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Charles D. and Mary Vaux Walcott
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EARLY TERTIARY APHELISCUS AND PHENACODAPTES AS PANTOLESTID INSECTIVORES

(With Two Plates)

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INTRODUCTION

Examination in 1954 of *Phenacodaptes* material in the Paleocene collections at Princeton University, believed pertinent to a review of Eocene artiodactyls then underway, led to rather inconclusive results. Dr. Jepsen's tentative suggestion (1930, p. 519) of such a relationship may, nevertheless, have merit.[1] More recent studies of the Knight faunas, however, involved certain pantolestids, and comparison of these among a wide range of both Eocene and Paleocene forms has convinced me that Cope's *Apheliscus* and Jepsen's *Phenacodaptes* are closely related and that both are pantolestids, although perhaps somewhat less closely related to the Pantolestinae than to the Pentacodontinae. Their relationships would seem possibly best illustrated by placing them both in the Apheliscinae as a subfamily of the Pantolestidae.

I am indebted to Dr. Glenn L. Jepsen for permitting me to borrow and illustrate specimens of *Phenacodaptes sabulosus* in the Princeton collections, and to Dr. George G. Simpson and Mrs. Rachel H. Nichols for sending me materials of *Apheliscus insidiosus* and *Pentacodon inversus* from the collections of the American Museum. The pencil drawings of specimens shown in the accompanying plates were made by Lawrence B. Isham, scientific illustrator for the Department of Geology in the U. S. National Museum.

PREVIOUS INTERPRETATIONS OF RELATIONSHIP

Apheliscus insidiosus was described by Cope (1874, p. 14) from the lower Eocene San Jose beds in New Mexico. He described it

[1] After this manuscript was submitted for publication, Dr. Jepsen showed me a note that he had placed in the collection drawer some time ago suggesting that *Phenacodaptes* be compared more carefully with *Apheliscus*.

first as a species of *Prototomus* and included it together with *"Prototomus" jarrovii* (=*Pelycodus jarrovii*) in the carnivores with *Prototomus* (=*Sinopa*) *viverrinus*. In 1875 (p. 16), however, he proposed the name *Apheliscus,* regarding it as "nearly allied to *Pantolestes,*" although at the same time he thought that the molar teeth suggested a relationship to *Anaptomorphus,* noting, nevertheless, that the premolars were "totally different." Cope's statement that the last lower molar lacked a heel would seem highly significant, but, if the meaning is here properly interpreted, it is surely an error, as may be seen from his illustration (1877, pl. 45, fig. 18). In addition to the described condition of the talonid of the third molar, Cope noted as distinctive in comparison with *Pantolestes* only the simplicity of the inner anterior tubercle of the lower molars.

Matthew (1918), in naming the family Apheliscidae, was very dubious as to its affinities, and while referring it to the Insectivora, considered that it might well be condylarthran, primate, or creodont. It should be noted, however, that at the time of his writing, such genera as *Aphronorus, Bessoecetor,* and *Phenacodaptes* were not known. Only large and comparatively aberrant *Pentacodon,* which he had recognized as a pantolestid insectivore (1909), and the Eocene members of the Pantolestinae were available for comparison.

Simpson (1937a) demonstrated the most logical arrangement for the pantolestids and pentacodonts, while adding the Paleocene genera *Bessoecetor* and *Aphronorus* to their respective subfamilies. He noted, moreover, the resemblance of *Apheliscus* to the Pentacodontinae in characters of the fourth premolars, but considered, however, that the molar structure was widely different. Nevertheless, his suggestion that *Apheliscus* might be an offshoot of the same stock seems particularly pertinent and certain of the lacking evidence for such an hypothesis may lie in *Phenacodaptes.* The family, however, was retained *incertae sedis,* questionably in the Insectivora in his 1945 classification.

Saban (1954), evidently following Simpson's suggestion, included the Apheliscidae with the Pantolestidae in the superfamily Pantolestoidea. His including Shikama's Endotheriidae, created for the Manchurian Jurassic *Endotherium,* as a subfamily of the Pantolestidae, however, seems surprising. McDowell (1958) rejected certain features of Saban's classification and in discussing the family Apheliscidae regarded it as *incertae sedis,* but noted that the teeth are "reconcilable with those of *Mixodectes.*" McKenna, on the other hand, in a field conference guidebook (1955) has the Clark Fork species *Apheliscus nitidus* listed as a condylarth.

Older but more recently described *Phenacodaptes sabulosus* is from

the Silver Coulee or Tiffanian horizon of the Polecat Bench formation in the Big Horn Basin. The possibility of a relationship to artiodactyls was tentatively suggested by Jepsen (1930) because of resemblances noted to such genera as *Diacodexis* and *Bunophorus,* evident in certain features of the molars. Simpson, however, in his classification of the mammals (1945) cited *Phenacodaptes* as a condylarth under ?Mioclaeninae *incertae sedis.*

COMPARISON OF *APHELISCUS* AND *PHENACODAPTES*

A lower jaw of *Apheliscus,* referred to *A. insidiosus,* in the National Museum collection (No. 19162) from the Gray Bull beds in the Big Horn Basin, exhibiting P_2-M_1 inclusive (see pl. 1, fig. 1), shows that the form and relative proportions of the lower premolars are strikingly like those in *Phenacodaptes* (see pl. 1, figs. 3, 4). The relatively small size of P_2 and particularly of P_3 in comparison with P_4 is quite alike in the two. P_4 is a little more slender in *Apheliscus* and the distinctive talonid seen in this tooth of *Phenacodaptes* is more sectorial and essentially better developed or exaggerated in *Apheliscus.* Both have a strongly developed primary cusp and only slight evidence of a paraconid. There is no metaconid on P_4 in the known material of *Apheliscus.* It is usually absent, but may be weakly developed in some specimens of *Phenacodaptes.* The lower molars differ noticeably in the anteroposteriorly shorter trigonid and more elongate talonid in *Apheliscus* (see pl. 1, fig. 2); moreover, they are relatively more slender than in *Phenacodaptes.* There is, nevertheless, a rather marked similarity in many details, particularly in form of the cusps and crest surrounding the talonid basin, and in the shape of the basin. The compressed trigonid of *Apheliscus* is rather less like that in *Phenacodaptes,* although the paraconid is absent or very much reduced on the posterior two molars of both forms. In M_1 of *Phenacodaptes,* however, this cusp is moderately well defined as an anterior crest from the protoconid, whereas in *Apheliscus* only a slight median cuspule remains.

The upper cheek teeth of *Apheliscus insidiosus* (see pl. 2, fig. 1) may appear a little less like those of *Phenacodaptes* (see pl. 2, fig. 2) than perhaps do the lower teeth, although both exhibit the comparatively small and subequal second and third upper premolars and enlarged fourth. The more noticeable differences between the two in upper teeth include less development of the cingulum, particularly on P^4, and the transversely narrower molars of *Apheliscus.* Moreover, the hypocone, though distinctive on M_1 and M_2 of *Phenacodaptes,* is weak or absent in Gray Bull *Apheliscus.* It is important to

note, however, that the upper teeth seen in Clark Fork *Apheliscus nitidus* seem intermediate in most, if not all, of these respects. A comparison of Matthew's figure (1918, fig. 24) for the Clark Fork specimen, which Simpson (1937b) made the type of *A. nitidus,* with P^4 and M^1 in *Phenacodaptes sabulosus,* here shown in plate 2, figure 2, reveals little to distinguish them. The Sand Coulee lower teeth of *Apheliscus,* figured by Matthew (1918, fig. 24) also seem to show a little less compression of the trigonid than more typical Gray Bull specimens.

The foregoing comparisons strongly suggest that *Phenacodaptes,* or at least a very closely related form, gave rise to *Apheliscus.* The succession may well have been *Phenacodaptes sabulosus–Apheliscus nitidus–Apheliscus insidiosus.* In the course of this postulated development it would seem that the principal tendency was toward the transverse narrowing of the teeth, both upper and lower series; the loss or weakening of the cingulum in the upper series; the increasingly *Pentacodon*-like development of P^4; the relative increase in length of talonid of the lower teeth, P_4 as well as the molars; together with the shortening of the lower molar trigonids.

RELATIONSHIPS OF *APHELISCUS* AND *PHENACODAPTES*

The most nearly comparable development to that illustrated in the *Phenacodaptes–Apheliscus* line would seem to be among the pantolestids. The suggested comparison is perhaps not so close to the *Bessoecetor–Propalaeosinopa–Palaeosinopa–Pantolestes* succession as it is to the middle Paleocene Pentacodontinae. The premolar development would seem rather like that in both *Aphronorus* (see pl. 2, figs. 3 and 4) and *Pentacodon* (see pl. 2, figs. 5 and 6), except that there tends to be no metaconid on P_4 or tritocone (uncertain for *Pentacodon*) on P^4 in the apheliscids. *Aphronorus,* moreover, differs in having somewhat higher crowned, more definitely insectivore teeth. The upper molars of *Aphronorus* show better developed and more laterally directed anteroexternal and posteroexternal styles and the lower molar trigonids are a little higher and show better development of the paraconid.

Much larger *Pentacodon* has a more enlarged fourth premolar, but the upper molars (not previously illustrated) do not show the distinctive outer styles seen in *Aphronorus.* Also the trigonids of the lower molars do not appear to be so elevated, but, like *Aphronorus* and unlike the apheliscids, show a prominent and forward-placed paraconid. The talonid construction, nevertheless, is much alike in the two subfamilies, except for relative length.

The mental foramen, the position of which, as Simpson (1937a, p. 120) notes, has been unduly emphasized, may warrant comment. It exhibits a comparatively small posterior opening somewhat farther forward in the Apheliscinae than in Pentacodontinae or Pantolestinae. It is variable in *Phenacodaptes* and is observed in positions beneath the anterior part of P_4 to the posterior part of P_3. A larger opening is noted beneath P_1 or P_2. In a specimen of *Apheliscus* (U.S.N.M. No. 19162), these foramina were noted beneath posterior portion of P_3 and beneath P_1. In *Aphronorus* the posterior foramen may be small and varies in position from beneath M_1 to the posterior part of P_4. An equally large or larger anterior opening is seen below P_2. In *Bessoecetor* foramina were noted beneath the posterior part of both M_1 and P_2, and in one specimen, U.S.N.M. No. 9442, anterior foramina were observed below the posterior portions of both P_2 and P_3. In Bridger *Pantolestes* I have seen only the well-developed foramen beneath M_1.

Among the Insectivores outside of the Pantolestidae I find a rather more remote relationship to the mixodectids indicated. There would appear to be rather less to suggest affinities with other orders. Among these, however, perhaps the condylarths should be considered. The relatively low trigonids of the lower molars seem indicative of a possible condylarthran relationship, and a form such as *Choeroclaenus* among the mioclaenine hyopsodonts is not too different from *Phenacodaptes* but there is, nevertheless, a more inflated appearance to the molar cusps and the premolars would appear to have little or nothing to recommend them. The possibility that the *Phenacodaptes–Apheliscus* line represents condylarth development rather paralleling that of pentacodonts cannot be entirely disregarded, but the same reasoning might apply equally well were they to be regarded as belonging to such other orders as primates, creodonts, or artiodactyls. Comparison with *Pentacodon* and *Aphronorus* appears rather more pertinent and better accounts for a number of minor details of similarity not easily dismissed.

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EXPLANATION OF PLATES

Plate 1

Apheliscus and *Phenacodaptes* from the early Tertiary of Wyoming

Figs. 1, 2. *Apheliscus insidiosus* Cope: 1, Right ramus of mandible (U.S.N.M. No. 19162), lateral and occlusal views. 2, Left ramus of mandible (A.M. No. 15696), lateral and occlusal views. All four times natural size. Gray Bull lower Eocene, Big Horn Basin, Wyoming.

Figs. 3, 4. *Phenacodaptes sabulosus* Jepsen: 3, Right ramus of mandible (P.U. No. 13926), lateral and occlusal views. 4, Left ramus of mandible (P.U. No. 13391), lateral and occlusal views. All four times natural size. Silver Coulee (Tiffanian) upper Paleocene, Big Horn Basin, Wyoming.

Plate 2

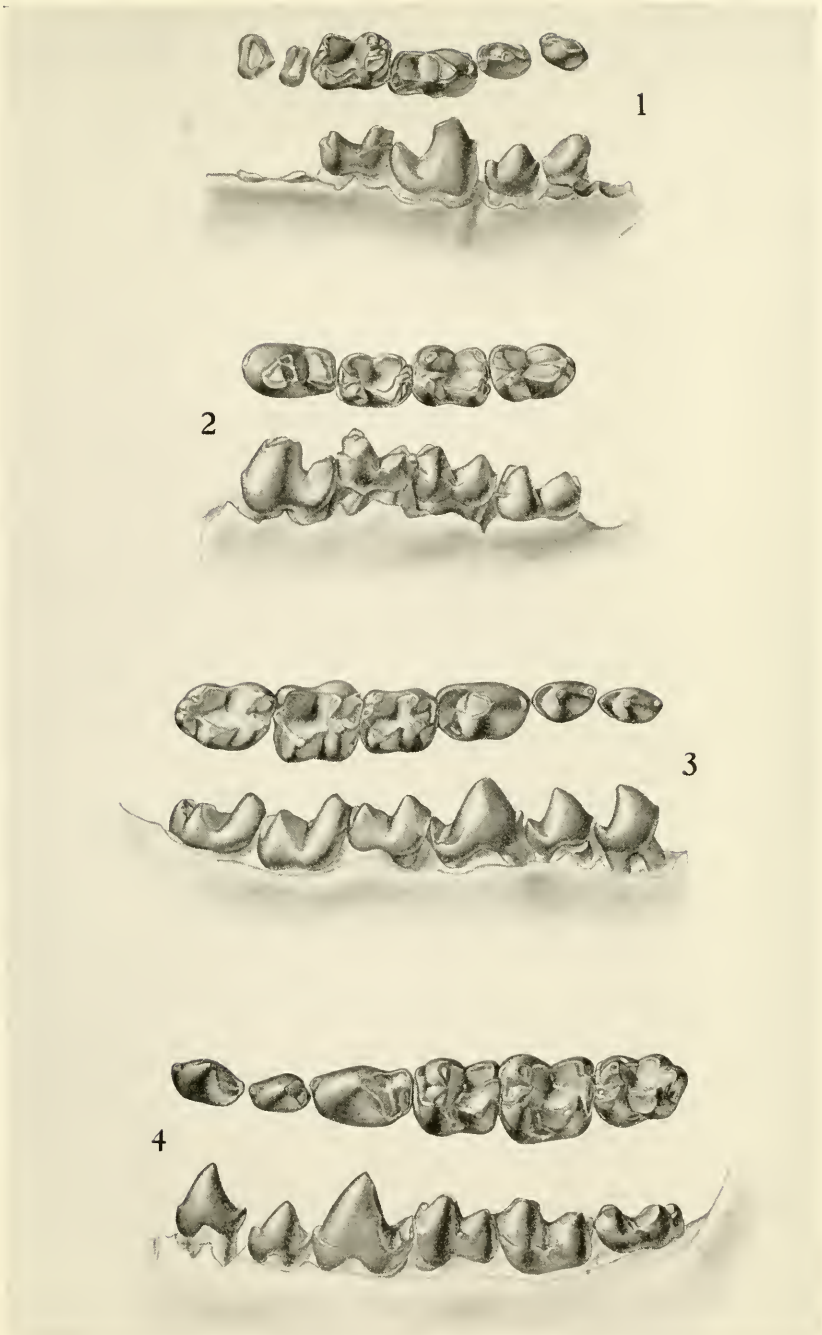
Apheliscinae and Pentacodontinae from the early Tertiary of the Rocky Mountain Region

Fig. 1. *Apheliscus insidiosus* Cope: Left upper cheek teeth (A.M. No. 15696), occlusal view. Four times natural size. Gray Bull lower Eocene, Big Horn Basin, Wyoming.

Fig. 2. *Phenacodaptes sabulosus* Jepsen: Right upper cheek teeth (P.U. No. 13977), occlusal view. Four times natural size. Silver Coulee (Tiffanian) upper Paleocene, Big Horn Basin, Wyoming.

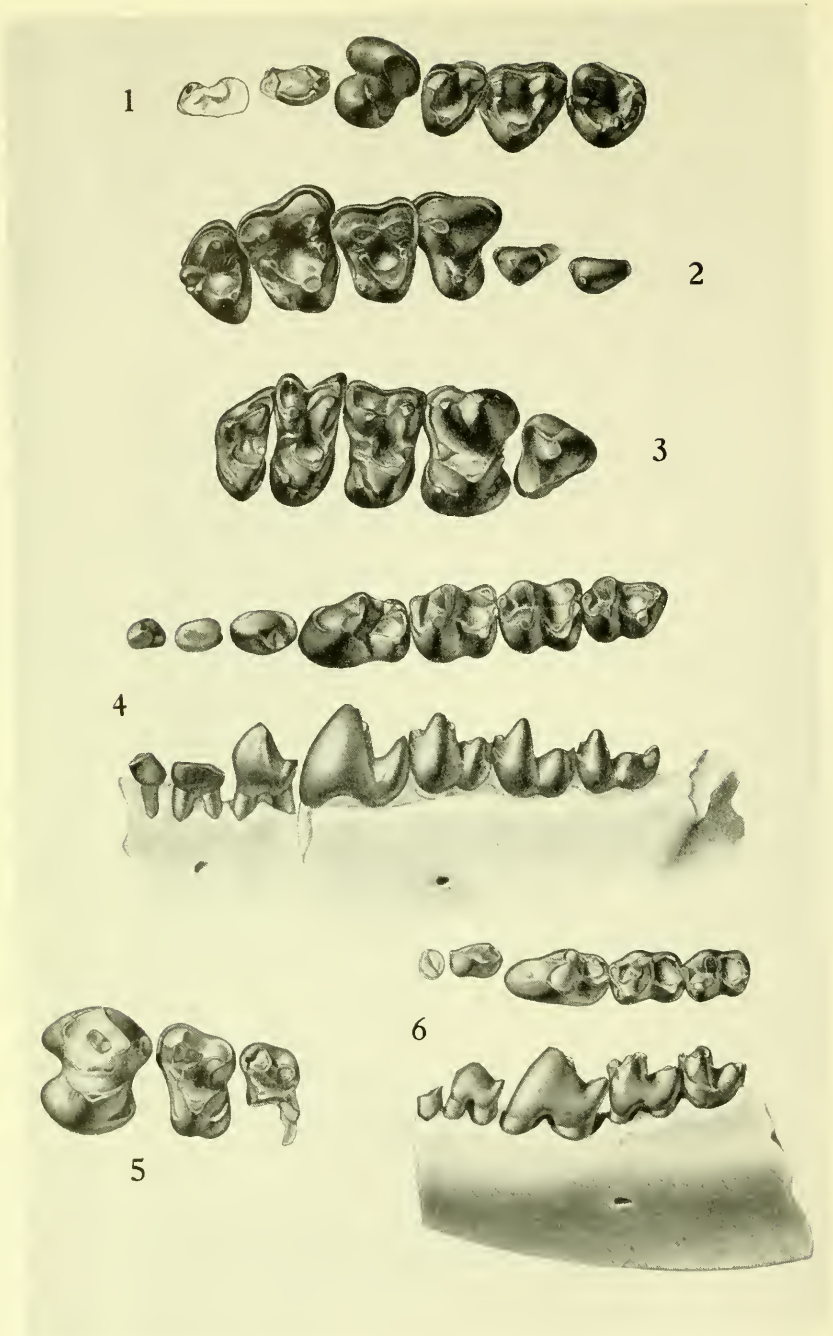
Figs. 3, 4. *Aphronorus fraudator* Simpson: 3, Right upper cheek teeth (U.S.N.M. No. 9561, P^4 from U.S.N.M. No. 9564), occlusal view. 4, Left ramus of mandible (U.S.N.M. No. 6177, type specimen, with molars restored from U.S.N.M. No. 9289, P_1 to P_3 from U.S.N.M. Nos. 9537 and 9291), lateral and occlusal views. All four times natural size. Fort Union middle Paleocene, Crazy Mountain area, Montana.

Figs. 5, 6. *Pentacodon inversus* (Cope): 5, Left upper cheek teeth (U.S.N.M. No. 15502), occlusal view. 6, Left ramus of mandible (A.M. No. 17038), lateral and occlusal views. All twice natural size. Torrejon middle Paleocene, San Juan Basin, New Mexico.



APHELISCUS AND PHENACODAPTES FROM THE EARLY TERTIARY OF WYOMING

(See explanation of plates at end of text.)



APHELISCINAE AND PENTACODONTINAE FROM THE EARLY TERTIARY OF THE ROCKY MOUNTAIN REGION

(See explanation of plates at end of text.)