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The Affinities of *Apterodon* (Mammalia, Deltatheridia, Hyaenodontidae)

BY FREDERICK S. SZALAY¹

INTRODUCTION

Recently, Van Valen (1965, 1966) has suggested, after examining the available evidence in detail, that the genus *Apterodon* is not a hyaenodontid but probably belongs to the arctocyonid-derived condylarth family Mesonychidae. The purpose of the present paper is to re-examine the relatively well-known Fayum material referred to three species of *Apterodon* and to compare the evidence with that derived from the mesonychid and hyaenodontid dentition and cranium.

The dental nomenclature used in this paper is that of Van Valen (1966), with some modification by me.

I am grateful to Drs. Malcolm C. McKenna and Leigh Van Valen for reading the manuscript and improving it with helpful suggestions. I am especially grateful to Dr. Malcolm C. McKenna for preparing a cast of the type specimen of *Apterodon gaudryi* Fischer, 1880, in the Muséum National d'Histoire Naturelle in Paris.

¹ Department of Vertebrate Paleontology, the American Museum of Natural History; Department of Zoology, Columbia University.

SYSTEMATICS

CLASS MAMMALIA LINNAEUS, 1758

ORDER DELTATHERIDIA VAN VALEN, 1965

FAMILY HYAENODONTIDAE TROUESSART, 1885

APTERODONTINI SZALAY, NEW TRIBE

TYPE GENUS: *Apterodon* Fischer, 1880.INCLUDED GENERA: *Apterodon* only.

DIAGNOSIS: Hyaenodontids with complete eutherian dental formula; premolars simple; paraconules and metaconules greatly reduced but still present on upper molars; postvallum and prevallid shear greatly reduced but still distinctly present on upper and lower molars; cusps on upper and lower molars tending to be bulbous and subjected to heavy apical wear; protocone completely reduced on P⁴; metaconids completely reduced on the lower molars.

APTERODON FISCHER, 1880

TYPE SPECIES: *Apterodon gaudryi* Fischer (see figs. 1, 2).

INCLUDED SPECIES: The type species, *Apterodon macrognathus* Andrews, 1906; *Apterodon altidens* Schlosser, 1910,¹ *Apterodon minutus* Schlosser, 1910,¹ and *Apterodon flonheimensis* Andreae, 1887 (the type species of *Dasyurodon* Andreae, 1887).

DIAGNOSIS: Same as for the tribe.

REMARKS: I have not been able to revise the genus, because the specimens are widely scattered in museums outside the United States.

The type of *Apterodon* (*A. gaudryi*) has never been figured before; to make a generic evaluation of the African material, therefore, is an uncertain task. Through the courtesy of Dr. Malcolm C. McKenna, who has prepared a cast of the dentition of the type specimen of the genotype, photographs of this cast can be published (see figs. 1 and 2). As the partially erupted M₃ indicates, the type represents an immature animal. *Apterodon gaudryi* is known to me only from the type; consequently I have no knowledge of the extent of size and morphological variation within this species. Comparisons, therefore, are extremely limited and are necessarily restricted to the structure of the P₄ and the lower molars.

Concerning size, the type of *A. gaudryi* could represent a small indi-

¹ Both *A. altidens* and *A. minutus* were named, but not described, by Schlosser (1910) in his brief, preliminary report of the then new Fayum mammals of Egypt. Schlosser (1911), in his large monograph on the Fayum fauna, described and figured these taxa, citing them as "new species."

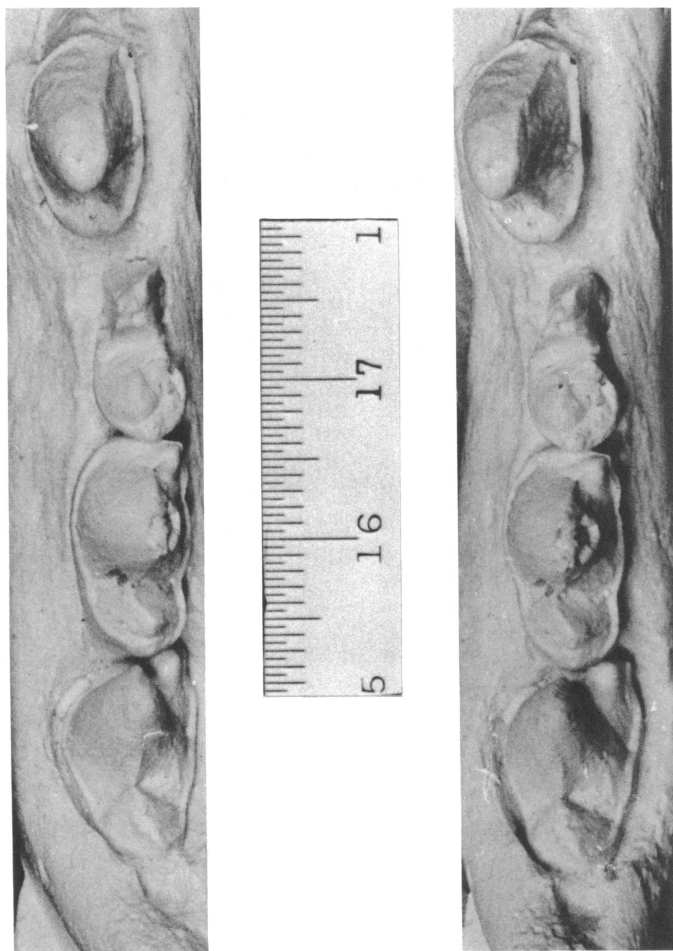


FIG. 1. Cast, A.M.N.H. No. 12391, of the type of *Apterodon gaudryi* Fischer, 1880, left P_4 (or dP_4), broken M_1 , M_{2-3} ; from the Phosphorites du Quercy, France. $\times 2$.

vidual in the population of the Fayum *Apterodon macrognathus*, the latter species being relatively well represented in the American Museum collection by several mandibles with teeth (A.M.N.H. Nos. 13239, 13240, 13241, and 13245). In addition to the few subtle morphological differences between *A. macrognathus* and *A. gaudryi*, the minimum sample known to me of the latter species also prevents my synonymizing the Fayum species with *A. gaudryi*.

The paraconids on M_2 and M_3 of *Apterodon gaudryi* may be relatively smaller than those of *A. macrogathus*. The talonid of the partially erupted M_3 of the type of *A. gaudryi* appears to be relatively slightly less elongated than that of any of the specimens of the African species known to me. There are no noticeable differences between the P_4 of *A. gaudryi* (which may be a dP_4) and the lower fourth premolars known to me of the *A. macrogathus* sample.

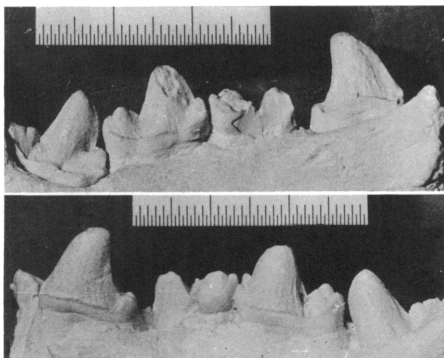


FIG. 2. Lingual (above) and buccal (below) views of the dentition of the type of *Apterodon gaudryi* Fischer, 1880. $\times 1$.

For the present, then, it appears best to retain the specific distinctness of *A. macrogathus* and *A. gaudryi*, although this distinction may not be, by any means, certain.

SUGGESTED SIMILARITIES OF *APTERODON* TO MESONYCHIDS

As Van Valen (1966) has pointed out, both Cope (1881) and Winge (1924) held that *Apterodon* very probably had mesonychid affinities. Van Valen (at the suggestion of S. B. McDowell, Jr., in Van Valen, 1966) specifically listed the following features as being similar to those of mesonychids but not to those of known hyaenodontids (the following is either *verbatim* or shortened from Van Valen): (1) relatively short snout as compared with length of skull; (2) relatively little divergence of tooth rows; (3) well-developed preglenoid process; (4) palatine extending only to level of junction of P^4 and M^1 ; (5) joint jugular and carotid foramina; (6) shallow masseteric fossa; (7) masseteric ridge not continuing below top of horizontal ramus; (8) distance from posterior border of lower canine to posterior border of M_3 less than length of mandible posterior

to M_3 ; (9) constriction in anterior and posterior margins of upper molars so that protocone is a distinct lobe; (10) relatively large parastyle on molars; (11) height of protocone of molars relatively great as compared with paracones; (12) protocones of molars massive; (13) protocone lobes of molars lacking conules; (14) posterior upper premolars taller than molars; (15) grinding mode resulting in heavy wear on molars.

The following characteristics of *Apterodon* were noted by Van Valen as being similar to those of some hyaenodontids, but not to those of mesonychids: relatively long basicranium; no alisphenoid canal; virtual absence of protocone from P^4 ; vertical protoconids and low or no talonids on the lower premolars.

DISCUSSION

The evidence presented by Van Valen and the information gathered by me are discussed below under two general categories: (a) the hyaenodontid, and (b) the mesonychid,¹ dentitions and crania and their degree of similarity or dissimilarity to those of *Apterodon*. Great caution has been exercised to utilize evidence derived from the excellent collection of proviverrine hyaenodonts and mesonychids in the American Museum of Natural History rather than that from the literature.

Points 2 and 9 to 15, as numbered above in the sequence in which Van Valen listed them, are concerned with the suggested similarities between the dentition of *Apterodon* and that of mesonychids. The recently considerably enlarged genus *Proviverra*² is probably the best-known representative of the primitive proviverrine condition, both dentally and in cranial morphology.

In *Apterodon* and *Proviverra* the upper incisors are aligned transversely and form a rather direct row of teeth in the premaxilla, the anterior border of the incisors forming a line nearly diagonal to the longitudinal axis of the cranium. In both of these genera there is a rather pronounced diastema between the upper canine and the most lateral upper incisors. In all mesonychids known to me the upper incisors are aligned in a semicircle, and the diastema between the upper incisors and the canine is relatively smaller than that in *Apterodon*. The diastema is virtually

¹ In several instances reference is also made to triisodontine arctocyonids.

² Van Valen (1965), in a generic revision of the tribe Proviverrini, synonymized *Sinopa*, *Prorhyzaena*, *Geiselotherium*, and *Leonhardtina* with *Proviverra*. Van Valen is followed, although on the basis of the evidence presented by him I cannot evaluate the validity of his judgments. In referring to *Proviverra* I generally mean *Proviverra* (= *Sinopa*) *grangeri* of the Bridger Formation, one of the best-known proviverrines.

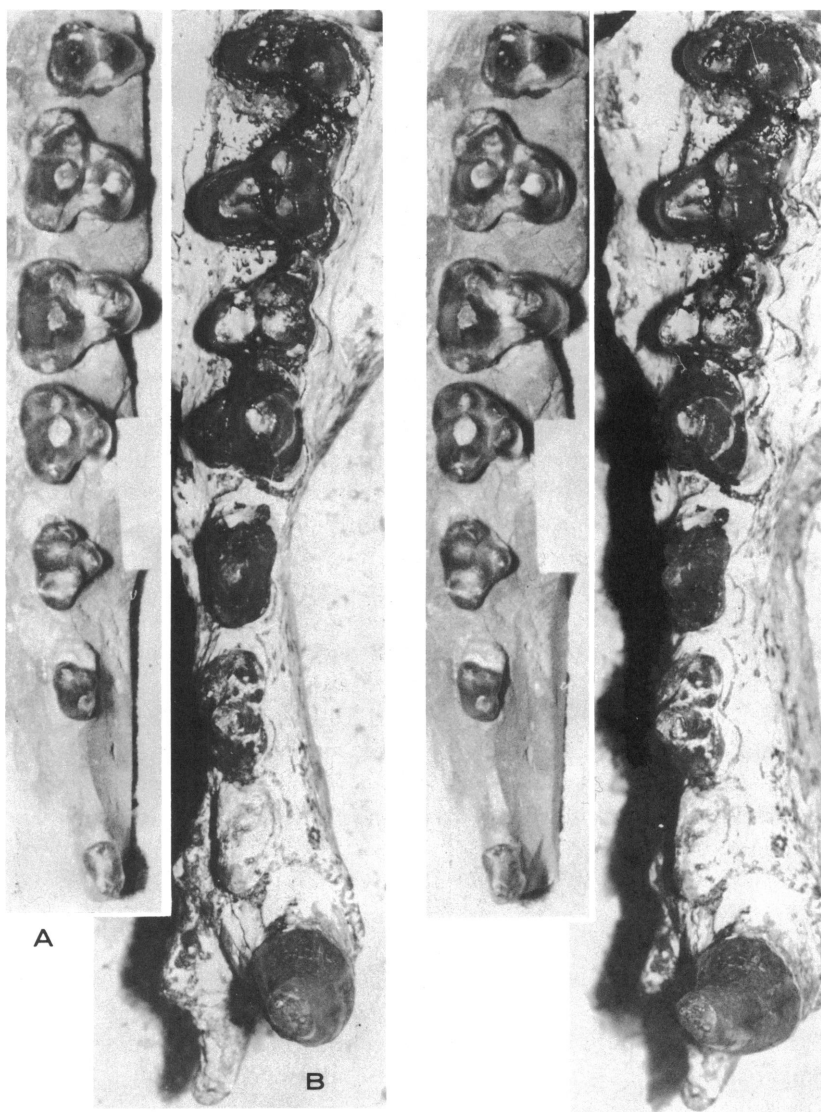


FIG. 3. A. Left upper dentition of *Dissacus saurognathus*, A.M.N.H. No. 776. $\times 1$. The individual teeth of the composite dentition are more separated from one another than they were in the maxilla. B. Right upper dentition of *Apterodon macrognathus*, A.M.N.H. No. 13237. $\times 1.55$.

absent from *Synoplotherium* and *Mesonyx*. Known specimens of *Dissacus* do not have the anterior region of the muzzle preserved.

P⁴ of *Apterodon* is distinctly larger and much taller than the following M¹ (see figs. 3 and 6). Excluding *Andrewsarchus* (see footnote below), this condition is not known to me in any mesonychid specimen (as against point 14). In the primitive genus *Dissacus*, P⁴ (as well as, to some degree, P³) is semimolariform, with a low paracone, small metacone, and a protocone; it is distinctly smaller than M¹. The P⁴ in *Mesonyx* and *Harpagolestes* remained smaller than the first molar.¹ In hyaenodontids, however, there is a tendency for P⁴ to be relatively larger than M¹.

In primitive proviverrines the paracone and metacone are connate and subequal on M¹ and M². On these teeth there is a large and pronounced metastylar area (very probably a remnant of the primitive eutherian broad stylar shelf) posterobuccal to the metacone. These conditions are identical in *Apterodon*. In *Dissacus* and in the more advanced mesonychids such as *Mesonyx* and *Harpagolestes* the metacone is invariably smaller than the paracone, and the metastylar area is relatively much smaller than in the proviverrines.

Cleaning one of the two known skulls of *Apterodon macrognathus* (A.M.N.H. No. 13237) in the collection of the American Museum of Natural History revealed the presence of a small paraconule (as against point 13) on M¹ and M² (see fig. 3B). An undescribed specimen of cf. *Apterodon altidens* (A.M.N.H. No. 13268) clearly shows the small paraconule and metaconule on dP⁴ and M¹ (see fig. 4B). The upper molars of all mesonychids lack the paraconule and the metaconule (see fig. 3A). Among the proviverrines, *Tritemnodon* from the Bridger Formation of North America, although clearly in a different lineage from *Apterodon*, also shows the trend toward reduction of the conules to vestiges on the upper molars. This trend presumably was initiated independently several times from a *Proviverra*-like ancestral condition, in which the paraconule and metaconule are very strong, distinct cuspsules on the molars.

Point 9 is not a feature of *Apterodon* shared only with mesonychids. Figures in Van Valen (1965) of the upper molars of *Prototomus torvidus* (fig. 4B of Van Valen), of *Prodissopsolis phonax* (fig. 4D of Van Valen) and of *Prodissopsolis theriodis* (fig. 4F of Van Valen) show clearly that the constriction of the anterior and posterior margins of the upper molars (so that the protocone is a distinct lobe) occurred quite regularly among

¹ In *Andrewsarchus*, a Late Eocene Asiatic mesonychid, the P⁴ is very large, is transverse, and lacks a protocone, as is the case in *Apterodon*. The bunodont molars, the peculiar specialization of the upper incisors, and the characteristic basicranial region of this aberrant mesonychid, in my opinion, bar any possibility of affinity between *Andrewsarchus* and *Apterodon*.

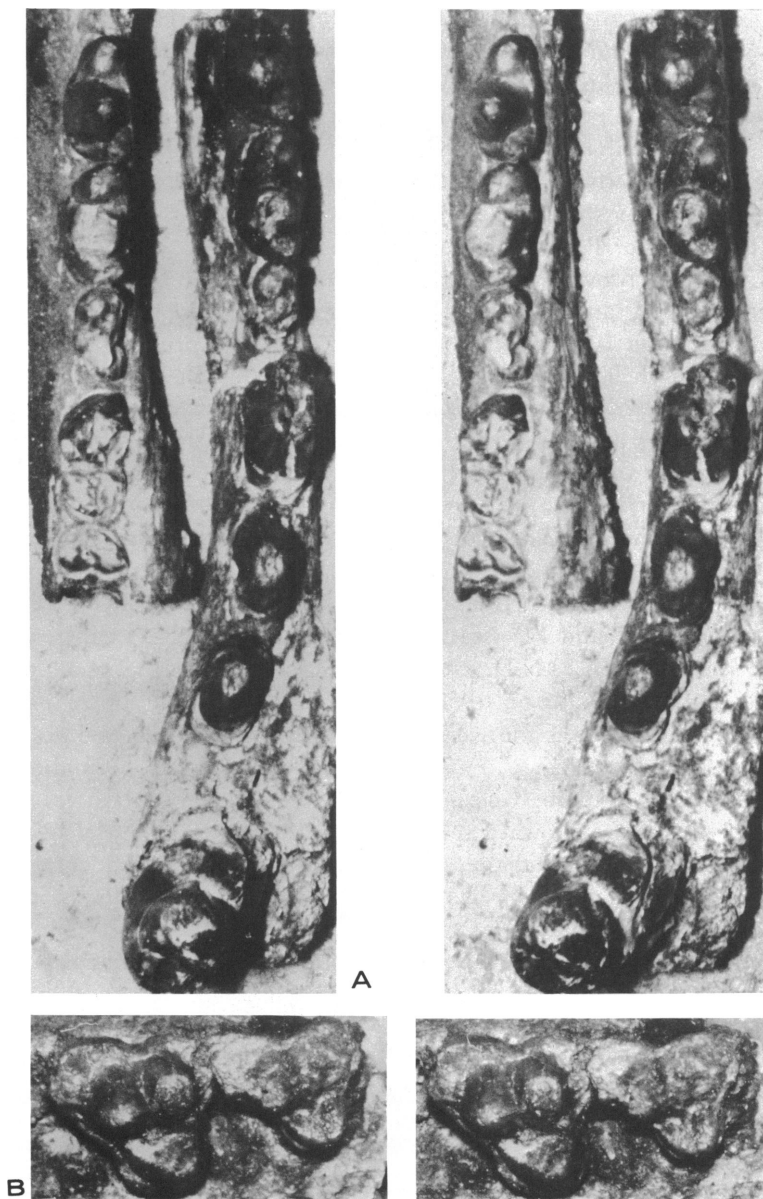


FIG. 4. A. Left lower dentitions of *Apterodon macrognathus*, A.M.N.H. Nos. 13240 (left) and 13239 (right). $\times 1$. B. dp^4 and M^1 of *Apterodon* cf. *A. altidens*, A.M.N.H. No. 13268. Note P^4 under dp^4 . $\times 1.55$.

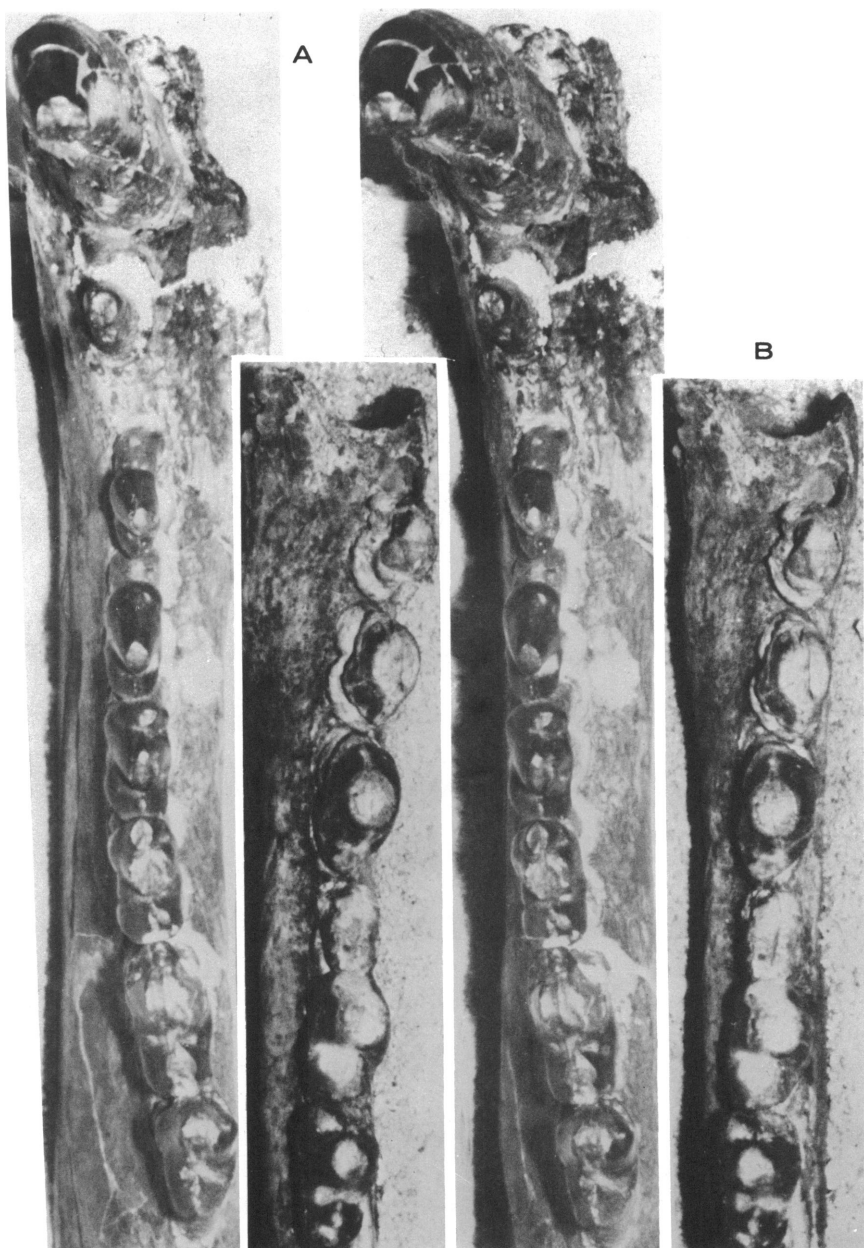


FIG. 5. A. Left lower dentition of *Dissacus saurognathus*, A.M.N.H. No. 2454. $\times 0.9$. B. Right lower dentition of *Apterodon macrognathus*. $\times 1$.



FIG. 6. Lateral view of a skull of *Apterodon macrognathus*, A.M.N.H. No. 13237. $\times 0.67$.

proviverrine hyaenodontids. It is a similarity shared by *Apterodon* and the mesonychids without any special meaning of affinity.

The parastylar area of the molars of *Apterodon*, in my opinion, is not relatively larger than that of *Proviverra* (as against point 10).

P¹⁻⁴ of *Apterodon*, *Proviverra*, *Pterodon*, and *Megalopterodon* (see plates in Dashzeveg, 1964) are very similar, the protoconid is a distinctly erect major cusp on the premolars, and the paraconid is lacking on the P₄ of these taxa (see figs. 4A and 5B). The lower premolars in mesonychids have characteristically trenchant talonids and strongly posteriorly inclined protoconids. The P₄ of *Dissacus* (and of all later mesonychids, with the possible exception of *Hapalodectes*) bears a strong and distinct paraconid (see fig. 5A), as does that of the triisodontine *Eoconodon*.

On the lower molars of *Apterodon* the paraconid is unmistakably anterolingual to the protoconid; there are no traces of a metaconid. There was a weak but indisputable prevallid shear between the molars of *Apterodon*. This shear was best developed between the anterobuccal surface of the trigonid of M₃ and the posterolingual border of M², as in all proviverrines and hyaenodontines. The lower molars of mesonychids such as *Dissacus* and *Pachyaena* (but not the more advanced ones) unmistakably have a relatively distinct metaconid connate with the protoconid (as in *Dissacus*) or as a vestigial nubbin on the uppermost third of the lingual wall of the protoconid (as in *Pachyaena*). The talonid basin is absent lingual to the trenchant talonid crest (transformed from the cristid obliqua), and prevallid shearing is completely lacking. The paraconid on the mesonychid molars is invariably anterior to the protoconid, and it is not anterolingual even in genera with the most trenchant lower teeth, such as *Hapalodectes*. There is no evidence among mesonychids for even the slightest trace of prevallid shear. Whatever shear had evolved occurred between the buccal wall of the protoconid and the lingual slopes of the paracone and metacone. The posterior wall of the upper molars of mesonychids was never involved in shearing against the proto-cristid of the trigonids.

The M₃ of *Apterodon* (and of almost all proviverrines) is the largest of the lower molars. The earliest mesonychids already show a clear trend toward the reduction of M₃.

The cheek-tooth row of *Apterodon* and the known proviverrines is characterized by a horizontal tooth row and a graded height relationship between the individual premolars and between the individual lower molars (see figs. 9 and 10), i.e., each premolar is smaller than the one following it and each molar is similarly larger than the one preceding it. P₄ is the tallest of the premolars, and it is much taller than M₁, which



FIG. 7. Ventral view of a skull of *Apterodon macrognathus*, A.M.N.H. No. 13236. $\times 0.52$.



FIG. 8. Dorsal view of a skull of *Apterodon macrognathus*, A.M.N.H. No. 13236. $\times 0.52$.

is the least tall of the molars. From M_1 to M_3 there is again the characteristic increase in size, as seen in the premolars (this is point 14; it does not, however, indicate an *Apterodon*-mesonychid affinity but, on the contrary, strongly supports the close relationship of *Apterodon* and the proviverrines). Points 2, 11, 12, and 15 above are valid similarities.

Points 1 and 3 to 8 are features of the cranium and mandibles of *Apterodon* suggested by Van Valen to show mesonychid affinities of the genus. Of these various points, 1 and 8 are very probably the result of the same changes that affected the cranium and mandibles of *Apterodon*. Such changes, the relatively short facial skull compared to the cerebral cranium and the relatively shorter horizontal ramus of the mandible compared to the entire length of the mandible, are features of *Apterodon* that are also characteristic of mesonychids. The relatively long and broad basicranial region (particularly the prominent and convex basioccipitals and basisphenoids) of *Apterodon* is striking (see fig. 7), a condition shared with *Proviverra* (particularly the cast of the type of *Proviverra grangeri*, A.M.N.H. No. 11494; the original is in the United States National Museum). In mesonychids the basicranial region invariably is very strongly compressed anteroposteriorly, and it is small in relation to the whole mesonychid skull. The slight shortening of the facial skull of *Apterodon* occurred without any observable effect on the osteology of the basicranium.¹

In my opinion, the two skulls of *Apterodon macrognathus* (A.M.N.H. Nos. 13236 and 13237) do not confirm the joint nature of the jugular and carotid foramina (point 5). The ear region of both skulls is badly broken, and whether certain foramina were confluent, or there was breaking out of bone between them, cannot be determined.

The mere fact that the preglenoid process of *Apterodon* is large and well developed (point 3) is a feature shared with mesonychids. Instead of viewing one fact out of context, however, we can examine the structures that are in close morphogenetic dependence on one another—in this case the entire zygomatic portion of the squamosal and its relation to the posterior part of the cranium. In *Apterodon*, *Proviverra*, and *Hyae-*

¹ The lengthening or shortening of the facial skull relative to the cerebral cranium is a relatively well-known feature of the two morphogenetically rather independent units of the whole mammalian skull, their relative growth in relation to each other being allometrically related. Evidence for the independent change of the facial skull is known in fairly well-established lineages in the fossil record (e.g., in horses), in closely related living species (e.g., the spectrum displayed from the relatively short-faced macaques to the long-faced baboons and mandrills), and in various breeds of domestic mammals (e.g., the short- and long-faced breeds of dogs).

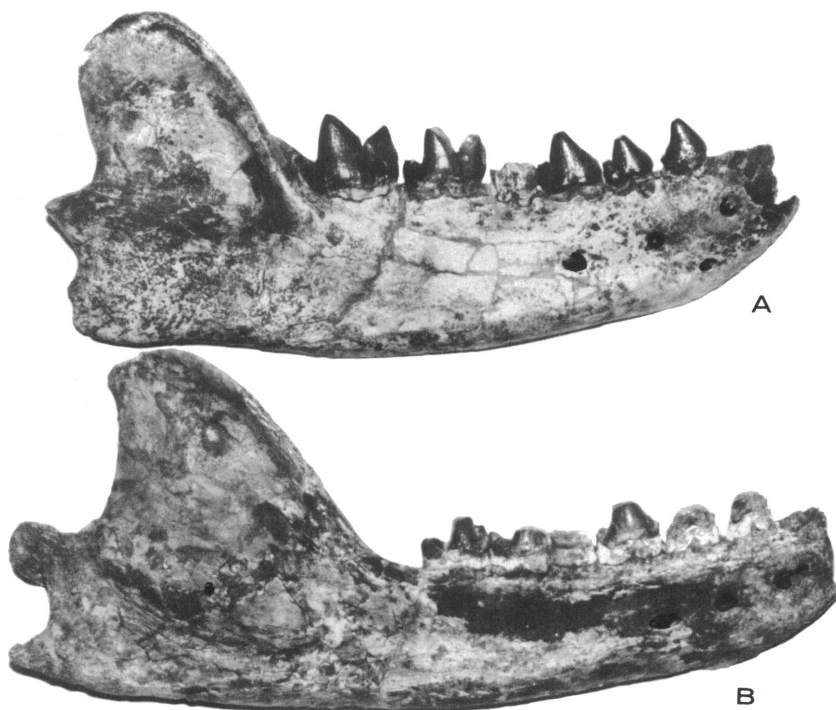


FIG. 9. Lateral view of mandibles. A. *Pterodon phiomensis*, A.M.N.H. No. 13253. B. *Apterodon macrognathus*, A.M.N.H. No. 13241. Both $\times 0.47$.

nodon the glenoid fossa is in contact medially with the anterior segment of the basicranium, and the glenoid fossa is about at the level where the posterior portion of the pterygoid crest extends posteriorly. In these genera the squamosal and the basicranium are a closely integrated unit. In mesonychid skulls, such as those of *Mesonyx*, *Synoplotherium*, *Pachyaena*, *Harpagolestes*, and *Andrewsarchus*, the entire glenoid fossa, with its strong preglenoid and postglenoid processes, is invariably offset laterally and ventrally from the basicranium proper.

A small postglenoid foramen is clearly present in *Apterodon* (A.M.N.H. No. 13237) as in *Proviverra*. Van Valen (1966) also cited the presence of a minute postglenoid foramen in A.M.N.H. No. 3359, a fragmentary specimen of *Dissacus navajovius*, and, as he stated, the foramen is present in the triisodontine and other arctocyonids.

In mesonychids the sagittal crest is relatively larger and the brain is relatively smaller than in *Apterodon*, or in any hyaenodontid known to me.

Each known mandible of *Apterodon macrognathus* in the American Museum

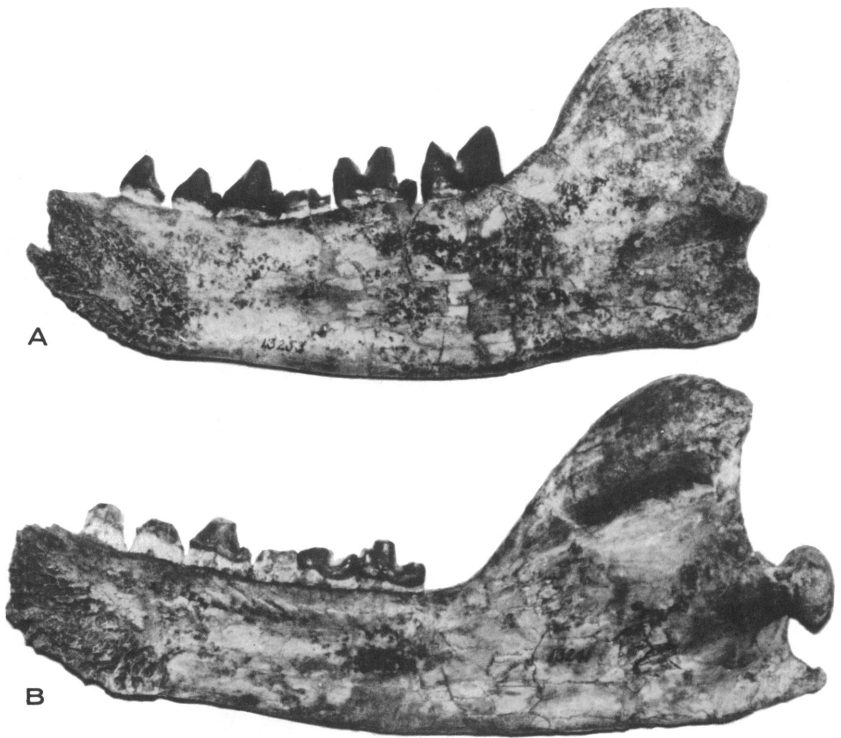


FIG. 10. Medial views of mandibles. A. *Pterodon phiomensis*, A.M.N.H. No. 13253. B. *Apterodon macrognathus*, A.M.N.H. No. 13241. Both $\times 0.47$.

collection from the Fayum beds of Egypt has a series of three to four large mental foramina; in no case is this number fewer than three. This feature is shared by *Apterodon* with *Pterodon* and species of *Proviverra*. No mesonychid mandible known to me has more than two mental foramina.

I cannot confirm the suggestion that the palatine extends past the level of the protocone of P^4 in any proviverrine; adequate cranial evidence is lacking for *Dissacus* and the various species of *Proviverra* so that I cannot confirm or contradict point 4 or discuss its significance.

A specimen (A.M.N.H. No. 15996) of the earliest known mesonychid, *Dissacus navajovius* from the Torrejonian of North America, shows a strong and distinct masseteric crest and hence a well-defined masseteric fossa (points 6 and 7 refer essentially to the same feature of the mandible). However, a trend in mesonychids toward a shallowing of the masseteric fossa is clearly observable in several species. *Apterodon* shares this feature with the mesonychids.

In *Apterodon*, and in primitive proviverrines such as *Proviverra*, the maxilla is broadly in contact with the frontal. In the condylarth mesonychids the large lacrimal prevents a maxilla-frontal contact.

CONCLUSIONS

As is shown in the above presentation and discussion, the undoubted hyaenodontid affinity of *Apterodon* is confirmed. All the very few similarities to the mesonychids are the result of a rather superficial convergence to the latter group of mammals.

The more immediate relations of *Apterodon* very probably lie with some unknown genera of proviverrines. It is my belief that *Apterodon* should be classified as belonging to a separate tribe derivable from the proviverrines, whether the latter are called a subfamily or merely one of the tribes of the Hyaenodontinae.

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