to the tympanic, because we have no primitive condition in this part of the skull of *Hyænodon*. This part is very much shortened, appearing in the relatively short distance between the processus postglenoideus and the processus paroccipitalis.

NIMRAVUS

1. *Nimravus debilis* (COPE). Peabody Museum, Yale University, No. 10045; John Day Valley, Oregon. Described by G. F. Eaton, 1922, Amer. Journ. Sci., (5) IV.

"TYMPANIC RING."—Eaton's "tympanic ring" in my opinion, needs a more thorough consideration.

If it really is an annulus tympanicus it is out of place, especially the rostral horn, which in the natural condition we should expect at a shorter distance from the foramen postglenoideum. The shallow groove just mesially from the foramen postglenoideum perhaps indicates the place of attachment of the rostral horn of the tympanic. In relation to this, the plane of this "tympanic ring" differs from that of the annulus tympanicus in all other mammals. These planes of the right and the left "tympanic ring" in this specimen cross each other in a line which at the level of the auditory region lies on the dorsal side of the basis cranii, while the planes of true annuli tympanici will always meet each other on the ventral side of the auditory region. The abnormal position of this tympanic ring is due to the fact that its plane runs from the dorsomesial to the ventrolateral direction. If it really is an annulus tympanicus which is out of place, its shape must have been changed, as the distance between the point which lies against the mastoid process and the extremity of the

rostral horn is much larger than it could have been if this rostral extremity was attached to the skull at a shorter distance from the foramen postglenoideum. No sulcus tympanicus for the attachment of the tympanic membrane is present in the rostral horn and the middle portion, while the dorsorostral side of the caudal horn shows matrix. Another difficulty in considering this ring as a true annulus tympanicus is the fact that it seems to be a hollow cylindrical rod filled with matrix. This cylindrical rod-like condition is shown by the two extremities over a distance of about 5 mm. The portion of the "tympanic ring" between these two extremities is a flat mass, mesially showing matrix, and laterally

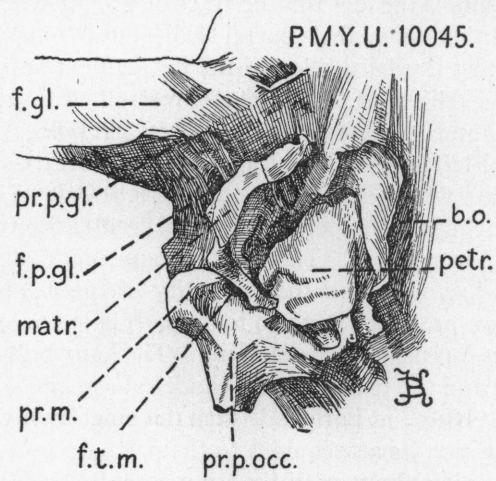

Fig. 13. *Nimravus debilis* (Cope). Peabody Museum, Yale University, No. 10045. Ventral view. Natural size.

covered with bone. According to the position of this "tympanic ring" one would suppose that its rostral horn and its just described middle portion agree much more with a septum in the bulla. Its position is the strongest argument for considering it as a septum or a part of a septum in the bulla. A groove present on the lateral side of the extremity of the rostral horn of the "tympanic ring" could owe its origin to the tuba auditiva. The portion of the bulla on its lateral side no doubt must have been very small in comparison with the caudomesial portion, but this occurs in many cases. The conditions found in the middle portion of the "tympanic ring" could be considered as an indication of a double structure of a septum bullæ. Here, as we have seen already, a bony

covering lies laterally against a mass of matrix, which perhaps is separated from a mesial covering of bone which has disappeared. This lateral bony covering is about 5 mm. high and flat, lying in the plane of the "tympanic ring" and thus at about right angles to the external surface of the bulla, which we have to expect from this point of view. Against this consideration of the double septum bullæ is the circumstance that this lateral bony covering bends over the dorsal margin of the mass of matrix. It teaches us that if it is a septum, its dorsal margin remained at a relatively great distance from the promontorium and that the radius of this dorsal margin was relatively large. Another difficulty in considering this as a septum is the fact that no trace of a bony extension, either in the lateral direction or in the ventral wall of the tympanic cavity, is present. The most caudal portion of the tympanic ring is very remarkable. This touches the skull at two points: rostrally it touches the processus mastoideus and caudally with its extreme point it reaches the petrosal. On the left side of the skull, which lacks nearly all of the above described features which are shown on the right side of the skull, this extreme tip attached to the petrosal is preserved and seems to indicate that it is a natural condition. Then this extreme point which is attached to the petrosal does not form the extremity of the caudal horn of the tympanic, but we probably have to look for this in the portion which reaches the processus mastoideus caudally. The bony bridge between the mastoid process and the petrosal is a cylindrical rod and could be a tympanohyal which is fused at both ends with the neighboring elements. In my opinion, however, its attachment to the petrosal lies perhaps too far mesialward to homologize it with the tympanohyal and then perhaps it could be a remnant of the mesial portion of the bulla. This bony bridge forms the rostromesial boundary of an aperture which seems to be the fissura tympano-mastoidea or the foramen stylomastoideum primitivum.

We may conclude that the "tympanic ring" should not be called a true annulus tympanicus without further evidence; that there are indications that there has been perhaps a more developed bulla. This is perhaps also indicated by the vertical wall of the basioccipital and by its raised lateral margins.

DAPHÆNUS

1. *Daphænus hartshornianus.* A. M. N. H. No. 9757; White River Formation, Lower *Oreodon* Beds, Squaw Creek, Big Badlands, South Dakota; Amer. Mus. Exp., 1892.
2. *Daphænus vetus.* A. M. N. H. No. 9759; Big Badlands, South Dakota.

3. *Daphænus* sp. A. M. N. H. No. 12450; Corall Draw, Big Badlands, South Dakota.
4. *Daphænus vetus.* U. S. N. M. Wash., No. 658, Genotype; Oligocene, White River Formation, South Dakota; Dr. John Evans.

TYMPANIC.—In all these specimens we find the well-known "small bulla" formed by the tympanic. The plane of the tympanic membrane shows a rather small inclination. This "small bulla" is but little inflated. The wide porus acusticus externus (there is no cylindrical auditory tube) lies in the caudal part of the bulla, as especially the rostromesial part of

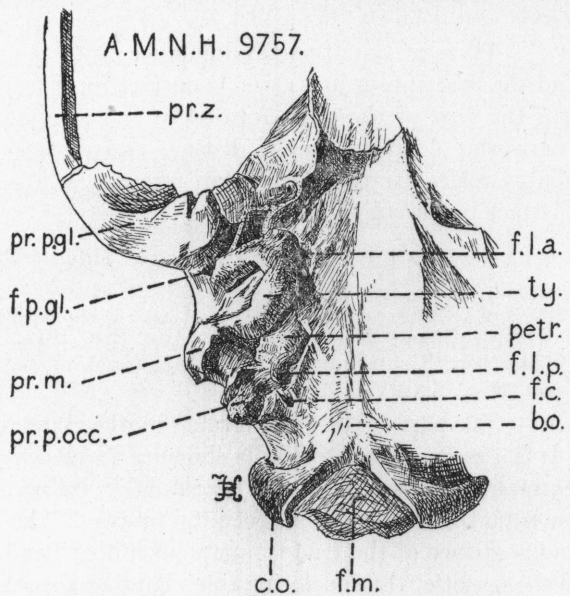

Fig. 14. *Daphænus hartshornianus.* A. M. N. H. No. 9757. Ventral and a little obliquely caudal view. Natural size.

the tympanic is broadened; this part ends in a bony tuberosity which is probably related to the entrance of the Eustachian tube. Its caudal margin remains at a considerable distance from the base of the paroccipital process which is directed obliquely downward and backward. There is every reason to believe that there has been an entotympanic as well, of which no trace is left. Apparently it was either cartilaginous or a loosely attached bone. It is pertinent in this respect to note that the bone of the center and of the caudal horn of the tympanic bends dorsalward toward the periotic and thus covers the mesiocaudal wall of the true tympanic chamber, which is thus more or less enclosed by the tym-

panic. This dorsalward bent wall forms the tympanic half of the septum bullæ. The entotympanic part of the septum bullæ was probably free from the tympanic septum. Traces of its attachment to the tympanic at all events are not visible.

PARADAPHÆNUS

1. *Paradaphænus cuspigerus* (COPE). A. M. N. H. No. 6852; type; John Day Formation.
2. *Paradaphænus cuspigerus* (COPE). A. M. N. H. No. 6853; type of *Amphicyon entoptychi* Cope; John Day Formation, *Diceratherium* Beds.

TYMPANIC.—There are no principal differences with the tympanic in *Daphænus* and the description just given is correct for *Paradaphænus* as well. Perhaps the part of the bulla formed by the tympanic is a little higher and narrower. Moreover the distinct rostromesial tuberosity, which is probably related to the Eustachian foramen, is absent or at all events less distinct in *Paradaphænus*.

PLIOCYON

1. *Pliocyon medius* MATTHEW. A. M. N. H. No. 17207; type; Snake Creek Beds, 23 miles South of Agate, Nebraska; Amer. Mus. Exp., 1916. Described by W. D. Matthew, 'Contributions to the Snake Creek Fauna,' Bull. Amer. Mus. Nat. Hist., XXXVIII, 1918.

TYMPANIC.—The part of the bulla formed by the tympanic is highly developed. It is a strongly inflated bulla showing a well developed bony cylindrical external auditory meatus. Its caudal margin remains at a great distance from the base of the paroccipital process. The bony covering of the under surface of the true tympanic chamber bends up dorsalward toward the periotic, thus enclosing this chamber also on the caudal and mesial sides. As there is strong reason to suppose the presence of an entotympanic, this dorsalward bent margin forms the tympanic part of the septum bullæ.

ENTOTYMPANIC.—The peculiarity of this specimen is the presence of a piece of bone which can not be anything else than the remainder of an entotympanic. The base of the paroccipital process seems to give rise to a bony ridge or plate which runs forward and reaches the caudal end of the tympanic, where the proper bulla passes into the bony cylindrical external auditory meatus. Then it seems to bend lateralward, lying caudally against the cylindrical external auditory meatus. This ridge or plate, at all events its center, must be the entotympanic. Strong reasons for this belief are the following: it occupies the place of the lateral wall of the bony entotympanic chamber; it forms the mesial wall of the fissura

tympano-mastoidea, which then lies at the normal place between the bulla and the mastoid process; finally, the contact of this entotympanic takes place with the mesiorostral margin of the paroccipital process. Now in the fossil Canidæ, in which the stout and not leaf-like; broadened paroccipital process runs obliquely downward and backward, showing a free top, the rostromesial margin of the paroccipital process often sends forward a bony plate or ridge which reaches the caudal margin of the bulla.

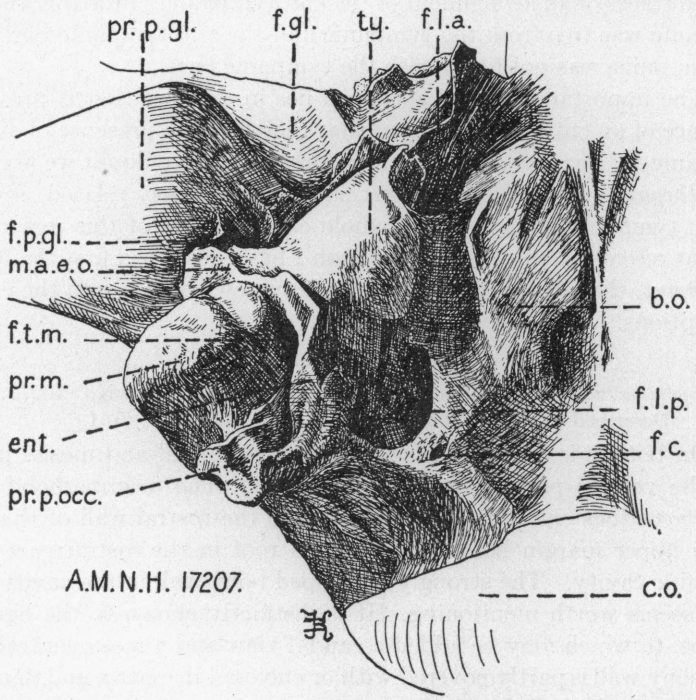

Fig. 15. *Pliocyon medius.* A. M. N. H. No. 17207. Ventral and a little caudo-lateral view. Natural size.

over which it can be spread out more or less. I found this in *Mesocyon coryphæus* (Cope) (A. M. N. H. No. 6859), *Cynodesmus* (*Canis*) *brachypus* (A. M. N. H. No. 8140), *Cynodesmus thomsoni* (A. M. N. H. No. 12874), *Tomarctus brevirostris* (A. M. N. H. Nos. 18242, 18243, 18244,) and *Ælurodon sævus* (A. M. N. H. No. 8311). These are all reasons to believe that the entotympanic participates in this bony ridge or plate running from the paroccipital process toward the tympanic. There is no distinct suture between the paroccipital process and the entotympanic. It is

impossible to give exact information on the extension of the entire entotympanic. No doubt it has lain on the caudal side of the tympanic chamber, but it seems impossible to say whether or not it has lain also on its mesial side, and how far it has extended rostralward; whether or not it has covered the groove (sulcus caroticus?) between the mesial side of the tympanic bulla and the lateral margin of the basioccipital. On the caudal and the mesiocaudal and mesial margin of the tympanic we find no traces of an attachment of the entotympanic. Probably the entotympanic was free from the tympanic and the entotympanic part of the septum bullæ was not fused with the tympanic part.

The importance of this specimen lies in the fact that it proves the presence of an entotympanic, and that therefore the presence of an entotympanic in *Daphænus* is still more probable. No doubt we may compare *Daphænus* and *Pliocyon*, first as they are closely related, secondly as the tympanic bullæ and the whole configuration of this region show evident resemblances. For that reason I have described first the bulla in *Daphænus*, though I could hardly add any new character to the existing descriptions.

OLIGOBUNIS

1. *Oligobunis darbyi.* Peabody Museum, Yale University No. 10272; type. Described by M. R. Thorpe, 1921, Amer. Journ. Sci., (5) I.

On both sides the bulla lacks the entire caudal and mesial portion and the ventral part of the rostral portion. The neighborhood of the porus acusticus externus is preserved, also the rostral wall of the bulla, whose upper margin bends and forms a roof in the rostral part of the tympanic cavity. The strongly developed bony wall in the cavity of the bulla seems worth mentioning. It is distinctly shown in the figure by Thorpe, to which may be added a caudal view and a mesioventral view. This bony wall is partly covered with or enclosed in matrix and thus could not be studied in all details, but yet can be determined rather certainly as the margo sulci tympanici or crista tympanica which stands back from the inner surface of the bulla. This means that the hypotympanic sinus extends far lateralward along the under surface of the external auditory meatus and thus we can also say that the bony external auditory meatus projects freely into the cavity of the bulla. Indications for this belief are the relatively small radius of this wall, which has the form of half a cylinder, its close approximation to the porus acusticus externus, and especially also the fact that its rostral and caudal part strongly bend lateralward, in all these characters agreeing with the place and form o the original narrow tympanic annulus. The fact that the rostral par

bends so strongly lateralward makes it probable that the ostium tympanicum tubæ lies on its mesial side, and in that case this bony wall cannot be a septum bullæ formed by tympanic and entotympanic. If this bony wall is really the crista tympanica which projects into the cavity of the bulla, the bony recessus meatus can be called well developed.

Eomoropus

1. *Eomoropus armarorum* (Cope). A. M. N. H. No. 5090; type; Cope Coll., Eocene, Washakie Formation, S. Bitter Creek, Washakie Basin, Wyoming; 1873. Described by E. D. Cope, 1881, 'The Systematic Arrangement of the Order Perissodactyla,' Proc. Amer. Philos. Soc., and in U. S. Geolog. Survey of the Territories, 'The Vertebrata of the Tertiary Formations of the West,' Book I, 1883, and by Osborn, Bull. Amer. Mus. Nat. Hist., XXXII, Art. 14.

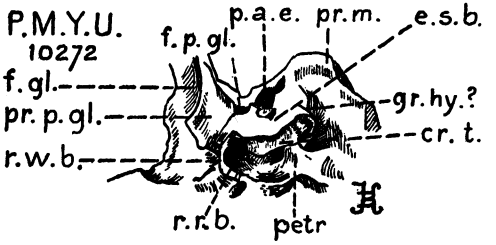

Fig. 16

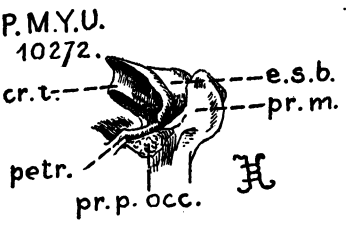

Fig. 17

Fig. 16. *Oligobunis darbyi.* Peabody Museum, Yale University, No. 10272. Ventral and a little obliquely mesial view. Natural size.

Fig. 17. *Oligobunis darbyi.* Peabody Museum, Yale University, No. 10272. Caudal view. Natural size.

Entotympanic.—Although it is not certain, it does not seem to me impossible that an entotympanic is present. This would be the element that lies between the mesial margin of the tympanic, and the lateral margin of the basis cranii. It is the element which is called petrosal by the authors cited above. Reasons for my belief that it could be an entotympanic as well are the following. We can expect an entotympanic in this group, as this element of the bulla occurs among the perissodactyls. It occupies the place of the entotympanic. If my opinion is true, it occupies the dorsal half of the mesial wall of the bulla, the ventral half of this wall being formed by the tympanic, which shows a sharp under margin. The tympanic does not gradually pass into the entotympanic (their adjacent margins form a groove and the convexities of their surfaces are different) but this is rather a common feature and constitutes or forms no objection to my opinion. An indication of the correctness of

my opinion perhaps may be the level of this bony element. The ventral margin of the entotympanic lies in about the same plane as the ventral margin of the basis cranii, whose under margin is rather rounded in the transverse plane. Now in skulls of the recent tapir and rhinoceros which at the time of this investigation were at my disposal, and also in the fossil *Moropus* (A. M. N. H. Nos. 14427 and 14378), the ventral surface of the petrosal lies on a more dorsal level than the center of the ventral surface of the basis cranii. The skull of *Eomoropus* is crushed, but it does not seem that crushing can have changed fundamentally this relative position.

CÆNOTHERIUM

1. *Cænotherium* sp. Princeton No. 11579; St. Gerard le Puy, France.

BULLA.—The bulla in the ventral view is V-shaped, the two legs being connected rostromesially and running from this place caudolaterally. The mesiocaudal leg is formed by the proper bulla, the laterorostral leg is formed by the external auditory meatus. The latter does not run in the laterocaudal direction only, but also runs obliquely upward. Thus the porus acusticus externus opens laterocaudo-dorsalward. The two legs of the V are separated by the vagina processus hyoidei, which in the ventral view of the skull occupies half the length of the longitudinal axis of the bulla, which, starting in a rostromesial position, runs laterocaudally. Both margins of the vagina lie close together; rostrally they diverge, enclosing an open pit. Just behind this deep pit the caudomesial margin of the vagina forms a small bony process. This process projects forward and downward and in the ventral view of the skull lies on the lateral side of the deep pit that forms the rostral end of the vagina processus hyoidei. In various places the thin layer of compact bone of the outer surface of the bulla fails and shows the spongy structure of the bulla. This cancellous structure is present not only in the caudomesial leg of the V, i.e., in the bulla proper, but also in the rostral portion of the laterorostral leg of the V. Thus, at all events, the proximal portion of the under wall of the external auditory meatus is cancellous.

EPOREODON

1. *Eporeodon occidentalis* MARSH. Peabody Museum, Yale University, No. 12316 (575); Upper Oligocene (Upper John Day), Bridge Creek, John Day Valley. Described by M. R. Thorpe in Amer. Jour. Sci., (5) II, 1921.
2. Many other Oreodontidæ in the Peabody Museum of Yale University.

DESCRIPTION.—Thorpe's remark on the natural casts of this specimen of *Eporeodon occidentalis*, which are divided into anterior and pos-

terior hemispheres, interested me in respect to the possibility of a compound structure of the bulla. For that reason I looked through the entire collection of the Oreodontidæ of the Peabody Museum, in so far as it was at hand during the provisional arrangement of the Museum at the time of my visit.

Looking through all these specimens I found that in *Eporeodon* as a rule the bulla is preserved, that the surface of the bulla never shows a distinct suture or line; a transverse groove may occur but is never distinct enough to indicate with any certainty a compound structure; the surface was seldom partly broken away and then it always showed the cavity filled with matrix and did not show a trace of a septum as described by Thorpe, but this was perhaps due to the matrix and to the way in which the bulla is broken. Bullæ of other species and genera as well did

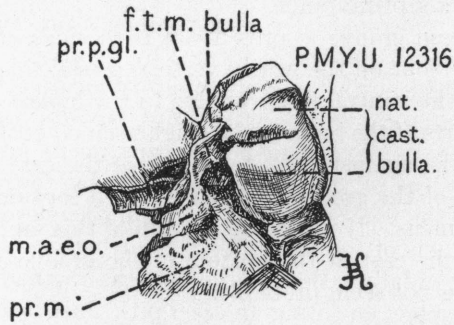

Fig. 18. *Eporeodon occidentalis* Marsh. Peabody Museum, Yale University, No. 12316. Ventral view. Natural size.

not show a suture, line or groove, distinct enough to indicate with any certainty a compound structure of the bulla. The well-known difference in size of the bullæ in the Oreodontidæ is not due to a difference in length (there is no considerable difference in the distance to the paroccipital process) but to a considerable difference in breadth, evident through the size of the space between the bulla and the basis cranii. This evidently shows that the small bulla in the Oreodontidæ is not due to the lack of a caudal or entotympanic chamber. All these facts show that the compound structure of the bulla in the Oreodontidæ is very doubtful and also that the septum in Thorpe's specimen of *Eporeodon occidentalis*, which caused the division of the natural casts of the bullæ into anterior and posterior hemispheres, is probably not a septum bullæ formed by tympanic and entotympanic. Further information might give us the

knowledge of the place of entrance of the lumen of the external bony auditory meatus into the cavity of the bulla. If this division is really caused by a septum bullæ, the anterior hemisphere must be the true tympanic chamber into which the external auditory meatus enters. At my request, the matrix which filled the external bony auditory meatus of a specimen of *Eporeodon leptacanthus* (P. M. Y. U. No. 11017) was perforated. If the course of the lumen of the external bony auditory meatus, in relation to the neighborhood, especially to the pit for the hyoid arch, is the same in both specimens, it shows that this lumen entered the cavity of the bulla either behind the transverse groove of the natural cast or perhaps at the level of this groove, partly in front, partly behind it. At all events, it does not distinctly enter into the rostral hemisphere. Thus, also, this seems to show that the groove in the natural cast of the bulla is not formed by a septum bullæ.

This transverse groove is present on both sides of the skull. On both sides it is absent on the nearly vertical mesial side of the cast and very distinct on the ventral side, running to the lateral side of the cast. The preserved parts of the bulla in the neighborhood of the external bony auditory meatus lie against the lateral side of the cast and conceal the dorsolateral part of the groove. Perhaps it is a septum radiating from the sulcus tympanicus. If the dorsal margin of this septum is preserved in the matrix of the cast at the bottom of the groove it must be very thin, but this does not seem probable.

LITERATURE CITED

ABEL, O. 1912. 'Palæobiologie.'
1919. 'Die Stämme der Wirbeltiere.'
1920. 'Lehrbuch der Paläozoologie.'

ADAMS, G. J. 1896. 'The Extinct Felidæ of North America.' Amer. Journ. Sci., (4) I (whole number, CLI), pp. 419–444.

ALLEN, GLOVER M. 1913. 'A New *Mylodon*.' Mem. Mus. Comp. Zoöl., Harvard College, XL, No. 7, p. 317, etc., 4 Pls.

ALLEN, J. A. 1904*a*. 'The External Ear Bone in Certain Rodents.' Bull. Amer. Mus. Nat. Hist., XX, pp. 135–138.
1904*b*. 'A Fossil Porcupine from Arizona.' Bull. Amer. Mus. Nat. Hist., XX, pp. 383–384.

AMEGHINO, F. 1889. 'Contribucion al Conocimiento de los Mamiferos fosiles de la Republica Argentina.' Atlas, Buenos Aires, Pls. I–XCVIII.

ANDREWS, C. W. 1915. 'A Description of the Skull and Skeleton of a peculiarly modified Rupicaprine Antelope (*Myotragus balearicus* Bate), with a notice of a new variety, *M. balearicus* var. *major*.' Philos. Trans. Roy. Soc. London, Series B, 206, pp. 281–305, Pls. XIX–XXII.

ANTHONY, H. E. 1917. 'Two New Fossil Bats from Porto Rico.' Bull. Amer. Mus. Nat. Hist., XXXVII, pp. 565–568, Pl. LVI.

BOEHM-TIETJE, KATHARINA, 1921. 'Ueber Vorkommen und Bedeutung des "Ossiculum accessorium mallei,"' Inaug.-Diss. Göttingen.

BONDY, GUSTAV. 1907. 'Beiträge zur vergleichenden Anatomie des Gehörorgans der Säuger. (Tympanicum, Membrana Shrapnelli und Chordaverlauf).' Anatomische Hefte, Heft 106, Bd. XXXV, Heft 2, pp. 293–408, Taf. X–XIII.
1908. 'Ueber die Entwickelung des Tympanicum und der Shrapnellschen Membran des Schweines.' Anat. Hefte, Heft 113, Bd. XXXVII, Hefte 3, pp. 591–602, Taf. XXXI–XXXIII.

BRAUN, M. 1906. 'Bemerkungen über das Zungenbein von *Mustela martes*.' Zool. Anz., Bd. XXIX, pp. 674–675.

BROOM, R. 1911. 'On the Structure of the Skull in Cynodont Reptiles.' Proc. Zoöl. Soc., London, II, pp. 893–925.
1914. 'On the Structure and Affinities of the Multituberculata.' Bull. Amer. Mus. Nat. Hist., XXXIII, pp. 115–134, Pls. XI, XII.

BROWN, BARNUM. 1903. 'A New Genus of Ground Sloth from the Pleistocene of Nebraska.' Bull. Amer. Mus. Nat. Hist., XIX, pp. 569–583.
1908. 'The Conard Fissure, a Pleistocene Bone Deposit in Northern Arkansas: with Descriptions of Two New Genera and Twenty New Species of Mammals.' Mem. Amer. Mus. Nat. Hist., IX, part 4, pp. 157–208, Pls. XIV–XXV.

BURMEISTER, H. 1867. 'Fauna Argentina-Primera parte: Mamiferos fosiles.' Anales del Museo publico de Buenos Aires, I, pp. 87–300, Pls. V–XIV.

CARLSSON, ALBERTINA. 1910*a*. 'Die Macroscelididæ und ihre Beziehungen zu den übrigen Insectivoren.' Zoologische Jahrbücher, Abt. Systematik, Bd. XXVIII, pp. 349–400.

1910*b*. 'Die genetischen Beziehungen der madagassischen Raubtiergattung Galidia.' Zoologische Jahrbücher, Abt. Systematik, Bd. XXVIII, pp. 559–602.

1911. 'Ueber *Cryptoprocta ferox*.' Zoologische Jahrbücher, Abt. Systematik, Bd. XXX, pp. 419–470.

1914. 'On the Fossil Carnivores *Cynodictis intermedius* and *Cynodon gracilis* from the Phosphorites of Quercy.' Proc. Zoöl. Soc., London, I, pp. 227–230.

1920. 'Ueber *Arctictis binturong*.' Acta Zoologica, Bd. I, pp. 337–380.

1921. 'Einige Bemerkungen betreffs H. Pohle's Aufsatz "Zur Kenntnis der Raubtiere. II. Die Stellung der Gattungen *Amphictis* und *Nandinia*."' Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin, Jahrgang, 1921, pp. 70–75.

1922. 'Ueber die Tupaiidæ und ihre Beziehungen zu den Insectivora und den Prosimiæ.' Acta Zoologica, Ärg. 3, Häfte 2–3, pp. 227–270.

CLAUDIUS, M. 1867. 'Das Gehörorgan von *Rhytina Stelleri*.' 'Mémoires de l'Académie impériale des sciences de St. Pétersbourg, VIIe Série, Tome XI, No. 5, pp. 1–15, 2 Taf.

COPE, EDWARD D. 1873*a*. 'On the Extinct Vertebrata of the Eocene of Wyoming Observed by the Expedition of 1872, with Notes on the Geology.' Sixth Annual Report of the United States Geological Survey of the Territories for the Year 1872. F. V. Hayden, U. S. Geologist. Washington, pp. 545–649.

1873*b*. 'On the Flat-clawed Carnivora of the Eocene of Wyoming.' Proc. Amer. Philos. Soc., Phila., XIII, pp. 198–209.

1879. 'On the Genera of Felidæ and Canidæ.' Proc. Acad. Nat. Sci. Phila., pp. 168–194.

1880*a*. Idem, in Ann. and Mag. Nat. Hist., Series 5, V, pp. 36–45, 92–107.

1880*b*. 'On the Foramina Perforating the Posterior Part of the Squamosal Bone of the Mammalia.' Proc. Amer. Philos. Soc. Phila., XVIII, pp. 452–461.

1880*c*. 'On the Extinct Cats of America.' American Naturalist, XIV, No. 12, pp. 833–858.

1881*a*. 'On the Nimravidæ and Canidæ of the Miocene Period.' Bull. U. S. Geol. and Geogr. Surv. of the Territories, VI, pp. 165–181.

1881*b*. 'On the Canidæ of the Loup Fork Epoch.' Bull. U. S. Geol. and Geogr. Surv. of the Territories, VI, pp. 387–390.

1881*c*. 'The Systematic Arrangement of the Order Perissodactyla.' Proc. Amer. Philos. Soc., XIX, pp. 377–401.

1882. 'On the Systematic Relations of the Carnivora Fissipedia.' Proc. Amer. Philos. Soc., XX, pp. 471–475.

1883. Idem, in Ann. and Mag. Nat. Hist., Series 5, XII, pp. 112–116.

COPE. E. D., AND W. D. MATTHEW. 1915. 'Hitherto Unpublished Plates of Tertiary Mammalia and Permian Vertebrata.' Prepared under the direction of Edward Drinker Cope for the U. S. Geological Survey of the

Territories with description of plates by W. D. Matthew. Amer. Mus. Nat. Hist.—U. S. Geol. Surv.

DAWKINS. W. BOYD. 1878. 'The British Pleistocene Mammalia.' Monograph on the British Mammalia of the Pleistocene Period. Order Carnivora. London.

DENINGER, K. 1909. 'Ueber *Babirusa*.' Berichten der Naturforschenden Gesellschaft zu Freiburg i. B., Bd. XVII, 3, pp. 179–200, Taf. I–III.

DEPÉRET, CHARLES. 1892. 'La faune de Mammifères miocènes de la Grive-Saint-Alban (Isère) et de quelques autres localités du Bassin du Rhone.' Archives du Muséum d'Histoire Naturelle de Lyon, Tome cinquième, Mémoire No. II, pp. 1–96, Pls. I–IV.

DILG, C. 1909. 'Beiträge zur Kenntnis der Morphologie und postembryonalen Entwicklung des Schädels bei *Manatus inunguis* Natt.' Inaugural-Dissertation Bern, pp. i–iv, 83–145, Taf. VIII–XIII. Idem, in Gegenbaur's Morphologisches Jahrb., Bd. XXXIX, pp. 83–145, Taf. VIII–XIII.

DOUGLASS, EARL. 1907. 'New Merycoidodonts from the Miocene of Montana.' Bull. Amer. Mus. Nat. Hist., XXIII, pp. 809–822.

EATON, G. F. 1922. 'John Day Felidæ in the Marsh Collection.' Amer. Journ. Sci., IV, pp. 425–452.

FILHOL, H. 1883. 'Notes sur quelques Mammifères fossiles de l'époque miocène.' Archives du Muséum d'Histoire Naturelle de Lyon, Tome III, pp. 1–99.

FREUND, LUDWIG. 1908. 'Beiträge zur Entwickelungsgeschichte des Schädels von *Halicore dugong* Erxl.' Denkschriften der Medic.-Naturwiss. Gesellschaft zu Jena, Bd. VII. Richard Semon, Zoologische Forschungsreisen, Bd. IV, pp. 557–626.

GAILLARD, CLAUDE. 1899. 'Mammifères miocènes nouveaux ou peu connus de la Grive-Saint-Alban (Isère).' Archives du Muséum d'Histoire Naturelle de Lyon, Tome VII, pp. 1–79, Pls. I–III.

GAUPP, E. 1908. 'Zur Entwickelungsgeschichte und vergleichenden Morphologie des Schädels von *Echidna aculeata* var. *typica*.' In Zoologische Forschungsreisen in Australien und dem Malayischen Archipel von Prof. Dr. Richard Semon, III Bd., Monotremen und Marsupialier, II, 2 Theil. Denkschriften der Med. Naturwiss. Gesellschaft zu Jena, Bd. VI, 2 Theil, pp. 539–788.

1913. 'Die Reichertsche Theorie (Hammer-, Amboss-, und Kieferfrage).' Arch. f. Anat. u. Entw. gesch., 1912, Suppl. Bd. zur Anat. Abt., pp. i-xiv, 1–416.

GIDLEY, J. W. 1906. 'A New Ruminant from the Pleistocene of New Mexico.' Proc. U. S. Nat. Mus., XXX, pp. 165–167.

1909. 'Notes on the Fossil Mammalian Genus *Ptilodus*, with Descriptions of New Species.' Proc. U. S. Nat. Mus., XXXVI, pp. 611–626, Pl. LXX.

1921. 'Pleistocene Peccaries from the Cumberland Cave Deposit.' Proc. U. S. Nat. Mus., LVII, pp. 651–678, Pls. LIV, LV.

GRANGER, WALTER, AND GREGORY, WILLIAM K. 1917. 'A Revision of the Eocene Primates of the Genus *Notharctus*.' Bull. Amer. Mus. Nat. Hist., XXXVII, pp. 841–859, Pls. CIII–CVII.

GRAY, A. A. 1913. 'Notes on the Comparative Anatomy of the Middle Ear.' Journ. Anat. and Physiol., XLVII, (3) VIII, pp. 391–413, 12 text figs.

GREGORY, WILLIAM K. 1903. 'Adaptive Significance of the Shortening of the Elephant's Skull.' Bull. Amer. Mus. Nat. Hist., XIX, pp. 387–394.

1910. 'The Orders of Mammals.' Bull. Amer. Mus. Nat. Hist., XXVII, pp. 1–524.

1913*a*. 'Critique of Recent Work on the Morphology of the Vertebrate Skull, especially in Relation to the Origin of Mammals.' Journ. Morph., XXIV, No. 1, pp. 1–42.

1913*b*. 'Relationship of the Tupaiidæ and of Eocene Lemurs, especially *Notharctus*.' Bull. Geol. Soc. America, XXIV, pp. 247–252.

1915. I. 'On the Relationship of the Eocene Lemur *Notharctus* to the Adapidæ and to other Primates.' II. 'On the Classification and Phylogeny of the Lemuroidea.' Bull. Geol. Soc. America, XXVI, pp. 419–446.

1916. 'Studies on the Evolution of the Primates. Part II. Phylogeny of Recent and Extinct Anthropoids, with Special Reference to the Origin of Man.' Bull. Amer. Mus. Nat. Hist., XXXV, pp. 258–355.

1920. 'On the Structure and Relations of *Notharctus*, an American Eocene Primate.' Studies on the Evolution of the Primates, III. Mem. Amer. Mus. Nat. Hist., N.S., III, part 2, pp. 49–243, Pls. XXIII–LIX.

1924. (With G. K. Noble.) 'The Origin of the Mammalian Alisphenoid Bone.' Journ. Morph. and Physiol., XXXIX, No. 2, pp. 435–463.

HANKE, HERBERT. 1914. 'Ein Beitrag zur Kenntnis der Anatomie des äusseren und mittleren Ohres der Bartenwale.' Jenaische Zeitschr. f. Naturwissenschaft, Bd. LI, pp. 487–524.

HAY, OLIVER P. 1916. 'A Contribution to the Knowledge of the Extinct Sirenian *Desmostylus hesperus* Marsh.' Proc. U. S. Nat. Mus., XLIX, pp. 381–398, Pls. LVI–LVIII.

1917. 'Descriptions of Two Extinct Mammals of the Order Xenarthra from the Pleistocene of Texas.' Proc. U. S. Nat. Mus., LI, pp. 107–123, Pls. III–VII.

HUXLEY, THOMAS H. 1865. 'On the Osteology of the Genus *Glyptodon*.' Philos. Trans. Roy. Soc. London, CLV, pp. 31–70, Pls. IV–IX.

KAMPEN, P. N. VAN. 1904. 'De tympanaalstreek van den zoogdierschedel.' Acad. proefschrift Amsterdam, pp. i-xii, 1-379.

1905. 'Die Tympanalgegend des Säugetierschädels.' Morpholog. Jahrbuch, Bd. XXXIV, pp. 321-722.

1907. 'Die Anheftung des Zungenbeins am Schädel bei *Putorius putorius* L.' Zool. Anz., Bd. XXXI, Nos. 21–22, pp. 695–696.

1915. 'De phylogenie van het entotympanicum.' 'Het parasphenoid.' Tijschr' Ned Dierk. Ver., (2) XIV, II, Verslagen, pp. xxiv, xxxii-xxxiii.

1922. 'Parasphenoid und Basitemporalia der Säugetiere.' Bijdragen tot de Dierkunde uitgegeven door het Koninklijk Zoölogisch Genootschap Natura Artis Magistra te Amsterdam, Afl. 22, pp. 53–58.

KELLOGG, LOUISE. 1912. 'Pleistocene Rodents of California.' Univ. Calif. Publs. Geol., VII, No. 8, pp. 151–168.

KLAAUW, C. J. VAN DER. 1922*a*. 'Ueber die Entwickelung des Entotympanicums.' Academisch proefschrift Universiteit Leiden, pp. i-x, 1-50, 4 Pls.

1922*b*. The same paper in Tijdschr. d. Ned. Dierk. Ver. (2) Dl. XVIII, Afl. 2, pp. 135–176, Taf. II–V.

1923. 'Die Skelettstückchen in der Sehne des Musculus stapedius und nahe dem Ursprung der Chorda tympani.' Zeitschr. f. d. gesamte Anatomie, Iste Abt. Zeitschr. f. Anat. und Entw. gesch., Bd. LXIX, Hefte 1–3, pp. 32–83.

1924*a*. 'Bau und Entwickelung der Gehörknöchelchen. Literatur 1899–1923.' Ergebnisse der Anatomie und Entwicklungsgeschichte, Bd. XXV, pp. 565–622.

1924*b*. 'Over de ontwikkeling van de tympanaalstreek bij eenige zoogdieren.' Nederl. Tijdschr. voor Geneeskunde, 68e jaargang, 2e Helft, No. 15, pp. 1922–1926.

1924*c*. 'Waarnemingen in Amerikaansche musea over de tympanaalstreek von fossiele zoogdieren.' Tijdschr. d. Ned. Dierk. Vereen. (2) Dl. XIX, Afl. 3, pp. cxviii-cxix.

LEIDY, JOSEPH. 1847. 'On a New Genus and Species of Fossil Ruminantia: *Poëbrotherium wilsoni*.' Proc. Acad. Nat. Sci. Phila., III.

1853. 'On Fossil Mammals from Nebraska.' Proc. Acad. Nat. Sci. Phila., VI, pp. 392–394.

1854. 'The Ancient Fauna of Nebraska, or a Description of Remains of Extinct Mammalia and Chelonia, from the Mauvaises Terres of Nebraska.' Smiths. Contr., VI, pp. 1–126, Pls. I–XXIV.

1855. 'A Memoir on the Extinct Sloth Tribe of North America.' Smiths. Contr., VII, Art. 5, pp. 1–68, Pls. I–XV.

1856. 'Notice of Some Remains of Extinct Vertebrated Animals.' Proc. Acad. Nat. Sci. Phila., VIII, pp. 163–165.

LEPSIUS, G. R. 1882. '*Halitherium schinzi*, die fossile Sirene des Mainzer Beckens. Eine vergleichend-anatomische Studie.' Abhandlungen des Mittelrheinischen geologischen Vereins, Bd. I, pp. 1–200, i-viii, Pls. I–X.

LILLIE, D. G. 1910. 'Observations on the Anatomy and General Biology of some Members of the Larger Cetacea.' Proc. Zoöl. Soc. London, II, pp. 769–792.

LOOMIS, F. B. 1910. 'Osteology and Affinities of the Genus *Stenomylus*.' Amer. Journ. Sci., (4) XXIX, pp. 297–323.

1920. 'On *Ticholeptus rusticus* and the Genera of Oreodontidæ.' Amer. Journ. Sci., (4) L, pp. 281–292.

LORENZ VON LIBURNAU, L. 1905. '*Megaladapis edwardsi* G. Grandidier.' Denkschriften der Kais. Akademie der Wissenschaften, Math.-Nat. wiss. Klasse, Bd. LXXVII, pp. 451–490, Taf. I–VI.

LULL, R. S. 1920. 'New Tertiary Artiodactyls.' Amer. Journ. Sci., (4) L, pp. 83–130.

1921. 'New Camels in the Marsh Collection.' Amer. Journ. Sci., (5) I, pp. 392–404.

1922. 'Primitive Pecora in the Yale Museum.' Amer. Journ. Sci., (5) IV, pp. 111–119.

LYDEKKER, R. 1885*a*. 'Note on Three Genera of Fossil Artiodactyla, with Description of a New Species.' The Geological Magazine, London, New Series, Decade III, 2, pp. 63–73.

1885*b*. 'Catalogue of the Fossil Mammalia in the British Museum (Natural History).' Part II, containing the Order Ungulata, Suborder Artiodactyla.

1887. 'Catalogue of the Fossil Mammalia in the British Museum (Natural History).' Part V, containing the Group Tillodontia, the Orders Sirenia, Cetacea, Edentata, Marsupialia, Monotremata, and Supplement. London.

MARSH, O. C. 1891. 'A Horned Artiodactyle (*Protoceras celer*) from the Miocene.' Amer. Journ. Sci., (3) XLI (whole number, CXLI), pp. 81–82.

1894. 'Miocene Artiodactyles from the Eastern *Miohippus* Beds.' Amer. Journ. Sci., (3) XLVIII (whole number, CXLVIII), pp. 175–178.

MATTHES, ERNST. 1912. 'Einige Bemerkungen über das Gehörorgan von Walen und Sirenen.' Anatom. Anzeiger, Bd. XLI, Nos. 20–22, pp. 594–599.

MATTHEW, W. D. 1893–1903. 'Fossil Mammals of the Tertiary of Northeastern Colorado.' Mem. Amer. Mus. Nat. Hist., I, part 7, pp. 353–447, Pls. XXXVII–XXXIX.

1901. 'Additional Observations on the Creodonta.' Bull. Amer. Mus. Nat. Hist., XIV, pp. 1–38.

1902*a*. 'A Skull of *Dinocyon* from the Miocene of Texas.' Bull. Amer. Mus. Nat. Hist., XVI, pp. 129–136.

1902*b*. 'On the Skull of *Bunælurus*, a Musteline from the White River Oligocene.' Bull. Amer. Mus. Nat. Hist., XVI, pp. 137–140.

1902*c*. 'The Skull of *Hypisodus*, the Smallest of the Artiodactyla, with a Revision of the Hypertragulidæ.' Bull. Amer. Mus. Nat. Hist., XVI, pp. 311–316.

1904. 'A Complete Skeleton of *Merycodus*.' Bull. Amer. Mus. Nat. Hist., XX, pp. 101–129.

1906. 'The Osteology of *Sinopa*, a Creodont Mammal of the Middle Eocene.' Proc. U. S. Nat. Mus., XXX, pp. 203–233, Pl. XVI.

1907. 'A Lower Miocene Fauna from South Dakota.' Bull. Amer. Mus. Nat. Hist., XXIII, pp. 169–219.

1908. 'Osteology of *Blastomeryx* and Phylogeny of the American Cervidæ.' Bull. Amer. Mus. Nat. Hist., XXIV, pp. 535–562.

1909. 'The Carnivora and Insectivora of the Bridger Basin, Middle Eocene.' Mem. Amer. Mus. Nat. Hist., IX, Part 6, pp. 291–559, Pls. XLII–LI.

1910*a*. 'On the Skull of *Apternodus* and the Skeleton of a New Artiodactyl.' Bull. Amer. Mus. Nat. Hist., XXVIII, pp. 33–42.

1910*b*. 'On the Osteology and Relationships of *Paramys* and the Affinities of the Ischyromyidæ.' Bull. Amer. Mus. Nat. Hist., XXVIII, pp. 43–72.

1910*c*. 'The Phylogeny of the Felidæ.' Bull. Amer. Mus. Nat. Hist., XXVIII, pp. 289–316.

1913. 'A Zalambdodont Insectivore from the Basal Eocene.' Bull. Amer. Mus. Nat. Hist., XXXII, pp. 307–314.

1918. 'Contributions to the Snake Creek Fauna with Notes upon the Pleistocene of Western Nebraska. American Museum Expedition of 1916.' Bull. Amer. Mus. Nat. Hist., XXXVIII, pp. 183–229, Pls. IV–X.

1915. (With Walter Granger.) 'A Revision of the Lower Eocene Wasatch and Wind River Faunas.' (By W. D. Matthew.) Part I. Order Feræ (Carnivora), Suborder Creodonta. Bull. Amer. Mus. Nat. Hist., XXXIV, pp. 4–103.

1918. (With Walter Granger.) 'A Revision of the Lower Eocene Wasatch and Wind River Faunas.' (By W. D. Matthew.) Part V. Insectivora (continued), Glires, Edentata. Bull. Amer. Mus. Nat. Hist., XXXVIII, pp. 565–657.

MERRIAM, J. C. 1906. 'Carnivora from the Tertiary Formations of the John Day Region.' Univ. Calif. Publ., Bull. Dept. Geol., V, No. 1, pp. 1–64, Pls. I–VI.

1909. 'The Skull and Dentition of an Extinct Cat Closely Allied to *Felis atrox* Leidy.' Univ. Calif. Publ., Bull. Dept. Geol., V, No. 20, pp. 291–304, Pl. XXVI.

MILLER, GERRIT S., JR. 1906. 'Notes on Malayan Pigs.' Proc. U. S. Nat. Mus., XXX, pp. 737–758, Pls. XXXIX–LXIV.

1907. 'The Families and Genera of Cats.' Smithsonian Institution, U. S. Nat. Mus., Bull. 57.

OSBORN, H. F. 1893–1903. 'The Extinct Rhinoceroses.' Mem. Amer. Mus. Nat. Hist., I, part 3, pp. 75–164, Pls. XII*a*–XX.

1896. 'The Cranial Evolution of *Titanotherium*.' Bull. Amer. Mus. Nat. Hist., VIII, pp. 157–197.

1902*a*. 'Dolichocephaly and Brachycephaly in the Lower Mammals.' Bull. Amer. Mus. Nat. Hist., XVI, pp. 77–89.

1902*b*. 'American Eocene Primates and the Supposed Rodent Family Mixodectidæ.' Bull. Amer. Mus. Nat. Hist., XVI, pp. 169–214.

1904. 'An Armadillo from the Middle Eocene (Bridger) of North America.' Bull. Amer. Mus. Nat. Hist., XX, pp. 163–165.

1913. '*Eomoropus*, an American Eocene Chalicothere.' Bull. Amer. Mus. Nat. Hist., XXXII, pp. 261–274.

1892. (With J. L. Wortman.) 'Characters of *Protoceras* (Marsh), the New Artiodactyl from the Lower Miocene.' Bull. Amer. Mus. Nat. Hist. IV, pp. 351–371.

1894. (With J. L. Wortman.) 'Fossil Mammals of the Lower Miocene White River Beds. Collection of 1892.' Bull. Amer. Mus. Nat. Hist., VI, pp. 199–228.

OWEN, RICHARD. 1840. 'The Zoology of the Voyage of H. M. S. "Beagle," during the Years 1832 to 1836.' Edited and Superintended by Charles Darwin. Part I. Fossil Mammalia. London; pp. i-iv, 1-111, Pls. I–XXXII.

1842. 'Description of the Skeleton of an Extinct Gigantic Sloth, *Mylodon robustus* Owen, with Observations on the Osteology, Natural Affinities and Probable Habits of the Megatherioid Quadrupeds in General.' London; pp. 1–176, Pls. I–XXIV.

1856. 'On the *Megatherium* (*Megatherium americanum*, Cuvier and Blumenbach). Part III. The Skull.' Philos. Trans. Roy. Soc. London, CXLVI, Part 2, pp. 571–589, Pls. XXI–XXVI.

1858. 'On the Scelidothere (*Scelidotherium leptocephalum* Owen).' Philos. Trans. Roy. Soc. London, CXLVII, pp. 101–110, Pls. VIII, IX.

1859. 'On the Fossil Mammals of Australia. Part I. Description of a mutilated Skull of a large Marsupial Carnivore (*Thylacoleo carnifex* Owen), from a calcareous conglomerate stratum, eighty miles S. W. of Melbourne, Victoria.' Philos. Trans. Roy. Soc. London, CXLIX, pp. 309–322, Pls. XIV, XV.

1866. 'On the Fossil Mammals of Australia. Part II. Description of an almost entire skull of the *Thylacoleo carnifex* Owen, from a freshwater deposit, Darling Downs, Queensland.' Philos. Trans. Roy. Soc. London, CLVI, pp. 73–82, Pls. II–IV.

PALMER, R. W. 1913*a*. 'Note on the Lower Jaw and Ear Ossicles of a Fœtal *Perameles*.' Anat. Anz., Bd. XLIII, Nos. 19–20, pp. 510–515.

1913*b*. 'The Brain and Brain-case of a Fossil Ungulate of the Genus *Anoplotherium*.' Proc. Zoöl. Soc. London, pp. 878–893.

PARKER, W. NEWTON. 1882. 'On some Points in the Anatomy of the Indian Tapir (*Tapirus indicus*).' Proc. Zoöl. Soc. London, pp. 768–777.

PAVLOW, MARIE. 1892. 'Études sur l'histoire paléontologique des Ongulés. VI. Les Rhinoceridæ de la Russie et le développement des Rhinoceridæ en général.' Bull. Soc. Imp. Nat. Moscou, N.S., T. VI, pp. 137–221, Pls. III–V.

POCOCK, R. I. 1916*a*. 'On the Course of the Internal Carotid Artery and the Foramina Connected Therewith in the Skulls of the Felidæ and Viverridæ.' Ann. and Mag. Nat. Hist., (8) XVII, pp. 261–269, Pls. X, XI.

1916*b*. 'On the Hyoidean Apparatus in the Lion (*F. leo*) and Related Species of Felidæ. Ann. and Mag. Nat. Hist., (8) XVIII, pp. 222–229.

1916*c*. 'On the Tooth-change, Cranial Characters and Classification of the Snow-Leopard or Ounce (*Felis uncia*).' Ann. and Mag. Nat. Hist., (8) XVIII, pp. 306–316.

1916*d*. 'The Structure of the Auditory Bulla in Existing Species of Felidæ.' Ann. and Mag. Nat. Hist., (8) XVIII, pp. 326–334.

1916*e*. 'The Tympanic Bulla in Hyænas.' Proc. Zoöl. Soc. London, I, pp. 303–307.

1921. 'The Auditory Bulla and Other Cranial Characters in the Mustelidæ.' Proc. Zoöl. Soc. London, pp. 473–486.

POHLE, HERMANN. 1917. '*Pseudobassaris riggsi*, gen. nov., spec. nov., für *Amphictis* spec. Riggs.' Sitzungsberichte der Gesellsch. Naturforschender Freunde zu Berlin, pp. 403–411.

1920. 'Zur Kenntnis der Raubtiere. II. Die Stellung der Gattungen *Amphictis* und *Nandinia*.' Sitzungsberichte der Gesellsch. Naturforschender Freunde zu Berlin, pp. 48–62.

PRELLER, WILHELM. 1907. 'Zur Kenntnis der Morphologie und postembryonalen Schädelmetamorphose von *Hydrochœrus capybara* im Vergleich mit den Schädeln der übrigen Caviiden und Beschreibung und Vergleichung zweier Schädel von *Dinomys branickii*.' Archiv für Naturgeschichte, 73e Jahrgang, Bd. I, pp. 377–422.

REINHARDT, J. 1878. 'Kaempedovendyr—Slaegten *Cælodon*.' Vidensk. Selsk. Skr., 5 Raekke, naturvidenskabelig og mathematisk Afd., XII, 3, Kjöbenhavn, pp. 255–350, T. I–V.

1879. 'Beskrivelse af Hovedskallen af et Kaempedovendyr, *Grypotherium darwinii*, fra la Plata. Landenes plejstocene Dannelser.' Vidensk. Selsk. Skr., 5 Raekke, naturvidenskabelig og mathematisk Afd. XII, 4, Kjöbenhavn, pp. 351–380.

REVILLIOD, P. 1917. 'Contribution a l'étude des Chiroptères des terrains tertiaires. Première partie.' Mémoires de la Société paléontologique Suisse, XLIII, pp. 1–62, Pl. I, 13 figs.

REYNOLDS, SIDNEY H. 1902. 'A Monograph of the British Pleistocene Mammalia. Part I. The Cave Hyæna.' The Palæontographical Society, II, pp. 1–25, Pls. I–XIV. London.

1906. 'A Monograph of the British Pleistocene Mammalia. Part II. The Bears.' The Palæontographical Society, II, pp. 1–35, Pls. I–VIII. London.

1909. 'A Monograph of the British Pleistocene Mammalia. Part III. The Canidæ.' The Palæontographical Society, II, pp. 1–28, Pls. I–VI. London.

1911. 'A Monograph of the British Pleistocene Mammalia. Part IV. The Mustelidæ.' The Palæontographical Society, II, pp. 1–28, I–VI. London.

RIDEWOOD, W. G. 1922. 'Observations on the Skull in Fœtal Specimens of Whales of the Genera *Megaptera* and *Balænoptera*.' Philos. Trans. Roy. Soc. London, Series B, CCXI, pp. 209–272.

RIGGS, ELMER S. 1896*a*. '*Hoplophoneus occidentalis*.' Kansas Univ. Quart., V, No. 1, pp. 37–52, Pl. I.

1896*b*. 'A New Species of *Dinictis* from the White River Miocene of Wyoming.' Kansas Univ. Quart., IV, No. 4, pp. 237–241.

1898. 'On the Skull of *Amphictis*.' Amer. Journ. Sci., (4)V. pp. 257–259.

ROUVIÈRE, H., AND J. DELMAS. 1913. 'Note sur le Développement du canal carotidien chez l'homme.' Comptes rendus hebdomadaires des séances et mémoires de la Société de Biologie, pp. 737, 738.

SCHLOSSER, MAX. 1887. 'Die Affen, Lemuren, Chiropteren, Insectivoren, Marsupialier, Creodonten und Carnivoren des Europäischen Tertiärs und deren Beziehungen zu ihren lebenden und fossilen Aussereuropäischen Verwandten. I Theil.' Beiträge zur Paläontologie Œsterreich-Ungarns und des Orients, Bd. VI, pp. 1–224, Taf. I–IX.

1890. 'Die Affen, Lemuren, Chiropteren, Insectivoren, Marsupialier, Creodonten und Carnivoren des Europäischen Tertiärs und deren

Beziehungen zu ihren lebenden und fossilen Aussereuropäischen Verwandten. III Theil (Schluss).' Beiträge zur Paläontologie Œsterreich-Ungarns und des Orients, Bd. VIII, pp. 1–106.

1899. 'Ueber die Bären und bärenähnlichen Formen des Europäischen Tertiärs.' Paläontographica, Bd. XLVI, pp. 95–148, Taf. XIII, XIV.

1921. 'Beiträge zur Kenntnis der Säugetierreste aus dem untersten Eocaen von Reims.' Palaeontographica, Bd. LXIII, Lief, 5–6, pp. 97–147, Taf. XV, XVI.

SCHMIDT, MARTIN. 1913. 'Ueber Paarhufer der Fluviomarinen Schichten des Fajum. Odontographisches und Osteologisches Material.' Geologische und Palaeontologische Abhandlungen herausgegeben von E. Koken, Neue Folge, Bd. XI, Heft 3, pp. 1–112, Taf. I–IX, 22 figs.

SCHULTE, H. VON. W. 1917. 'The Skull of *Kogia breviceps* Blainville.' Bull. Amer. Mus. Nat. Hist., XXXVII, pp. 361–404, Pls. XXXV–XLIII.

SCOTT, W. B. 1889. 'Notes on the Osteology and Systematic Position of *Dinictis felina* Leidy.' Proc. Acad. Nat. Sci. Phila., pp. 211–244.

1890. 'Beiträge zur Kenntnis der Oreodontidæ.' Morphol. Jahrb. Bd. XVI, pp. 319–395, Taf. XII–XVI.

1891*a*. 'On the Osteology of *Poëbrotherium:* a Contribution to the Phylogeny of the Tylopoda.' Journ. Morphol., V, pp. 1–78.

1891*b*. 'On the Osteology of *Mesohippus* and *Leptomeryx* with Observations on the Modes and Factors of Evolution in the Mammalia.' Journ. Morphol., V, pp. 301–406.

1895*a*. 'The Osteology and Relations of *Protoceras*.' Journ. Morphol. XI, pp. 303–374, Pls. XX–XXII.

1895*b*. 'The Mammalia of the Deep River Beds.' Trans. Amer. Philos. Soc. Phila., XVIII, New Series, pp. 57–185, Pls. I–VI.

1896. 'Die Osteologie von *Hyracodon* Leidy.' Festschrift zum 70-sten Geburtstage von Carl Gegenbaur, II, pp. 351–384, Taf. I–III.

1899. 'The Selenodont Artiodactyls of the Uinta Eocene.' Trans. Wagner Free Institute of Science of Phila., VI, pp. 1–121, Pls. I–IV.

1903*a*. (Editor) 'Mammalia of the Santa Cruz Beds. Part I. Edentata. 1. Dasypoda.' Reports of the Princeton University Expeditions to Patagonia, 1896–1899, V, pp. 1–106, Pls. I–XVI.

1903*b*. (Editor) 'Mammalia of the Santa Cruz Beds. Part I. Edentata. 2. Glyptodontia and Gravigrada.' Reports of the Princeton University Expeditions to Patagonia, 1896–1899, V, pp. 107–227, Pls. XVII–XXXV.

1904. (Editor) 'Mammalia of the Santa Cruz Beds. Part I. Edentata. 3. Gravigrada.' Reports of the Princeton University Expeditions to Patagonia, 1896–1899, V, pp. 227–364, Pls. XXXVI–LXIII.

1905. (Editor) 'Mammalia of the Santa Cruz Beds. Part II. Insectivora. Part III. Glires.' Reports of the Princeton University Expeditions to Patagonia, 1896–1899, V, pp. 365–499, Pls. LXIV–LXXI.

1910. (Editor) 'Litopterna of the Santa Cruz Beds.' Reports of the Princeton University Expeditions to Patagonia, 1896–1899, VII, Part 1, pp. 1–156, Pls. I–XX.

1912. (Editor) 'Toxodonta of the Santa Cruz Beds.' 'Entelonychia of the Santa Cruz Beds.' Reports of the Princeton University Expeditions to Patagonia, 1896–1899, VI, parts 2, 3, pp. 111–300, Pls. XIII–XXX.

1913. 'A History of Land Mammals in the Western Hemisphere.' New York.

SEFVE, IVAR. 1915. '*Scelidotherium* Reste aus Ulloma, Bolivia.' Bull. Geol. Inst. Univ. Upsala, XIII, pp. 61–92, Pls. X–XIV.

SINCLAIR, WILLIAM J. 1906. 'Marsupialia of the Santa Cruz Beds.' Reports of the Princeton University Expeditions to Patagonia, 1896–1899, IV, part 3, pp. 333–460, Pls. XL–LXV.

1908. 'The Santa Cruz Typotheria.' Proc. Amer. Philos. Soc., XLVII, pp. 64–78.

1909. 'Typotheria of the Santa Cruz Beds.' Reports of the Princeton University Expeditions to Patagonia, 1896–1899, VI, part 1, pp. 1–110, Pls. I–XI.

1914. 'A Revision of the Bunodont Artiodactyla of the Middle and Lower Eocene of North America.' Bull. Amer. Mus. Nat. Hist., XXXIII, pp. 267–295.

STEHLIN, H. G. 1912. 'Die Säugetiere des schweizerischen Eocæns. Siebenter Teil, erste Halfte: *Adapis*.' Abh. schweiz. paläont. Ges., XXXVIII.

STANDING, H. F. 1908. 'On Recently Discovered Subfossil Primates from Madagascar.' Trans. Zoöl. Soc. London, XVIII, pp. 59–162.

STEINMANN, G. AND L. DÖDERLEIN. 1890. 'Elemente der Paläontologie.'

STOCK, CHESTER. 1913. '*Nothrotherium* and *Megalonyx* from the Pleistocene of Southern California.' Univ. Calif. Publ., Bull. Dept. Geol., VII, No. 17, pp. 341–358.

1914. 'Skull and Dentition of the Mylodont Sloths of Rancho la Brea.' Univ. Calif. Publ., Bull. Dept. Geol., VIII, No. 18, pp. 319–334, 6 figs.

1917. 'Further Observations of the Skull Structure of Mylodont Sloths from Rancho la Brea.' Univ. Calif. Publ., Bull. Dept. Geol., X, No. 11, pp. 165–178, Pls. III–IV.

STROMER V. REICHENBACH, E. 1912. 'Lehrbuch der Paläozoologie.' II Teil: Wirbeltiere.

TEILHARD DE CHARDIN, PIERRE. 1914–1915. 'Les Carnassiers des Phosphorites du Quercy.' Annales de Paléontologie, Tome IX, pp. 103–192, Pls. XIII–XX.

1922. 'Les Mammifères de l'éocène inférieur français et leurs gisements.' Annales de Paléontologie, Tome XI, pp. 1–116 (pp. 1–8 in Tome X), Pls. I–VIII.

THORPE, M. R. 1921*a*. 'Two New Fossil Carnivora.' Amer. Journ. Sci., (5) I, pp. 477–483.

1921*b*. 'John Day Eporeodons with Descriptions of New Genera and Species.' Amer. Journ. Sci., II, pp. 93–111.

1921*c*. 'Two New Forms of *Agriochœrus*.' Amer .Journ. Sci., (5) II, pp. 111–119.

1922*a*. 'Oregon Tertiary Canidæ, with Descriptions of New Forms.' Amer. Journ. Sci., (5) III, pp. 162–176.

1922*b*. 'A New Genus of Oligocene Hyænodontidæ.' Amer. Journ. Sci., (5) III, pp. 277–287.

1923. 'The Primitive and Carnivore-like Characters of the Merycoidodontidæ.' Amer. Journ. Sci., (5) VI, pp. 239–246.

TOULA, F. 1902. 'Das Nashorn von Hundsheim *Rhinoceros* (*Ceratorhinus* Osborn) *hundsheimensis*, nov. form. Mit Ausführungen über die Verhältnisse von elf Schädeln von *Rhinoceros* (*Ceratorhinus*) *sumatrensis*.' Abh. d. k. k. Geologischen Reichsanstalt, Bd. XIX, Heft I, pp. 1–92, Pls. I–XII. Wien.

TROXELL, E. L. 1917. 'An Oligocene Camel, *Poëbrotherium andersoni*, n. sp.' Amer. Journ. Sci., XLIII, pp. 381–389.

1920*a*. 'A Tiny Oligocene Artiodactyl, *Hypisodus alacer*, sp. nov.' Amer. Journ. Sci., (4) XLIX, pp. 391–398.

1920*b*. 'Entelodonts in the Marsh Collection. Part II. The Genus *Archæotherium*.' Amer. Journ. Sci., L, pp. 361–386.

1921*a*. 'The American Bothriodonts.' Amer. Journ. Sci., (5) I, pp. 325–339.

1921*b*. 'New Amynodonts in the Marsh Collection.' Amer. Journ. Sci., II, pp. 21–34.

TRUE, F. W. 1910. 'Description of a Skull and Some Vertebræ of the Fossil Cetacean *Diochotichus vanbenedeni* from Santa Cruz, Patagonia.' Bull. Amer. Mus. Nat. Hist., XXVIII, pp. 19–32, Pls. I-V.

TURNER, H. N. 1851. 'On the Arrangement of the Edentate Mammalia.' Proc. Zoöl. Soc. London, XIX, pp. 205–221.

TURNER, WM. 1913. 'Observations on the Auditory Organ in the Cetacea.' Proc. Roy. Soc. Edinburgh, XXXIV, pp. 10–22.

VOIT, MAX. 1923. 'Ueber einige Befunde in der Gegend des Gelenkteiles des primordialen Unterkiefers der Wirbeltiere.' Anat. Anz., Bd. 57, Ergänzungsheft (Verh. Anat. Ges. Heidelberg, 1923), pp. 68–77.

WATSON, D. M. S. 1916. 'The Monotreme Skull: A Contribution to Mammalian Morphogenesis.' Philos. Trans. Roy. Soc. London, Series B, CCVII, pp. 311–374.

WEITHOFER, ANTON. 1888. 'Beiträge zur Kenntnis der Fauna von Pikermi bei Athen.' Beiträge zur Paläontologie Oesterreich-Ungarns und des Orients, Bd. VI, pp. 225–292, Taf. X–XIX.

WEITHOFER, K. A. 1890. 'Die Fossilen Proboscidier des Arnothales in Toskana.' Beitrage zur Palaontologie Oesterreich-Ungarns und des Orients, Bd. VIII, pp. 107–240, Taf. I–XV. Wien.

WINGE, HERLUF. 1888. 'Jordfundne og nulevende Gnavere (Rodentia) fra Lagoa Santa, Minas Geraes, Brasilien. Med Udsigt over Gnavernes indbyrdes Slaegtskab.-Rongeurs fossiles et vivants de Lagoa Santa, Minas Geraes, Brésil. Avec un aperçu des affinités mutuelles des Rongeurs (Extrait du mémoire danois par les soins de l'auteur).' E Museo Lundii, Förste Bind., pp. 1–200, Taf. I–VIII.

1893*a*. 'Jordfundne og nulevende Flagermus (Chiroptera) fra Lagoa Santa, Minas Geraes, Brasilien. Med Udsigt over Flagermusenes indbyrdes Slaegtskab.—Chauves-souris fossiles et vivantes de Lagoa

Santa, Minas Geraes, Brésil. Avec un aperçu des affinités mutuelles des Chiroptères (Aperçu du mémoire danois, publié par les soins de l'éditeur).' E Museo Lundii, Andet Bind, Förste Halvbind, Kjöbenhavn, pp. 1–92, Pls. I, II.

1893*b*. 'Jordfundne og nulevende Pungdyr (Marsupialia) fra Lagoa Santa, Minas Geraes, Brasilien. Med Udsigt over Pungdyrenes Slaegtskab. Marsupian fossiles et vivants de Lagoa Santa, Minas Geraes, Brésil. Avec un aperçu sur les affinités des Marsupian. (Résumé du mémoire danois, publie par les soins de l'éditeur).' E Museo Lundii, Andet Bind, Förste Halvbind, Kjöbenhavn, pp. 1–149, Pls. L–LV.

1895*a*. 'Jordfundne og nulevende Aber (Primates) fra Lagoa Santa, Minas Geraes, Brasilien. Med Udsigt over Abernes indbyrdes Slaegtskab. Singes (Primates) fossiles et vivants de Lagoa Santa, Minas Geraes, Brésil. Avec un aperçu des affinités mutuelles des Primates. (Résumé du mémoire danois, publié par les soins de l'éditeur) E Museo Lundii, Andet Bind, Andet Halvbind, Kjöbenhavn, pp. 1–57, Pls. I, II.

1895*b*. 'Jordfundne og nulevende Rovdyr (Carnivora) fra Lagoa Santa, Minas Geraes, Brasilien. Med Udsigt over Rovdyrenes indbyrdes Slaegtskab.—Carnivores fossiles et vivants de Lagoa Santa, Minas Geraes, Brésil. Avec un aperçu des affinités mutuelles des Carnassiers. (Résumé du mémoire précédent, publié par les soins de l'éditeur.)' E Museo Lundii, Andet Bind, Andet Halvbind, Kjöbenhavn. pp. 1–130, Pls. I–VIII.

1906. 'Jordfundne og nulevende Hovdyr (Ungulata) fra Lagoa Santa, Minas Geraes, Brasilien. Med Udsigt over Hovdyrenes indbyrdes Slaegtskab.' E Museo Lundii, Tredie Bind, Förste Halvbind, Kjöbenhavn, pp. 1–239, Pls. I–IX.

1915. 'Jordfundne og nulevende Gumlere (Edentata) fra Lagoa Santa, Minas Geraes, Brasilien. Med Udsigt over Gumlernes indbyrdes Slaegtskab.' E Museo Lundii, Tredie Bind, Andet. Halvbind, Kjobenhavn, pp. i–lv, 1–321, Pls. I–XLII.

WOODWARD, ARTHUR SMITH. 1900. 'On Some Remains of *Grypotherium* (*Neomylodon*) *listai* and Associated Mammals from a Cavern near Consuelo Cove, Last Hope Inlet, Patagonia.' Proc. Zoöl. Soc. London, pp. 64–79, Pls. V–IX.

WORTMAN, J. L. 1895. 'On the Osteology of *Agriochœrus*.' Bull. Amer. Mus. Nat. Hist., VII, pp. 145–178.

1898. 'The Extinct Camelidæ of North America and Some Associated Forms.' Bull. Amer. Mus. Nat. Hist., X, pp. 93–142.

1901. 'Studies of Eocene Mammalia in the Marsh Collection, Peabody Museum.' Amer. Journ. Sci., (4) XII, pp. 281–296.

1902*a*. 'Studies of Eocene Mammalia in the Marsh Collection, Peabody Museum.' Amer. Journ. Sci., (4) XIII, pp. 197–206.

1902*b*. 'Studies of Eocene Mammalia in the Marsh Collection, Peabody Museum.' Amer. Journ. Sci., (4) XIII, pp. 433–448.

1903. 'Studies of Eocene Mammalia in the Marsh Collection, Peabody Museum.' Amer. Journ. Sci., (4) XVI, pp. 345–368.

1921. 'On Some Hitherto Unrecognized Reptilian Characters in the Skull of the Insectivora and Other Mammals.' Proc. U. S. Nat. Mus., LVII, pp. 1–52.

1899. (With W. D. Matthew.) 'The Ancestry of Certain Members of the Canidæ, the Viverridæ and Procyonidæ.' Bull. Amer. Mus. Nat. Hist., XII, pp. 109–138, Pl. VI.

WYMAN, J. 1850. 'Notice of Remains of Vertebrated Animals found at Richmond, Virginia.' American Journal of Science and Arts, Second Series, X, pp. 228–235.

ZITTEL, KARL A. VON. 1893. 'Handbuch der Palæontologie. I Abtheilung. Palæozoologie. Bd. IV. Vertebrata (Mammalia).'

1911. 'Grundzüge der Paläontologie (Paläozoologie). Neubearbeitet von F. Broili, E. Koken, M. Schlosser. II Abteilung. Vertebrata.' 2e Aufl.

1923. 'Grundzüge der Palæontologie (Palæozoologie). Neubearbeitet von F. Broili und M. Schlosser. II Abteilung. Vertebrata.' 4e Aufl. Mammalia bearbeitet von M. Schlosser, pp. 402–689.

LIST OF ABBREVIATIONS IN THE FIGURES

art. s. st. hy. = articulation surface for the stylohyal.
b. o. = basioccipital.
b. s. = basisphenoid.
c. c. = canalis caroticus
c. o. = condylus occipitalis.
cr. t. = crista tympanica.
d. p. ent. = dorsal portion of the entotympanic.
ent. = entotympanic.
e. o. = exoccipital.
e. s. b. = external surface of the bulla.
f. c. = foramen condyloideum.
f. c. p. = foramen caroticum posterius.
f. gl. = fossa glenoidea.
f. l. a. = foramen lacerum anterius.
f. l. p. = foramen lacerum posterius.
f. m. = foramen magnum occip.
f. p. gl. = foramen postglenoideum.
f. st. m. = foramen stylomastoideum primitivum.
f. t. aud. = foramen tubæ auditivæ.
f. t. m. = fissura tympano-mastoidea.
gr. hy.? = groove for the hyoid?
m. a. e. o. = meatus auditorius externus osseus.
mand. = mandibula.
matr. = matrix.
nat. cast bulla = natural cast of the bulla.
oss. acc. m. = ossiculum accessorium malleoli.
p. a. e. = porus acusticus externus.
petr. = petrosal.
pr. m. = processus mastoideus.
pr. p. gl. = processus postglenoideus.
pr. p. occ. = processus paroccipitalis.
pr. z. = processus zygomaticus.
pter. = pterygoid.
rec. epit. = recessus epitympanicus.
r. r. b. = rostral roof of the bulla.
r. s. c. = roof of the sulcus caroticus.
r. w. b. = rostral wall of the bulla.
s. c. = sulcus caroticus.
s. ent. = septum bullæ, pars entotympanici.
s. occ. = supraoccipital.
s. ty. = septum bullæ, pars tympanici.
ty. = tympanic.
ty. hy. = tympanohyal.
v. s. ent. = ventral surface of the entotympanic.
* = bone.
x = bony element (see text).

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