

**Article IV.—THE POSITION OF THE “SPARASSODONTS”:
WITH NOTES ON THE RELATIONSHIPS AND HISTORY
OF THE MARSUPIALIA**

BY HORACE ELMER WOOD, II

• Repeated controversies concerning the relationships of the extinct South American carnivorous marsupials (e.g., *Borhyæna*, *Prothylacinus*, *Cladosictis*, *Amphiproviverra*) have arisen during the past thirty years, and no conclusion has yet been reached which satisfies all the students of this problem. The question came up in a discussion between Prof. William K. Gregory and myself and I am writing this paper at his suggestion. He has given invaluable advice and assistance at each stage of the work. I am indebted to Dr. W. D. Matthew for permission to use the fossil “sparassodonts” in the American Museum, as well as for a critical reading of the manuscript. I am also under obligations to Mr. H. C. Raven of the American Museum for various helpful suggestions. The drawings are the work of Mr. Malcolm McGregor Jamieson.

Ameghino (1892) founded a separate suborder of marsupials, the Sparassodonta, composed of the carnivorous South American marsupials. He regarded them as genetically intermediate between typical polyprotodont marsupials and creodonts. He placed the four genera named above in separate families. Sinclair first (1905, 1906) gave convincing evidence that the “sparassodonts” were true polyprotodont marsupials, in no sense ancestral to or allied with the creodonts. He also classified them as members of the family Thylacinidæ, united to *Thylacinus* by many striking resemblances. This had already been suggested vaguely by Lydekker and Bensley. At the time, Matthew (1907) accepted this unreservedly.

Tomes (1906) came to Ameghino's aid by announcing that the enamel of a single damaged tooth of *Borhyæna* had the histological structure of the fissipedes and the inadapative creodonts, rather than that of the marsupials. This was recently refuted by Carter (1920) from more adequate material. He showed that the enamel structure of *Borhyæna*, *Cladosictis* and *Pharsophorus* was of typical carnivorous polyprotodont type.

Except for Tomes's paper the reference of the “sparassodonts” to the polyprotodonts passed unchallenged. Their union with *Thylacinus* in the family Thylacinidæ was also accepted until Matthew in “Climate and Evolution” (1915, delivered orally a number of years earlier) denied that the “sparassodonts” were related to any Australian form more

closely than by descent from a common didelphid ancestor. Scott (1913) supported Sinclair's reference of the "sparassodonts" to the Thylacini-dæ. Gidley (1915), Loomis (1921) and Osgood (1922) took a position somewhat intermediate between Sinclair and Matthew, regarding all these forms as "Thylacinidæ," but apparently deriving both Australian and South American forms from hypothetical Paleocene thylacines in Holarctica.

Although Matthew denied the possibility of any southern land connection between Australia and South America on isostatic grounds, he admitted the probability of an early Tertiary elevation of the southern continents to the edge of the continental shelf (1915, p. 283); and, although doubting its probability, he considered the possibility of the transportation of a hystricomorph rodent across the Atlantic Ocean from Africa to South America (pp. 229-231). The transportation of a small thylacine from the edge of the continental shelf south of Tasmania to Antarctica, and thence of a descendant across the narrow deep-water channel to South America, is equally conceivable. Although any assumption of this type is difficult to accept and requires strong proof, such a discontinuous bridge would result in a partial mingling of faunas (the particular migrants chosen being determined partly by chance, partly by their adaptability to sea-travel). That something of the kind may have taken place is suggested by the striking resemblance—sometimes extending to specific identity—of the Tertiary invertebrate faunas of Patagonia, New Zealand and Australia,—a similarity not shared with any other region. (For a further discussion of this question see Ortman, 1902, Matthew, 1915, Barbour, 1916, Loomis, 1921.)

I have reviewed the literature on the southern land bridge, but I have not attempted to discuss the subject further, as it involves balancing against one another unproved and contradictory hypotheses. I am not competent to discuss the evidence for or against isostasy, or its implications, or the potency of natural rafts as transporting agents. Any final decision as to relationship should, however, be based chiefly on structure—and the paleontological record, when legible—rather than on present geographic distribution or unproved theories of crustal movement.

Matthew's morphological conclusions, as given in "Climate and Evolution," are as follows:

The near resemblance between the modern Australian *Thylacinus* and the Borhyænidae of Tertiary South America has been used as an argument for an Antarctic connection between the two. Such a hypothesis will not bear close examination. The resemblance is not closer than between parallel adaptations in distinct families of true Carnivora whose genealogy has been more or less completely traced back

through independent lines of descent from unspecialized common ancestors. It is not closer, for instance, than that between the Oligocene Felidæ and the modern *Cryptoprocta* of Madagascar, whose common descent from an unspecialized placental carnivore (Viverrid or Miacid), analogous to the marsupial didelphyids, is generally admitted. The common characters distinguishing thylacinids and borhyænids from the didelphyids are, without exception, such as would naturally be assumed independently in adaptation to predaceous terrestrial life and have been so assumed in numerous independent parallel adaptations of the same sort among placental Carnivora. On the other hand, *Thylacinus* has retained certain didelphyid characters which are already lost by the most primitive of the Borhyænidæ (palatal vacuities, posterior position of the orbits, an external lachrymal duct, double perforation of the basi-sphenoid), while in other features (brain development, cursorial specialization, etc.) it is more progressive. The Borhyænidæ are more progressive in the reduction of the last molar, in the differentiation of enamel from dentine,¹ less so in the cursorial adaptation of the limbs and feet.

Descent from a common ancestral type is undoubtedly shown, but some at least of the above differences point back to Didelphyidæ as this common type. The characters which Sinclair uses to separate the thylacines are the reduced number of incisors, the carnassial specialization of the molars and especially the loss of the metaconid. Every one of these features, besides numerous other common characters which he does not specify, may be paralleled in two or more distinct lines of Carnivora whose common ancestors are not more predaceously specialized than *Didelphys*. The loss of the metaconid occurs in *Cyon*, *Ischyrocyon*, *Simocyon* and *Enhydrocyon* among the Canidæ, in all the post-Oligocene Felidæ, in *Gulo*, *Megalicteis*, *Mustela*, etc., among the Mustelidæ, in the later Hyænidæ, in *Hyænodon* and *Pterodon* among the Hyænodontidæ, in *Patriofelis* among the Oxyænidæ, in all the later Mesonychidæ. Each one of these genera is independently descended from genera in which the metaconid is well developed. In every case, it is simply a stage in predaceous adaptation of the molars, nor can it be assigned any other significance in the marsupial carnivores. There is, in short, no evidence for assuming a closer affinity between thylacines and borhyænids than common descent from didelphyid ancestors and there is strong evidence against such an assumption.

Granting that any one, or that several, of the characters linking the "sparassodonts" with *Thylacinus* might be due to parallelism, such an explanation becomes more difficult to accept in geometric ratio as this list is multiplied, unless other characters link the "sparassodonts" with the Didelphidæ while separating them from *Thylacinus*, which is apparently not the case. That the "sparassodonts" lack part of the common didelphid heritage which is retained in *Thylacinus* does not prove them to be an independent and more immediate offshoot from the didelphids, especially since in most of these characters they are more progressive than *Thylacinus*.

In the instances of parallelism given above by Dr. Matthew, the members of each family are still clearly distinguishable as to family; even

¹But see Carter, 1920. H. E. W.

though it may be difficult to state that difference in words. Figs. 1-47—or, better still, the actual specimens,—show that *Thylacinus* fits in most naturally among the “sparassodonts.”

In this paper I have attempted to give a fair summary of the osteological characters of didelphids, “sparassodonts,” *Thylacinus* and dasyurids, usually omitting general polyprotodont characters and those of purely specific or generic value. This is based, for living marsupials and *Amphiproiverra*, on material in the American Museum of Natural History. Most of the characters for *Borhyaena*, *Prothylacinus* and *Cladosictis* are taken from Sinclair's monograph (1906). The numbers, unless otherwise indicated, refer to American Museum specimens. It is often necessary to list separately characters which are, or which may be, complementary to each other.

The following characters indicate thylacine affinities for the “sparassodonts”: 2, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 17, 18, 19, 24, 25, 32, 34, 35, 36, 39, 40, 41, 43, 44, 45, 48, 49.

These give no light on this question: 3, 14, 27, 28, 29, 30, 31, 33, 37, 38, 42, 46, 47.

These characters suggest didelphid affinities for the “sparassodonts”: 1, 15, 16, 20, 21, 22, 23, 26.

A valid objection may be raised to this summary as it stands. Where two characters, listed separately, are necessarily complementary to each other, they should be counted as only a single unit. Going over these tables, uniting characters clearly complementary to each other, omitting the neutral characters and italicizing the more important ones, we get the following summary: thylacine affinities: 2, 4, 5, 6, (7 & 8), 9, 10, 11, 12, 13, 17, 18, 19, 24, 25, 32, 34, 35, 36, 39, 40, 41, 43, 44, 45, 48, 49; didelphid affinities: 1, 15, 16, (20 & 21), 22, 23, 26. I omit the neutral characters, as they are either highly variable within the limits of each group, or else the “sparassodonts” differ from all the others (as, for example, in regard to the number of premolars replaced). In this respect the “sparassodonts” are separated as widely from the Didelphidæ as from *Thylacinus*.

Of the characters favoring thylacine affinities these are underlined as more important: the dental formula $I_{\frac{4-3}{3}} C_{\frac{1}{1}} P_{\frac{3}{3}} M_{\frac{4}{4}}$; the reduction of the protocone; the high shearing metastyle; the parastyle plastered on the paracone; the loss of the mesostyle; the approximation of the paracone and metacone; the narrow shearing M^4 ; the absence of the metaconid (see Figs. 1-16); the thickened, but not down-turned, posterior edge of the palate (see Figs. 32-47); the very wide temporal

fossæ; the retracted tips of the nasals (see Figs. 17-31); the free atlanteal intercentrum of *Borhyæna*, *Amphiproviverra* and *Thylacinus*; the long, proximally constricted, transverse process of the atlas; the halberd-shaped neural process of the axis; the long spiked neural processes of the cervical vertebræ 3-7; the number of rib-bearing vertebræ; the flat ilium; the position of the acetabular notch, and the great reduction of the marsupial bones. These characters may be considered as defining the family Thylacinidæ. In all these, the Thylacinidæ (of Sinclair) differ from all the didelphids examined (whatever their habits and food) and very often from *Dasyurus* and even from *Sarcophilus*, which are just as purely carnivorous as any of the Thylacinidæ and should, therefore, possess all the "habitus" characters which are an essential part of the equipment of a carnivorous polyprotodont marsupial. Most of these characters are apparently not immediately dependent on one another; and although, unquestionably, many of them are associated with the carnivorous habits of the Thylacinidæ, they are not *all*, at least, *necessary* modifications for a carnivorous life in a polyprotodont marsupial, since, of these nineteen characters, eight differ from both *Dasyurus* and *Sarcophilus*. These are: the dental formula; the parastyle plastered on the paracone; the absence of the mesostyle; the absence of the metaconid; the thickened, but not down-turned, posterior border of the palate; the number of rib-bearing vertebræ; the flat ilium, and the great reduction of the marsupial bones. Only *Sarcophilus*, of the dasyurids examined, has the abnormally wide temporal fossæ of the thylacinids; and none of the dasyurids has the free atlanteal intercentrum found in *Borhyæna*, *Amphiproviverra* and *Thylacinus* (but fused in *Prothylacinus* and *Cladosictis*).

I found only seven characters tending to support Matthew's view of the didelphid affinities of the "sparassodonts." These are: the geographical separation of Australia and South America; the closed palate of the "sparassodonts" (approximated in *Caluromys*, *Antechinomys* and some specimens of *Dasyurus*); the virtual loss of the bar enclosing the foramen at the postero-external corner of the palate in *Thylacinus*; the naso-lachrymal contact seen in the "sparassodonts" and a few didelphids; the position of the orbits; the arrangement of the lachrymal foramina; and the shape of the postorbital process of the jugal. The geographical occurrence of the forms under discussion is not a morphological character, and its possible meanings are discussed elsewhere. The closed palate is presumably secondary and independently acquired in each family (in the "sparassodonts," *Dasyurus* and *Caluro-*

mys). In any case, it separates the "sparassodonts" from the didelphids nearly as completely as from *Thylacinus*. The loss of the bar from the palate is valid as far as it goes, but such losses occur rather easily. The relative position of the orbits is largely determined by the lengthening or shortening of the face, which are decidedly "habitus" characters. It is, therefore, rather variable and not a very safe guide. The nasolachrymal contact is a valid character, although its value is somewhat reduced by its great variability, not only within the family but inside the genus, species, and even between the two sides of the same individual. The same thing is true of the position of the lachrymal foramina and the shape of the postorbital process of the jugal.

Without denying some weight to the arguments given above for the Didelphidae as the nearest relatives of the "sparassodonts," I feel that this summary shows a strong preponderance of characters uniting them to *Thylacinus*. The reader must decide whether parallelism will explain so striking a similarity.

Scott (1917), apropos of Nuttall's blood tests, says: "A close relationship is shown to exist between all Marsupials, with the exception of the Thylacine." This would seem to furnish support for the view that *Thylacinus* is not a dasyurid and hence is probably a "sparassodont." Its value as evidence is greatly diminished, however, by the fact that, except for didelphids, *Thylacinus* and *Parameles* were the only polyprotodonts tested, and that the serum was considered of unsatisfactory quality by Nuttall (1904).

The Cænolestidae of South America are also of interest in this connection. They furnish a parallel case, either connecting with the Australian Peramelidae and Phalangeridae, or being parallel derivatives from some opossum. Osgood (1921) and Gregory (1922) both see their closest relatives among the Australian forms. This strengthens, by just so much, the argument for some real relation between the two faunas.

Osgood (1921) emphasizes what he regards as the isolated position of *Myrmecobius*, not only from the dasyurids, but from the marsupials in general, going back to a Jurassic ancestor with more than seven cheek teeth. The reasons for regarding *Myrmecobius* as an aberrant dasyure have been given by Bensley (1903), Gidley (1915) and Gregory (1920). Osgood's monograph does not seem to invalidate their reasoning. He admits that *Myrmecobius* is derived from generalized marsupials, yet one of the most uniform and, presumptively, most primitive marsupial characters is the presence of not more than seven post-canine teeth. Consider also these statements on page 131 of his article: "Whatever the

case may have been with respect to the history of the extra molar teeth of *Myrmecobius*, the view that all the living families of Marsupials were well differentiated early in the Tertiary seems to be well founded. Therefore, without reference to possibly archaic characters other than the teeth, it is still possible to believe in an early predidelphid origin for *Myrmecobius*." Since opossums are known from the Upper Cretaceous, this does not bar them from ancestry to all other marsupials. It may be justifiable, in view of the possible geological antiquity of the type (*Myrmecoboides*, Gidley, 1915), and the unusual "habitus" characters, to make a separate family, the Myrmecobidæ, as has already been done for the Thylacinidæ; although it would be equally logical to regard it as a subfamily of the Dasyuridæ.

In this connection, I wish to point out that more time can be allowed for the radiation of the marsupials than has often been assumed. We know that the opossum, at least, has come down from the Upper Cretaceous without material change. *Wynyardia* is firmly imbedded in the literature as an Eocene or Oligocene diprotodont with polyprotodont affinities and has often been used as a means of dating the origin of the diprotodonts. A discussion of Spencer's paper (1900) between Dr. William K. Gregory and myself led to an attempt to discover these supposed polyprotodont affinities. Spencer lists the following "dasyurid" characters in *Wynyardia* (see Figs. 48-57):

"1. Proportionate length to the breadth of the skull 100:67. This approximates most nearly to *Dasyurus* and shows a decidedly greater proportionate width than in the Phalangeridæ." There is a much closer resemblance both in ratio and proportions to such a diprotodont as *Bettongia* (No. 6346), or *Phascolarctus cinereus* (No. 42178). Even if this were not true, however, such a ratio would mean nothing, since *Dasyurus* and *Wynyardia* have entirely different shapes as seen from above. An accidental equivalence of ratios of length to breadth, if it occurred, would mean nothing. A superficial approach to this ratio is found in *Phascogale*, *Thylacinus* and *Borhyæna*. It is presumably secondary in all these forms. In *Phascogale* it is associated with the enormous bullæ—a "habitus" feature.

"2. Lambdoidal crest well developed, as in *Dasyurus*." It is equally so in *Trichosurus vulpecula*, No. 249, and *Pseudochirus cooki*. This, therefore, is hardly valid as a dasyure character.

"3. Sagittal crest strongly developed, resembling that of Dasyuridæ and species of *Didelphys*." On the whole, it is probably more like *Trichosurus*, since the sunken area in the frontal region between

the V-shaped forks of the sagittal crest is much alike in *Trichosurus* and *Wynyardia*.

"5. The wide sweep and upward curvature of the zygomatic arches, as in *Dasyuridæ*." This is the only one of these characters that appears to be valid. Even here, however, *Wynyardia* is probably closer to *Bettongia*, or even *Trichosurus*.

"7. The transverse elongation of the glenoid cavity, the downward-produced plate of bone which forms the boundary, is not connected with any structure forming part of the auditory passage. In this respect, it agrees with *Dasyuridæ* and *Perameles*, and differs markedly from the *Phalangeridæ*, amongst which it forms the anterior part of a bony auditory canal." By this the author apparently means that in *Wynyardia* and the *Dasyuridæ* the tympanic ring is not coössified with the postglenoid process as it is in *Trichosurus*. As they are not coössified in *Phascolarctus cinereus*, No. 42178, and various other diprotodonts, the value of this character as a link with the polyprotodonts is nullified.

Among the more striking diprotodont characters are: the chunky premaxillæ; the masseteric process beneath the zygoma; the profile of the skull from above; the V-shaped basin in the frontal region inside the forking sagittal crest; the naso-lachrymal contact (probably secondary for marsupials and primitive for diprotodonts); the descending curve of the sagittal crest to the rear, as seen from the side, and the entirely diprotodont shape of the mandible. Compare the figures of *Dasyurus*, *Wynyardia* and *Trichosurus*.

Wynyardia is also much more recent than the date—Eocene or Oligocene—ascribed to it by Spencer. Frederick Chapman, the Australian geologist, in an oral communication to William K. Gregory, refers it to the *Turritella warburtoni* zone of the Lower Pliocene. This geological level, entirely aside from the morphological evidence cited above, eliminates *Wynyardia* as a possible link between polyprotodonts and diprotodonts. It seems reasonable to regard it as a slightly primitive phalanger.

There is therefore no reason why the preliminary stages in the adaptive radiation of the marsupials may not have taken place by the Upper Cretaceous or Paleocene, except that the scanty marsupial remains of that time are apparently all didelphids (except *Myrmecoboides*, if it is a marsupial). This hypothesis is an expansion of the suggestion of Gidley (1915) and Loomis (1921) that a marsupial adaptive radiation from didelphids into dasyures, thylacines and pre-diprotodonts may

have taken place in the northern hemisphere, after which the didelphids, thylacines and pre-diprotodonts would have entered South America, while the dasyures, thylacines and pre-diprotodonts would have entered Australia. This hypothesis combines the strongest elements in the views of Sinclair and Matthew, avoiding their more difficult assumptions, but a new difficulty, in view of the rather frequent occurrence of the Didelphidæ, is the absence from the northern hemisphere of the remains of the other three families postulated. To fall back on "the imperfection of the geological record" in a way merely begs the question. Possibly these unknown and hypothetical forms may have belonged to the long-lost upland fauna of the later Cretaceous.

The alternative to the hypothesis tentatively expressed above is some more direct connection between the faunas of Australia and South America.

CONCLUSIONS

1. The closest structural relations of the "sparassodonts" are with *Thylacinus*, and, in the absence of any direct evidence of "parallelism," they should be included with it in the family Thylacinidæ, defined as above. *Thylacinus*, however, was not descended from any known "sparassodont."

2. *Myrmecobius* is closely related to the Dasyuridæ in its "heritage" features. It is not a "Mesozoic survival,"—certainly not in the sense that its extra teeth are inherited directly from a Jurassic form with extra teeth.

3. *Wynyardia* is now assigned to the Pliocene instead of the Eocene or Oligocene. It is a true diprotodont in every way, and does not connect the diprotodonts and polyprotodonts.

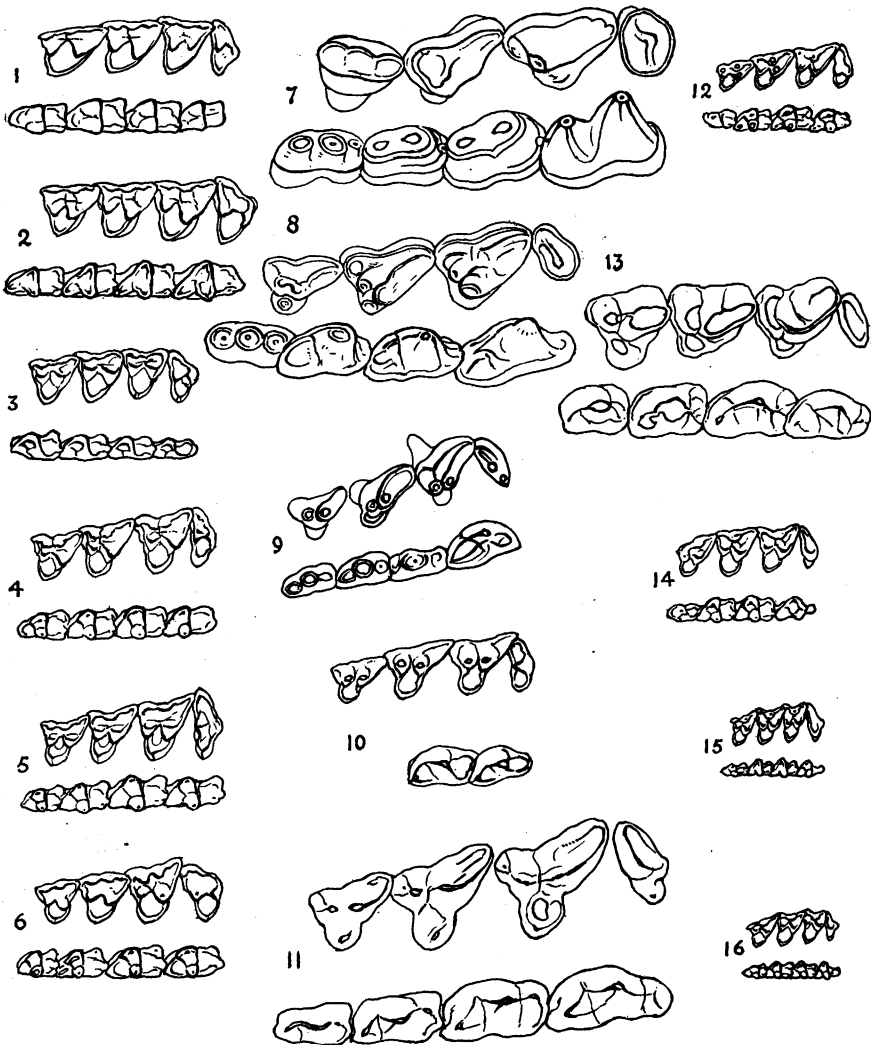
4. The paleogeographic concomitants of the statements above are uncertain. There may have been a discontinuous southern connection between South America and Australia during the late Cretaceous or early Tertiary. Or perhaps the marsupial adaptive radiation began in Holarctica by the Upper Cretaceous. By the Paleocene the Didelphidæ and, perhaps, the Dasyuridæ, Myrmecobidæ, Thylacinidæ and the pre-diprotodonts were already in existence. The competition of the placentals would then have limited the marsupials (except the opossum) to South America (with opossums, thylacines and pre-diprotodonts) and Australia (with myrmecobids, dasyures, thylacines and pre-diprotodonts).

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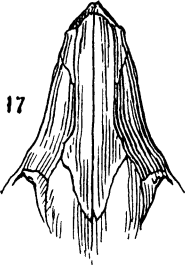
FIGURES 1 to 57

- Fig. 1. *Philander* sp. No. 2072. $\times 4$.
- Fig. 2. *Metachirus* sp. No. 244. $\times 2$.
- Fig. 3. *Caluromys derbianus*. No. 10058. $\times 2$.
- Fig. 4. *Chironectes minimus*. No. 33027. $\times \frac{1}{2}$.
- Fig. 5. *Marmosa chapmani*. No. 4773. $\times 3$.
- Fig. 6. *Didelphys virginiana*. No. 242. $\times \frac{1}{4}$.
- Fig. 7. *Borhyaena tuberata*. Princeton Univ. No. 15701. (After Sinclair.) $\times 1$.
- Fig. 8. *Prothylacinus patagonicus*. P. U. No. 15700. (After Sinclair.) $\times 1$.
- Fig. 9. *Cladosictis lustratus*. P. U. No. 15170. (After Sinclair, lower teeth reversed.) $\times 1$.
- Fig. 10. *Amphiproviweria mazaniana*. No. 9254. $\times 1$.
- Fig. 11. *Thylacinus cynocephalus*. No. 35504. $\times 1$.
- Fig. 12. *Dasyurus viverrinus*. No. 16669. $\times 1$.
- Fig. 13. *Sarcophilus ursinus*. No. 35106. $\times 1$.
- Fig. 14. *Phascogale cristicaudata*. No. 15009. $\times 2$.
- Fig. 15. *Antechinomys laniger*. No. 15012. $\times 2$.
- Fig. 16. *Sminthopsis crassicaudata*. No. 15013. $\times 2$.

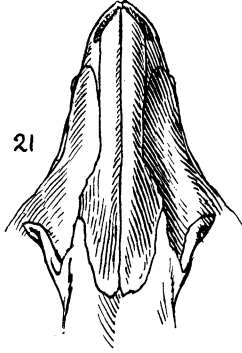


- Fig. 17. *Philander* sp. No. 2702. $\times 2$.
Fig. 18. *Metachirus* sp. No. 244. $\times 1$.
Fig. 19. *Caluromys derbianus*. No. 10058. $\times 1$.
Fig. 20. *Chironectes minimus*. No. 33027. $\times 1$.
Fig. 21. *Marmosa chapmani*. No. 4773. $\times 2$.
Fig. 22. *Didelphys virginiana*. No. 240. $\times 1$.
Fig. 23. *Borhyaena tuberata*. P. U. No. 15701. (After Sinclair.) $\times 1$.

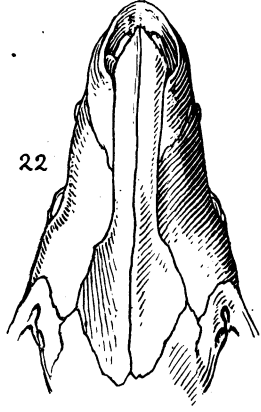
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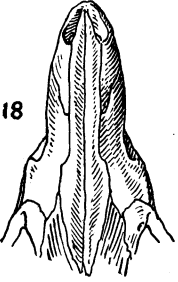
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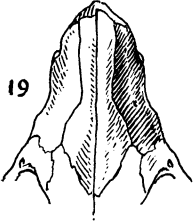
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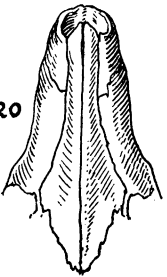
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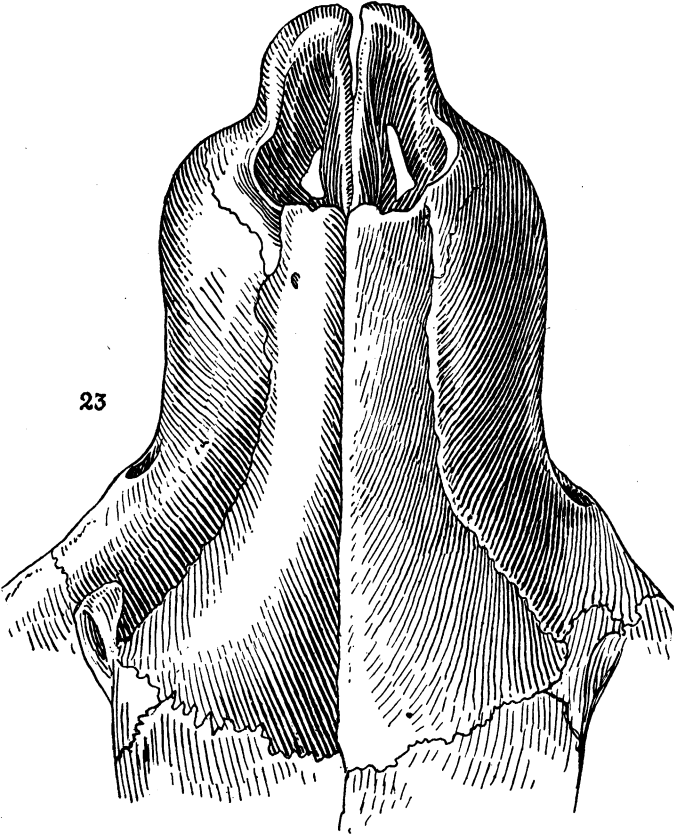
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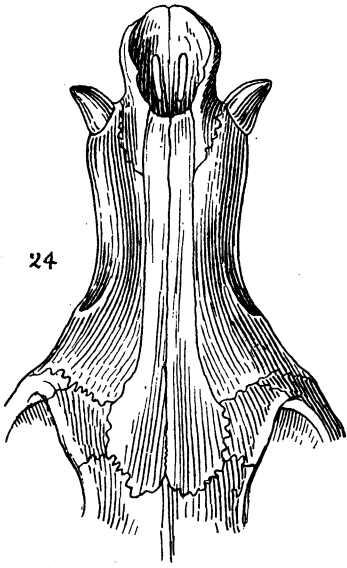
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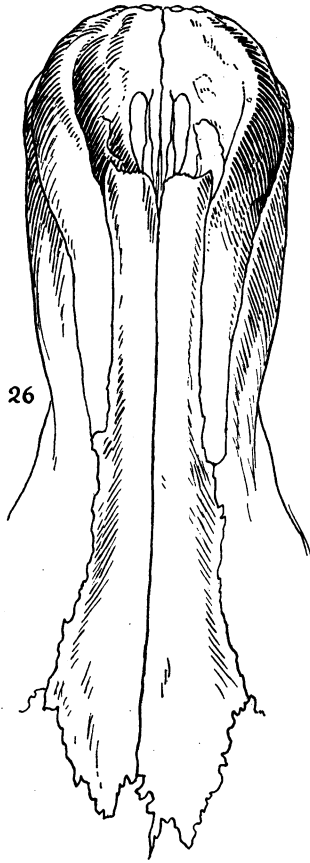
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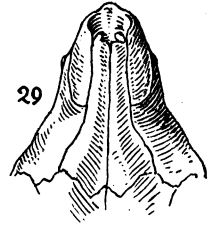
- Fig. 24. *Cladosictis lustratus*. P. U. No. 15046. (After Sinclair.) $\times 1$.
Fig. 25. *Amphiproviverra mazaniana*. No. 9254. $\times 1$.
Fig. 26. *Thylacinus cynocephalus*. No. 35504. $\times 1$.
Fig. 27. *Dasyurus viverrinus*. No. 16669. $\times 1$.
Fig. 28. *Sarcophilus ursinus*. No. 35106. $\times 1$.
Fig. 29. *Phascogale cristicaudata*. No. 15009. $\times 2$.
Fig. 30. *Antechinomys laniger*. No. 15012. $\times 2$.
Fig. 31. *Sminthopsis crassicaudata*. No. 15013. $\times 2$.



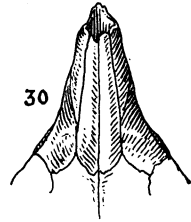
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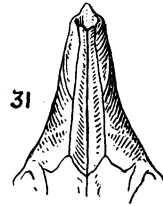
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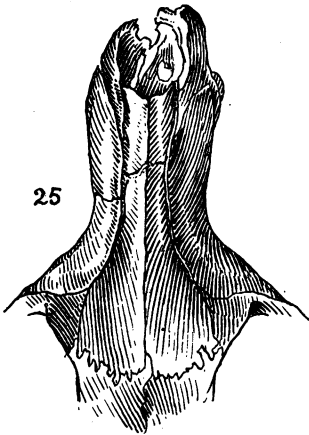
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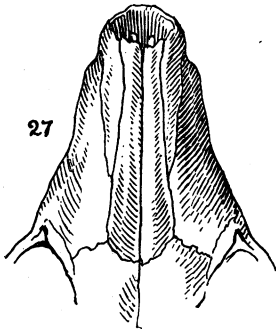
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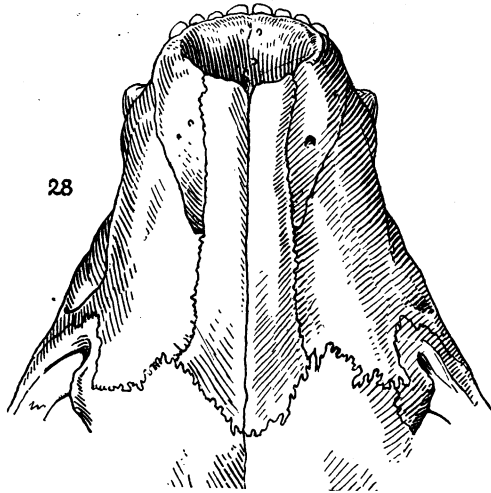
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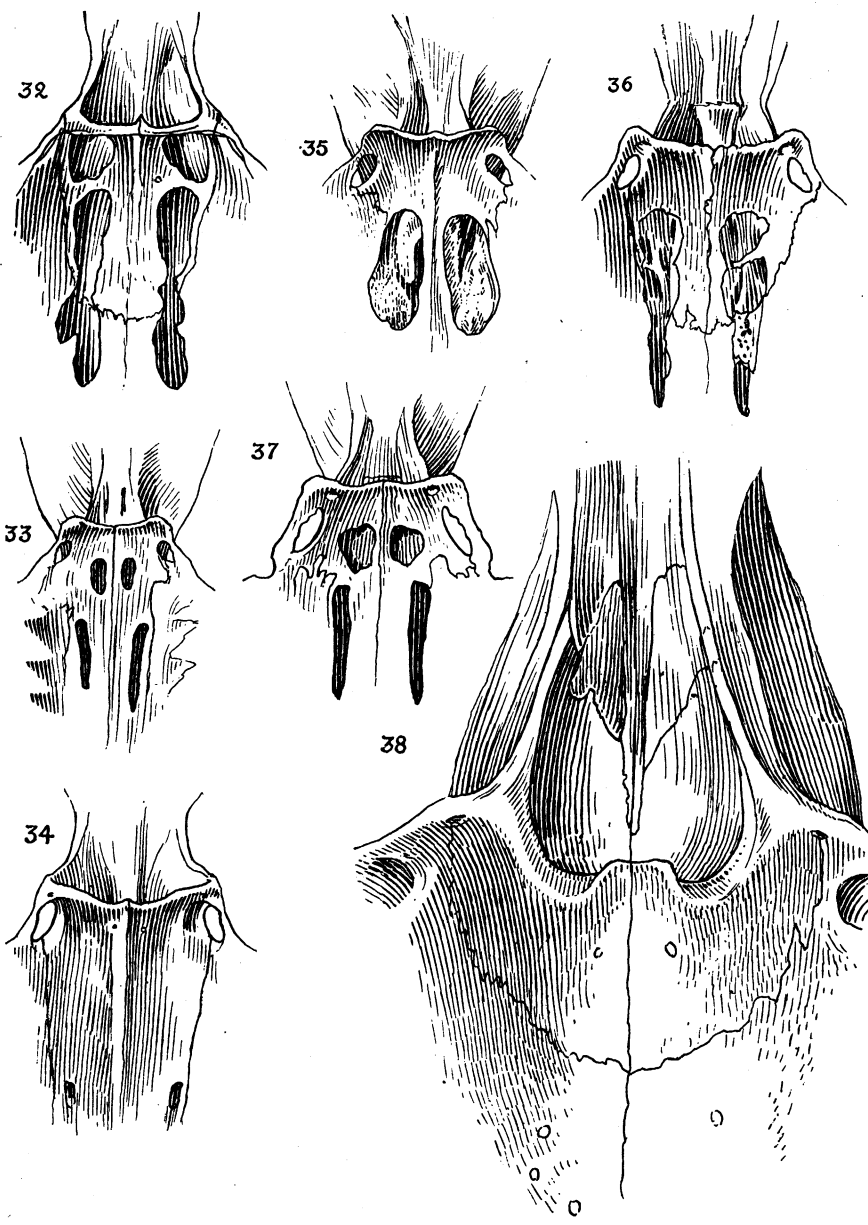


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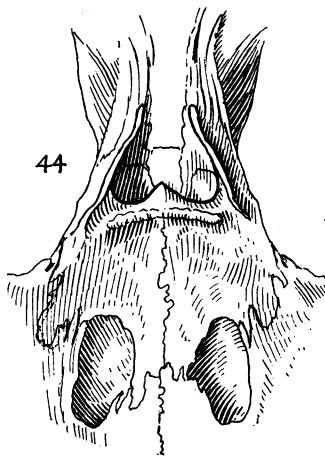
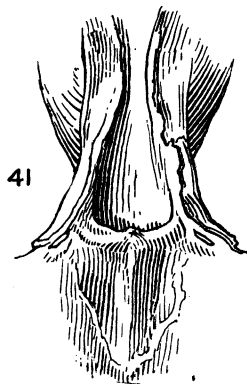
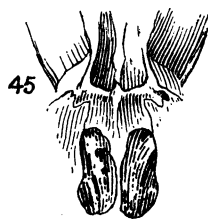
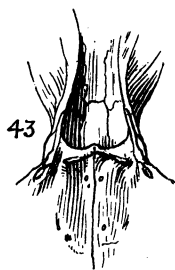
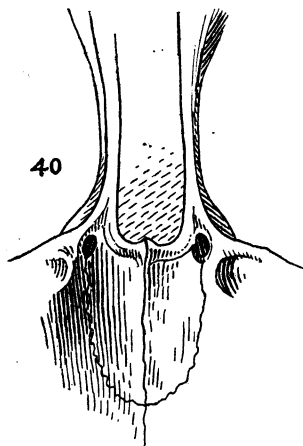
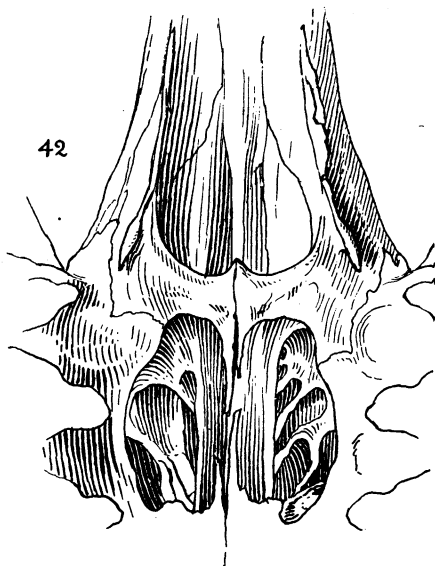
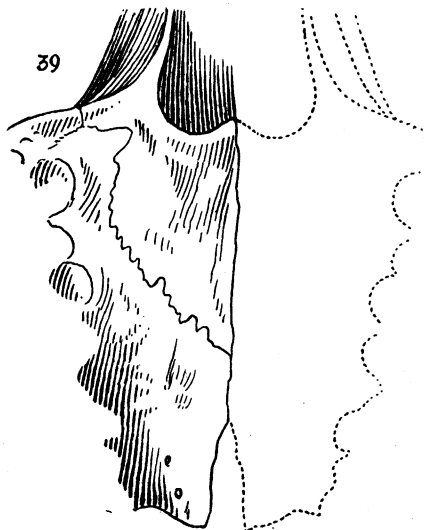


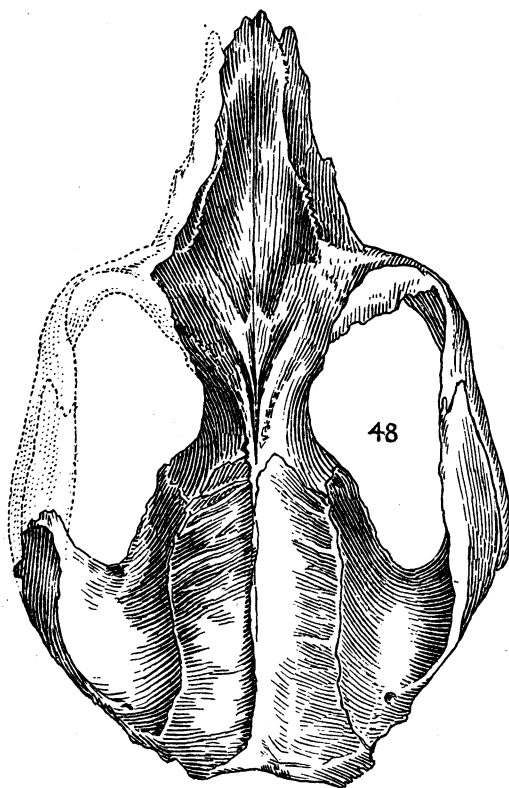
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- Fig. 32. *Philander* sp. No. 2072. $\times 4$.
Fig. 33. *Metachirus* sp. No. 244. $\times 2$.
Fig. 34. *Caluromys derbianus*. No. 10058. $\times 2$.
Fig. 35. *Chironectes minimus*. No. 33027. $\times \frac{3}{2}$.
Fig. 36. *Marmosa chapmani*. No. 4773. $\times 3$.
Fig. 37. *Didelphys virginiana*. No. 240. $\times \frac{5}{4}$.
Fig. 38. *Borhyæna tuberata*. P. U. No. 15701. (After Sinclair.) $\times 1$

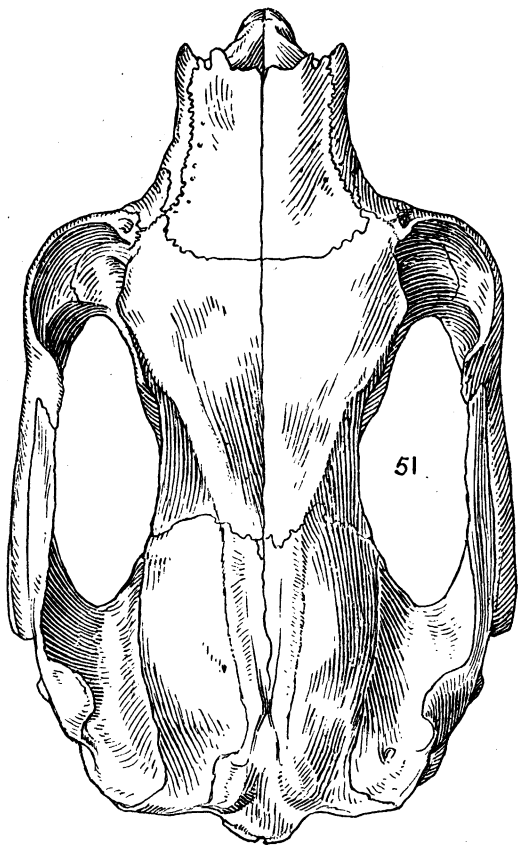
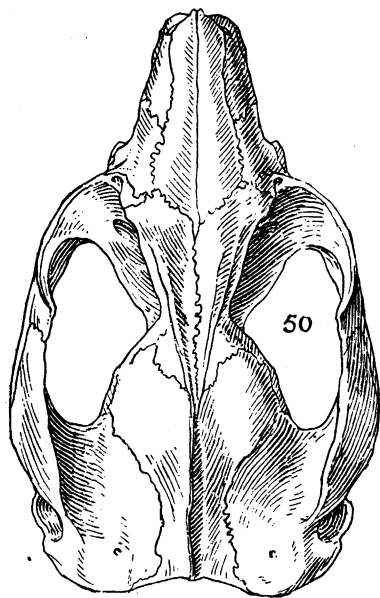
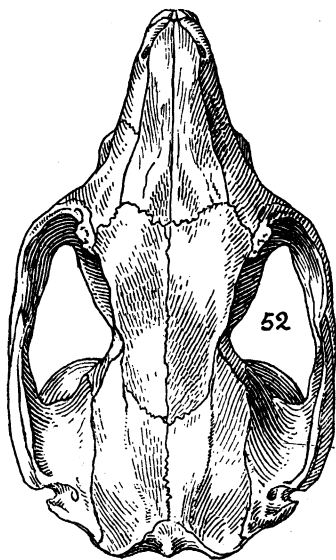
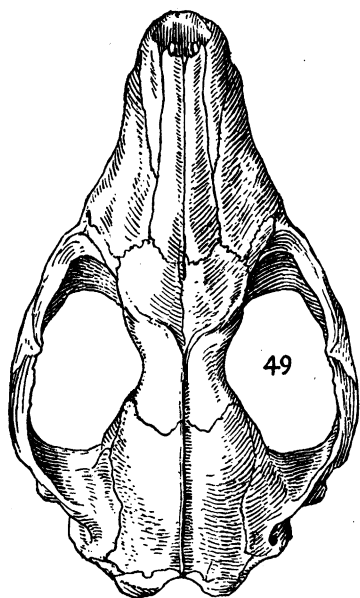


- Fig. 39. *Prothylacinus patagonicus*. P. U. No. 15700. (After Sinclair.) $\times 1$.
Fig. 40. *Cladosictis lustratus*. P. U. No. 15046. (After Sinclair.) $\times 1$.
Fig. 41. *Amphiproviverra mazaniana*. No. 9254. $\times 1$.
Fig. 42. *Thylacinus cynocephalus*. No. 35504. $\times 1$.
Fig. 43. *Dasyurus viverrinus*. No. 16669. $\times 1$.
Fig. 44. *Sarcophilus ursinus*. No. 35106. $\times 1$.
Fig. 45. *Phascogale swainsoni*. Raven Coll. 91. $\times 2$.
Fig. 46. *Antechinomys laniger*. No. 15012. $\times 2$.
Fig. 47. *Sminthopsis crassicaudata*. No. 15013. $\times 2$.

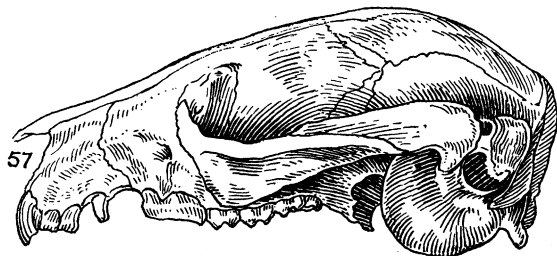
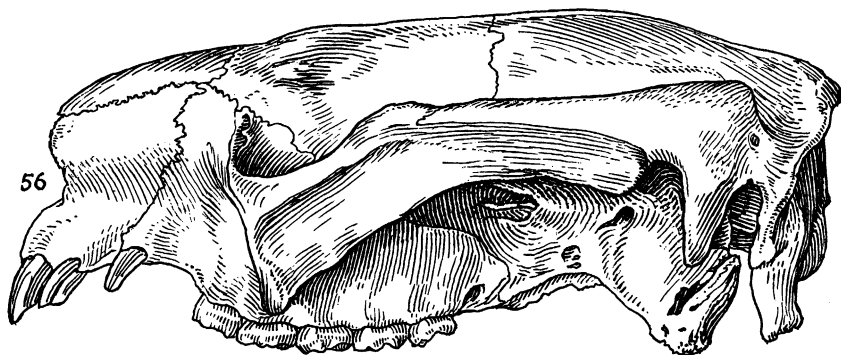
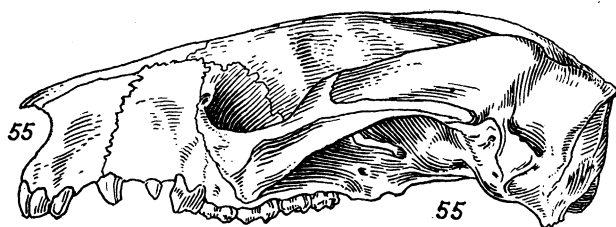
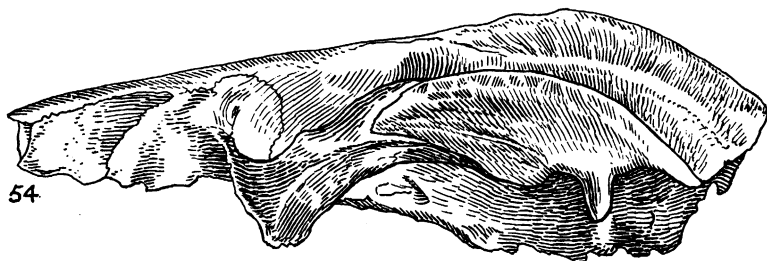
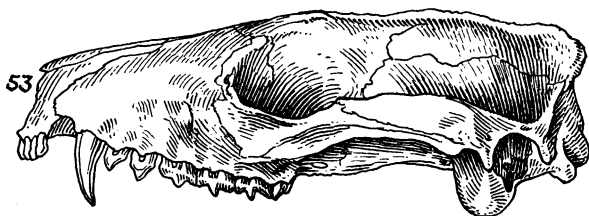




- Fig. 48. *Wynyardia bassiana*. (After Spencer.) $\times 1$.
 Fig. 49. *Dasyurus viverrinus*. No. 16669. $\times 1$.
 Fig. 50. *Trichosurus vulpecula*. No. 249. $\times 1$.
 Fig. 51. *Phascolarctus cinereus*. No. 42178. $\times 1$.
 Fig. 52. *Bettongia* sp. No. 6364. $\times 1$.



- Fig. 53. *Dasyurus viverrinus*. No. 16669. $\times 1$.
Fig. 54. *Wyngardia bassiana*. (After Spencer, reversed.)
Fig. 55. *Trichosurus vulpecula*. No. 249. $\times 1$.
Fig. 56. *Phascolarctus cinereus*. No. 42178. $\times 1$.
Fig. 57. *Bettongia* sp. No. 6364. $\times 1$.



NAME AND SPECIMEN	1. LOCALITY	2. DENTAL FORMULA	3. DECIDUOUS TEETH	4. PROTOCONE	5. METASTYLE SHEARING BLADE	6. PARASTYLE	7. Ps:Ms	8. MESOSTYLE	9. PA:ME	10. M ⁺	11. FIRST UPPER INCISORS	12. TIP OF UPPER JAW	13. TRIGONID	14. SYMPHYSIS	15. PALATAL VACUITIES	16. POSTERO-EXTERNAL CORNER OF PALATE	17. POSTERIOR EDGE OF PALATE	18. TEMPORAL FOSSA	19. ANTERIOR TIPS OF NASALS	20. POSTERIOR ENDS OF NASALS	21. NASAL LACHRYMAL BONES	22. POSITION OF ORBITS	23. LACHRYMAL FORAMEN	24. SUPRA-ORBITAL CREST	25. POSTORBITAL PROCESS OF FRONTAL	26. POSTORBITAL PROCESS OF JUGAL
<i>Thylamys keaysi</i> No. 16472	Peru	$I\frac{3}{2}C\frac{1}{1}P\frac{3}{3}M\frac{4}{4}$		Slightly higher than in <i>Didelphis</i>	Low	Large free cusp	Ps>Ms	Free cusp	Widely separate	Crushing	Enlarged and approximated	Pointed	Mtd>Pad	Ligamentous	Present	Pierced by foramen	High transverse ridge, notched by remnants of two foramina	Normal	Protracted	Very slightly spread	Widely separate	Anterior	Double or single; inside orbit	Absent	Absent	Present
<i>Philander</i> species No. 2072	South America	$I\frac{3}{2}C\frac{1}{1}P\frac{3}{3}M\frac{4}{4}$		Slightly lower than in <i>Didelphis</i>	Low	Fairly large, free cusp	Ps>Ms	Free cusp	Widely separate	Crushing	Enlarged and approximated	Pointed	Mtd>Pad	Ligamentous	Present	Pierced by foramen	High transverse ridge, notched by remnants of two foramina	Normal	Protracted	Very slightly spread	Widely separate	Anterior	Double; just inside orbit	Absent	Absent	Present
<i>Metachirus</i> species No. 244	Colombia	$I\frac{3}{2}C\frac{1}{1}P\frac{3}{3}M\frac{4}{4}$		As in <i>Didelphis</i>	Low	Large free cusp	Ps>Ms	Free cusp	Widely separate	Crushing	Enlarged and approximated	Pointed	Mtd>Pad	Ligamentous	Present	Pierced by foramen	High transverse ridge, pierced or notched by two foramina	Normal	Protracted	Slightly spread	Widely separate	Median	Double; on edge of orbit	Absent	Small	Absent
<i>Caluromys derbianus</i> No. 10058	Costa Rica	$I\frac{3}{2}C\frac{1}{1}P\frac{3}{3}M\frac{4}{4}$		Slightly lower than in <i>Didelphis</i>	Low	Small free cusp	Ps>Ms	Free cusp	Widely separate	Crushing	Enlarged and approximated	Pointed	Mtd>Pad	Ligamentous	Almost lost	Pierced by foramen	High transverse ridge, notched by remnants of two foramina	Normal	Protracted	Widely spread	Distinctly separate	Anterior	Double; on edge of orbit	Slight	Very large	Absent
<i>Chironectes minimus</i> Nos. 30752, 33027	Nicaragua	$I\frac{3}{2}C\frac{1}{1}P\frac{3}{3}M\frac{4}{4}$		Slightly lower and sharper than in <i>Didelphis</i>	Low	Very large, free cusp	Ps>Ms	Free cusp	Widely separate	Crushing	Enlarged and approximated	Broad point	Mtd>Pad	Ligamentous	Present	Pierced by foramen	High transverse ridge, pierced by two foramina	Normal	Protracted	Widely spread	Almost in contact	Anterior	Single; inside orbit	Absent	Large	Absent or slight
<i>Marmosa chapmani</i> Nos. 4473, 6123	Trinidad	$I\frac{3}{2}C\frac{1}{1}P\frac{3}{3}M\frac{4}{4}$		As in <i>Didelphis</i>	Low	Large free cusp	Ps>Ms	Free cusp	Widely separate	Crushing	Enlarged and approximated	Pointed	Mtd>Pad	Ligamentous	Present	Pierced by foramen	High transverse ridge, pierced by two foramina	Normal	Protracted	Slightly spread	Widely separate	Median	Double; inside orbit	Slight	Small	Small and blunt
<i>Didelphis virginiana</i> Nos. 238, 240, 616, 7370, 16675 <i>D. mesamericana</i> Nos. 6120, 16743	North America	$I\frac{3}{2}C\frac{1}{1}P\frac{3}{3}M\frac{4}{4}$	DP3	Prominent, blunt, almost on level with other cusps	Low	Large free cusp	Ps>Ms	Free cusp	Widely separate	Wide Crushing	Enlarged and approximated	Pointed	Mtd>Pad	Ligamentous	Present	Pierced by foramen	High transverse ridge, pierced by two foramina	Normal	Protracted	Widely spread	Separate or in contact	Anterior	Double; on edge of orbit; or single; inside orbit	Absent	Small or well-developed	Absent or minute
<i>Borhyaena tuberata</i> <i>B. exocata</i> After Sinclair	Patagonia	$I\frac{3}{3}C\frac{1}{1}P\frac{3}{3}M\frac{4}{4}$	DC DP3	Minute and very low		Small, plastered on paracone		Absent	Approximated	Shearing	Uniform with other incisors	Rounded	Mtd absent	Fused	Lost	Pierced by foramen	Thickened, no ridge	Very wide	Retracted	Widely spread	Wide or narrow contact	Markedly anterior	?Single; well inside orbit		Absent	Small
<i>Prothylacinus patagonicus</i> After Sinclair	Patagonia	$I\frac{3}{3}C\frac{1}{1}P\frac{3}{3}M\frac{4}{4}$	DP3	Very low		Fairly large, plastered on paracone		Absent	Approximated	Shearing			Mtd absent	Fused	Lost	Pierced by foramen	Thickened, no ridge	Very wide				Markedly anterior	?Single; well inside orbit			Absent
<i>Cladosictis petersoni</i> <i>C. lustratus</i> After Sinclair	Patagonia	$I\frac{3}{3}C\frac{1}{1}P\frac{3}{3}M\frac{4}{4}$	DC DP2 DP3	Very low		Fairly large, plastered on paracone		Absent	Approximated	Shearing	Uniform with other incisors	Rounded	Mtd absent	Ligamentous	Lost	Pierced by foramen	Thickened, no ridge	Wide	Retracted	Widely spread	Wide contact	Markedly anterior	?Single; well inside orbit	Large	Fair	Absent or minute
<i>Amphiproboscidea mazoniana</i> No. 9254, also after Sinclair	Patagonia	$I\frac{3}{3}C\frac{1}{1}P\frac{3}{3}M\frac{4}{4}$	DP3	Very low	High	Small, plastered on paracone		Absent	Approximated	Shearing	Approximated	Rounded	Mtd absent	Ligamentous	Lost	Pierced by foramen	Thickened, no ridge	Wide	Retracted	Widely spread	Wide contact	Markedly anterior	Single; well inside orbit	Large	Fair	Minute
<i>Thylacinus cynocephalus</i> Nos. 35504, 42259	Tasmania	$I\frac{3}{3}C\frac{1}{1}P\frac{3}{3}M\frac{4}{4}$	DP3	Very low	High	Fairly large, plastered on paracone		Absent	Approximated	Shearing	Uniform with other incisors	Rounded	Mtd absent	Ligamentous	Present	Bar enclosing foramen nearly lost	Thickened, no ridge	Wide	Retracted	Slightly spread	Widely separate	Median	Double; one inside orbit, one outside	Present	Fair	Sharp spike
<i>Dasyurus viverrinus</i> Nos. 16669, 35721, 42998	Australia	$I\frac{3}{3}C\frac{1}{1}P\frac{3}{3}M\frac{4}{4}$	DP3	Much lower than in <i>Didelphis</i> , with accessory pl, ml	High	Forms transverse ridge with paracone	Ps<Ms	Free cusp	Separate	Shearing	Uniform with other incisors	Rounded	Mtd>Pad	Ligamentous	Present or closed and spongy	Pierced by foramen; bar sometimes lost	Low transverse ridge, notched by two foramina	Fairly wide	Retracted	Slightly spread	Widely separate	Slightly anterior	Single; inside or on edge, or outside	Present	Fair	Sharp spike
<i>Sarcophilus ursinus</i> Nos. 35106, 35535	Tasmania	$I\frac{3}{3}C\frac{1}{1}P\frac{3}{3}M\frac{4}{4}$	None	Very low and small	High	Forms transverse ridge with paracone		Absent	Approximated	Shearing	Uniform with other incisors	Rounded	Mtd minute	Fused	Present	Bar enclosing foramen nearly lost	Low transverse ridge, notched by two foramina	Very wide	Retracted	Slightly spread	Widely separate	Slightly anterior	Single; on edge of orbit	Present	Good	Sharp spike
<i>Phascogale cristicavata</i> No. 15009 <i>P. ? macdonnellensis</i> No. 15011 <i>P. flavipes</i> <i>P. swainsoni</i> Raven Collection	Australia	$I\frac{3}{3}C\frac{1}{1}P\frac{3}{3}M\frac{4}{4}$		Much lower and sharper than in <i>Didelphis</i>	High	Forms transverse ridge with paracone	Ps<Ms	Free cusp	Separate	Shearing	Approximated	Rounded	Mtd>Pad	Ligamentous	Present	Pierced by foramen; bar sometimes lost	Low transverse ridge, unnotched	Fairly wide	Retracted	Widely spread	Widely separate	Markedly anterior	Double; inside orbit	Present	Absent	Small, blunt
<i>Antechinomys laniger</i> No. 15012	Australia	$I\frac{3}{3}C\frac{1}{1}(P\text{-form})P\frac{3}{3}M\frac{4}{4}$		Much lower than in <i>Didelphis</i>	Fairly high	Forms transverse ridge with paracone	Ps<Ms	Free cusp	Separate	Shearing	Approximated	Pointed	Mtd>Pad	Ligamentous	Closed by thin sheet of bone	Bar enclosing foramen lost	Low transverse ridge, unnotched	Fairly wide	Retracted	Very slightly spread	Widely separate	Anterior	Double; one inside, one outside orbit	Present	Absent	Wide, low
<i>Sminthopsis crassicaudata</i> No. 15013	Australia	$I\frac{3}{3}C\frac{1}{1}P\frac{3}{3}M\frac{4}{4}$		Distinctly lower and sharper than in <i>Didelphis</i>	Fairly high	Forms transverse ridge with paracone	Ps<Ms	Free cusp	Separate	Shearing	Approximated	Pointed	Mtd>Pad	Ligamentous	Present	Bar enclosing foramen lost	Low transverse ridge, notched by two foramina	Fairly wide	Retracted	Very slightly spread	Widely separate	Anterior	Single; on edge of orbit	Present	Absent	

NAME AND SPECIMEN	27. POSTORBITAL CONSTRICTION OF SKULL	28. TYMPANIC BULLA AND COMPONENTS	29. PAROCCIPITAL PROCESS	30. CONDYLAR FORAMEN	31. OCCIPUT	32. ATLAS	33. BACKWARDLY DIRECTED SPIKE ON ATLAS INTER- CENTRUM	34. ATLANTAL TRANSVERSE PROCESS	35. NEURAL PROCESS OF AXIS	36. NEURAL PROCESSES ON C3-7	37. LONGEST NEURAL PROCESS ON	38. VERTEBRAL ARTERY PIERCING TRANSVERSE PROCESS OF	39. VERTEBRAL FORMULA	40. ANTECLINAL VERTEBRA	41. SACRAL VERTEBRÆ COÖSSIFIED WITH PELVIS	42. ACROMION	43. ILIUM IN CROSS-SECTION	44. ACETABULUM	45. MARSUPIAL BONES	46. PATELLA	47. ECTOCUNEIFORM	48. HALLUX	49. TERMINAL PHALANGES
<i>Thylamys keaysi</i> No. 16472	Slight	Well-developed; alisphenoid, tympanic, periotic, mastoid																					
<i>Philander</i> species No. 2072	Slight	Perfect; alisphenoid, tym- panic, periotic	Absent			Solid ring	Absent	Short and little con- stricted proximally	Reduced to small ridge.	Almost lost	C7	C2-7	D12, L7, S2	D11?	2		Flattened tri- angle	Widely open on to ischium	Large	Unossified		Complete, divergent	
<i>Melachirus</i> species No. 244	Some	Incomplete alisphenoid bulla as in <i>Didelphis</i>	Long, rod-like, directed down and back	Double	Descends to level of basis cranii																		
<i>Caluromys derbianus</i> No. 10058	Some	Incomplete alisphenoid bulla, slightly better than in <i>Didelphis</i>	Long, longitudi- nally plate-like, directed back and down	Double	Descends to level of basis cranii																		
<i>Chironectes minimus</i> Nos. 30752, 33027	Very great	Incomplete alisphenoid bulla, slightly better than in <i>Didelphis</i>	Short, rod-like, directed down	Double	Does not descend to level of basis cranii																		
<i>Marmosa chapmani</i> Nos. 4473, 6123	Some	Incomplete; alisphenoid, tympanic	Short, longitudi- nally plate-like, directed down	Double	Does not descend to level of basis cranii	Solid ring	Absent	Short and little con- stricted proximally	Hooked back over C3	Reduced and stubby	C2	C2-7	D12, L7	D11?		Fairly short, wide, tri- angular	Flattened tri- angle	Open on to ischium	Large	Unossified			
<i>Didelphis virginiana</i> Nos. 238, 240, 616, 7370, 16675 <i>D. mesamericana</i> Nos. 6120, 16743	Considerable	Incomplete alisphenoid bulla	Long, rod-like, par- occipital directed down and slightly back	Double	Descends to level of basis cranii	Solid ring	Minute or absent	Short and little con- stricted proximally	Stout, not projecting back over C3	High and thick	C3, 4	C2-7	D12, L7, S2	D11	2	Short, wide, triangular	Flattened tri- angle	Open on to ischium	Large	Unossified	Variable; unsupport- ed by cuboid (3 specimens) or largely supported (1 spec- imen)	Complete, divergent	Uncleft
<i>Borhyaena tuberata</i> <i>B. exarata</i> After Sinclair	Some	Alisphenoid bulla com- menced	Transverse, plate- like, well-devel- oped	Double	Descends far be- low basis cranii, even below con- dyles	Free inter- centrum	Present	Long and constricted proximally	Halberd-shaped, hooked back over C3	Long and spiked	C7	C2-7											Cleft
<i>Prothylacinus patag- onicus</i> After Sinclair			Short, stout, rod- like, directed back, down, and out	Double	Descends below level of basis cranii	Solid ring	Absent	Long and constricted proximally	Halberd-shaped, hooked back over C3	Long and spiked		C2-7		D10	1		Flat	Open on to obtur- ator foramen		Ossified	Partly supported by cuboid	Reduced to metatarsal	Cleft
<i>Cladosictis petersoni</i> <i>C. lustratus</i> After Sinclair	Considerable					Solid ring	Absent	Long and constricted proximally	Halberd-shaped, hooked back over C3	Long and spiked	C7	C2-7	D13, L6, S2	D10	1	Long, narrow parallelogram	Flat	Open on to obtur- ator foramen	Absent		Partly supported by cuboid	Reduced to metatarsal	Uncleft
<i>Amphiprociaverra mazaniana</i> No. 9254, also after Sinclair	Great	Alisphenoid bulla com- menced	Transverse, plate- like, well-devel- oped	Single	Descends far be- low level of basis cranii, even below con- dyles	Free inter- centrum	Absent	Long and constricted proximally												Ossified	Chiefly supported by cuboid	Divergent, dis- tal end un- known	Uncleft
<i>Thylacinus cynoceph- alus</i> Nos. 35504, 42259	Some	Alisphenoid bulla not quite complete	Long, diagonal, rod-like, with ex- panded base, di- rected down and back	Double	Descends to level of basis cranii	Free inter- centrum	Present	Long and constricted proximally	Halberd-shaped, hooked back over C3	Long and spiked	C7	C2-7	D13, L6, S2	D10	1	Short, stout parallelogram	Flat	Open on to obtur- ator foramen	Vestigial	Unossified	Chiefly supported by cuboid	Absent	Cleft
<i>Dasyurus viverrinus</i> Nos. 16669, 35721, 42993	Considerable	Perfect alisphenoid-tympanic bulla	Diagonal, rod-like, with expanded base, directed down and back	Double	Descends far be- low level of basis cranii	Solid ring	Large or absent	Long and constricted proximally	Halberd-shaped, bent back over C3	Long and spiked	C7	C2-6 C7 pierced or not	D12, L7, S2	D9	1	Long, narrow, triangular	Rather flat	Open on to obtur- ator foramen	Large	Unossified	Partly or slightly sup- ported by cuboid	Reduced to metatarsal	Cleft
<i>Sarcophilus ursinus</i> Nos. 35106, 35535	Very great	Perfect alisphenoid-tympanic bulla	Stout, short, rod- like, directed back and down	Double	Descends below level of basis cranii	Solid ring	Present	Long and constricted proximally	Halberd-shaped, bent back over C3	Spiked	C7	C2-7 Bar below lost on C7	D11, L8, S3	D9	2		Rather flat	Open on to obtur- ator foramen	Large	Unossified	Partly supported by cuboid	Reduced to metatarsal	Cleft
<i>Phascogale cristicau- data</i> No. 15009 <i>P. ? macdonnellensis</i> No. 15011 <i>P. flavipes</i> <i>P. swainsoni</i> Raven Collection	Some	Perfect: alisphenoid, tym- panic, periotic, squamosal, exoccipital, mastoid	Absent, region in- volved in bulla	Double	Crowded high up skull by bulla	Solid ring	Short	Medium and con- stricted proximally	Halberd-shaped, somewhat or not at all bent back over C3	Lost except on C7	C2	C2-6	D12, L7, S2	D9?	1	Long, narrow, triangular	Rather flat	Open on to obtur- ator foramen		Unossified	Partly or slightly sup- ported by cuboid	Complete but small, not divergent	
<i>Antechinomys laniger</i> No. 15012	Some	Perfect: alisphenoid, tym- panic, periotic, squamosal, exoccipital, mastoid	Absent, region in- volved in bulla	Double	Crowded high up skull by bulla				Almost lost	Almost lost	C2		D13, L6	D9			Rather flat	Open on to obtur- ator foramen		Unossified		Absent	
<i>Sminthopsis crassi- caudata</i> No. 15013	Some	Perfect: alisphenoid, tym- panic, periotic, mastoid	Absent, region in- volved in bulla	Double	Crowded high up skull by bulla					Absent			D13, L6, S3			Long, narrow, triangular	Rather flat	Open on to obtur- ator foramen		Unossified		Complete but very small, not divergent	

