

# THE MONOTREMES AND THE PALIMPSEST THEORY

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## INTRODUCTION

### THE AMBIGUOUS MONOTREMES AND THE SEARCH FOR THEIR ANCESTORS

THE "DUCK-BILLED PLATYPUS" or "duck mole" (*Ornithorhynchus*) of Australia is popularly supposed to be "a missing link between animals [mammals] and birds," but modern zoologists regard it rather as a kind of link between mammals and the later mammal-like reptiles of Triassic age. It has been abundantly shown that the bird-like features of the platypus are due solely to convergent evolution. But in spite of the enormous amount of study that has been devoted to the platypus and its relative, "echidna" (*Tachyglossus*), they have not hitherto been securely tied in with any known extinct or recent group of mammals, and their anatomical structure abounds in peculiar features of debatable derivation.

Fossil remains of monotremes in the Pleistocene deposits of Australia (Owen, 1884) differ but little from the existing forms, and the earlier fossil history of the group is unknown. On account of their egg-laying habits and of the resemblances in the reproductive organs to birds and reptiles, the monotremes were referred by De Blainville (1834) to a distinct subclass of mammals named "Les Ornithodelphes" in contrast to the second subclass, "Les Didelphes" (marsupials), and a third, "Les Monodelphes" (placentals). De Blainville was followed in essentials by Gill (1870), Huxley (1872, 1880), and most later authors. Mivart (1866), chiefly on the basis of the reptilian characters of the reproductive organs, even regarded the monotremes as wholly separate from the other mammals and assumed that the mammals were of diphyletic origin (M. Weber, 1928, p. 22). Essentially the same conclusion has been reached for other reasons by the paleontologists Matthew (1927, p. 948) and Simpson (1928, p. 183), who separated the Monotremata very widely from the Marsupialia and Placentalia, placing them on the extreme margins of their phylogenetic diagrams, far away from the marsupials and placentals and at the end of a totally unknown line leading back to a possible deriva-

tion from the therapsid stock in the Trias (Simpson), or Permian (Matthew).

But Max Weber (1904) cited numerous characters tending to show that in spite of their "reptilian features" and peculiar specializations the monotremes are true mammals, and in "The orders of mammals" (1910, pp. 144-162) I gave a fairly extensive analysis of a wide range of monotreme characters and concluded (p. 158) that "the ancestral lines of Marsupials and Monotremes converge into a common source which had already acquired many essentially mammalian characters." In the second edition of "Die Säugetiere," Weber and Abel (p. 39) state in substance that they endorse the conclusions of Gregory (1910), namely, that the monotremes are derived from true mammals that were also the ancestors of the marsupials and placentals, and that the Mammalia are thus monophyletic.

Broom (1914) noted several points of resemblance in the structure of the skull between the Lower Eocene multituberculate "*Poly-mastodon*" (*Taeniolabis*) and the modern *Ornithorhynchus*. He concluded (p. 134) that "from a Middle Jurassic herbivorous Multituberculate there probably arose the line which after considerable specialization and degeneration resulted in the Monotremes."

Simpson (1937, pp. 759, 760), after an intensive analysis of the available material, concluded that such resemblances as there are between the monotreme basicranium and that of the multituberculate *Psilodus* are superficial and that there is no good evidence for the transformation of multituberculates into monotremes.

In the course of a review of the history of the theory of trituberculy (1934a, p. 263) I referred in passing to the problem of the origin of the monotremes as follows: "There are so many deep-seated mammalian characters of the brain, hair, milk glands, etc., of monotremes that a separate derivation from Triassic reptiles is very difficult to accept. My tentative hypothesis is, therefore,

that the *Ornithorhynchus* is an excessively specialized derivative from the Australian phalangeroid stem, that its 'beak' represents an enormously hypertrophied rhinarium of the type seen in *Phascolarctos* and that the two V's of its upper molars correspond with those of *Phascolomys*; also that the 'reptilian' characters of its reproductive organs have arisen from a neotenuous arrest of ontogenetic phases that are transient in the diprotodonts; that excessive aquatic adaptation accounts for many of the other specializations of the skeleton."

In discussing the evidence from the development of the teeth upon the problem of the origin of the monotremes, Green (1937) referred to the previous suggestions as follows: "Recently, Gregory (1934, p. 262) states that Simpson's figures (1929) suggest to him a possible derivation of the teeth of *Ornithorhynchus* by excessive degeneration from a 'somewhat *Caenolestes*-like stage'. A little later on I show that I agree with Simpson in considering any derivation from a tritubercular type of tooth to be most unlikely. Gregory goes a step farther and puts forward the 'tentative hypothesis' that *Ornithorhynchus* is an extremely specialized derivative from the Australian phalangeroid stem. He suggests that the 'beak' of *Ornithorhynchus* represents an enlargement of such a rhinarium as is seen in *Phascolarctus*, and he compares the double 'V' pattern of the upper molars with that of *Phascolomys*. He dismisses the 'reptilian' characters of, for example, the reproductive organs of *Ornithorhynchus* by saying that they have arisen 'from a neotenuous arrest of ontogenetic phases that are transient in the diprotodonts'. I fail to see any material evidence in favour of such a view; it can surely only be looked upon as a despairing attempt to draw *Ornithorhynchus* into the 'recognized' mammalian fold."

### THE PALIMPSEST THEORY

For many years past the problem of the origin and relationships of the monotremes has been discussed from time to time with graduate students of the Columbia University course on the evolution of the mammals,

and with my late colleague, Henry Cushier Raven, whose collecting in Australia (1921-1922) had made considerable material available to us. Frequent study of monotreme skeletons in comparison with those of marsupials and placentals, together with a re-study of other evidence cited in the literature, led to the present attempt to apply the general methods of what may now be called the "palimpsest theory" to the problem of the origin of the monotremes. According to this theory, which I have hitherto set forth, but without naming it, in various papers on "Habitus and heritage" (1910, pp. 111, 112; 1922, 1929, 1936a, 1936b), the entire picture of the habits, behavior, physiology, and morphology of any animal type at a given geologic period is due to a complex of "habitus" and "heritage." The former is the totality of habits and anatomical characteristics that have been assumed during the latest life habits of the type; the heritage, on the other hand, is the totality of habits and characteristics inherited from earlier life habits. Obviously habitus and heritage are correlative terms, and the remainders of the successive habitus of the remote ancestors become incorporated into the heritage of later times. In general the habitus tends to overlay and obscure more remote heritage features, somewhat as the later writing on a palimpsest hides the partly erased image of the earlier writing. According to this system, all the successive habitus of the ancestors are prerequisite for the final habitus of their descendant. This is the factual basis for the belief by some specialists in a sort of phylogenetic predestination, which is perhaps misnamed orthogenesis.

### POSTULATES AND PROPOSITIONS

For the purpose of the present work I shall assume the general validity of Simpson's conclusions that the monotremes have not been derived from the multituberculates and that they are at least not demonstrably derived from the microcleptids, the triconodonts, the docodonts, or any other known Mesozoic mammals. I am of course not denying that the monotremes, in common with, and perhaps even to a greater degree than,



other recent mammals, retain parts of the ground plan of the Triassic cynodonts and other progressive therapsid reptiles. On the other hand, I shall attempt to apply the palimpsest theory to the following theses: (1) that the existing monotremes are, on the whole but with certain exceptions, far more

specialized away from the primitive mammalian type than are any of the known marsupials; (2) that the monotremes have been derived, probably within the Australasian region and by relatively rapid divergence, from the ancestors of some of the Australian marsupials.

## SURVEY OF EVIDENCE

### HABITS AND BODY FORM

THE DUCK-BILLED PLATYPUS is well adapted for a peculiar combination of habits which are separately shown in part in ducks, beavers, otters, muskrats, moles, seals, sirenians, and other partly aquatic or partly fossorial vertebrates. Its spatulate bill variously suggests the bills of ducks, spoonbill ibises, spoonbill sturgeons, and spoonbill dinosaurs. With it, it snaps up and shears water shrimps, probes the mud, and probably picks up bits of stems and weaves a very bird-like nest for its young. However, many other mammals (e.g., meadow mice, muskrats, etc.) build nests quite as bird-like. According to Fleay (1944) the wet leaves and grass are carried into the burrow by the curled-up tail (? another suggestion of marsupial habits). It lays small but sizable eggs well filled with yolk and protected by a thin horny shell. It probably incubates the eggs, and the young break out by vigorous use of the "egg-tooth" on top of the bill. The right and left oviducts remain completely separate down to the long cloaca (hence the word "Ornithodelphia," bird womb); there is a shell gland in each oviduct. The penis in some ways recalls that of reptiles, and the testes remain abdominal, never descending into a scrotum.

As if to emphasize this claim for relationship with the birds, the male monotremes exhibit a large curved spur projecting backward from their ankles, like the spurs of a cock. But these spurs, like the fangs of an adder, are each pierced by a duct and connected with a large gland containing albuminous fluid. Thus equipped, the males, at least during the breeding season, can and do inflict wounds that are poisonous to other animals. The spurs are probably also used as claspers in breeding and fighting (Burrell, 1927, pp. 76-104).

At least in captivity, the platypus, like some of the shrews, consumes an enormous amount of food in proportion to its weight (Burrell, 1927, p. 216).

The platypus has typical mammalian blood corpuscles of about the same size as

those of man (Burrell, 1927, p. 56). Wood Jones (cited by Burrell, 1927, pp. 56-58) states that during the period of partial hibernation or estivation the temperature of the echidna tends to follow the temperature of the outside air, "but this fall in winter temperature is found in all hibernating or partially hibernating animals; and it can only be said that the Monotremes are animals having a rather low body temperature, but, nevertheless, being truly homeothermic (or 'warm-blooded') within certain limits of temperature and in the non-hibernating period. They have a typically good mammalian heat-regulating mechanism, effective between 27.6° C. and 32.6° C.; and it is only when the temperature is raised or lowered beyond these limits that the regulation tends to break down and they behave as poikilothermic animals."

The body of the duckbill is well rounded transversely and somewhat wider than high. Its very large tail is flattened dorsoventrally somewhat as in the beaver, and with its aid the creature dives and swims very quickly. Thus the body form belongs to the "flat-boat type," along with those of plesiosaurs and other surface-swimming and diving types. The very short, strong legs are adapted for a crawling position, with the elbows and knees raised and sharply everted (Burrell, 1927, pp. 12, 52). In this it suggests certain Permian reptiles, but the crooked pose of the limbs (pl. 1) greatly facilitates rapid digging and swimming and quick passage through the winding tunnels. The hands are very large, more or less seal-like, armed with large claws used in digging, but with a broad webbed margin used in swimming; this can be folded in when walking or digging. The hind feet are similar but shorter, more spreading. The "duck-mole" is a fast and tireless digger and makes very long winding tunnels with underwater openings and large nursing chambers along the river banks (Burrell, 1927, pp. 105-136).

The "spiny anteater," "porcupine," or echidna (*Tachyglossus*) is thoroughly terrestrial and feeds chiefly on ants and insects,

probing the earth with its long pointed bill and lapping up the ants with its sticky prehensile tongue. Wood Jones (1923, pp. 43, 44) writes of the echidna's digging habits as follows:

"The animal is a burrower of the most remarkable kind, and its powers of clinging to, and sinking into the earth, can hardly be appreciated by those who have not witnessed the process. If an *Echidna* be placed upon a hard surface into which it is unable to burrow, it is capable of making off at a good pace, but the moment that it encounters ground into which it can dig, it ceases all attempts to escape by shuffling along and proceeds at once to sink directly downwards into the earth. In this process it does not burrow in head first, as do most burrowing animals, but it sinks in, in a way that can only be described as all-over-at-once. If it be interfered with in the preliminary stages of this process of digging itself in, it will be found that the animal appears to be miraculously stuck to the ground; and, once it has started to descend, it is almost impossible to arrest its progress and draw it back.

"Although these extraordinary powers of digging are commonly said to be the natural endowment of an animal which obtains its food by 'digging up the ant or termites' nests with its powerful limbs,' this time-honoured explanation is far from satisfactory. The digging of *Echidna* in its normal manifestation is certainly a protective mechanism; it is an elaborated method of avoiding its enemies, rather than a perfected means of obtaining its food. Even when it is quite unable to dig below the surface, it still shows its wonderful powers of clinging to the earth, for given any irregularities of surface of which it can take advantage, it will manage to wedge itself so securely, by the aid of its stout feet and its bristles, that it is practically impossible for an enemy to dislodge or even to injure it. In the same way it will wedge itself into the corner of its cage when confined; and an extension of the same process permits it to ascend to the corner of its box in a manner rather surprising in an animal which has, apparently, so little adaptation to climbing activities. Its strength is very remarkable, and it is difficult to devise any cage in which

it can be kept under observation, for its stout little limbs and powerful claws are capable of tearing a way through most materials.

"Some idea of the strength of the animal may be gained from the experience of an Adelaide zoologist who put an *Echidna* in his kitchen for the night. Next morning all the furniture—the heavy dresser, the table, chairs, boxes, etc.—was found moved from the walls towards the middle of the room. The gas stove, which was fixed by its pipe, alone withstood the animal's efforts at removal."

#### HAIR AND MILK GLANDS

Wood Jones (1923, p. 46) notes that "The Platypus is clothed with a dense fur, which consists of a beautifully soft woolly underfur, concealed by a longer, harsher coat of shining hairs. The general colour of the dorsal surface of the head and body, and of the outer aspect of the limbs, is a deep umber brown, looking, of course, a great deal darker when the animal is wet. The ventral surface and the inner aspect of the limbs is slightly paler than the general body colour. . . . Hair extends only just beyond the wrist upon the back of the manus; but on the pes, hair is present right down to the extremities of the digits."

These are of course wholly mammalian, completely unreptilian conditions. The co-existence of woolly under fur and longer harsher outer hairs is paralleled among seals and other aquatic mammals. Thick woolly fur is also found among the phalangeroids; e.g., the hairy-nosed wombat has the "coat fairly long, soft and silky" (Wood Jones, 1924, p. 266), while the common wombat has the "coat fairly long but coarse and harsh. Underfur sparse or absent" (*ibid.*, p. 264). Thus the hairy coat of the platypus, at least in its macroscopic characters, is completely mammalian. In enlarged cross sections of hairs, the observations of Poulton (1894) and of Spencer and Sweet (1899) show that some hairs of the platypus are from the first not radially symmetrical in section, as usually in mammals, but flattened dorsoventrally, with the cortical layers thicker on the dorsal surface. The arrangement of the platypus hairs and hair bundles into groups, as figured by

De Meyere (cf. Weber, 1927, vol. 1, fig. 10), suggests those of the beavers and the otters.

In the echidna the outer hairs for the most part are enlarged and spine-like, but in both the Tasmanian echidna (*Echidna aculeata setosa* Thomas) and the New Guinea *Zaglossus* the spines are slender and the hair is long. The nearest parallels to this spinous development are to be found among the centetoid insectivores and hystricomorph rodents. In a young echidna (Römer, 1898, pl. 1, fig. 11) in certain regions of the body each spine hair protrudes from the apex of a broadly triangular, scale-like structure. These structures are arranged in rows which alternate and overlap in an irregular, scale-like manner. They are not, however, true scales and are indeed less reptilian in structure than are the scales of the scaly anteater (*Manis*), whose mammalian status is indisputable. In the other direction, there are no known reptiles whose scales even remotely approach the furry coat of the platypus. To assume that the platypus merely parallels other mammals in possessing this and other diagnostic mammalian characters and that its ancestors separated from the mammalian stock in Triassic times is to push the principle of parallelism beyond the limit of available evidence and to beg the question at issue.

The presence and functional value of milk-giving glands on the ventral surface of the female is another diagnostic mammalian character possessed by the monotremes, and the ability of the young to suck or imbibe this milk is another. That the mammary areas are not supplied with projecting nipples to which the young could be attached, as in the marsupials, may well be connected in the platypus with the high specialization for aquatic life and the inconvenience and risk involved if the young were attached to the body in swimming and digging.

The nesting habit is perhaps only second in survival value to the habit of keeping the young in safe underground chambers; even the entrance to these chambers may be temporarily closed up during the mother's absence on food-getting forays (Burrell, 1927, pp. 129-132). And since the monotremes are indubitable mammals and not birds, their entire nesting and breeding complex may

well be a relatively recent acquisition.

In the monotremes there is a powerful development of the mammalian panniculus carnosus muscles (Ruge, 1895), and by their means the echidna can erect its spines and wave them when it is digging. The limbs, like those of the platypus, are widely everted at the knees and elbows and digging is facilitated by a somewhat screw-like movement of the paddle-like hind feet. As here interpreted, the digging habitus of echidna is even more specialized than that of the platypus and is merely convergent towards the crawling and digging habitus of certain Permian reptiles.

#### MUZZLE AND FOREHEAD

The skin covering the broad, flattened bill of the platypus is thus described by Wood Jones (1923, pp. 46, 47): "The naked skin of the flattened muzzle, or 'beak,' is of a suffused purplish, slate-colour above and pale flesh-coloured, or mottled below; and it is extremely delicate in texture. The dorsal surface is finely marked by minute pores, somewhat like those seen on the skin of the palm of the human hand. From the flattened dorsal portion of the beak a free fold of the same delicate naked skin is carried back over the anterior part of the fur-covered face. This fold forms a sort of shield, extending backwards almost as far as the eye. . . . The lower (or mandibular) portion of the muzzle is covered by skin similar in texture to that of the maxillary portion, but the little pores or pits are arranged more definitely in a linear series. From the lower jaw, as from the upper, a folded back portion, like the turned back cuff of a sleeve, overlaps the fur-covered throat." The linear arrangement of the little pores on top of and below the beak is admittedly convergent towards the somewhat similar arrangement of lateral line pits on the head of many fishes. "That the whole of the soft skin of the beak is a highly important sense organ," writes Wood Jones (p. 52), "is quite definite. The minute structure of the tactile organs in the skin and their connections with the nerves tell us this; and so do the observations of Bennett—'if the mandibles were touched they darted away immediately, the parts appearing to be remark-



ably sensitive.' " The lateral margins of both the upper and lower jaws of the bill bear obliquely transverse lamellae or sharp ridges, which may serve to give the platypus a firm hold upon the fresh-water shrimps and even to aid in shearing off their appendages. These lamellae may also let the water and fine mud drain outward while the shrimp or other prey

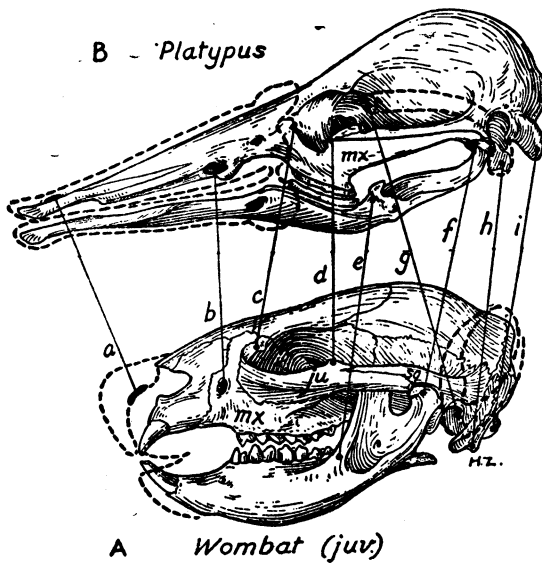


FIG. 1. Skulls of young wombat, representing a diprotodont marsupial, and platypus, the latter showing greater specialization. Broken lines indicate position of rhinarium and "bill," also of external ears. Guide lines connect homologous points and indicate differential shifts in growth rates toward platypus stage.

is firmly held in the mouth. Their analogies with the ridges on the bills of certain ducks are again obviously convergent.

But since this spatulate bill is evidently not inherited from reptiles, from what structure found among other mammals could it have evolved? Some years ago Raven suggested that it was truly homologous with the rhinarium, a hairless area of naked skin on the noses of the koala and other phalangers, wombats, and *Notoryctes*. This hint was indeed the first clue to the present possible solution of the entire monotreme problem which is here proposed. Presumably the ancestral monotreme had a large rhinarium even before it took to mud-grubbing habits.

In the "week-old" young platypus figured by Burrell (1927, pl. 23, p. 134) the muzzle is relatively short, and even in the young of "about three weeks" the concave lips are said to be "adapted for sucking" (*op. cit.*, pl. 33, fig. 2, p. 206).

In an embryo American opossum, Selenka (1887, quoted by McCrady, 1938, p. 168) found the mouth surrounded by a great cornified oral shield (fig. 17), which he interpreted as a remnant recalling the beak of the platypus. The latter, however, may rather be a specialization of a more primitive muzzle shield, of which both the "egg-tooth" (os carunculae) of the foetal platypus and the rhinarium of certain marsupials may also be remnants. All these structures in turn may represent fragments of the epidermal muzzle tissue of reptiles, but the bill of the platypus may have begun its present specializations in fairly early developmental stages—where indeed among other mammals many new specializations first begin to appear.

It is evident from Burrell's observations that the bill of the platypus is of vital importance to the animal and, as the analogies cited above suggest and as already noted, spatulate bills have likewise been evolved independently in several widely different groups of vertebrates. In the platypus line, as the muzzle became very large, the sensory skin of the rhinarium extended downward around the under side of the lower jaw and backward to form the flaps or collar above and below.

The paired oval nostrils of the platypus (fig. 2) are on top of the bill near the front end and open upward. The small eyes are also dorsally placed and look upward and outward, as do those of crocodiles, hippopotami, and other semi-aquatic vertebrates. The ear holes likewise are well seen in the top view and open chiefly upward. All these are merely indications of surface-floating habits.

The bill or beak of the echidna tapers toward the rather pointed end and is nearly round above. Wood Jones (1923, p. 42) notes that the snout is sensitive and that there is a slight tendency for the whole snout to be turned upward at its tip. Australians sometimes call the echidna the "sticky beak" for obvious reasons. With its cylindrical and

strongly protrusile sticky tongue it pulls in a variety of small insects, especially ants. The analogies here are chiefly with various placental anteaters, especially the edentate tamandua, and with the zalambdodonts *Echinops* and *Oryzoryctes*. The New Guinea *Zaglossus* (fig. 2), with its greatly elongate snout and subglobose cranium, convergently

resembles the kiwi among birds.

The eyes of the echidna are laterally placed, and its ear slit lies behind the cheek, in accordance with its terrestrial habits.

In connection with the flattening of the muzzle, the olfactory chamber of the platypus (fig. 3) has been squeezed into a pair of small tunnels on either side of the midline,

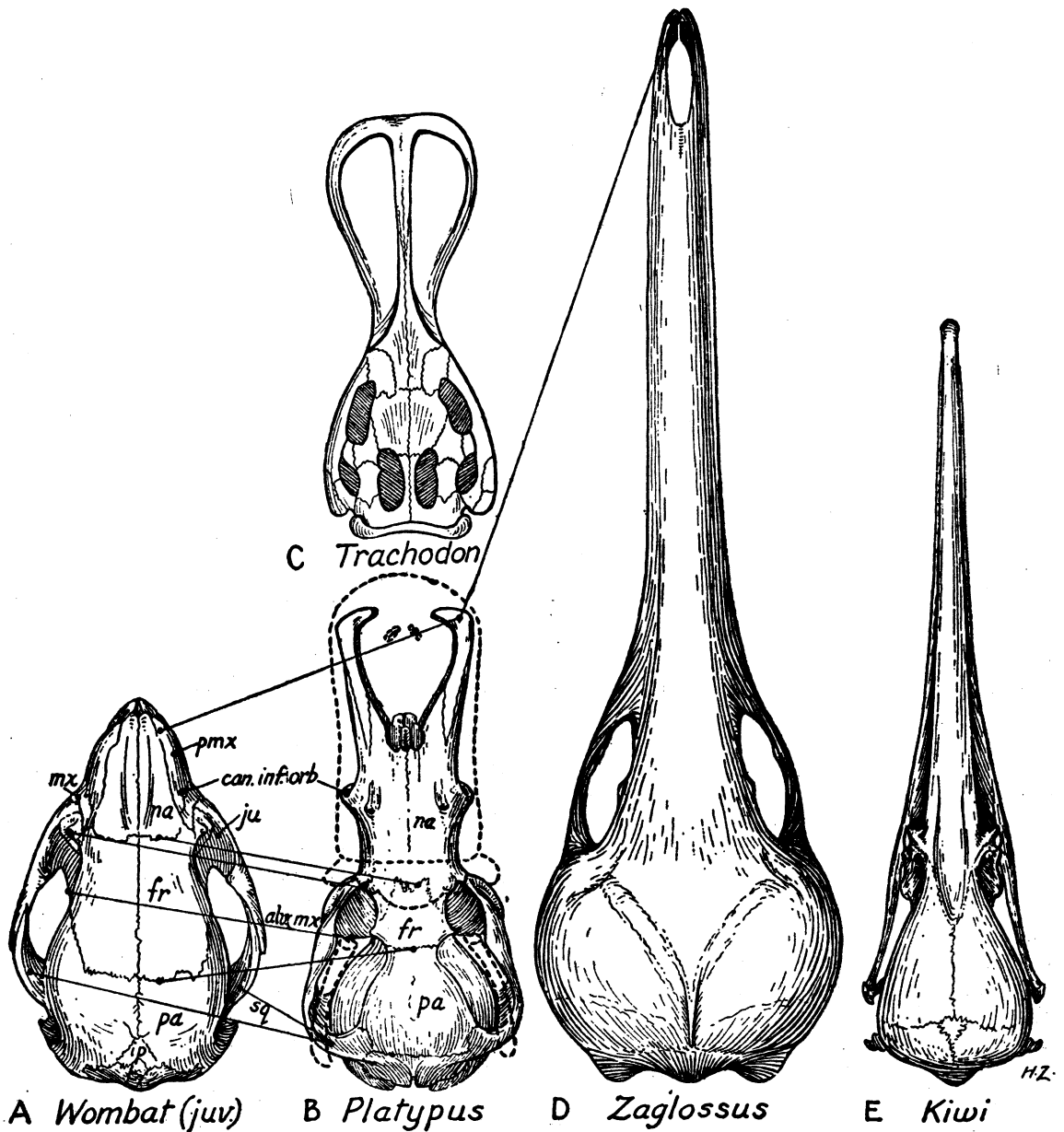


FIG. 2. Adaptive divergence (A, B, D) and convergence (B-C, D-E) in skull form; dorsal views.

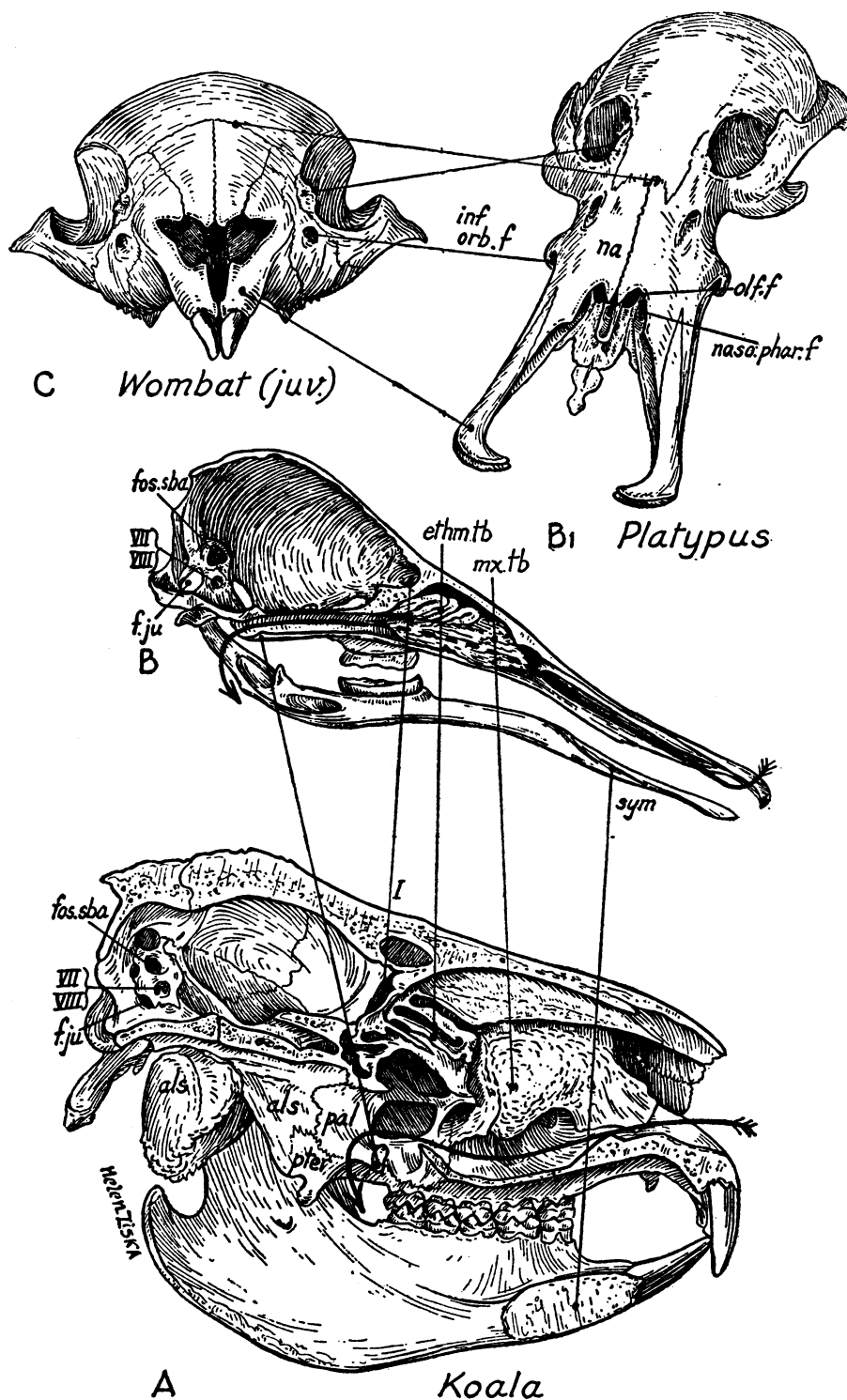


FIG. 3. Nasal chamber and nasopharyngeal canal in relation to endocranium. Although highly specialized and superficially bird-like in its cranium and bony bill, the platypus retains mammalian ethmo-turbinals and maxillo-turbinals.

the inner one ending posteriorly in the olfactory foramen, fitting into the bony ethmoid plug; the lateral tunnel runs backward and downward and leads to the posterior nares, which lie above the backwardly produced, flat plates of the bony palate. According to Paulli (cited by Weber, 1928, p. 31), the turbinals of the platypus are reduced, and, besides the nasoturbinal, they include only three endoturbinals with four olfactory folds. In the echidna, on the other hand, the olfactory organs are very large and highly developed, including, besides the insignificant nasoturbinal, seven vertically directed endoturbinals with four olfactory scrolls.

The Jacobson's organs of the platypus are highly differentiated in the shell-like process of the lateral cartilaginous wall and in its extension forward above the mouth. Attempts to see here a relationship of this organ with that of the reptiles are rejected by Seydel, since in none of its principal points does it differ from that of other mammals (Weber, *ibid.*).

#### TEETH AND JAWS

In the dried skull of the platypus there is a superficial and convergent resemblance to the "duck-bill" dinosaurs (fig. 2C), the bill in both groups being supported by flattened prolongations of the premaxillae, maxillae, and mandible. There is also a superficial suggestion of the head of the long-jawed mastodonts (fig. 4B), some of which likewise have a spatulate scoop on the front end of the mandible, with a median channel for the tongue, a long ante-molar diastema, grinding dental plates, and a dorsally placed, rounded mandibular condyle. These long-jawed mastodonts were eventually derived from a *Moeritherium*-like stage in which the skull as a whole to some extent suggests that of a phalangeroid marsupial with procumbent lower incisors. And, as the sequel suggests, it is not improbable that the platypus also has been derived from a more normal mammal with more or less procumbent incisors.

The muzzle or bill of the platypus is admittedly a peculiar and specialized organ for the prehension of food and for the detection of food when probing in the mud. That the loss of incisor teeth beneath the skin of the muzzle is a relatively recent event connected

with the evolution of the duck-bill is suggested by the presence of transitory traces of five incisors on each side of the lower jaw, as recorded by Green (1937, p. 394). Thus the not very remote ancestors of the monotremes may have been descriptively "polyprotodont," and for other reasons also they may have been marsupials.

The four horny dental plates of the platypus (figs. 1B, 6B) arise from the proliferation of the epithelial tissue around the proximal ends of the roots of the cheek teeth. This tissue cornifies around the complex roots, forming a mould of them, of which traces may be seen after the teeth have been worn down and cast out. The horny upper and lower plates themselves are thereby placed in favorable positions to articulate accurately with each other (fig. 1B), and they immediately take over the function of crushing and comminuting the shrimps and other small objects with which, along with much mud, the animal stuffs its cheek pouches (Burrell, 1927, p. 73). This substitution of horny plates for true molars was probably part of the radical transformation away from more normal mammalian dentition and terrestrial habits into the unique dentition and aquatic habits of the platypus.

The development and morphology of the teeth of *Ornithorhynchus* are the subject of a fine monograph by H. L. H. Green (1937), who made serial sections of the dental laminae in a series of stages of foetal specimens. The incisor portion of the dental lamina of the upper jaw forms early but rapidly disappears; traces of a tooth in the position of a canine are often retained until later stages. In the lower jaw there are the germs of five incisors on each side, but these also disappear later. Green interprets the full dental formula as:  $I_3^0 C_1^1 Pm_2^2 M_3^3$ . There is evidence of one milk tooth in each jaw, this being in the premolar region and recalling the conditions in marsupials. The enamel is degenerate. The roots are numerous but very short and stunted, and they are arranged in a complex irregular pattern.

Careful comparisons are made with other mammalian dentitions, especially the Triassic Microleptidae (p. 404), but "... as the teeth of *Ornithorhynchus* are so degenerate,



it is unwise to base monotreme relationships on the present structure of their teeth" (p. 419).

A series of "epithelial nodules" associated with the teeth are "constant in number and

the degenerating dental lamina to produce secondary polyisomeres, as do also the accessory cusplets and wrinkles on the molar crowns and the numerous complex molar roots.

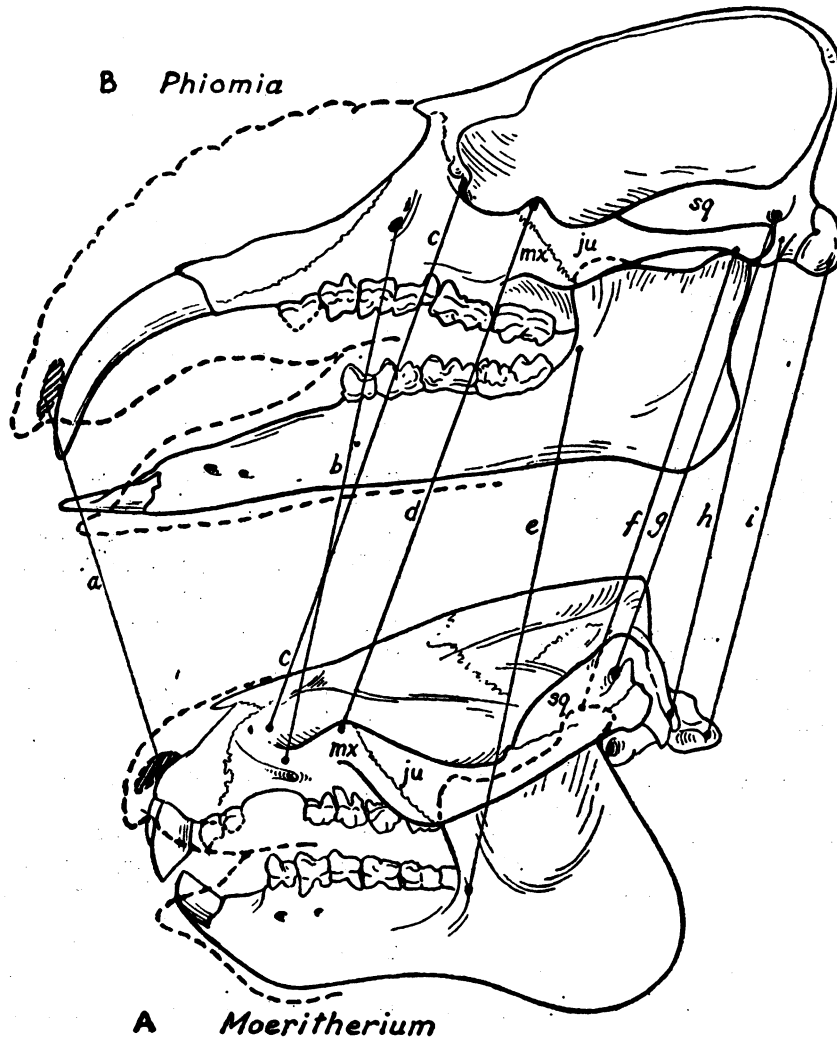


FIG. 4. Skulls of primitive (A) and long-jawed (B) proboscideans. After Osborn. Comparison of guide lines with those of figure 1 indicates more or less parallel changes and differential shifts in growth rates in passing from more primitive to more specialized stages.

position" (p. 411) and appear to be "derived from the degenerated apices of the teeth" (p. 413). "In no sense can the epithelial bodies be considered as representing vestigial remains of a milk dentition" (p. 415). They seem to me rather to be abortive attempts of

The small vestigial molars of the platypus were very carefully described and figured and the phylogenetic evidence analyzed by Simpson (1929), who showed that they differ from those of microcleptids, multituberculates, *Desmostylus*, triconodonts, and panto-

therians, and from all known tuberculo-sectorial or therian types. He also finds nothing to indicate the derivation of the tuberculo-sectorial type from one essentially like that of the platypus. He further concludes that there is nothing like this dentition among mammal-like reptiles, although "... a simple (but

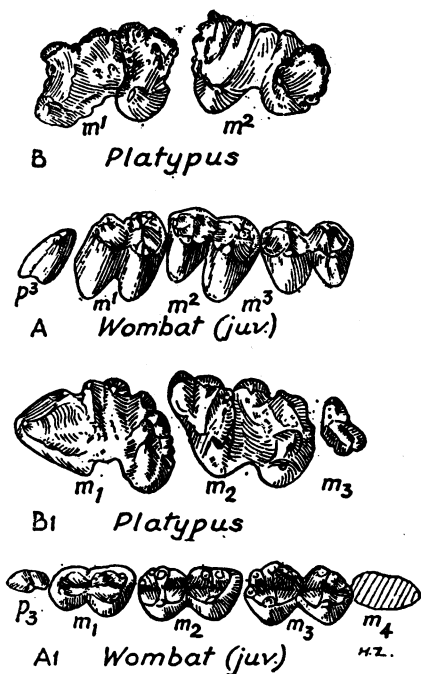


FIG. 5. Unworn molar crowns of young wombat ( $\times 2$ ) and platypus ( $\times 4$ ). B, B 1, After Simpson. The platypus molar crowns, although plainly degenerate in detail, seem to retain traces of two main V's separated by deep transverse valleys, as in the wombat.

absolutely hypothetical) origin might be assigned to such teeth by the action of processes which did occur in the theromorphs. This would involve primary longitudinal differentiation into two main cusps, and transverse differentiation through the up-growth of cingula, as suggested in *Diademodon* or *Pachygenelus*, on opposite sides of upper and lower teeth."

In so far as the molars of the platypus (fig. 5B) are: (1) anteroposteriorly elongate, (2) divided into two moieties by transverse valleys, (3) with reversed upper and lower patterns, they agree with those of *Phasco-*

*larctos*, *Phascalomys*, the kangaroos, *Myrmecobius*, and others. Although, as noted by Simpson, the lower molars are wider than the uppers, they conform otherwise more or less to normal occlusal relationships, the external borders of the uppers projecting beyond those of the lowers and the main anteroexternal cusp of the lowers fitting into the space between two upper molars.

Possibly the greater width of the lower molar crowns may be associated with the slight downward and outward slope of the occlusal plane of the lower molars and with the transverse rocking movements of each half mandible. For such movements the long, very narrow symphyseal contact of the two half mandibles seems to be adapted, and even in adult jaws the symphyseal contact is slender and flexible. Thus the symphyseal region is pretty surely both retrogressive and specialized, and the horny false-molar plates are still more highly specialized.

In short, although the ancestral pre-mono-treme molar type is not known, the marked difference, especially in the roots, between the degenerate and vestigial molars of the platypus and the unreduced molars of marsupials does not appear to me to forbid a relationship which seems to be indicated by other sources of evidence.

Among other specializations in the region of the jaws of the platypus are the following:

With the reduction of the true molars and the development of large, horny, false-molar plates, the alveolar regions of the maxillae (fig. 1) have formed a pair of strong, wide bases for their horny plates. The bases are braced in front by the wide proximal end of the bony rostrum, dorsally by the flat frontals (fig. 2B), ventrally by the maxillo-palatal plates (fig. 6B), and dorsolaterally by the wide and strong zygomatic arches (figs. 1B, 2B, 6B). The latter are formed in part by large zygomatic processes of the maxilla, which in turn are braced dorsoposteriorly by equally strong zygomatic bars of the squamosal. The jugals (fig. 1B) have been reduced to vestigial postorbital processes. The zygomatic arches extend far backward, and the fulcrum for the mandible are placed far to the rear (fig. 6B), where they are braced internally by the side wall of the braincase.

The postglenoid process of each side is absent, but there is a large inwardly and downwardly extended glenoid articular surface (figs. 6B, 8B). This is braced medially against a prominent downwardly and back-

capital process. The wide glenoid articular surface is concave transversely and slightly convex longitudinally. It permits the mandible to slide forward, and upon it rolls the transversely convex condyle of the mandible.

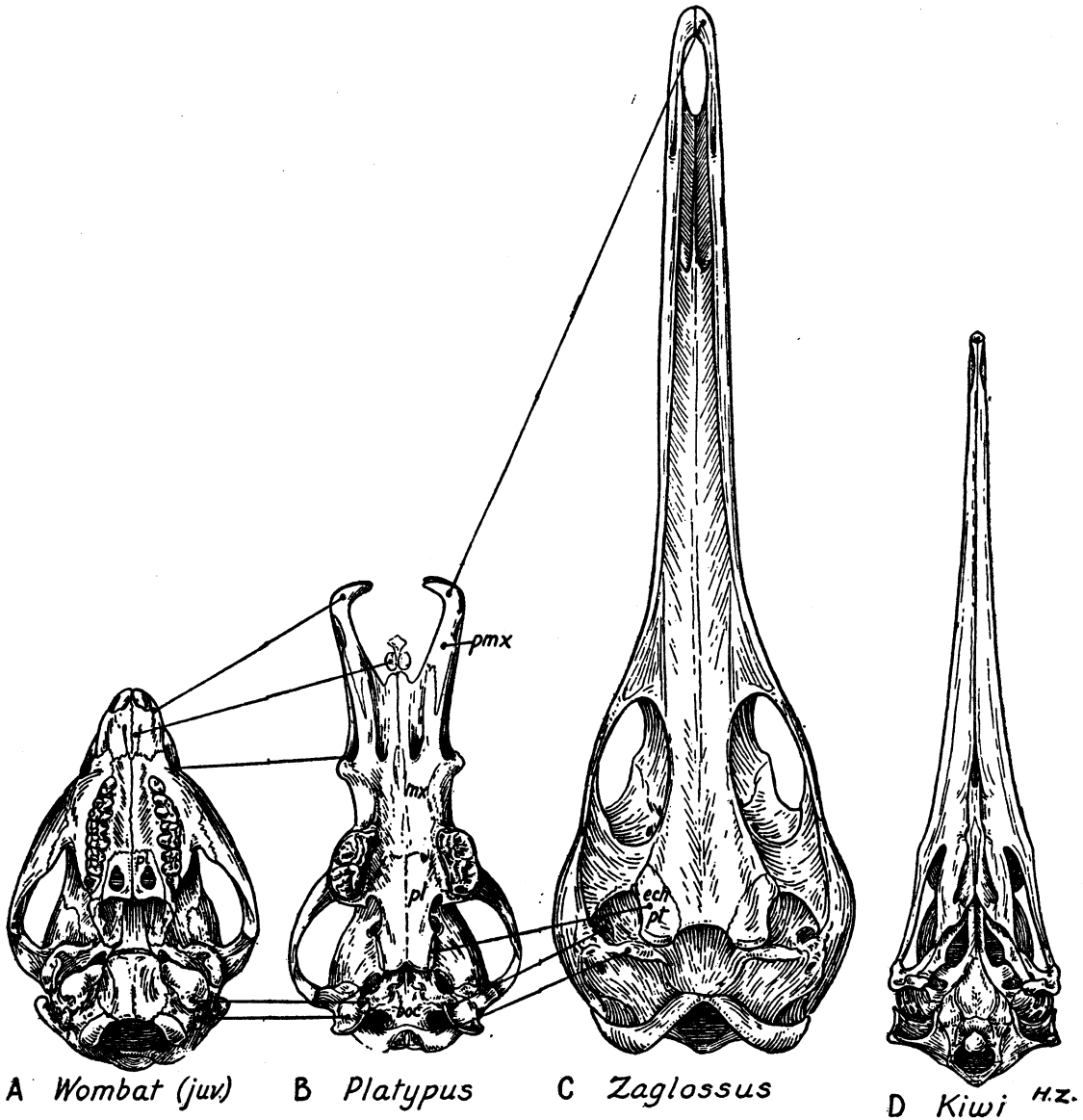


FIG. 6. Adaptive divergence (A, B, C) and convergence (C, D) in skull form; palatal views. Guide lines indicate great forward growth of bill and backward growth of palate in end stage of monotremes.

wardly directed process which has been homologized with the crista parotica of the lizard chondrocranium (Watson, 1916, pl. 25) and seems to be the conjoined mastoid and paroc-

In all this the essentially normal mammalian temporo-mandibular joint retains little to recall even the progressive reptilian conditions of the cynodonts, and as it stands today

this joint (fig. 1B) could rather easily be derived from that of a young wombat (fig. 1A). Nor does the embryonic jaw of the platypus (De Beer, 1937, pl. 105) retain more than the usual embryonic mammalian relations to the persistent Meckel's cartilage and the anlage of the incus. In the absence of a mandibular meniscus (or interarticular disc) both monotremes agree with the Australian polyprotodonts and contrast with the diprotodonts

the elongate and divergent flat symphyseal bars and the strong bases for the horny molar plates, together with the transversely rounded condyles, may now be noted. Behind the horny molar plates the jaw curves upward to support the elevated condyles (fig. 7B); these, as in herbivorous mammals, lie far above the plane of the lower molars. The entire coronoid process, instead of projecting well above the condyle as in typical herbi-

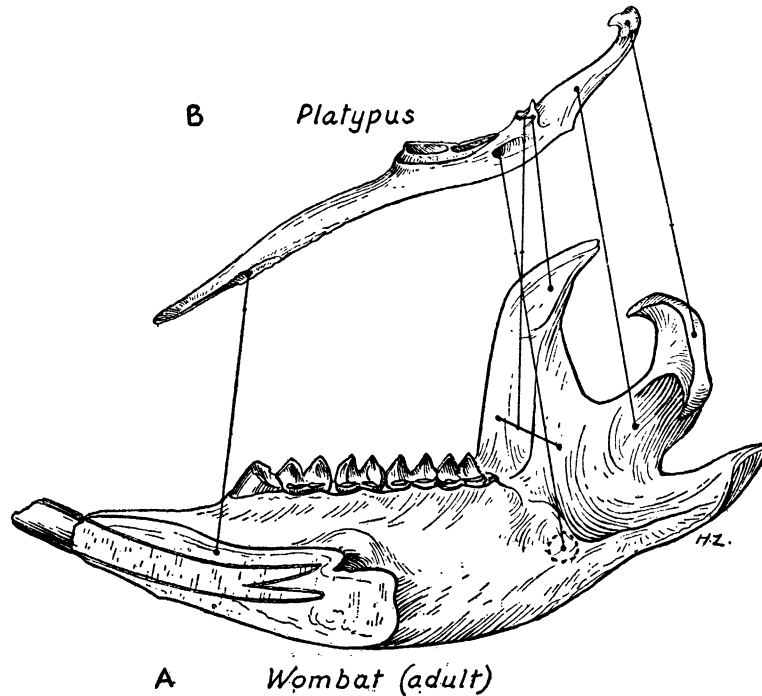


FIG. 7. Right half of mandible, medial aspect, showing extreme specialization in the platypus.

(Abbie, 1939b). Whatever may be the explanation of this difference, it does not separate monotremes from all marsupials. Nor does the contrast between Australian polyprotodonts and diprotodonts seem to indicate a diphyletic origin of the marsupials. Evidently the meniscus has often dropped out without lethal results.

In the echidnas the entire loss of all teeth has led to the reduction of the maxillary process of the zygomatic arch to a slender bar (fig. 6C), as well as to the reduction of the mandible to a pair of long splints.

In the mandible of the platypus (fig. 7B)

vores, is a very small projection which is far below and in front of the condyle (fig. 1B). The angle of the mandible has disappeared, the lower rear border of the jaw being partly covered by the large detrahens mandibulae muscle (Adams, 1919, pp. 111-114). Above the detrahens area is a large curved rim, and medial to the latter is a deep fossa (fig. 1B) into which the zygomatic and anterior branches of the masseter are inserted. A strong, obliquely placed ligament bounds the temporalis muscle anteriorly and runs down to the vestigial coronoid process of the mandible. This ligament may help to snap the jaw



shut after it is lowered by the detrahens mandibulae. The pterygoideus externus muscle (of mammals) is well developed and runs as usual from the outer side of the ala temporalis to the inner side of the mandibular condyle. On the inner side of the mandible (fig. 7B) is a very large foramen for the mandibular branch of the trigeminus (Huber, 1930a, fig. 22B, p. 179). Above the foramen

is a small hook for the tendon of the mylohyoid.

The musculature of the jaws of the platypus has become very complex, probably in connection with other factors, especially (1) the evolution of a great spatulate bill or muzzle lying far in front of the fulcrum of the jaws, which is near the rear end of the skull; and (2) the necessity for imparting to the

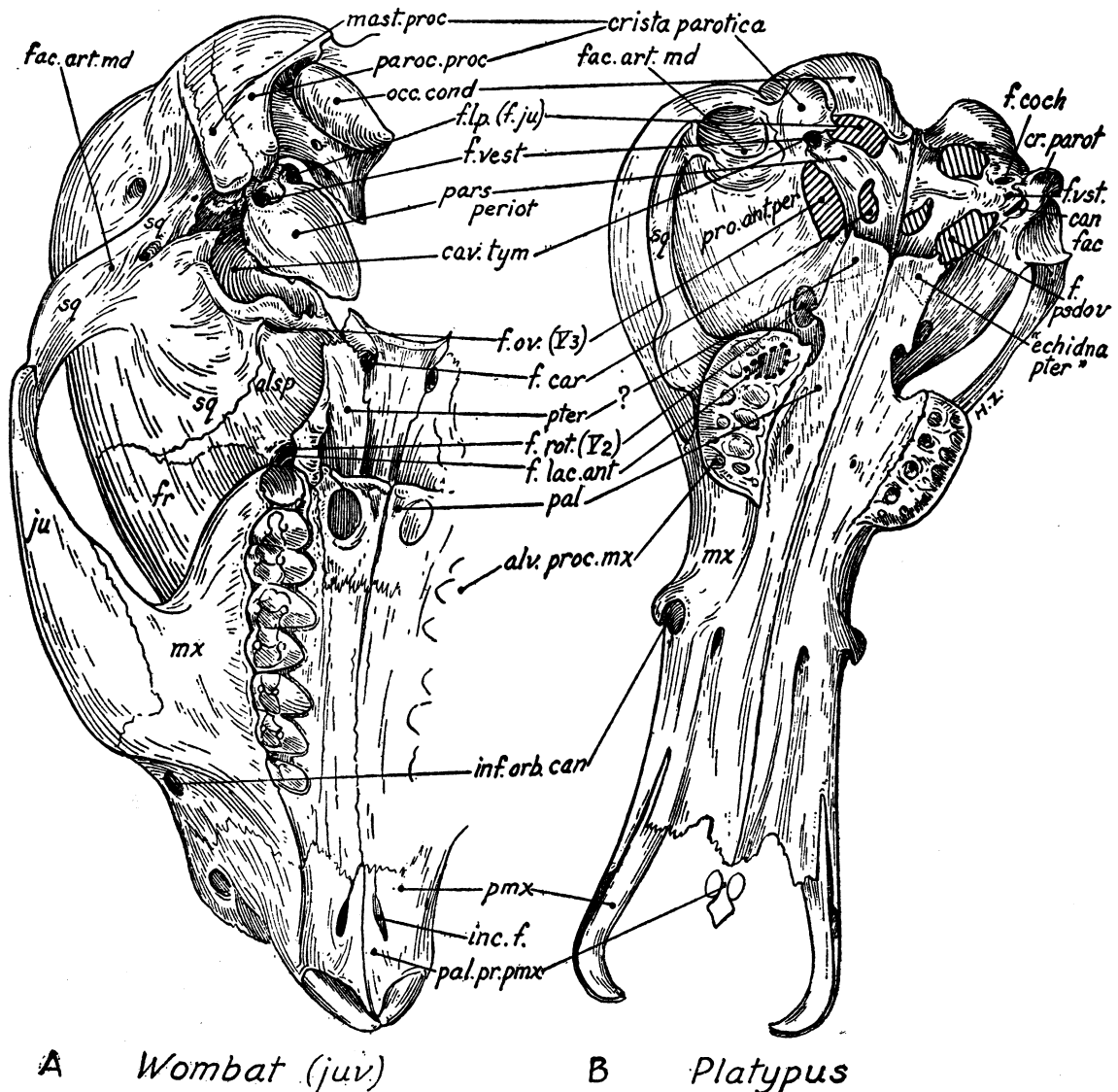


FIG. 8. Oblique inferior view of skulls to show (in B): (1) backward displacement of articular support for mandible (fac. art. md.); (2) crowding and marked diminution of auditory and basioccipital region; (3) backward shift of main foramina. The minute epitympanic cavity is overarched by the conjoined mastoid and paroccipital processes which form the "crista parotica."

mandible complex longitudinal sliding, snapping, and transverse rolling and chewing movements.

Adams sums up as follows (1919, p. 112):

"Monotremes have the following peculiar conditions of the jaw muscles: They have no true digastric. The masseter and temporal muscles are massed together [and tend to form new slips]. They have no pterygoideus internus. Presence of the detrahens mandibulae [interpreted as a derivative of the masseter and as a functional substitute for the lost digastric]. Extensive development of the mylohyoid group of muscles." Adams concludes that "The monotremes are so different from other animals in their myology that it is probably correct to assume that they split off from the mammalian stem at a very early period."

But from evidence that is being considered in the present paper it seems probable to me that many of the great and striking peculiarities of the monotremes are due rather to their extreme specialization away from the monotreme-marsupial stem.

Edgeworth in his great work on "The cranial muscles of vertebrates" (1935, p. 73) suggests that the detrahens existed as a separated fasciculus of the levator mandibulae externus in primitive mammals with an incudo-Meckelian jaw joint.

The presence of the detrahens mandibulae only in the monotremes is also cited by Westoll (1945, p. 115) as an item in support of the suggestion that mammals are not monophyletic. But these suggestions can hardly neutralize the many other items in which the monotremes exhibit typical mammalian characters. Moreover, the detrahens mandibulae, as already noted, plays an important part in the complex anteroposterior and rolling movements of the jaw, which is uniquely specialized in the platypus.

#### PALATE, TONGUE, AND LARYNX

The fore part of the bony palate of the platypus (fig. 6B) is formed in the usual mammalian way from maxillary plates of the maxillae and palatines. The large vacuity in the dried skull in front of the palate is covered in life by the dermal floor of the

muzzle, which is supported laterally by marginal rostral prolongations of the premaxillae. The little "dumb-bell bones" in the middle of the rostral vacuity are regarded by Broom (1932, pp. 318-320) as homologues of the reptilian "prevomers," but according to Parrington and Westoll (1940, pp. 323-325) they represent vestiges of the palatal processes of the premaxillae. In that case there would be no difficulty in deriving the conditions in the platypus from those seen in a young wombat and other diprotodonts. In the dorsal view of the embryo platypus skull the very large ascending processes of the premaxillae support a prominent os carunculae or so-called egg-tooth (De Beer, 1937, pl. 105, fig. 4). This is a strikingly sauropsidian character which is not found in viviparous mammals with small or no egg yolk and shell-less eggs.

The rear part of the bony palate (fig. 6B) is without palatal vacuities and ends posteriorly in thin edges on the palatines, which are without either thickened rims or ascending flanges to embrace the vomer. These conditions contrast widely with the stout cross-bar at the rear end of the palate and large palatal vacuities in typical marsupials. They are, however, approached to some extent in *Myrmecobius*, which, perhaps in conformity with the lengthening of the tongue and elongation of both the face and the bony palate, has lost its palatal vacuities and retains only a slender transverse palatal bar. The evident analogies with the backwardly prolonged palate of the placental anteaters (*Myrmecophaga*, *Tamandua*, etc.) raises the suspicion that the monotremes are highly specialized also in their bony palate. This suspicion may even extend to the phyletic significance of the well-known "echidna pterygoids" (fig. 6B, C).

At the rear end of the palatal bridge surrounding the nasopharyngeal ducts lie the "echidna pterygoids" on either side, and ventral to these are the "mammalian pterygoids," the latter in contact with the cranial base. As to the homologies of these two, Watson (1916), De Beer (1937, p. 297), and Parrington and Westoll (1940) differ more or less in detail, but all agree that they have been derived from known elements in the

cynodonts and are also homologous with known elements in the other mammals. In any case, in respect to the entire configuration of the palatal region the monotremes agree in essentials with other mammals that have backwardly produced palates, but the monotreme palates are only superficially similar to those of ichthyosaurs, crocodilians, and other reptiles with backwardly produced palates.

The tongue of the platypus (cf. Wood Jones, 1923, fig. 33) includes a wide posterior part, lying between the false-molar plates, and a narrower anterior part, lying in the space between the rostral bars of the mandible. The upper surface of the tongue is covered with small papillae, and when the mouth is closed the tongue presses against the flat surface of the backwardly elongated bony palate.

There are pockets or cheek pouches at the root of the rostrum, slightly in front of, and lateral to, the false-molar plates. Burrell (1927, p. 73) reports that he frequently found them stuffed with mud and the debris of small creatures which had been cut up by the transverse ridges on the upper and lower margins of the bill.

The sensitiveness of the muzzle is due to the marked development of the cutaneous branches of the superior maxillary branch of the trigeminus (Huber, 1930a, fig. 21, p. 178). The superficial facial muscles are well developed above the cheeks around the eyes and cheek pouches (Ruge, 1895; Huber, 1930a, fig. 5, p. 143), especially in the platypus, whereas in reptiles only the primitive sphincter colli is present (Huber, 1930a, fig. 3, p. 141).

In the anatomy of the larynx, according to Göppert (1901, p. 627) echidna is more primitive than the platypus in some features, more specialized in others; but both agree in basic characters which unite the monotremes with the higher mammals and separate them sharply from the reptiles. In certain features they agree with the marsupials and contrast with the placentals, and in others they are peculiarly specialized.

#### EARS: OUTER, MIDDLE, AND INNER

"The auditory sense" in the platypus, according to Burrell (1927, p. 67), "is undoubtedly acute. The creature [when floating on the surface] dives on hearing an unaccustomed noise just as rapidly as on seeing an unaccustomed movement." Eye and ear are indeed close to each other. The external ears of the platypus (fig. 1B) are a pair of curved cartilaginous tubes which arch over the roots of the zygomatic processes of the squamosal and continue forward under the skin to open just behind the eyes. Citing Bennett's statement concerning "the twitching of the facial furrow at the region of the ear-hole," continues Burrell (p. 67), "I find that the platypus is actually capable of 'cocking' it [the 'facial furrow'] to act as a temporary auricle to pick up sounds." In this connection it may be noted that Huber (1930a, fig. 5A, p. 143) shows a small slip of the superficial facialis system immediately behind the eye and above the ear-hole, which probably opens the orifice. Immediately before the creature dives, according to Burrell, the senses of hearing and seeing are rendered inoperative, "principally by means of a watertight furrow which simultaneously envelops the orifice of both ear and eye. . . ." (p. 72).

The rear part of the external ear tube leads downward, behind the glenoid region (fig. 1B), curving forward below the parotic process to the very small tympanic membrane (Watson, 1916, fig. 8, p. 325). This membrane in turn is stretched upon the minute, horse-shoe-shaped tympanic bone. The tympanic membrane, which blocks the lower end of the outer ear tube, is nearly horizontal in position, as in embryos of typical mammals; but as a whole the middle ear region is specialized away from a more typical mammalian condition (Weber, 1928, pp. 32, 33), especially in the great reduction of the cavity of the middle ear, which lies within and partly medial to the longitudinally compressed parotic process (fig. 8). However, the topographic relations of the platypus tympanic region of the skull to the surrounding bony parts are essentially

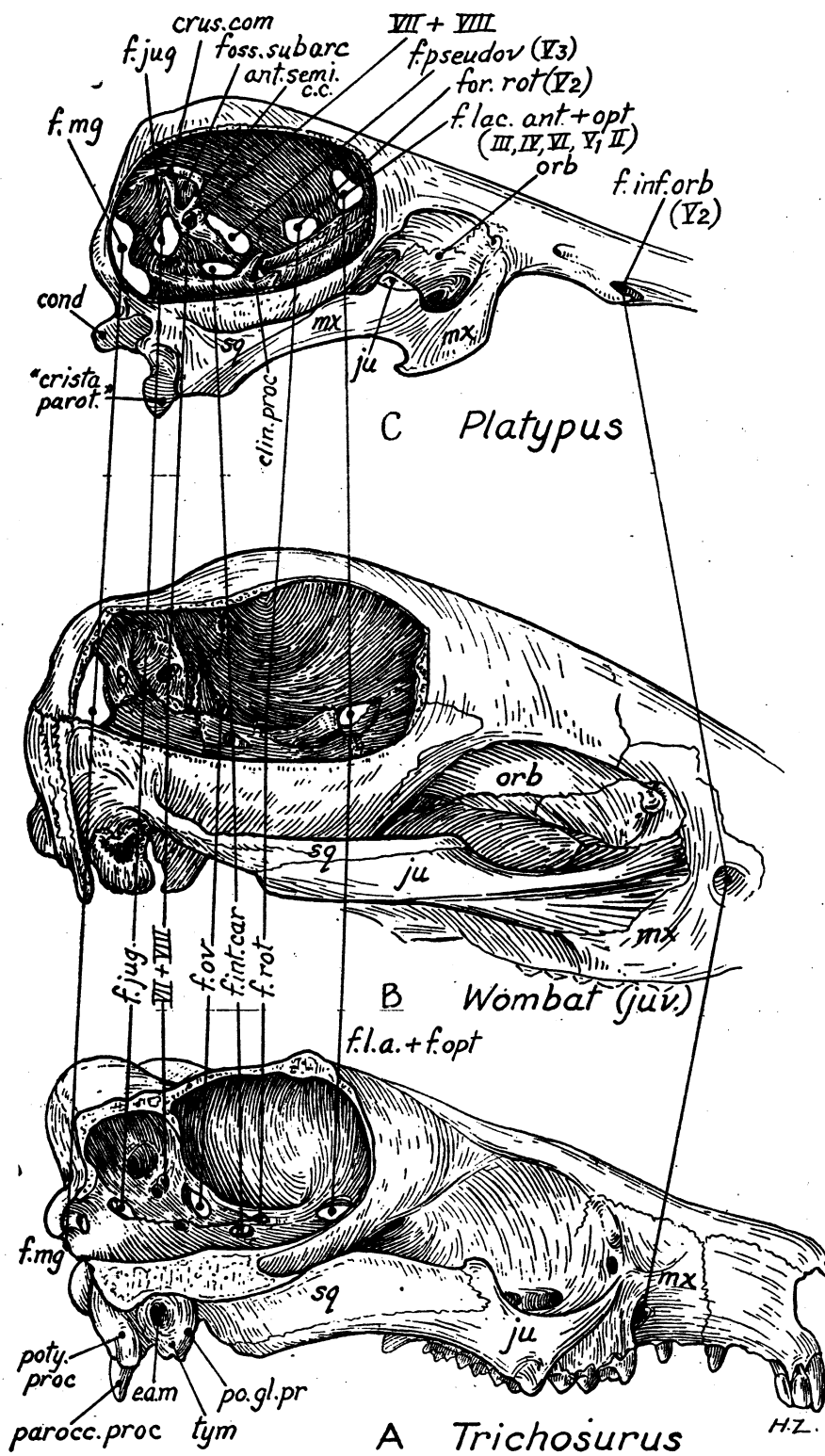


FIG. 9. Endocranium and main cranial nerve foramina. In the platypus some of the foramina have expanded into fenestrae but still conform in general to the marsupial pattern.

similar, except in proportions, to those in marsupials (cf. Van Kampen, 1905, fig. 10, p. 390; fig. 11, p. 393; fig. 12, p. 397); but the tubo-tympanal passage is regarded by Van Kampen (p. 393) as very primitive because it is merely a recess from the pharynx. This is another feature that suggests an arrest of development at a certain stage, followed by new specializations.

A comparison of the acoustic region of the skull of the platypus (figs. 6B, 8, 9) with those of marsupials suggests that in the former both the auditory part of the periotic and the tympanic cavity have been, as it were, squeezed in between the very large backwardly displaced condyle of the jaw and the even larger anterodorsal extension of the occipital condyle, while the crista parotica, extending downward, has quite overshadowed the dwindling tympanic chamber. Moreover the jugular foramen has for some reason become enormous, thus further restricting the space available for the cavity of the middle ear. Finally, the need for bracing the thin, large-domed skull against the powerful forces of the nuchal and masticatory muscles, as well as against the axial muscles that suddenly depress the head, has, as it were, encouraged the opposite periotic bones to form a pair of forwardly and inwardly directed trusses which converge to the stiff basicranial axis (figs. 8, 9). Toward its outer end each periotic expands dorsoposteriorly to form a conspicuous superstructure for housing the semicircular canals and supporting the cranial wall (fig. 9).

In the construction of the otic region of the skull, the echidna seems rather to be a derivative of the platypus than the reverse. Its land-living and ant-eating habits have permitted or encouraged later specializations which have to some extent obscured or wiped out those of the platypus. Thus the jaws of the echidna have become reduced to mere stylets, and the tongue is the dominant organ. The brain has expanded transversely, pushing the cranial wall of the periotic laterally and greatly enlarging the space available for the middle ear and the auditory ossicles, which have become far larger than those of the platypus.

In embryonic and foetal stages, the mal-

leus of the platypus, like that of all other mammals, is formed from the proximal end of Meckel's cartilage, and the incus corresponds in position and is homologous with the reptilian quadrate. But in these and other features the embryonic jaws of the platypus do not retain the form of these elements in cynodonts but are in the main completely mammalian (cf. De Beer, 1937, pls. 105-108).

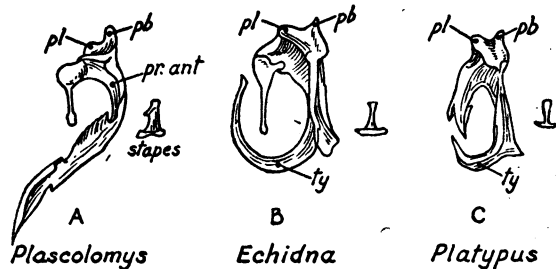


FIG. 10. Ossicula auditus. After Doran.

Concerning the auditory ossicles of the adult monotremes, Doran in his immortal work (1879, pp. 487-488) writes thus:

"I leave such important questions as What bones are the homologues of the mammalian malleus and incus in the Sauropsida? to distinguished authorities in the united branches of morphology and embryology. Next, I hardly need remind the anatomist that, as far as the ossicles are concerned, the Monotremata wear a perfectly mammalian uniform, having malleus, incus, and stapes. If any theorist consider this Order more Sauropsidan than mammalian, on account of the most marked feature in the first two bones, he must, for the same reason, place the Porcupines and Cavies nearly as low in the scale, and decidedly in an inferior position to the Marsupials; and as for the stapes, it is of a type precisely imitated in the placental *Manis*."

The progressive loss of the stapedia foramen, as shown in Doran's plate 64, culminates in the imperforate, columella-like stapes of the monotremes and of many marsupials. The obvious resemblance to many avian stapes adds to the list of characters in which the monotremes merely converge toward sauropsidan conditions, and in which the monotreme characters were far more prob-

ably derived from primitive marsupial conditions. The malleus and incus of the monotremes (*idem*, pl. 64, figs. 35–37) are most nearly approached (fig. 10) by those of *Phascolomys* and *Phascolarctos*, as clearly recognized by Doran (*ibid.*, pl. 64, figs. 32–34). The tympanic bone retains its embryonic horseshoe shape, whereas in Australian marsupials it is usually inflated. The “goniale” (Gaupp), which as in other mammals is fused to the malleus to form the anterior process, is exceptionally large in both monotremes and marsupials. In monotremes it fuses with the tympanic.

A noteworthy and presumably primitive feature of the inner ear is the failure of the cochlea to achieve more than a three-quarter turn (Weber, 1928, vol. 2, p. 32). This could be owing either to an arrest of development or to the retention of primitive mammalian conditions. Simpson (1928, p. 85) reports that in a Mesozoic mammal, *Triconodon*, the cochlear cavity was represented by an almost straight tube. In the echidna, with the great reduction of the size of the jaws and the transverse enlargement of the brain, the chamber of the middle ear and ossicula auditus have greatly increased in size, while the cochlear tube is well curved.

Most, or perhaps all, of the detailed differences in the configurations of the auditory complex in the echidna and the platypus seem to be readily explained on the hypothesis that the latter illustrates an earlier habitus which has achieved high specialization away from an older, more central mammalian type, and that in the echidna new specializations have overgrown the earlier ones. And direct comparison of the skulls indicates that on the whole the auditory region of the platypus, in spite of its curious specializations, seems to be easily derivable from conditions preserved in diprotodonts.

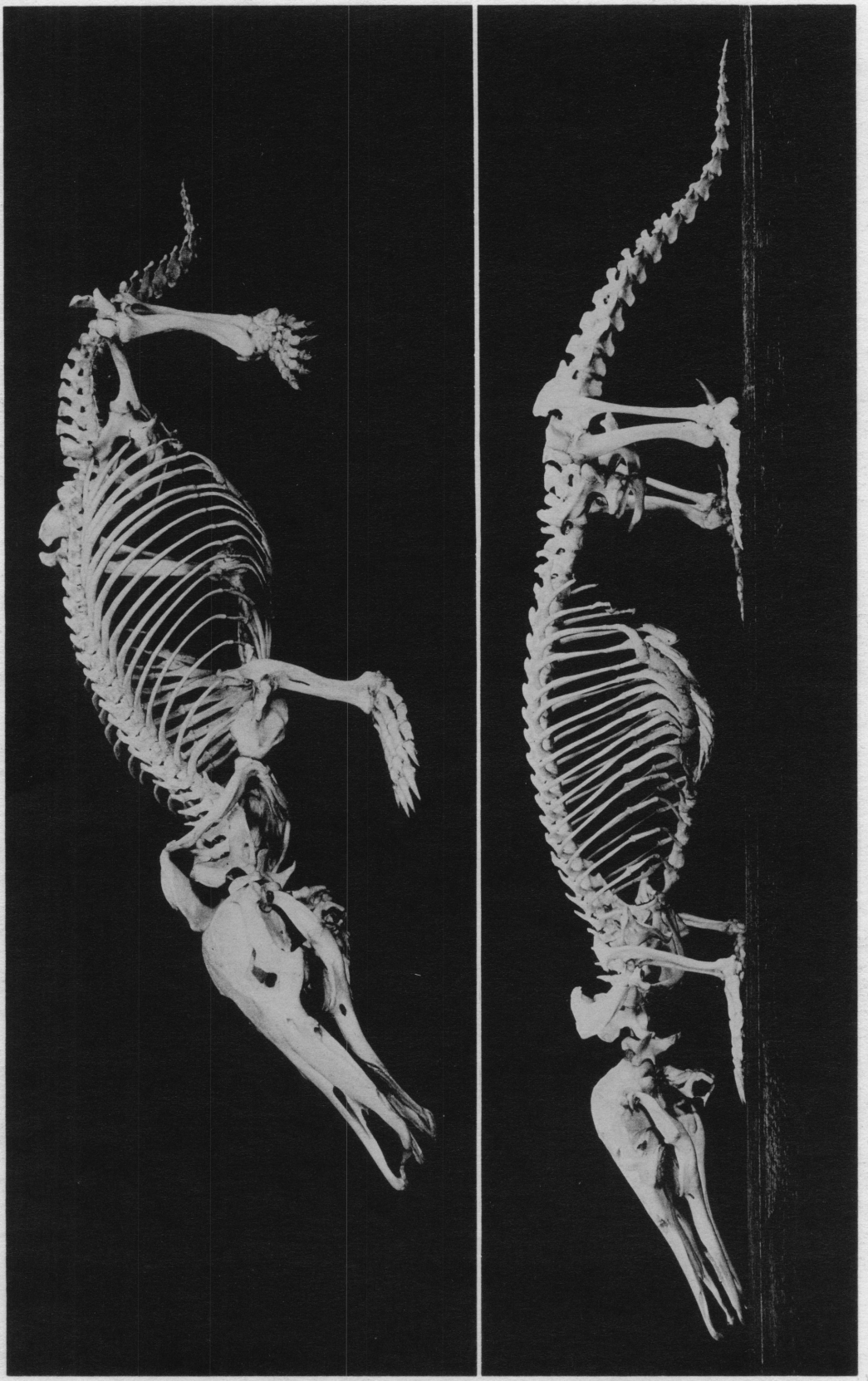
#### BRAINCASE AND BRAIN

The skull of the platypus is superficially bird-like, not only in its duck-like bill but in its well-rounded and thin-walled cranial dome (fig. 3B). But although most of its bones, except the dense petrous portion of the periotic, are thin, they are surprisingly strong. The great flattened bill is firmly hafted above

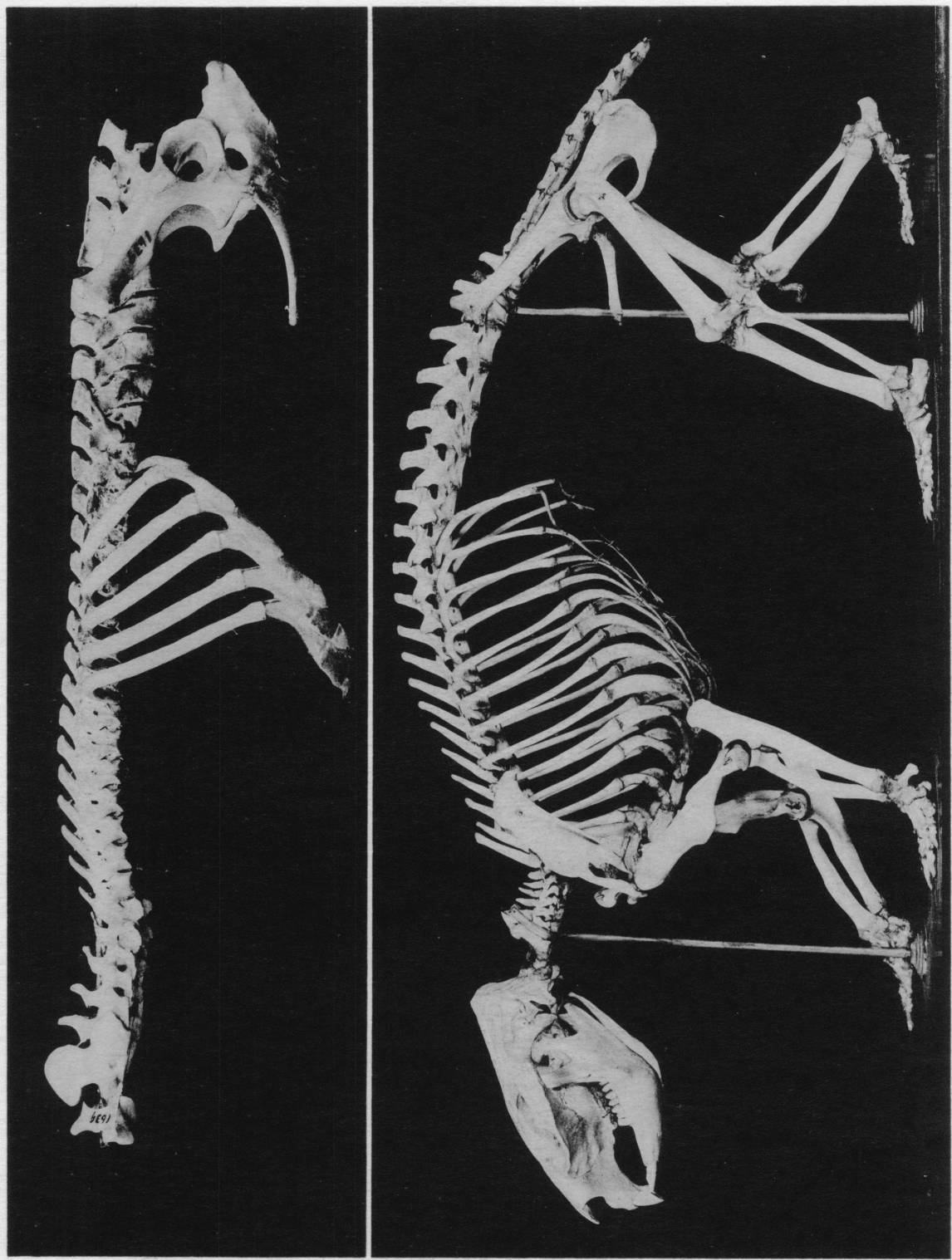
onto the bony forehead and below to the stiff, backwardly prolonged bony palate and its enclosed naso-pharyngeal ducts (fig. 3B). The palate in turn transmits its thrusts to the small basis cranii. This, as also noted above, is strengthened laterally by the side walls and by the truss-like paired periotics (fig. 9C), posteriorly by the excessively wide condyles and strong occipital wall. The condyles in turn permit wide movements of the entire head and transmit their loads to the thick neck and stoutly built cervical vertebrae. The roof of the cranial dome is stiffened by a large longitudinal beam, which seems to be an anterior extension of the tectum synoticum (Watson, 1916) and possibly an ossification of the falx cerebri.

Along with these and other peculiar specializations (such as the fusion of the mastoid and paroccipital processes, the marked transverse widening of the occipital condyles, the presence of a prominent median cleft above the foramen magnum, which in a very young skull is covered with a thin septum) are several important features in the platypus cranium which are regarded by morphologists as unusually primitive or reptilian. Here belong the great flat side wall below the parietal (fig. 8B), which is represented in Watson's model of the chondrocranium and which he names *processus anterior periotici*. However, this great flange closely resembles in its form and topographic relations the corresponding region of the side wall of the skull in diprotodonts (fig. 9A, B), which is part of the alisphenoid or *ala temporalis*. In Watson's sections of the chondrocranium of a foetal platypus (1916, figs. 8–14) this large plate (our fig. 9) occupies the territory which in other mammals belongs to the alisphenoid, and its ventral branch extends downward and inward to a point lateral to the semilunar (Gasserian) ganglion of the fifth nerve (Watson, 1916, fig. 14) and is connected below by an unossified strip with the *ala temporalis*. But posteriorly the dorsal flange of the same is broadly continuous with the periotic. And in the young echidna figured by Watson (*ibid.*, pl. 24) both branches plainly are continuous with the huge “pterotic process of the mastoid” (Van Bemmelen). In short, this entire dorsal





Platypus skeleton



*Upper.* Vertebral column, ribs, and pelvis of echidna.  
*Lower.* Wombat skeleton

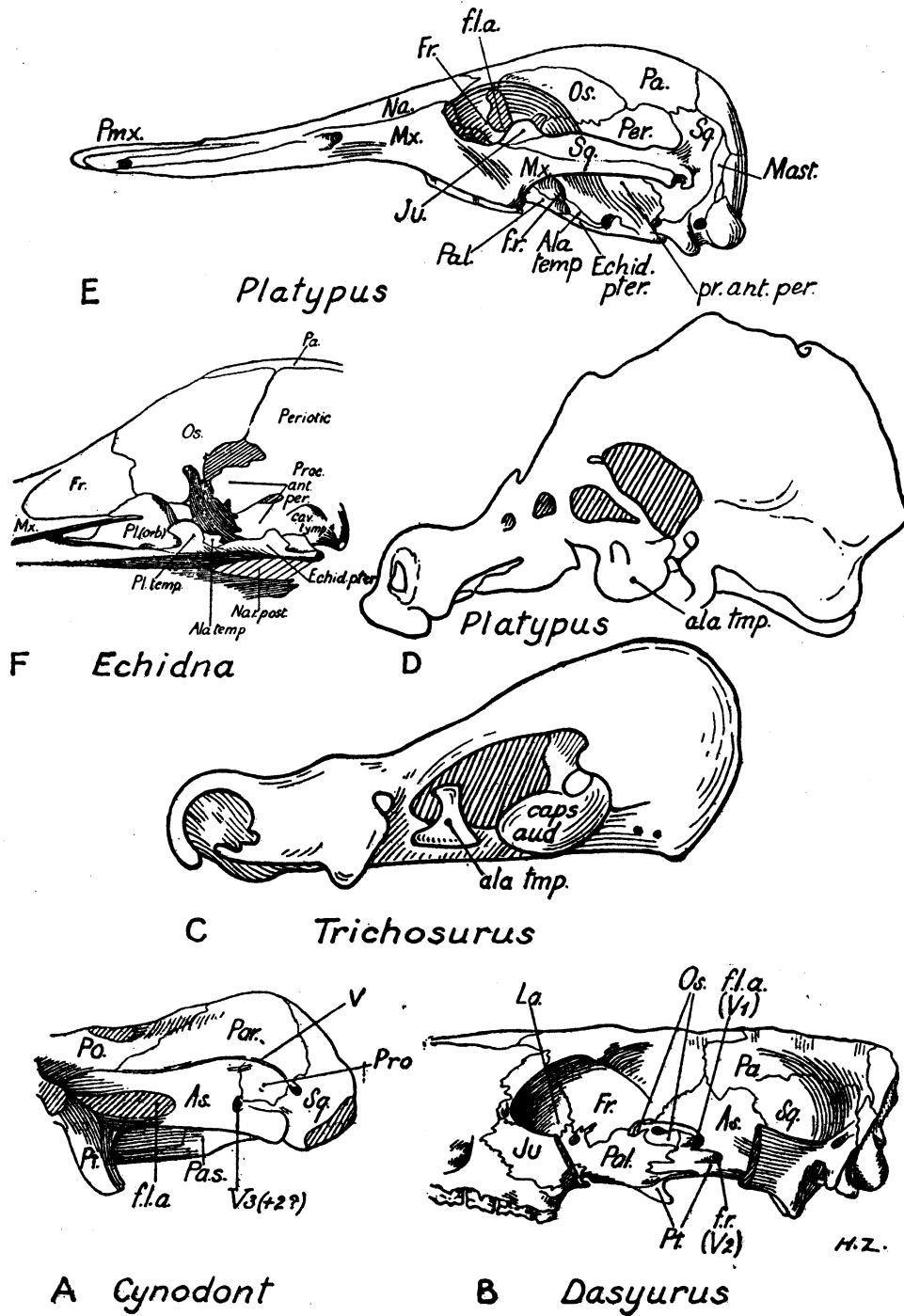


FIG. 11. Cynodont, marsupial, and monotreme braincase. A, F, After Watson; B, E, after Gregory and Noble; C, after Broom; D, after De Beer.

membrane bone plate of the anterior process of the periotic of monotremes is homologized by Watson (*ibid.*, p. 344) with the "anterior superior process of the Cynodont prootic" (fig. 11A) and therefore may well represent another persistent primitive metacynodont character of the monotremes. In that case, this dorsal plate of the side wall of the skull has been replaced in marsupials and placentals by the dorsal flange of the ala temporalis.

The ala temporalis or alisphenoid of monotremes (fig. 11) is a small, dorsally concave lateral flange from the basisphenoid, lying on each side beneath the Gasserian ganglion and not forming the side wall of the skull; it is homologous with the lower part of the alisphenoid of marsupials.

As a whole, the chondrocranium of the platypus (De Beer, 1937, pl. 106) is identical in basal plan with that of the diprotodont *Trichosurus*, as figured by Broom (1909, pls. 10-13), the most conspicuous difference being the reduction of the otic capsule in the platypus and its enlargement in *Trichosurus*.

The supraoccipital of the platypus forms a large median plate, which in the embryo is represented by the tectum synoticum of the chondrocranium. This plate has every appearance of being homologous with the supraoccipital of other mammals. The reptilian tabulars if present are not apparent as such. The prominent median slit above the foramen magnum in the adult skull is a remnant of a deep embayment in the chondrocranium of the 122-mm. stage (cf. De Beer, 1937, pl. 106), which must accommodate the projecting median lobe of the cerebellum. In a very young skull (estimated by Burrell at eight and a half weeks) this embayment is covered by membrane, which must have separated the medial lobe of the cerebellum from the ligamentum nuchae.

The braincase of the echidna is in some respects even more bird-like than that of the platypus, and the entire skull of its New Guinea relative *Zaglossus* (fig. 2) amazingly but superficially resembles that of the ant-eating bird *Apteryx*. In both cases (platypus and echidna) the cranial roof has been moulded chiefly by the large brain, since the temporal jaw muscles in the platypus do not

extend on top of the skull to form sagittal and lambdoidal crests, while the temporal muscles of the echidna are feeble and the lower jaws reduced almost to a vestige.

In general form the brain of the platypus is macrosmatic; the neopallium is smooth and much swollen posteriorly where it deeply overlies the primary brain roof and the anterior third of the cerebellum. The latter is richly convoluted and fissured. Thus the platypus has a mammalian brain, differing widely from the lizard type in the proportional development of its parts. The external surface of the echidna brain is much larger, well furrowed, and still more mammalian in appearance.

Internally the brains of both monotremes agree with the primitive marsupial type in lacking a corpus callosum; but according to Abbie (1941, pp. 88-90), they lack the fasciculus aberrans (a separate strand passing through the anterior commissure and penetrating the capsule), which is characteristic of the diprotodonts. The polyprotodont marsupials (including *inter alia* *Didelphis* and the bandicoots) also lack the fasciculus aberrans, and Abbie regards the monotreme brain as being essentially ancestral to both the diprotodont and placental types. Both monotremes have a more or less well-developed hippocampus, but both lack the corpus callosum of placentals. However, according to Abbie (1941, pp. 89, 90) both the monotreme and the marsupial brains provide the prerequisite conditions for the evolution of a corpus callosum.

#### VERTEBRAL COLUMN, RIBS, AND STERNUM

The platypus retains some, at first sight, very ancient and premammalian-looking features in its vertebral column and ribs, such as: the persistent sutural contact of the odontoid with the axis, the presence of the vertebral suture of the cervical ribs (except in very old individuals), the shortness of the lumbar region, in which only two presacral vertebrae are ribless. Moreover the centra of the dorsal and lumbar vertebrae, especially as seen from below, are similar-looking polyisomeres, with but little regional differentiation. But the centra of the neck are

widened and closely appressed, and behind the sacrum there is a sudden widening of the transverse processes from the root of the tail to near its distal end. The intercentral plates are reduced to thin discs, and the centra fit closely together with flat anterior and posterior faces. Such features suggest the secondarily checker-like centra of extinct marine reptiles and cetaceans and are often found in secondary polyisomeres. Essentially similar centra are retained in echidna, which, although thoroughly terrestrial, has apparently inherited part of the more primitive monotreme stage which is best preserved in the platypus.

The neural spines of the axis and third cervical of the platypus show marked enlargement and regional differentiation (fig. 12); in C4, 5, 6, 7, they grow shorter and gradually turn backward to D2; on D2, 3, 4, 5, they acquire spatulate tips; on D6–11, their tips are recurved, blunt to narrow. On D12–15, the spines increase a little in length and robustness; on D16, 17, their anterior border becomes concave; on L1, the spine points slightly forward; on L2, it is larger and nearly vertical. All these and many other features of the column are plainly related to the animal's exceptional abilities in diving, swimming, and digging. No doubt the same is true of other special features, such as the rapid diminution of the spinal foramina as we pass forward, from very large openings, beneath the zygapophysial articulations between L2 and S1, to the small foramen that perforates the side of the longitudinally extended base of the neural arch in the mid-dorsals. This foramen in turn then increases in size in successive vertebrae anteriorly until it merges with the larger and regular lateral interspinal exits of the cervical vertebrae. These curious and very specialized features are not found in the marsupials, in which the spinal nerve exits are intervertebral and quite normal for mammals generally, nor is there any indication of them in cynodonts.

Equally adaptive are the metapophyses which spring from the dorsolateral corner of the anterior zygapophyses (fig. 12). These metapophyses are a distinctly mammalian character and are not present in *Cynognathus*. But they are very well developed in *Phasco-*

*larctos*, *Phascolomys*, and apparently all other marsupials.

The hypapophyses (fig. 12) on the centra of D1–4 and C7–2 of the platypus have evidently been evoked by powerful flexors and abductors of the neck and head. On the ventral rim of the atlas there is a pair of long downwardly and backwardly divergent hypapophysial horns. Probably the scalenus and the rectus capitis magnus are lateral to these hypapophysial horns, and the longus colli is medial to them (cf. Evans, 1939, fig. 15, p. 83). These muscles play an important part both in quickly depressing the head when diving and in the sudden rolling up of the body into a ball. But the bony "horns" or branches on the ventral side of the platypus atlas have another important function. From their distal and ventral surfaces arises the omotrachelian muscle, which is inserted on the forwardly inclined blade of the scapula from the acromion upward (McKay, 1894, pp. 343–344).

This apparently unique development of large hypapophysial horns on the atlas is not shared by the echidna and does not seem to be indicated in any of the numerous marsupials examined. Large hypophysial processes on the second and other cervical vertebrae are, however, strongly developed in penguins—another bird-like convergence feature in the platypus.

From the distal ends of the large flat rib of the axis and of the other cervical ribs of the platypus arises the levator scapulae dorsalis. This is inserted on parts of the antero-internal surface of the scapular blade (cf. McKay, 1894, pp. 338–339). In swimming, the muscles named above would tend to depress the neck, and if used alternately would cause the neck to sway from side to side.

The vertebral formula of the platypus (pl. 2) has been somewhat differently reported by different observers, chiefly because of the transitional conditions between the thoracic (dorsal), lumbar, sacral, coccygeal, and caudal regions.

The comparative data have been set forth by Flower (1885, pp. 88, 89), Weber (1904), Gregory (1910, p. 152), Gregory and Camp (1918, p. 540), Weber (1928, p. 29). After

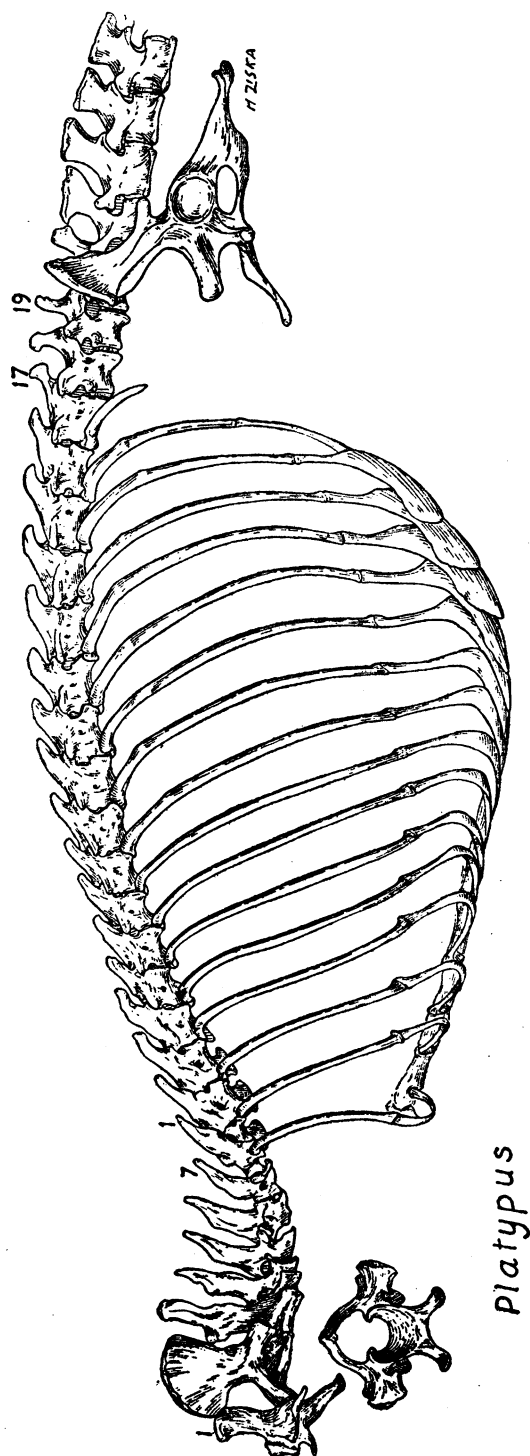


FIG. 12. Vertebral column, ribs, and pelvis of platypus.

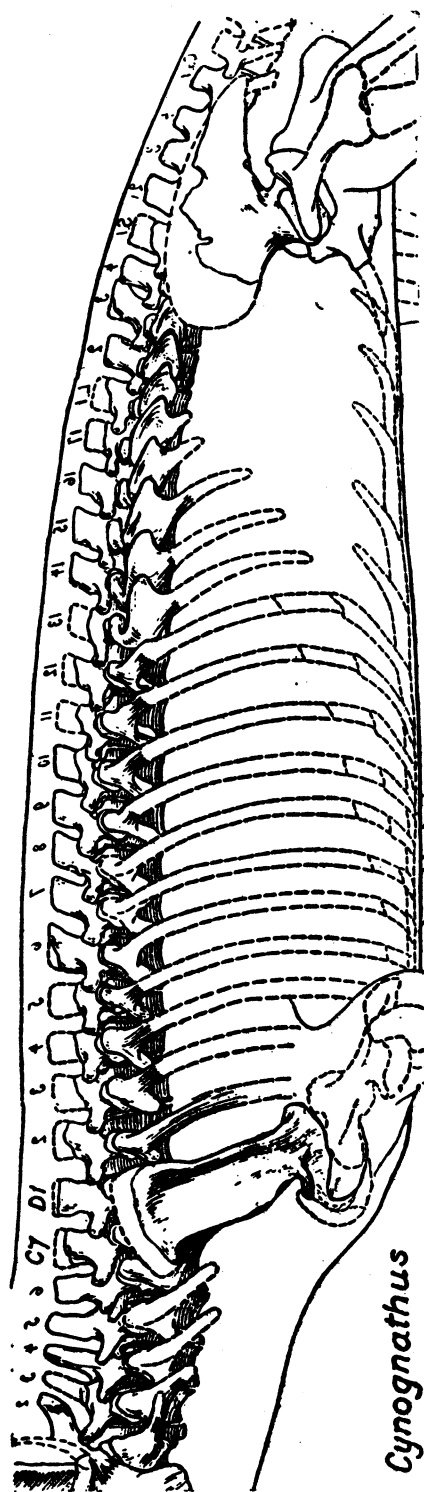


FIG. 13. Reconstruction of *Cynognathus* skeleton. After Gregory and Camp.

carefully reviewing the literature and available skeletons, I have compiled the data shown in table 1.

The presence of but two short sacrals improves the mobility of the column of the platypus both in front of and behind the fulcrum for the hind limbs, an obvious advantage in swimming and digging. The still more powerfully digging echidna has length-

dled; but in the platypus the powerful hind limbs refused to give ground to the lumbar. The echidna, on the other hand, may even have surrendered its last dorsal to the lumbar field as its sacrum appropriated the last lumbar. Such readjustments would be in line with much evidence that the sacrum does shift its attachment either backward or forward during the transformation from one

TABLE 1  
VERTEBRAL NUMBERS

	Cervical	Dorsal	Lumbar	Dorso-lumbar	Pre-sacral	Sacral	Sacro-Coccygeal	Sacral + Sacro-Coccygeal	Coccygeal + Caudal
	C	D	L	D+L	C+D+L	S	Scgl	S+Scgl	Cgl+Cd
Pelycosauria (Romer and Price, 1940)	7			20	27	2			60
<i>Moschops</i> (Gregory, 1926)	6-7			21-22	29	3	6 (est.)	9	?
<i>Cynognathus</i> (Gregory and Camp, 1918)	7			21	28	4	4	8	?
Platypus	7	17	2	19	26	2	0	2	20
Echidna	7	15	3	18	25	2	2	4	11
<i>Phascolomys</i>	7	15	4	19	26	2	2	4	8-15
<i>Phascolarctos</i>	7	11	8	19	26	2	2	4	9
<i>Didelphis</i>	7	13	6	19	26	2	3	5	23+
Placental primitives (est.)	7	14	6	20	27	3	1	4	

ened and strengthened the sacral complex.

In spite of its aquatic habits, the platypus has not increased the number of its lumbar. Possibly this may be due to the capture of two of the lumbar by the dorsal region and the secondary increase in the number of free ribs in connection with the widening of the thorax and the more oblique position of the large diaphragm. In Sirenia and whales, with dwindling hind limbs, the lumbar region lengthened as the sacro-iliac contact dwin-

type of habitus to another. In some of the sloths, for example, the sacrum has apparently slipped backward, increasing the number of dorso-lumbar from 19 to 28, and in *Hyrax* the number of dorso-lumbar rises to 30. In the orang, on the other hand, the sacrum has shifted upward, reducing the number of dorso-lumbar to 16.

From this it is apparent that in their vertebral formulae the monotremes are nearer to the marsupials than to the therapsids.



The ribs of the platypus (fig. 12), in conformity with the exceptional width of the thorax, spring outward widely from the vertebrae, their proximal fourth in the mid-dorsals being nearly horizontal; then they turn downward, backward, and outward, becoming more nearly vertical toward their lower end, where they meet peculiar flat and overlapping "ventral ribs," which curve forward toward the sternum. The capitula of middorsal ribs are embedded in bony sockets on or near the ventral sides of the centra and in contact with the intercentral discs. Even in the first dorsal rib the proximal end is slightly expanded vertically, but there is still only a single head with little or no trace of a separate tubercle.

The wide lateral swelling of the thoracic barrel leaves abundant space for large and long lungs and superficially recalls the well-rounded wide thoracic barrel of the aberrant pelycosaur *Casea*, of *Moschops*, and of other semi-aquatic reptiles. It even suggests the thorax of *Cryptocleidus*, a fully aquatic plesiosaur. All of these are obviously habitus features, and there is little or nothing that is purely reptilian in the vertebral column and ribs of either platypus or echidna. The same is true of the sternum, with its well-ossified pre-sternum and sternal segments. These secondary polyisomeres are not present as such in the known reptiles.

The diaphragm of the platypus, as described and figured by von Gössnitz (1901, pl. 13, fig. 1), is a completely mammalian structure. Although *Cynognathus* probably had the materials from which a diaphragm was later evolved, it had peculiar large, flattened, laterally projecting lumbar ribs, which grade back into the sacral ribs. No visible trace of such an arrangement is present in the monotremes.

#### PECTORAL GIRDLE AND LIMBS

The pectoral girdle of the platypus forms a large, strong, but rather lightly constructed crib for the suspension of the anterior half of the body (pl. 1), and it also serves as a platform and fulcrum for the powerful arms and very large hands. As noted above, the thorax is supported and held in place in a sling: dorsolaterally by muscles running from the

neck and thorax to the forwardly inclined and over-arching blades of the opposite scapulae; and ventrally by the pectoralis and other muscles running in from the limbs to the pectoral girdle and thorax. In running mammals (such as the horse), which have lost their clavicles, the thorax is slung dorsally only between the scapular blades by muscles such as the rhomboideus and the serratus, which run upward and outward from the thorax to the scapulae. On the other hand, even in such mammals as monkeys, with strong clavicles that meet the anterior segment of the sternum, the coraco-scapulae are not articulated with the sternum, and consequently both the scapulae and the clavicles are free to move in various directions. This greatly increases the freedom and length of stride of the fore limbs. At the other extreme, in the monotremes (fig. 14) the clavicles are firmly united with the interclavicles and the sternum, and the greatly enlarged scapulae are also firmly articulated with the sternum. The latter is tied to the ventral body wall and fixed by the ribs. Consequently the coraco-scapulae of monotremes are nearly fixed in the anteroposterior direction with reference to the floor of the crib-like structure mentioned above. They are also fixed laterally by the firm attachment to the clavicles at the acromion and by the close union of the latter with the wide, flat, T-shaped interclavicle. But in the vertical direction the entire pectoral girdle can move up and down a little, as does the forepart of the plastron of a box tortoise, by means of a nearly transverse, tripartite, cartilaginous hinge joint, running obliquely inward across the articular facets between the pillar-like coracoids and the presternum, and transversely across a similar articular surface between the interclavicle and the presternum. Thus the scapulo-coracoid connections are not completely rigid, and the expanded thin epicoracoid plates can slide a little upon the wide flat surface of the interclavicle.

In the retention of undiminished clavicles and interclavicles and of the contact between the coracoids and the sternum (fig. 14E), the monotremes are unquestionably reptilian in construction rather than mammalian, and this undisputed fact has been one of several

principal reasons why nearly all authors, including myself, have recognized the basic reptilian heritage of the platypus.

In the other direction, it is evident that the pectoral girdle of the platypus has become

many features of the clavicular-interclavicular arch and sternum.

The pectoral girdle, ribs, and sternum of the echidna are identical in plan with those of the platypus but are far more robust in ac-

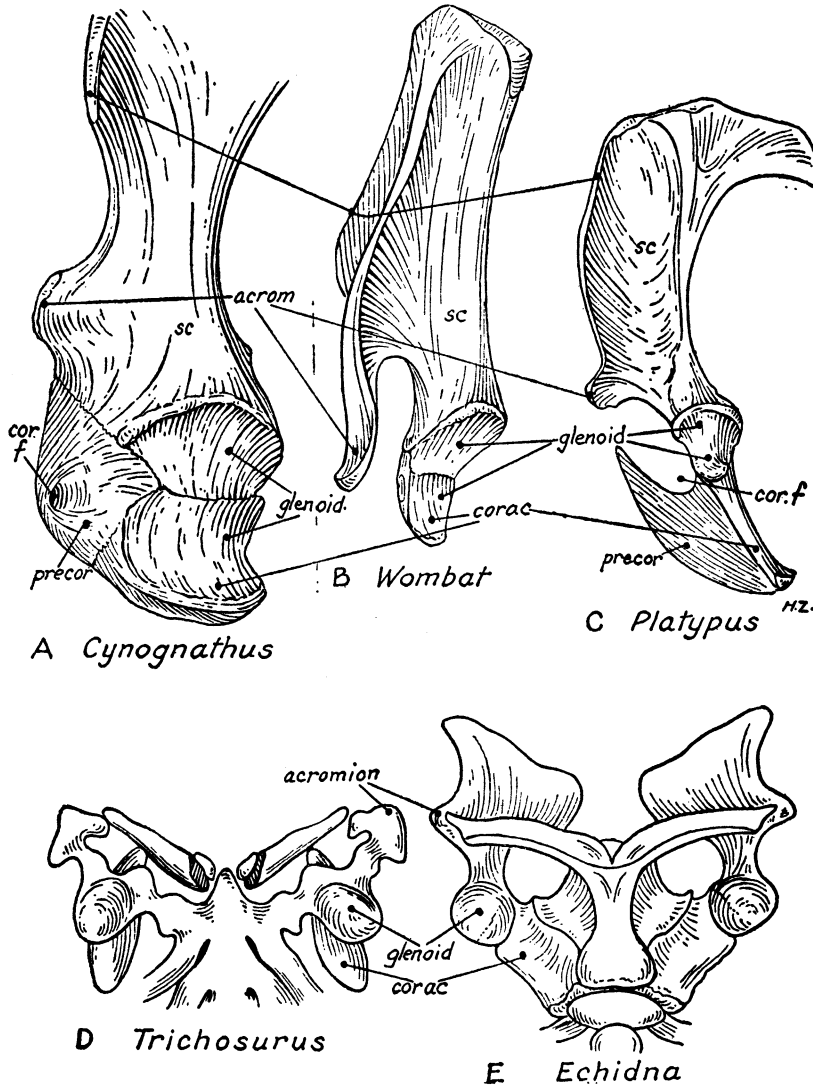


FIG. 14. Morphology of the coracoid. D, E, After Broom.

highly specialized: in the forward arching of the scapulae (pl. 1), in the eversion of their outer borders, in the prolongation of their posterodorsal border into a long hook, in the transverse lengthening and columnar form of the somewhat crocodilian coracoids, in the great expansion of the epicoracoids, and in

cordance with its far greater muscular power. As will be noted below, the evidence from several sources suggests that the ancestors of the echidna once passed through a more platypus-like stage.

Returning now to the problem of the relations of the platypus to the cynodonts, it is

also plain that in the pectoral girdle and sternum the forces and conditions that produce habitus features have, so to speak, concentrated on depositing new specializations but have by no means obliterated the heritage from remote therapsid ancestors. Brazier Howell (1937a, p. 192), although readily admitting the general reptilian source of the monotreme coracoids, as well as of other parts of the shoulder girdle, doubts the derivation of monotremes from known therapsids. "The theory of irreversibility of evolution," he writes, "is accepted by me only with extensive reservations, but it is difficult to see how the anterior coracoid of a tetrapod could become severely reduced, following the shifting of its musculature to other bones, as was clearly the case with the theriodonts of the Triassic, and could later take the reverse step to conform to monotreme conditions. The obvious conclusion is that monotremes could not have been derived from any of the 'mammal-like reptiles' of therapsid affinity of the types now known" (*ibid.*, p. 195).

But the supposed shifts between reptiles and therian mammals in the muscle areas of the coraco-scapular tract have been ably dealt with by Romer (1922, pl. 32, figs. 6-11, and pp. 551-554), and the derivation of monotremes as well as of all other mammals from the general therapsid stock rests upon many lines of evidence and need not be reconsidered here.

Again, Brazier Howell, in his excellent paper on "The swimming mechanism of the platypus" (1937b), shows in his figure 2 his theory of the homologies of the various coraco-scapulo-humeral muscles in the platypus, as compared with those of a typical therian mammal, and his arrangement does not differ very profoundly except in detail from those already proposed by Wilson and McKay (1893) and adopted by Gregory and Camp (1918) and Romer (1922). Yet he appears to make an unwarranted extrapolation beyond the direct evidence when he confidently affirms that the anterior and posterior coracoids and interclavicle of the platypus are "... of a type that renders it practically impossible that monotremes could have been derived from mammal-like reptiles

of the Triassic theriodont type from which therian mammals are assumed to have arisen."

Unyielding factualists have so set the style in taxonomy and morphology that, if their assertions were accepted, hardly any known type of animal could possibly have been derived even from any known past group. That many transformations, involving numerical changes and reversals of emphasis in growth, have taken place on a grand scale seems to be still unsuspected by all those who expect remote ancestors to show the same kinds of specializations as do their later descendants. One would certainly look in vain below the level of the Triassic theriodonts for any reptilian shoulder girdle that is as near to the monotreme type in basic features as are those of *Cynognathus* and the anomodonts. The great enlargement of the anterior coracoid plate and its muscles in the monotremes is to some extent convergent toward a similar enlargement of those parts in the aquatic nothosaurs and plesiosaurs. Although it is conceivable that the monotreme connection of the coracoids with the sternum is entirely secondary, not primary, it seems on the whole more probable that the remote ancestors both of the monotremes and the marsupials retained this contact and were in this feature definitely prototherian in stage.

Direct comparison of the scapulo-coracoid of *Cynognathus* (fig. 14A) and the anomodonts with that of the platypus indicates that in the latter there has indeed been an expansion of the anterior coracoid element (fig. 14C), whether we call it epicoracoid or precoracoid, just as there has been a transverse elongation of the posterior or true coracoid, producing a somewhat crocodilian or columnar shaft. This is associated with the general flattening of the body, and it lengthens the space available for the pectoralis, supracoracoideus, and other muscles, besides putting the glenoid facets in an advantageous position for the swimming or digging movements of the humerus.

Hanson (1920), cited by McCrady (1938, p. 163), observed in an opossum stage-33 embryo that the coracoid cartilage extended all the way from the scapula to the sternum without sutures. "Later in the same stage, the middle portion of the coracoid disappears

and the sternal and scapular ends remain in cartilaginous form. This is the condition when born. In later stages the sternal portion fails to ossify and is resorbed. The scapular portion becomes ossified and attached to the scapula as a typical mammalian coracoid process." Unfortunately, I have been unable to find any description of the actual development of the pectoral girdle in the platypus. But it is evident that there was a marked acceleration of growth of the coracoid plate, accompanying the great enlargement of the pectoral muscles. In short, the ontogeny of the pectoral girdle both in the American opossum and in the Australian "opossum" *Trichosurus*, as described by Broom (1899; 1932, p. 323), joins with much other evidence to indicate that divergent specializations toward the monotreme and marsupial stages took place while the common ancestors of the marsupials and monotremes were still in a prototherian or pre-marsupial stage.

In the echidna the coracoid column (fig. 14E) is much shorter transversely, and the glenoid facets are brought inward much closer to the midline of the sternum. Other evidence suggests that this marks a further specialization in the echidna, and it may well be partly a convergence toward the conditions in that ontogenetic stage of certain marsupials (fig. 14D) in which the coracoid column is very short and the glenoid facets are much nearer to the midline than they are in the adults.

The humerus of the platypus plainly reflects a similar combination of digging and swimming habitus with prototherian or cynodont heritage (cf. Gregory, 1910, p. 153; Gregory and Camp, 1918, p. 510; Howell, 1937b, pp. 218-222). It is much more specialized than that of an unidentified Jurassic mammal (Simpson, 1928, pp. 155-158, figs. 50-54) but not in the direction of the typical therians. In the extreme widening of the distal end, the platypus humerus (fig. 15) suggests the humerus of moles, *Chrysochloris*, and other animals that are extremely strong diggers. The head and proximal end of the humerus, instead of being nearly globular as in typical therians, as seen from the end is greatly widened, compressed, and folded around the coracobrachial mass to form a

wide fossa which faces downward and backward in the standing posture. The wide distal end of the humerus is twisted nearly at right angles to the general plane across the proximal end. By means of these and other adjustments the elbows are widely everted in the standing pose, and the plane across the projecting ento- and ecto-condyles is nearly horizontal.

"Examination of the articular surfaces [between the glenoid surface and the head of the humerus]," writes Howell (1937b, p. 218), "indicates that pure rotation of the humerus can take place through an arc of about 135 degrees, and that further movement at the elbow is sufficient to allow the forearm to sweep through an arc of fully 180 degrees without any deflection of the humeral axis whatever." The olecranon of the ulna (pl. 1) is very large and greatly produced into a crest on which the enormous triceps is inserted. From the olecranon and from the long ectocondylar process of the humerus very strong flexor muscles on the back of the wrist impart a powerful backward thrust to the hands in swimming (Howell, 1936, p. 429; 1937b, fig. 2 E, F). "It is clear," writes Howell (1937b, p. 217), "from the photographs and descriptions of Burrell (The Platypus, Sydney, 1927) and others, that the platypus swims by alternate thrusts of the fore feet. The integument of the manus is projected far beyond the nails, and on the forward thrust this extension is folded back against the palm, so that water resistance is reduced, while on the backward thrust the palmar extension is expanded, so that a greater 'purchase' is secured for propelling the animal. During aquatic progression the broad hind feet are held immobile, laterally, and in a horizontal position, and are used, in conjunction with the flattened tail, solely for equilibration. This method is theoretically inefficient for the reason that the animal never can travel faster than the speed at which it retracts the forelimbs. In contrast to this are the methods used by penguins, sealions, seals, and whales, which employ an oblique thrust against the water, utilizing somewhat the same principle which enables an iceboat to tack at a speed faster than the wind velocity."

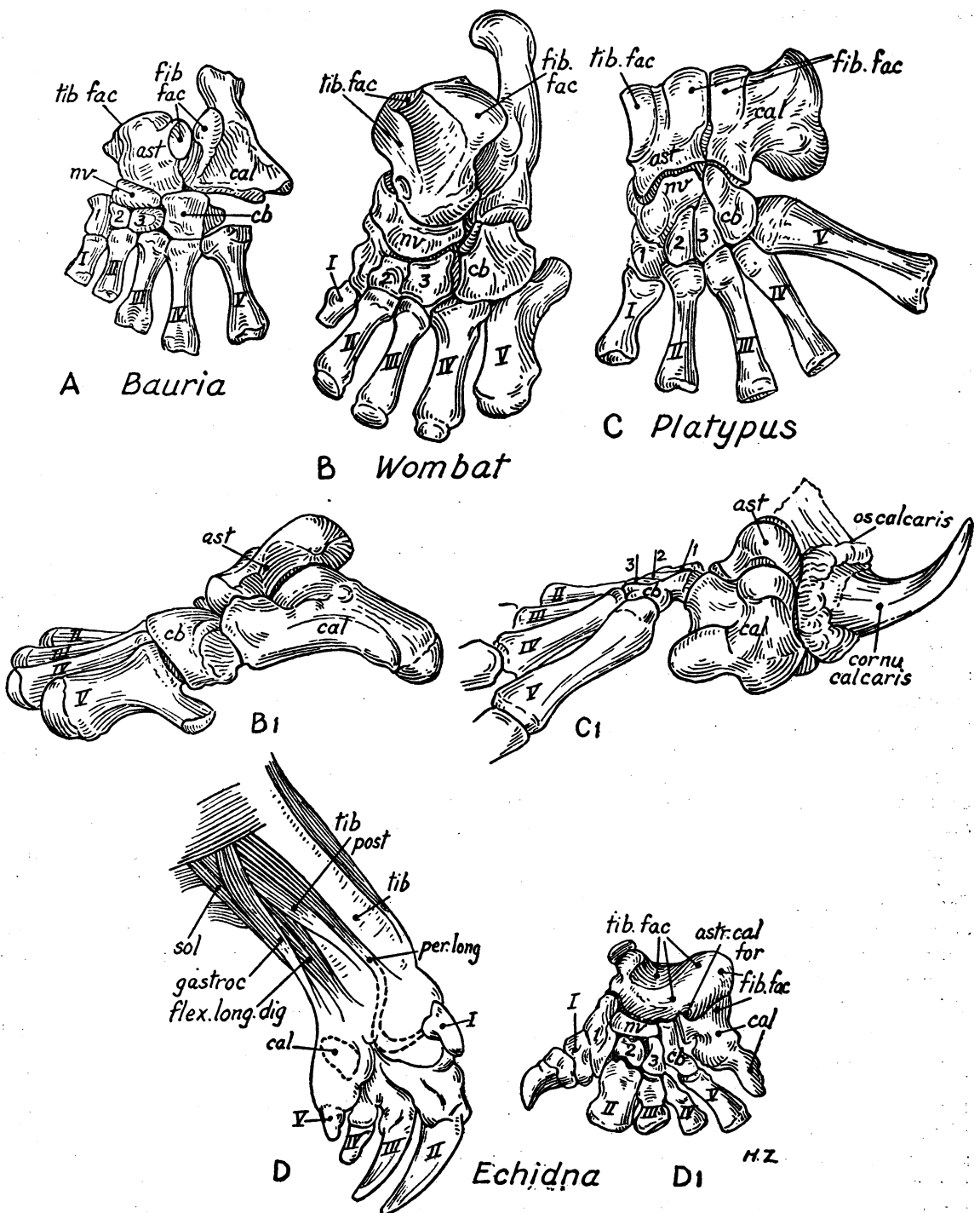


FIG. 15. Morphology of the pes. A, After Schaeffer; D, after Mivart; others original.

The echidna, with still more powerful fore limbs, quickly sinks almost vertically into the ground, tearing up the ground with the large claws of the fore feet and quickly kicking the dirt over its back with rotary and screw-like movements of the hind feet. Thus in many ways the monotremes converge toward and far surpass such Permian reptiles as *Diadectes* in their digging adaptations, and we need not suppose that their extreme specializations gave rise to the conditions observed in the pectoral girdle and limbs of the therian mammals.

### PELVIC GIRDLE AND LIMBS

Whereas the pectoral girdle of monotremes differs widely from those of all marsupials and placentals, the pelvis (fig. 12), including the epipubic bones, is of the general marsupial type, differing chiefly in proportions and special details that are mostly connected with the peculiar habits of the monotremes. The pelvis is relatively smaller than in marsupials, the ilio-ischial length into dorso-lumbar length being about  $3\frac{1}{2}$  in platypus as compared with  $2\frac{1}{2}$  and  $2\frac{1}{2}$ , respectively, in aboreal koala and *Didelphis*,  $2\frac{1}{2}$  in fossorial wombat. The pelvis as a whole is very similar in the two types of monotremes, that of the echidna being far more robust.

The ilium (fig. 12) differs from that of *Cynognathus* (fig. 13) and of the smaller cynodonts in not being at all helmet-shaped but more or less triquetrous in cross section near the top, with a medial surface for the sacrum, an anteroventral surface for the ilio-psoas, and a posterolateral surface for the deep gluteus muscles. In the uppermost cross sections of the ilium, however, the iliacus surface is wanting, and the crest of the ilium is produced anterodorsally, somewhat as in *Phascolarctos* but less elongate. This dorsally projecting crest of the ilium in monotremes is in a favorable position to give attachment medially to some part of the sacrospinalis muscles, dorsolaterally to the deep gluteus, dorsoposteriorly to the cruro-coccygeus (Pearson, 1926, figs. 1, 2).

From the anterior border of the pubis of the platypus (fig. 12) in front of the acetabulum springs a large forwardly and upwardly directed iliopectineal spine for the attach-

ment of the "sartorius" (ambiens) (Pearson, *ibid.*, p. 156). Ventrolaterally to this process is the smaller "pubic tubercle," directed laterally for Pearson's "adductor 1" (*ibid.*, pp. 157, 158). In the kangaroo the prominent pectineal process gives rise at its base to the psoas minor and at its tip to the pectineus (Elftman, 1929, pl. 9, fig. D), but in other marsupials the pectineus arises from the epipubic bone. The great enlargement of the iliopectineal spine and the separation of a pubic tubercle in monotremes are probably connected with the extreme development of their thigh muscles and with their digging habits.

Helga S. Pearson (1926, p. 153), after dissecting the pelvic and thigh muscles of a comparative series of reptiles and mammals, including the platypus, and carefully considering Romer's results in this field, concludes that "Most of the pelvic and thigh muscles of *Ornithorhynchus* can readily be brought into line with these [i.e., Romer's homologizations of reptilian and mammalian muscles]. As might be expected, they [the pelvic and thigh muscles of *Ornithorhynchus*] are essentially mammalian in their arrangement but sometimes still suggest a reptilian origin. A few appear to be unique."

The epipubic bones (fig. 12) of monotremes are essentially like those of the wombat, except that they are shorter and more sharply divergent from the midline. They are embedded in the muscular wall of the abdomen, and between them in the female is the opening of the pouch. As in marsupials, they are movably articulated with the anterior border of the pubis. In *Cynognathus*, Seeley's (1895) specimen likewise shows a flat articular facet on the anterior transverse border of the symphysis, which suggests that the cynodonts too had epipubic bones.

The hind limbs of the platypus, highly adapted for crawling, are widely everted, the knees being much above the level of the acetabula in standing (pl. 1). Thus, as in the fore limbs, there is pure convergence toward the bent-limbed pose of the Lower Permian reptiles (cotylosaurs, pelycosaurs). Whereas in the standing pose the head and potential neck of the femur in cynodonts and marsupials curved inward so that the great

trochanter is lateral to the acetabulum, in the monotremes (pl. 1) the neck and head are directed upward and inward, and the great trochanter is posterolateral to the acetabulum. The shaft of the femur is much flattened, more so than it is in digging edentates, and the distal end of the dorsal part of the intercondylic notch is replaced by a wide, smoothly rounded patellar surface; the ventral part of the notch still lodges the crucial ligaments for the tibia. The femur of the wombat distantly approaches that of the platypus in so far as the head of the femur is beginning to face upward, the greater and lesser trochanter are nearly in the same transverse plane, the upper half of the shaft is beginning to be flattened, and the patellar surface is rounded and extended transversely, with dorsally reduced intercondylic notch.

The internal trochanter of the platypus is nearly equal to the external trochanter and springs from the opposite (anteroventral) border of the femur. It is largely covered dorsally by the ilio-psoas and ventrally by the enlarged first division of the obturator externus+quadratus femoris? (Pearson, 1926, fig. 6, p. 161).

In spite of its specializations, the femur in the platypus is readily derivable in a general way from the primitive femoral stage that is represented in the oldest known mammalian femur, from the Stonesfield Slate (Middle Jurassic of England) (Simpson, 1928, figs. 46, 47, pp. 149-153). Simpson (p. 153) concludes that, although this femur resembles that of a monotreme in many essential respects and "... might even be described as a monotreme femur without the specialization seen in the recent forms ..." yet "... the characters held in common must be admitted in all probability to have occurred in the ancestry of all known mammals. They do not indicate that the femur is that of a monotreme but they do show that it is at a similar evolutionary level. It is prototherian, not necessarily in the sense of being a member of a natural group Prototheria, or of being related to the monotremes, but in an evolutionary sense, using the term prototherian to designate a grade of structure."

Another fossil femur from the Purbeck, or Upper Jurassic of England, is definitely more

progressive toward the primitive metatherian stage as represented in *Didelphis* (Simpson, *op. cit.*, pp. 153, 154).

Assuredly the Stonesfield and Purbeck femora, although indeterminate as to subclass and order, do suggest that even before the close of the Jurassic period some of the mammals were partly adapted for crawling, swimming, and digging, others for running and perhaps climbing.

The collective muscles of the platypus lower leg are greatly swollen, especially at their proximal ends (Meckel, 1826; Pearson, 1926). The very wide cruro-coccygeus (simulating a gluteus maximus+coccygeofemoralis), extending from the anterodorsal end of the ilium along the root of the tail and inserted on the flexor side of the tibia, tends both to adduct the tarsus and to flex the leg on the thigh. A very wide but rather thin sheet, the biceps femoris, passing outward from the stout ischial tuberosity, would further fold the lower leg upon the knee.

The upper end of the fibula (pl. 1) is prolonged into a high, expanded flabellum. Mivart (1866, p. 393) states that in *Echidna* the peroneus longus (pl. 53, fig. 3; our fig. 15) is a large muscle and arises from the anterior surface of the upper half of the fibula, including its singularly produced upper extremity. "The tendon of this muscle, running downward, passes obliquely inward (toward the tibia) and then dips down between the curiously reflected calcaneum and the peroneal border of the cuboid, and running along a groove on the plantar surface of that bone, and crossing the sole of the foot, is inserted into the plantar surface of the proximal phalanx of the hallux." Meckel (1836, pl. 6, fig. 35) describes this muscle in the same position in the platypus. In the wombat the flabellum of the fibula (pl. 2) is also pronounced but much less than in the monotremes. Probably the extreme dorsal extension of the fibula in the monotremes is a specialization but from a primitive or prototherian stage.

In the hind feet of the platypus (fig. 15) the metatarsals and digits form spreading webbed paddles which suggest those of some chelonians and are probably used in balancing and in turning as well as in digging. That they can



be waved obliquely back and forth is indicated by the loose hinge-like connection between the leg and the foot. There are two long oblique convex facets for the tibia and fibula on the proximodorsal surface of the astragalus and calcaneum (fig. 15C, C 1), and there is a ball-and-socket internal malleolar joint between the astragalus bearing the socket and the tibia, which has a bead-like projection in the midst of a circular articular track. The calcaneum has its tuber or heel directed not upward and backward, as in more normal mammals, but downward and outward (fig. 15C 2), so that it seems to have been pushed into a position nearly at right angles to its original one. Meanwhile the facets for the fibula and cuboid have retained much more of their primitive positions.

Still greater modifications are found in the echidna. The lateral tibial facet on the astragalus (fig. 15D) now forms a high, smoothly convex ball, while the internal trochlea is much reduced to make room for the large internal malleolar globe on the tibia, which is received into a large basin on the internal surface of the astragalus. The "head" or navicular facet is wide and flattened anteriorly. The calcaneum has a large internal facet for the astragalus; its outwardly and downwardly directed heel tapers to a blunt point. The cuboid is much reduced dorsoventrally and widened and flattened transversely. In various ways this foot suggests those of pareiasaurs, giant tortoises, *Diprotodon*, and others with wide tarsals and short metatarsals. But here there are large sickle-like claws for digging, which are operated by screw-like or undulating movements at the tibio-tarsal joint, as well as by powerful flexors of the digits.

The down-turned calcaneal tuber must cooperate with the excessively wide and short hallux and the other digits in grabbing hold of the earth with great strength, so that an enemy would find it very difficult to overturn the animal. Mivart's description and dissection (1865) show that in echidna (and presumably also in the platypus) the tendon of the peroneus longus (fig. 15D) takes its usual mammalian course, running down the back of the leg into a deep groove on the plantar surface between the calcaneum and the

cuboid and then bending inward to be inserted into the proximal end of the hallux. The down-turned tuber of the calcaneum is embedded in a huge plantar pad. A similar swollen pad lies beneath the short hallux, and there is a deep crease between these two pads, which must add to the effectiveness in grasping.

The gastrocnemius and soleus muscles are continued up onto the back of the flabellum fibulae. In Mivart's plate 53, figure 3 (1865), their tendons disappear under the thick integument of the foot, but with the swinging of the tuber around nearly at right angles to its normal position, these muscles must be inserted on the calcaneum nearer to the fulcrum than they would be if the heel were produced far behind the tibial shaft (fig. 15D); thus they seem to cooperate more effectively with the other flexors in thrusting the foot backward.

Comparison with the foot of the highly progressive therapsid *Bauria* (cf. Schaeffer, 1941a) again shows that while the platypus has retained the main tibio-fibular facets on the astragalus, its calcaneal process has been pushed around to the outer side.

The foot of the platypus appears to be far more specialized than that of *Phascalomys*. Its aberrant morphologic features may have been assumed during the intense and probably rapid adjustment to the peculiar and successful combination of both swimming and digging by a ground-living pre-marsupial ultimately of arboreal derivation.

#### REPRODUCTION AND EMBRYOLOGY

Since the early years of the nineteenth century, when it became known that the right and left oviducts of the platypus remained separate and opened into a single individual cloaca, the obvious resemblances to the conditions in the Sauropsida have been treated by generations of eminent exponents of *l'école des faits* as an ultimate fact, as if no further analysis were desirable or possible.

Chiefly upon the contrasting relations of the opposite oviducts to each other and to the cloaca in the monotremes, marsupials, and placentals rested De Blainville's subdivision of the mammiferous quadrupeds into three major grades or subclasses: "Les

Ornithodelphes," "Les Monodelphes," "Les Didelphes." Another hitherto unexplained fact of record has been the peculiar relations of the three-way "vaginae" of marsupials to

(1941) of the University of Sydney, Australia, to link these two sets of facts in terms of evolution (fig. 16), as best set forth in his own words and diagrams (p. 86):

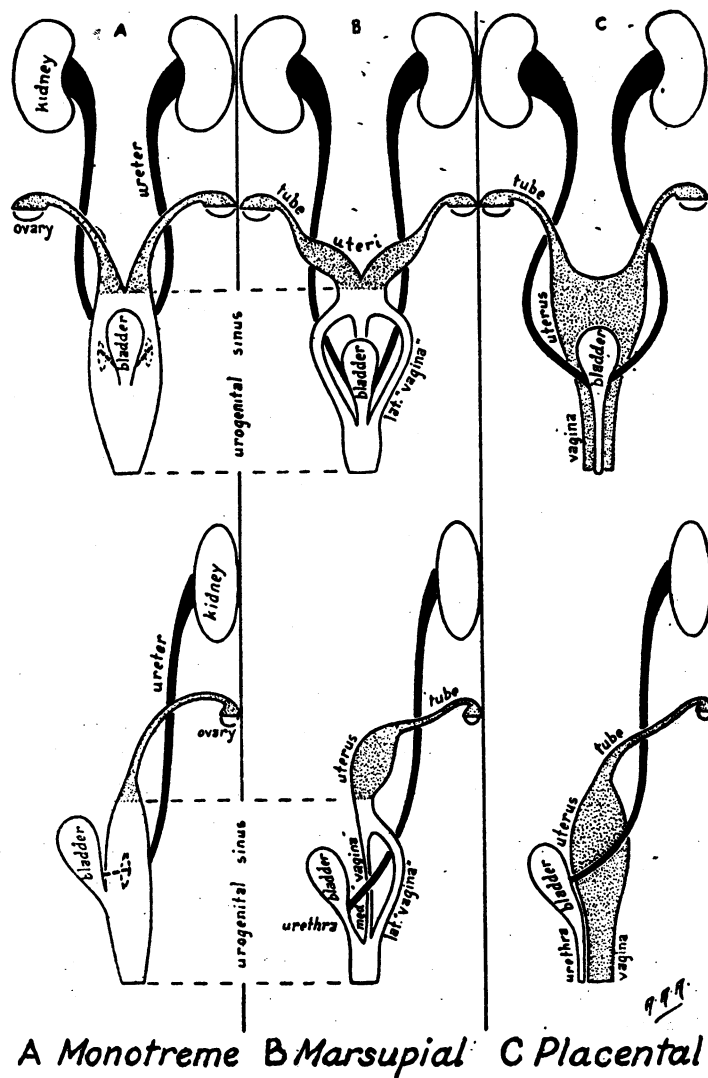


FIG. 16. Schematic representations of the reproductive systems in a monotreme (A), a marsupial (B), and a eutherian (C). Upper figure as seen from the ventral aspect; lower, from the left lateral aspect. Solid areas, ureters; stippled, Müllerian ducts. In A the broken lines indicate the course that the ureters would take to attain the marsupial condition. After Abbie.

the cloaca and oviducts and the complete absence of these structures in monotremes and placentals. It has remained for Abbie

"In sub-marsupials the urogenital sinus is relatively very long, reaching from the cloaca to in front of the bladder. The Müllerian

ducts open separately into its frontal end, the ureters enter its dorsal aspect, and the bladder opens off independently from its ventral surface (figure 1, A). The ureters do not reach the bladder. If, now, the ureters be prolonged right through the urogenital sinus to reach the bladder, the sinus would present two perforations separating three tubes. If the two lateral tubes are called 'lateral vaginae,' and the median tube the 'urethra' and 'median vagina,' and only what is left of the sinus below is allowed as 'urogenital sinus,' the condition would be precisely that found in marsupials (figure 1, B). It is suggested, then, that the 'lateral vaginae' really represent incompletely separated portions of the urogenital sinus, not the caudal continuation of the Müllerian ducts as is usually believed. On this argument the marsupial genital apparatus is simply an elaboration of the sub-marsupial—particularly monotreme—and possibly adapting an oviparous mechanism to a limited degree of viviparity.

"In the eutherian, differentiation of the urogenital apparatus carries the urethra and the single vagina behind it to the perineum (figure 1, C); this vagina does represent the fused lower ends of the Müllerian ducts. Such a condition could be derived from the marsupial by disappearance of the separated portions of the urogenital sinus ('lateral vaginae') and permanent establishment of the 'median vagina.' But if it is accepted that the various marsupial 'vaginae' are no more than portions of the urogenital sinus, such adjustments become unnecessary; it is necessary only to go to the ancestral marsupial structure, which is assumed here to be practically the same as that of monotremes, to reach a condition whence both the modern marsupial and the eutherian could readily be derived."

In the light of the foregoing, it seems that these three morphological patterns instead of constituting unbridgeable gaps between their respective subclasses, may now be viewed as allometric or heterogonic differences which accumulate during divergent evolution. Abbie, however, takes it for granted that the monotremes have preserved the original pattern and that the marsupial and placental patterns are divergent derivatives. It may

prove desirable for appropriate embryologic material to be examined for the purpose of testing Abbie's hypothesis more in detail, in order to discover, for example, whether the so-called triple "vaginae" of marsupials really arise in the way he suggests, and whether the monotreme pattern is not the result of temporary arrest at an early stage,

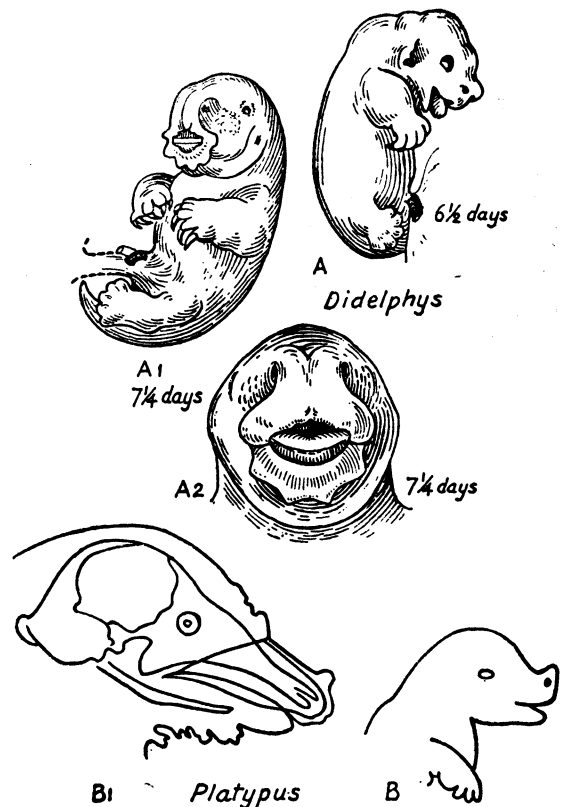


FIG. 17. Embryos of platypus and marsupial. A, After Selenka; B, B 1, after De Beer and Fell. In the earlier stage (B), the platypus resembles the marsupial (A); in a later stage (B 1), the "duck-bill" features are developing.

with subsequent development of yolk and shell glands delaying and preventing the conjunction of parts of the opposite oviducts.

Such an arrest at a low mammalian stage of development, with subsequent acceleration of new specializations, may well be the basis also for the apparently half-reptilian character of the male reproductive system in monotremes (cf. Weber, 1928, pp. 36, 37).

Dr. John Eric Hill and I have dissected the cloacal region of a male platypus and found the conditions exactly as described and figured by Meckel (1826, pl. 8, fig. 23), namely: that inside the preputial sack the large retracted glans is bilobate, the right and left halves turned in different directions; each half bears a group of several sharply pointed spines. Meckel describes the glans as bifid. There is a superficial suggestion of the bifid and spiny hemipenes of reptiles, but probably a true homology is with the distally cleft penis of various marsupials (cf. Weber, *op. cit.*, pp. 65, 68).

Even a brief review of the comparative embryology of the monotremes is beyond the scope of this paper, but it may be recalled that J. P. Hill (1910, p. 23) found evidence that the marsupials had been derived from early forms in which the eggs were provided with a tough membrane.

Newborn monotremes bear a striking general resemblance to newborn and foetal marsupials and share with them the great enlargement of the arms and hands as compared with the hind limb bud. This enables the newborn young to climb along the ventral surface of the mother to the pouch or lacteal depression. Burrell (1927) found that the young platypus has lips adapted for sucking, and Selenka (cited by McCarty, *vide supra*) found the muzzle of a newborn American opossum covered with an epidermal mask which strongly suggested the muzzle of the platypus. In the embryo platypus of stage 4 (De Beer and Fell, 1936, pl. 1, fig. b; our fig. 17B) the muzzle is very thick dorso-ventrally and extremely unlike the flattened beak that is already well under way in stage 5 (*idem*, pl. 1, fig. c; our fig. 17B 1). In stage 4 the head indeed is much more like that of a foetal *Didelphis* (fig. 17A).

## DISCUSSION AND CONCLUSIONS

1. THE FOREGOING FACTS and considerations seem to indicate that the phyletic relationship between the platypus and the echidna is relatively close, so that they do not merit more than family separation. The echidna bears the marks of secondarily terrestrial derivation from the aquatic platypus stock, and it has retained the platypus method of moving the limbs, but swims, as it were, in a dense medium.

The food habitus of the echidna is highly specialized, depauperate; by analogous cases with other long-tongued anteaters, its ancestors must have had more normal jaws and dentition. Moreover, it retains a *detrahens* mandibulae and other jaw muscles of monotreme type.

2. It has sometimes been assumed that the echidna is more primitive than the platypus, but it has lost all trace of teeth and has reached almost the limit of degeneration of the mandible. The platypus, on the contrary, is only now in the midst of a great transformation of the jaws and dentition involving the loss of true teeth and the evolution of substitutes in the form of horny dental plates. But in spite of the enormous differences between the echidna and the platypus in the jaws, the auditory ossicles and very many features throughout the skeleton remain alike in plan though differing in size; this again indicates that the wide differences between the platypus and the echidna have been effected in a relatively short period, perhaps from the Upper Eocene to the present time.

That the platypus in general is more primitive than the echidna is further indicated in the more archaic-looking pattern of its brain. Probably also the ancestors of the echidna had abandoned amphibious habits and become strong enough to dig in the forest and in dry ground. Thus they avoided the perils of frequent droughts and the drying up of streams, which must greatly limit the food supply of the platypus.

3. Between the monotremes and the marsupials there are many striking evidences of common phyletic heritage relationships. Later habitus specializations have to a great extent wiped out earlier specializations in

most parts of the skeleton, leaving only diverse and disconnected fragments of the older record. Nevertheless the platypus is essentially marsupial in type, in the presence of 19 dorsolumbar vertebrae and in the general characters of the cervical, dorsal, lumbar, and sacral regions. The general type of the temporo-mandibular joint of the platypus is far more nearly approached by marsupials than by cynodonts, and the muscles of the jaws diverge from the mammalian norm chiefly in such peculiar monotreme specializations as the separation of a *detrahens* mandibulae from the superficial levator muscle and the absence, at least of the posterior belly, of the digastric.

Even the chondrocranium of the platypus embryo, in spite of certain possibly reptilian or prototherian characters, far more nearly resembles as a whole the chondrocranium of the marsupial *Trichosurus* than it resembles that of any modern reptile.

The malleus and incus of monotremes (see above, p. 25) closely resemble those of the wombat, as clearly recognized by Doran. Their imperforate stapes resembles that of several marsupials and merely converges toward the columella of later reptiles and birds. The relatively great size of the anterior process of the malleus of the echidna is even exceeded in a young American opossum 49 days after birth (McCrady, 1938, p. 196).

Selenka (1887, p. 157) saw that the duck-like bill of the platypus is plainly only a specialization of the "oral shield"; this is well developed in embryo American opossums (stage 34) but in that form it degenerates rapidly, so that in the newborn there is only a trace of it left (McCrady, 1938, p. 168). Under the name "rhinarium" this structure persists, especially in some phalangeroids and in *Notoryctes*, but it never attains the remarkable size and specialization seen in the platypus.

The pouch of monotremes is a ventral depression lying between the marsupial bones, and it may be in either a partly degenerate or a primitive pre-marsupial stage. The latter may also be true of the lacteal glands and mammary areas.

The pelvis of the platypus is essentially marsupial in general build, differing chiefly in its shortness and in the emphasis of the pectineal tubercle. The ilium is not helmet-shaped as in cynodonts but essentially mammalian in all its relations. The sacrum differs very widely from the cynodont, but not from the marsupial type.

Monotremes obviously converge toward *Diadectes* and other Permian reptiles and even exceed them in the crookedness of their elbow joints and knee joints, but these adaptations to digging and swimming may readily have been derived from the far less extreme specializations of a wombat-like marsupial, merely by overemphasizing the bent-limbed posture and short-leggedness of embryo and young marsupials.

The skeleton of the hands and feet of the platypus suggest derivation from such a digging marsupial as the wombat, in which the older arboreal marsupial heritage characters have already nearly disappeared. The musculature of the platypus arm and hand is highly specialized and well adapted for the swimming and digging habits (Brazier Howell), and the same is true of the musculature of the hind limb (H. Pearson).

In the form and structure of the brain, the monotremes are far nearer to marsupials (cf. Abbie, 1941) than to either existing reptiles or the cynodont braincase described by Watson (1913).

Finally, the embryo and foetal stages of the platypus, as figured by De Beer, Burrell, and others, bear a remarkably close general resemblance to embryo and foetal marsupials, as figured by Semon and others.

4. If monotremes were the direct descendants of Triassic cynodonts and entirely free of all but remote parallel relationships to the marsupials, then many important monotreme specializations should not seem to be derivable from those of highly placed marsupials, rather than from the corresponding parts of Triassic cynodonts. The greatly reduced true molar teeth, for example, are doubtless specialized in possessing multiple roots and degenerate enamel and dentine. But in so far as the crown patterns include two more or less V-shaped moieties, they agree with those of *Phascolarctos* and *Phas-*

*colomys*, and the fact that they are now brachydont rather than hypsodont may be owing rather to an arrest in development with subsequent specialization in the degeneration of the teeth and elaboration of horny dental plates, than to the retention of a primitive condition.

5. Within the reptilian class the synapsid-theriodont ancestors of the mammals were at the opposite pole from the diapsid-archosaurs that gave rise to birds. Both indirect and direct evidence indicates that the theriodont and prototherian ancestors of all mammals, including the monotremes, laid eggs, that the right and left oviducts opened into a cloaca, and that the coracoids were in contact with the sternum; but not that the ancestral mammals built bird-like nests or had duck-like bills or tarsal spurs, or that they had pillar-like coracoids or greatly enlarged bony epicoracoids or twisted, sabre-like scapulae, or any of the features connected with widely everted elbows and knees and highly perfected swimming and digging habits. Similarly, other monotreme characters may be merely convergent toward reptilian characters.

6. For the present writer the question is left open whether the complete separation of the right and left oviducts in monotremes is a direct inheritance from reptiles or whether it came via a prototherian stage from the common ancestors of monotremes and marsupials, or, finally, whether it is partly owing to: (1) arrest of development at a stage in which the right and left oviducts were still separate, and (2) subsequent specialization toward a secondary increase in yolk, large eggs, and oviparous rather than ovo-viviparous habits.

In any event, the entire female reproductive system in the platypus is far less different from that of the wombat (e.g., Wiedersheim, 1907, p. 439, fig. 322C) than from that of the lizard (*idem*, p. 437, fig. 320). A failure to unite of the right and left uteri and the loss of the median "vagina" in the wombat would produce an arrangement like that of the platypus. And, as noted above, it has been shown by Abbie that merely by changing the rates of growth of the several parts, the monotreme reproductive pattern could give rise to that of marsupials and placentals.

7. Whatever may be the ultimate findings of embryologists regarding the origin of the diverse patterns of the female reproductive system in the three commonly recognized subclasses of mammals, we may at least, on the ground of Abbie's observations and deductions, seriously question the time-honored practice of selecting these diverse patterns of the reproductive system to be the first criteria of subclass value in the major classification of the Class Mammalia. This classification was set up at a time when the general paleontological history of the mammals and their origin from the Mesozoic therapsid stock were completely unknown, and it was not realized that with extremely rare exceptions skeletal characters afford the only known homologous terms in problems of phylogeny that involve both fossil and recent animals. Nor was it suspected at the time of De Blainville that the present habitus of any given animal represents, as it were, the telescoping and net residue of all earlier ancestral habitus beneath the surface layer of later habitus characters. Hence the ultimate criterion for the major classification of any given form should be not primarily its existing features but the determination of distant ancestral features which it may or may not have lost. If, for example, the relations of the embryonic membranes to the uterus should be given prior rank in classification, certain scincoid lizards might claim admission to the "Placentalia" (cf. Flynn, 1923). Or if the possession of a hairy covering were made an absolute criterion for admission to the Class Mammalia, adult and even foetal whales would fail to qualify, except for a few putative remains of bristles around the lips. And in the case of recent whales, even the skeleton is excessively disguised by later habitus features; but the skull of the early Tertiary *Eocetus* bears irrefutable evidence that the ancestors of the cetaceans were primitive placental mammals and that they were with high probability early Cenozoic members of the Order Carnivora.

8. The long prevalent misapplication of Dollo's "Law of Irreversibility," which in practice has been twisted to mean that remote ancestors must reveal the same kinds of specializations as their latest descendants, and that a specialization once acquired can never

be sloughed off and absorbed by a later specialization, has often obscured the essentially transformational, rather than orthogenetic, changes which do take place during a period of shifting from a given life zone to a very different one (Gregory, 1936b).

Huxley, Dollo, Bensley, and their successors all admit the arboreal origin of all the marsupials, and some of the signs of arboreal ancestry persist even in the excessively queer feet of *Diprotodon*. Different, but no greater, changes would be necessary to transform the pes of the wombat into that of the platypus. Even the cranium, jaws, and dentition of the platypus could be derived with fewer and smaller changes from those of the wombat or some other marsupial than from those of *Cynognathus*, and the same is true of many other parts of the skeleton, to say nothing of the brain (Abbie, 1941; Huber, 1930a), the facialis musculature (Huber, 1930a), and the musculature of even the fore limbs (cf. Brazier Howell, 1937).

9. Although the monotremes may have retained more of the "reptilian" characters in their reproductive methods, in their pectoral girdle, and various other features, their skeletons, including the adult skulls, jaws, dentitions, etc., are on the whole far more specialized than those of marsupials. The Cretaceous to Recent American didelphids seem indeed to be the more direct heirs of the progressive mammal-like reptiles; their Jurassic predecessors may have given rise to the Palaearctic early marsupial stock; the latter in turn may have given off the Australasian diprotodonts and, later, the monotremes.

10. The time when the monotremes and the marsupials separated from the prototherian stock can at present be estimated only indirectly and within wide limits. Probably no one would expect the earliest possible date to be much below the Upper Trias, or the latest nearer than perhaps Lower Eocene.

The evidence cited by Simpson (1928, p. 150) shows that by Middle Jurassic times in England the only known mammalian femur of that date was a little like that of the platypus in the arrangement of its proximal end and trochanters; but, as he is careful to point out, this by no means implies that monotremes were then already in existence.



In the next period (Purbeckian) another femur was on a step nearer to the *Didelphis* type. But the presumably very primitive didelphid marsupials are not definitely known before the Upper Cretaceous of Europe.

The total morphological advance in dental and skeletal systems from a primitive Paleocene creodont to a modern sperm whale (*Physeter*) seems to me far greater than that from a primitive Cretaceous marsupial (*Eodelphis*) to the modern platypus. Moreover, the existing morphologic gap between a sperm whale (*Physeter*) and a whalebone whale (*Balaena*) is very much greater than that between the platypus and a wombat. But from the work of Abel (1914) and Kellogg (1936), it seems highly probable that the phyletic lines leading backward respectively from *Physeter* and *Balaena* would merge in the common archaic stock of the Lower Eocene.

So far as known, the monotremes are closely associated only with the Pleistocene and Recent marsupial fauna of Australia and New Guinea, and by analogy with the history of the modernized placental orders, the adaptive branching of the Australasian marsupials need not have begun earlier than the beginning of the Paleocene. The monotremes may represent a semiaquatic branch of ground-living derivatives of an old arboreal stock.

Considering all this, I would tentatively place the branching off of the monotremes from the pre-marsupial stem as later than the beginning of the Tertiary period and the place as within the Australasian region.

In brief, I now propose to remove the monotremes from their isolated position in the subclass "Ornithodelphia" and to transfer them in the Order Monotremata to the Subclass **Marsupionta**<sup>1</sup> (new subclass), defined as didelphian, cloacate to trivaginate, oviparous or fetiparous, marsupiate mammals, typically with epipubic bones; primitively a large rhinarium (lost in tachyglossids); brain with hippocampus but without a corpus callosum; malleus with large anterior process (goniale).

The place of the monotremes in relation to other surviving groups would thus be as follows:

- Class Mammalia
  - Subclass Marsupionta
    - Order Marsupialia
    - Order Monotremata
  - Subclass Monodelphia (Placentalia)

This arrangement would get rid of the confusing terms Prototheria, Metatheria, Eutheria, Theria. The Multituberculata may be a very early side branch of the Marsupionta. The transition from the earlier Marsupionta to the Monodelphia may have occurred not by way of the monotremes but through the Mesozoic orders Triconodonta, Symmetrodonta, Pantotheria. From the construction of their jaws and teeth, I infer that the first two were essentially marsupionts, the third, primitive placentals.

<sup>1</sup> From *μάρσιπος, μάρσιπιον*, pouch; *ὄντα*, existing things.

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