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THE AFFINITIES OF THE BORHYAENIDAE

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In several recent papers (e.g., 1939) there has been occasion to mention my belief that the South American fossil borhyaenids are not immediately and exclusively related to any Australian marsupials. The evidence against this view has been published in considerable detail (e.g., by Sinclair, Wood, Cabrera, etc., see below), but the evidence for it has not been adequately summarized. This note is published to give a review of opinions and evidence, as briefly as is consistent with showing that there is a strong, if not a conclusive, case for the belief elsewhere expressed without discussion.

The earliest literature on the subject was largely concerned with whether the borhyaenids, or "sparassodonts" as Ameghino called them, were marsupials or placentals, a question no longer requiring comment.

Ameghino's definitive views are summed up in his great work of 1906. Here he says that all more or less carnivorous animals belong to a single natural group, his *Sarcobora*, divisible into *Pedimana* (didelphoids), *Dasyura* (Australian carnivorous marsupials), *Insectivora*, *Sparassodonta* (South American carnivorous marsupials, *Borhyaenidae sensu lato*), *Creodonta*, *Carnivora* (*Fissipedia* of other authors), and *Pinnipedia*. Ameghino's accompanying diagram shows the pedimanes giving rise to the sparassodonts and insectivores and then, considerably later, to the dasyures. The sparassodonts give rise to the creodonts and these to the pinnipeds and carnivores (fissipeds). The sparassodonts are shown as derived from pedimanes quite independently of the dasyures. These two groups are, then, supposed to be parallel but not closely related, not, for instance, more closely than sparassodonts and insectivores.

Although it is now generally abandoned, Ameghino's belief in marsupial-creodont relationships was by no means erratic or ill-founded in his day. For instance, Wortman, then the greatest authority on creodonts, as Ameghino was on borhyaenids, held similar views. This is now a dead issue, but Ameghino's belief that borhyaenids and dasyurids were independently derived from didelphoids is still important.

Sinclair (1906) made a penetrating analysis and gave detailed descriptions of the Santa Cruz borhyaenids. He assumed, as all students would today, that the borhyaenids may be allied to the marsupials or to the creodonts, but not to both, and he listed twenty marsupial characters of the borhyaenids. He concluded that the borhyaenids were marsupials, a conclusion that has not since been seriously challenged. This, his essential argument, does not indicate (nor did he say it indicated) special relationship to dasyures or to thylacines, but he went on to say that such a relationship exists. The evidence for this opinion was, however, incompletely given. Sinclair did not explicitly discuss thylacinid as opposed to dasyurid or didelphid affinities. His definition of the *Thylacinidae* in order to include *Thylacinus* and the borhyaenids but to exclude dasyures and opossums does not, in fact, do this. It excludes opossums only by the incisor formula, variable in any case (and some didelphoids are not excluded by this character), and by the absence of the metaconid, really excluding many borhyaenids that he meant to include. The definition excludes dasyurids only by this same feature which is not really diagnostic of borhyaenids. Sinclair's subsequent discussion assumed that the borhyaenids were

thylacinids and pointed out more differences from, than resemblances to *Thylacinus*.

The status of the problem as left by Sinclair was thus that he had proved the borhyaenids to be marsupials and had expressed the opinion that they were thylacinids without making out a serious case for this subsidiary conclusion.

This opinion was widely accepted at the time and has been maintained by many students ever since, but it was seriously questioned by Matthew (1915), who showed what I have mentioned above, that Sinclair had not really offered any evidence of thylacinid (as opposed merely to polyprotodont marsupial) affinities. He pointed out that the resemblance between borhyaenids and thylacines is no closer than has unquestionably arisen by parallelism from an undifferentiated ancestry in analogous cases among true carnivores. Matthew concluded that there was no evidence that this supposed relationship was closer than would be implied by derivation from primitive marsupials didelphid in structure.

Although he did not so put it, Matthew thus was supporting Ameghino's view of the parallel, not direct, relationships between borhyaenids and thylacinids plus dasyurids, while accepting Sinclair's important emendation that made all these forms marsupials not allied to the creodonts.

Wood (1924) made a thorough review of the specific problem of the position of the borhyaenids among the polyprotodont marsupials. He listed 49 anatomical characters and counted a vote of their bearing on the problem: 28 for thylacinid affinities, 8 for didelphid affinities, and 13 neutral. Counting complementary characters as one and omitting neutral characters, his final ballot was 27 for thylacinid relationships (18 important, 9 not) and 7 for didelphid affinities (2 important, 5 not).

Wood's general conclusion was that the borhyaenids were not only related to the Australian as opposed to the other American polyprotodonts (didelphids or didelphoids) but also that they were specifically related to *Thylacinus* as opposed to the

other Australian polyprotodonts, including *Dasyurus* and its allies. This was approximately Sinclair's opinion, which Wood made more explicit and backed with detailed stated evidence.

Cabrera (1927) pointed out that the opinions of Sinclair and of Wood were based on a small number of relatively late (Miocene) genera that did not adequately exemplify the whole complex of the borhyaenids. He accepted the evidence for Australian polyprotodont affinities but rejected the belief in specifically thylacinid affinities. He, therefore, recognized a superfamily Dasyuroidea with three families, Borhyaenidae, Dasyuridae, and Thylacinidae, believed to have evolved independently but more or less in parallel from a generalized dasyuroid ancestry.

Other opinions, based for the most part on these rather than on independent research, do not add significantly different theories. Thus Gregory (1910) said that Sinclair had proved thylacinid affinities. Scott (1913) also accepted this conclusion. Later (1937) he placed both borhyaenids and *Thylacinus* in the Dasyuridae, with some (but less definite) suggestion of special thylacine affinities among the dasyurids. Loomis (1914) accepted the general idea of Australian affinities but felt that reference to the Thylacinidae suggested too close a relationship and retained a family Borhyaenidae. He thus adumbrated Cabrera's theory, but gave no real evidence for it and did not clearly state it. Like Cabrera and unlike Sinclair and Wood, he was familiar with some of the pre-Santa Cruz borhyaenids, an important point in his trend away from the extreme suggested by Sinclair and later made concrete by Wood.

There are thus three authoritative theories now in the field:

(1) The borhyaenids were derived from generalized polyprotodonts, didelphoid by definition, independently of the dasyurids and thylacinids (Ameghino, Matthew).

(2) The borhyaenids are thylacinids (Sinclair, Wood).

(3) The borhyaenids are dasyuroids, but not specifically thylacinids, derived independently from the same generalized stock as the dasyurids and thylacinids (Cabrera).

My reasons for believing that the second of these theories is definitely incorrect and that the truth lies between the first and third, probably nearer the first, will be briefly summarized.

It has never been questioned that all the South American carnivorous marsupials (excluding those definitely didelphoid) are allied to each other. Whether classed as a suborder or order (as by Ameghino), a superfamily or family (as by Loomis, Cabrera, me, etc.), or as a subfamily or smaller group (as by Sinclair, Scott, Wood, etc.), no one seems to have questioned that they did have a common ancestry, nor is there any reason to question this now. The problem of affinities should, then, be approached from the point of view of the group as a whole, envisioning its diverse evolutionary trends as to potentialities and destiny and seeking an ancestry not for a few selected genera but for the whole known complex. The group includes not only the relatively uniform, normally specialized Santa Cruz forms, but also diverse more primitive and older genera and such extraordinarily aberrant and progressive forms as the younger *Thylacosmilus*.

If the borhyaenids are thylacinids, or closer to thylacinids than to either dasyurids or didelphids, there are only two possibilities:

(1) They were derived from a specifically thylacinid ancestry, or (2) the thylacinids were derived from them. The questions to be answered are: (1) did the borhyaenid ancestry have specifically thylacinid characters, and (2) was that ancestry structurally capable of giving rise to the thylacinids or did any known or inferable borhyaenid line definitely tend toward thylacinid basic (and not merely superficial) structure?

In this connection a first step is to take Wood's evidence, keenly observed and excellently digested but based on few genera, and to see whether it applies to the borhyaenid ancestry or to the borhyaenids as a whole and not only to these Miocene forms. The points that he considered important in this respect may be briefly reviewed from this broader point of view, facilitating reference by using the

numbers that he applied to the various characters.

2.—Dental formula. Didelphoids: $\frac{5-?.1.3.4}{4-3.1.3.4}$
 Dasyurines: $\frac{4.1.3-2.4}{3.1.3-2.4}$ *Thylacinus*: $\frac{4.1.3.4}{3.1.3.4}$
 Borhyaenids: $\frac{4-0.1.3-2.4}{3-0.1.3-2.4}$ All these could be derived from $\frac{5.1.3.4}{4.1.3.4}$. The largest lower for-

mula known for borhyaenids did occur among fossil didelphoids in which the upper formula is unknown. The incisive formula is unknown in the most primitive borhyaenids. The fact that I_3^4 is the thylacine count has no bearing on special affinities because it is also the dasyure count, and under these circumstances there is no reason to suppose that it was not derived in the borhyaenids separately from a didelphoid count. Borhyaenid reduction set in early—already in the Casamayor there is a genus with I_3^4 . This character is neutral, not an important thylacine resemblance.

4.—Protocone. Generally large in didelphoids and small in dasyuroids. In advanced borhyaenids it is often small, but in some primitive borhyaenids it is as large as in most didelphoids. This character favors didelphoid, more than dasyurine or thylacine, ancestry.

6-8.—Molar styles. In didelphoids the parastyle is free and larger than the mesostyle, which is also free. In *Thylacinus* the parastyle is large and plastered on the paracone, the mesostyle absent. In dasyurines the parastyle usually forms a transverse ridge with the paracone and is smaller than the mesostyle when this is present. In Santa Cruz borhyaenids the condition is about as in *Thylacinus*, although the difference from *Sarcophilus* is not striking. In *Borhyaena* styler reduction is advanced and in *Thylacosmilus* it is complete. On the other hand, in primitive borhyaenids, notably *Patene*, the styles are less reduced than in dasyurids and are essentially didelphoid. This is undoubtedly primitive and must have occurred in the borhyaenid ancestry, which thus must have been more didelphid than dasyurine or thylacine in this respect.

9.—Approximation of paracone and metacone. They are separated in didelphoids and primitive dasyurines, approximated in *Sarcophilus*, *Thylacinus*, and advanced borhyaenids. But in primitive borhyaenids and hence in the borhyaenid ancestry they were separated. Hence the character is opposed to thylacine relationship, indifferent between didelphoids and dasyuroids.

10.— M^4 , a relatively large tooth in most didelphoids and primitive dasyuroids, reduced and somewhat shearing in many borhyaenids and in more advanced dasyuroids. But here again the stages of reduction are to be found among the diverse borhyaenids and within this group the transformation was from an essen-

tially didelphoid to an essentially thylacine-like condition, as it was also among dasyuroids. The evidence opposes thylacine ancestry and is indifferent between didelphoid and dasyuroid.

13.—Metaconid. Present and large in most didelphoids and dasyurines, absent in *Thylacinus* and some borhyaenids. But other borhyaenids have a large metaconid and the reduction certainly occurred within that group. This character, too, opposes thylacine ancestry and is indifferent between didelphoids and dasyuroids.

17.—Palate. In didelphoids there is a ridge pierced or notched by two foramina. Dasyurines are similar but with a lower ridge and the foramina tend to be lost. In *Thylacinus* and advanced borhyaenids the ridge is represented only by thickening and the foramina are absent. This might favor thylacine relationships, but (a) the same condition is approached and practically reached by dasyurines, (b) this character is not known in any really primitive borhyaenid, and (c) the borhyaenid palate is otherwise very unlike that of any of the three other groups concerned.

19.—Nasals. Protracted in didelphoids, retracted in most borhyaenids and Australian forms. But in the borhyaenid *Arminiheringia* (an early form but specialized in dentition) the condition is intermediate and the character is not known in truly primitive borhyaenids (or in ancient didelphoids). The evidence is too imperfect to be adjudged other than neutral, or at best as possibly dasyuroid but not thylacine.

32, 34, 35, 36, 39.—Vertebrae. Without denying their importance, these may be lumped together because all are unknown in any pre-Santa Cruz or primitive borhyaenids and are also unknown in any Cretaceous or early Tertiary didelphoids, so that at best their evidence cannot be conclusive, however suggestive. In some striking respects the dasyurines show both didelphoid and thylacine characters in different genera, e.g., large or small neural processes on cervicals (35, 36), and these are manifestly adaptive characters dependent purely on size and power of the animals, not on affinities. As regards the free intercentrum of the atlas, borhyaenids show both conditions and nothing is shown except departure from a didelphoid-dasyuroid condition and the capacity to evolve a thylacine-like structure from this. The vertebral formula is not surely known in any borhyaenid and is doubtfully known in one species only. Even if the formula believed to be that of this species is correct, the loss of one rib, a common variation sometimes not even of generic value, would give the modern didelphid formula and in fact both occur among dasyurines. The known evidence of the vertebral column seems entirely inconclusive.

43, 45, 45.—Pelvis. These characters, also, are known for only a few borhyaenids, none ancient and none truly primitive, and the ancestral didelphoid repertory is not known. In two species of Santa Cruz borhyaenids the ilium is

known to be flattened and the acetabulum opens onto the obturator foramen, both dasyuroid characters and suggestive of such affinities, but not specifically thylacine. The probable absence of the epipubic bones in one species (and perhaps in others) of borhyaenids suggests their reduction in *Thylacinus*, which does, however, have them.

Thus of the 17 characters cited by Wood as important evidence of thylacine affinities, 3 seem to me really to favor didelphoid affinities, 7 seem to be almost completely neutral in the present state of knowledge, 3 are neutral as between didelphoid and dasyuroid but are opposed to specifically thylacine affinities, 2 favor dasyuroid affinities in general, one (retraction of nasals) may be placed in this category but could be considered neutral, and just one, probable absence of epipubic bones, might be taken as favoring thylacine affinities. Obviously this one character is a very slender basis for such a conclusion, and it is opposed, not reënforced, by the weight of the evidence. The question is not to be decided by a simple recount of the votes cast by Wood, any more than he thought the count decisive as such, but this is a convenient way to review the evidence.¹ This evidence seems to me strongly opposed to thylacine affinities, indeed conclusive against thylacine ancestry for the borhyaenids.

The other aspect of the problem, that borhyaenids might be ancestral to thylacines, is not so conclusively settled by these considerations. Some borhyaenids did develop characters like those of *Thylacinus* even though there is no good evidence that the borhyaenid ancestry as a whole had any of these characters. As Wood noted, no known borhyaenid could have this ancestral relationship. To prove the vague negative, that some unknown borhyaenid could not have been such an ancestor, is practically impossible, but neither is it urgently necessary to discount the unknown. Even a hypothetical borhyaenid combining all known *Thylacinus*-like characters of the group would

¹ Nor is the recount to be considered personally critical of Wood's conclusion, being based on evidence unknown when he wrote or not available to him. It is because his work was so careful that it is used as a basis for a revised opinion.

not make an acceptable ancestor for *Thylacinus*, because all known borhyaenids do have specializations that are absent in *Thylacinus*, as Sinclair and all later students have seen. To go back to a time when these were absent would be to go back to a pre-borhyaenid stage and to beg the question entirely.

The case for generally dasyuroid affinities, as in Cabrera's theory, is considerably better, but is almost on the same footing with the case for generally didelphoid affinities. Thus the ancestral borhyaenids probably had the nasals somewhat retracted, incisors somewhat reduced, and (with considerable uncertainty) may have had a slightly more carnassial type of molars than in modern opossums and a somewhat flattened ilium, with the acetabulum opening more on the oburator foramen than on the ischium. But, on equally strong evidence, they probably had molars distinctly more primitive, more didelphoid, than do living dasyuroids, and probably had the nasals widely expanded posteriorly, cutting off the frontals from the maxillas, more as in some didelphoids. In fact primitive dasyuroids and primitive didelphoids differ very little in structure and are hard to distinguish except geographically. If one postulates a dasyuroid primitive enough to be ancestral to the borhyaenid group as a whole, it is, practically speaking, indistinguishable from a didelphoid, for the dasyuroids are distinguished from didelphoids only by slight advances not known to have occurred in the borhyaenid ancestry. Cabrera's idea of independent borhyaenid and dasyurid derivation from a common ancestry seems to me entirely sound, but I do not think that ancestry can have been clearly distinct from the ancient (Cretaceous) didelphoids. As for *Thylacinus*, there seems to be abundant, conclusive evidence that it is merely a specialized dasyurid.

A common ancestry combining the primitive dasyuroid with the primitive didelphoid characters would be more didelphoid, that being the more conservative of the two lines. Such an ancestry for the Borhyaenidae is the only one well sup-

ported by the evidence now in hand. Given such a common ancestry, with the same genetic constitution at the beginning of divergence and with the same approximate repertory of mutational possibilities, and given similar environments, it seems not surprising but indeed inevitable that specialized animals evolved independently by adaptation for essentially identical ways of life would resemble each other as much as do, for instance, *Borhyaena* and *Thylacinus*. If they had any more immediate common ancestry, they would be expected to resemble each other still more than they do, and in characters less visibly adaptive.¹

Where the common ancestor of didelphids, dasyurids, and borhyaenids lived is a different question and one not to be discussed here. The conclusion that the common ancestry to be sought is, on present evidence, that of all three of these groups, and not that of two, excluding the other, does, however, put this question on quite a different footing. For instance it removes any particular reason for postulating a connection directly between Australia and South America, although in itself not disproving such a postulate.

As in many other cases, while I agree with all recent workers in rejecting certain of Ameghino's hypotheses regarding these animals, it appears that his more important conclusion regarding borhyaenid-dasyure affinities has been too lightly regarded and that this was essentially correct. The conclusion reached in this paper is also more or less consonant with those of both Matthew and Cabrera, or at least not vitally contradictory to either, but is nearer that of Matthew.

¹ Scott (1937) says that "to maintain that the Australian genera, on the one hand, and the South American genera, on the other, were independently derived from didelphid ancestors, involves such a degree of convergence as has never been admitted for any other group and for which there is no warrant." In the first place, I feel that he over-emphasizes the resemblance, which is great but hardly great enough for such emphatic statement. In the second place, the common ancestry was not didelphid in the strict modern sense but doubtless lacked some special characters of modern opossums and had some preserved in dasyurids and not in didelphids. And in the third place, this is not convergence (like, for instance, the far less striking horse-litopteran resemblance) but parallelism, which is on quite a different basis of probability.

REFERENCES

- AMEGHINO, F.
1906. "Les formations sédimentaires du Crétacé supérieur et du Tertiaire de Patagonie avec un parallèle entre leurs faunes mammalogiques et celles de l'ancien continent." *An. Mus. Nac. Buenos Aires*, XV, pp. 1-568.
- CABRERA, A.
1927. "Datos para el conocimiento de los dasiuroideos fósiles argentinos." *Rev. Mus. La Plata*, XXX, pp. 271-315.
- GREGORY, W. K.
1910. "The orders of mammals." *Bull. Amer. Mus. Nat. Hist.*, XXVII.
- LOOMIS, F. B.
1914. "The Deseado formation of Patagonia." *Concord, N. H.*
- MATTHEW, W. D.
1915. "Climate and evolution." *Ann. New York Acad. Sci.*, XXIV, pp. 171-318.
- SCOTT, W. B.
1913. "A history of land mammals in the Western Hemisphere." New York.
1937. "A history of land mammals in the Western Hemisphere. Revised edition rewritten throughout." New York.
- SIMPSON, G. G.
1939. "The development of marsupials in South America." *Physis, Rev. Soc. Arg. Ci. Nat.*, XIV, pp. 373-398.
- SINCLAIR, W. J.
1906. "Marsupialia of the Santa Cruz beds." *Repts. Princeton Univ. Exp. Patagonia*, IV, Pt. III, pp. 333-408.
- WOOD, H. E.
1924. "The position of the 'sparassodonts': with notes on the relationships and history of the Marsupialia." *Bull. Amer. Mus. Nat. Hist.*, LI, pp. 77-101.