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SURVIVAL OF PRIMITIVE NOTOUNGULATES AND CONDYLARTHS INTO THE MIOCENE OF COLOMBIA

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ABSTRACT. The late Miocene La Venta fauna from Colombia has yielded fossil remains of a primitive isotemnid-like notoungulate and a didolodont condylarth, both forms representing late survival of essentially early Tertiary mammalian types. The condylarth, a new genus related to *Ernestokokenia* and *Asmithwoodwardia*, is the largest known form and represents the latest known occurrence of the order. Hyopsodont affinites for *Ernestokokenia*, *Asmithwoodwardia*, and the new genus are discounted.

Stirton (1953) has published a preliminary report on the extensive late Miocene La Venta fauna from the upper Magdalena River valley southwest of Bogotá, Colombia. Most of the fauna has not been described, but papers by Cabrera (1929), Kraglievich (1928), Mook (1941), Reinhart (1951), Royo y Gomez (1942, 1946), Savage (1951a, 1951b), Stirton (1951), and Stirton and Savage (1950) have discussed some of the fauna in detail. In the present contribution a new genus of condylarth is described and a poorly represented primitive notoungulate is discussed. Both animals belong to groups known thus far only from the early Tertiary. Advanced interatheres, astrapotheres, toxodonts, and rodents indicate a post-Santacrucian age for the La Venta fauna; therefore it is believed that the occurrence of two primitive protungulates in the fauna indicates a long temporal range for these forms in the tropics, reminiscent of the occurrence of the hyaenodont creodont *Dissopsalis* in the late Tertiary Siwalik sequence in Pakistan. There is no strong evidence that either of the La Venta specimens has been reworked from older Tertiary deposits.

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Class **MAMMALIA**

Order NOTOUNGULATA

?Suborder TOXODONTA

?Family Isotemnidae, sensu lato

Undescribed genus and species

SPECIMEN: U. C. 42891, an eroded left M_3 with a portion of the hypoconulid chipped away. Found in a small concentration of remains which yielded about 100 teeth belonging to several kinds of rodents and assorted specimens representing crocodiles, fish, ?lizard, armadillo, ?glyptodont, small nothrothere, toxodontid, proterotheriid, and *Miocochilius*. Many of these fragments were water worn. All were dark brown in color.

LOCALITY: U. C. Loc. V-4525, in thirty-foot thick unit of alternating sandstones and claystones between the "Yellow Sandstone" and "Lower Red Bed" units south of Quebrada La Venta and traceable over the divide into the Rio Tatacoa drainage. Honda group, Department of Huila, Colombia.

FAUNA: La Venta.

AGE: Approximately Friasian, late Miocene.

DESCRIPTION: M_3 brachydont, incipiently lophodont; trigonid not extremely oblique, giving a nearly symmetrical outline instead of the typical advanced notoungulate oblique outline; trigonid occupying one-third or less of total length of tooth; paraconid absent; paralophid absent; metaconid high and marginal, placed more posteriorly than protoconid; metalophid without accessory cusp; hypoconid strong, placed more anteriorly than entoconid; entoconid marginal, with labially directed spur; hypoconulid elongate, with labial, anteriorly directed crest; anterior cingulum present, slightly cuspidate anterolingually; labial and lingual cingula very weak. Measurements: present total length of tooth 8.4 mm; estimated original total length 8.7 mm; height of metaconid above enamel base 5.5 mm; estimated height of hypoconid above enamel base 3.9 mm; maximum width of trigonid 5.2 mm; maximum width of talonid 4.4 mm.

COMMENTS: This specimen is apparently a primitive notoungulate allied to the primitive Isotemnidae (including the Oldfieldthomasiidae as a subfamily) and to such forms as *Henricosbornia*. Of the characters listed above, the shape of the trigonid, the lack of a metalophid accessory cusp and paraconid, and the presence of a labially directed entoconid spur seem most diagnostic, and point to relationship with primitive notoungulates like *Colbertia* de Paula Couto 1952a rather than to didolodonts or to lithopterns like *Wainka* or the referred specimens of *Protheosodon* figured by Loomis (1914, p. 42). Comparison with *Colbertia* is more favorable than with any other notoungulate genus, chiefly because in *Colbertia* the trigonid is less oblique than in such forms as *Henricosbornia*, *Notostylops*, and *Othnielmarshia*.

Stirton (1953, p. 614) considered the specimen a member of the La Venta fauna but suggested that it could possibly have been redeposited from older fossil-bearing rocks. This consideration was based on the primitive nature of the tooth, not on the fact that it appears to be peculiarly worn (Stirton, personal communication). Those surfaces in which wear occurs (other than that caused by occlusal attrition) show a smooth, even removal of enamel suggestive of solution rather than abrasion. Other than this wear, the tooth is quite well preserved, with no cracks in the enamel of the crown. In other details the specimen is preserved in precisely the same manner as other teeth from the same locality.

Order CONDYLARTHRA

Family Didolodontidae

Megadolodus molariformis, new genus and species

ETYMOLOGY: *Mega* Gr. large, great: *dolos* Gr. deceit; *odontos* Gr. tooth; *molariformis* L. shaped like a molar. In allusion to the large size of the genus, its relationship to the Casamayoran genus *Didolodus*, and to the uniquely advanced fourth lower premolar.

TYPE OF GENOTYPIC SPECIES: U. C. 39270, a fragmentary left mandible bearing M_1, the labial side of P_4, and the roots of P_3, M_2, and M_3.

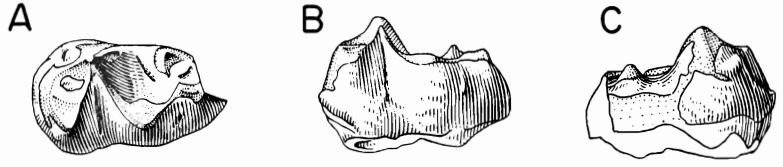

Fig. 1. Undescribed genus and species of ? Isotemnid, U. C. 42891, U. C. Loc. V-4932, La Venta fauna, Colombia. Left M_3. A., occlusal; B., labial; and C., lingual views. × 3.

TYPE LOCALITY: U. C. Loc. V-4932, 200 yards northeast of the railway bridge at kilometer 126 across Quebrada Balsillas, Neiva-Girardot Railway, 11 kilometers northeast of Villavieja, Department of Huila, Colombia. Variegated gray, buff, and rusty claystone containing much calcareous material, including nodules and concretions. San Nicolás unit, Honda group.

FAUNA: La Venta.

AGE: Approximately Friasian, late Miocene.

GENERIC AND SPECIFIC DIAGNOSIS: Easily the largest known condylarth; depth of jaw twice that of *Phenacodus primaevus* and *Paulogervaisia mamma* and three times that of *Didolodus multicuspis*. M_3 estimated 20 percent larger than that of *Paulogervaisia inusta*, the largest previously known condylarth. Measurements: P_3 estimated talonid width 9 mm; P_4 length 15.6 mm, estimated width 14 mm; M_1 length 16.5 mm, trigonid width 16.1 mm, talonid width 15.8 mm; M_2 estimated length 19 mm, estimated trigonid width 17 mm, estimated talonid width 16 mm; M_3 estimated trigonid width 18 mm. Jaw robust, depth under M_1 47 mm, maximum thickness below M_3 23 mm. ?Two mental foramina: one definitely below the talonid of P_4, possibly a second anterior to this, below the trigonid of P_4.

P_4 fully molariform, in contrast to all other members of the Didolodontidae and Phenacodontidae; trigonid robust, but not as large relative to the talonid as in *Didolodus*, *Ernestokokenia*, or *Asmithwoodwardia;* paraconid probably missing; protoconid a large, blunt cone giving rise to a paralophid typical of *Ernestokokenia*, *Asmithwoodwardia*, *Hyopsodus*, many phenacodonts, and some periptychids and arctocyonids; anterior cingulum weak; talonid with strong hypoconid and anterolingually directed metalophid bearing a trace of an accessory cusp; labial cingulum weak, non-cuspidate; hypoconulid probably weak; labial enamel moderately vertically crenulated.

M_1 with robust but short trigonid; paraconid totally absent; protoconid smaller than metaconid, connected to the latter by a strong, looping paralophid, as in P_4; anterior cingulum strong; talonid with strong hypoconid and anterolingually directed metalophid apparently lacking an accessory cusp, but with a small cuspule developed labial to it between the hypoconid and protoconid; entoconid opposite to and weaker than hypoconid, possessing strong anterior ridge directed toward metaconid; hypoconulid strong, with strong cingula directed downward both labially and lingually; labial cingulum developed only around base of protoconid and most anterior portion of base of hypoconid; lingual cingulum absent; labial enamel

moderately vertically crenulated, lingual enamel heavily crenulated in upper portions, especially on the metaconid, where three folds in the enamel are present. M_2 larger than M_1. M_3 as large as, or larger than M_2.

COMMENTS: The Miocene genus *Megadolodus* possesses a dentition which could belong only to a primate, primitive artiodactyl, arctocyonid, or condylarth. From the first three of these groups *Megadolodus* is differentiated by its possession of both a wide talonid basin and a distinctive looping paralophid connecting the protoconid to the metaconid. Both of these characters are possessed by certain Paleocene and Eocene arctocyonids and condylarths. Among these latter forms *Ernestokokenia*, *Asmithwoodwardia*, and some of their less well known relatives are closely similar to *Megadolodus* in known morphology. It is to these early Tertiary forms that we must turn for close comparison.[1]

The well known Casamayoran genus *Didolodus* differs from *Megadolodus* in that P_4 shows no indication of becoming molariform, a paraconid is present on the molars, a strong, litoptern-like metalophid accessory cusp is developed, the molars are somewhat more elongate, and the size of the animal was smaller.

The Riochican and Casamayoran genus *Ernestokokenia* (?including *Archaeohyracotherium*) is now fairly well known, thanks to the work of de Paula Couto (1952b). *E. parayirunhor* de Paula Couto differs from *Megadolodus* in that P_4 is somewhat less molariform (although much more molariform than in *Didolodus* or *Paulogervaisia*), a trace of a paraconid remains on the molars, the teeth are relatively narrower, the mental foramina are differently situated, and the size is considerably smaller.

Asmithwoodwardia, once one of the most poorly known didolodonts, is now the best known (de Paula Couto, 1952b). It occurs in the Riochican Itaborai fauna and in the Casamayor fauna. It is the smallest didolodont, whereas *Megadolodus* is the largest, but the two genera are comparable in important details. The P_4 of *Asmithwoodwardia* is considerably less molariform than in *Megadolodus* and somewhat less molariform than in *Ernestokokenia*. It is more molariform than in *Didolodus*. M_1 of *Asmithwoodwardia* lacks any trace of a paraconid, as in *Megadolodus* and the North American Eocene genus *Hyopsodus*. No metalophid accessory cusp is present, in agreement with the condition in *Megadolodus* and the Itaborai species of *Ernestokokenia* and in contrast to the condition in *Didolodus*, *Lamegoia*, some phenacodonts, and many of the more advanced species of *Hyopsodus*. As in *Ernestokokenia*, the molars of *Asmithwoodwardia* are more elongate than the quadrate molars of *Megadolodus*. Finally, the looping paralophid in *Asmithwoodwardia* is closely similar to that of *Megadolodus* and *Ernestokokenia*, as well as to that of *Hyopsodus* and some of the phenacodonts.

Megadolodus is morphologically more similar to *Ernestokokenia* and *Asmithwoodwardia* than to such forms as *Didolodus*, *Lamegoia*, and *Paulogervaisia*. This similarity is accepted here as indicating actual relationship.

[1] Stirton (1947) has described a new genus, *Lophiodolodus*, from the Oligocene Chaparral fauna, found near Tolima, Colombia, comparing it with the didolodonts. I suspect that *Lophiodolodus* is a sirenian; for this reason the genus does not enter into the present discussion.

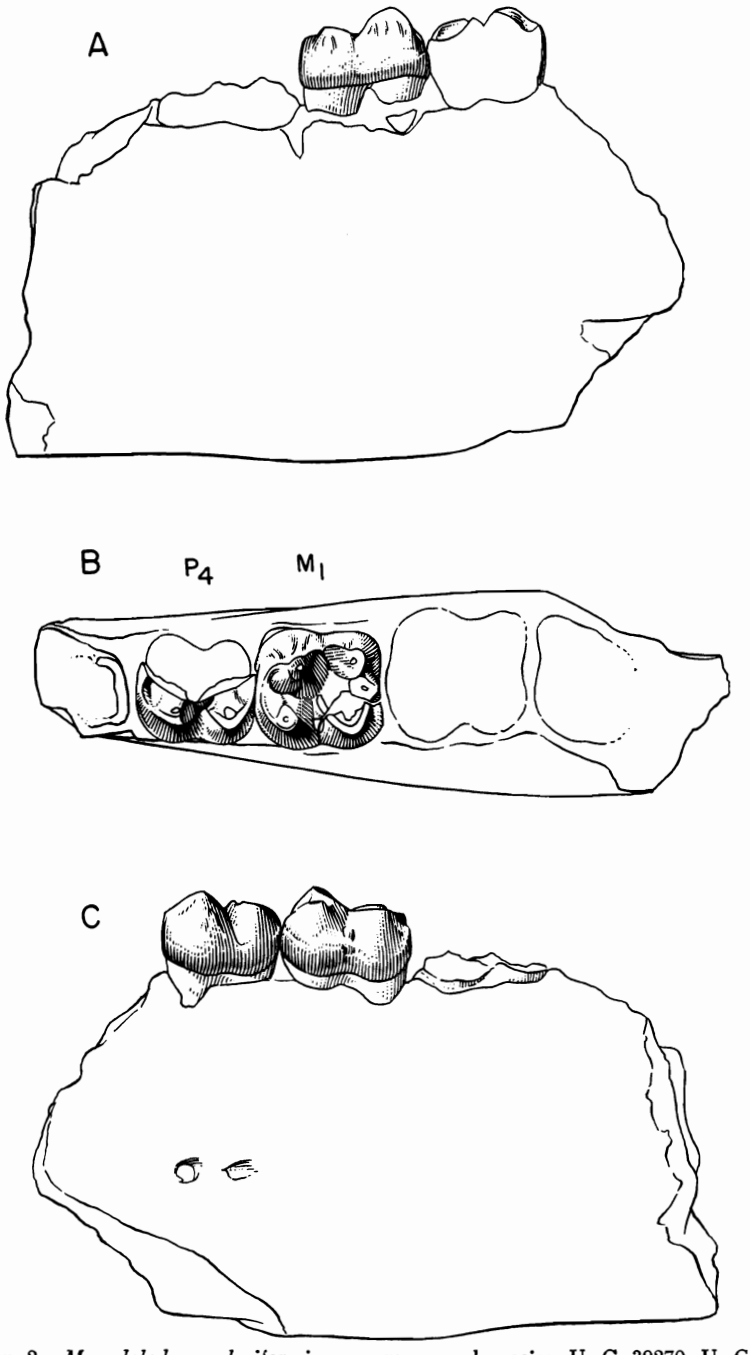

Fig. 2. *Megadolodus molariformis*, new genus and species, U. C. 39270, U. C. Loc. V-4932, La Venta fauna, Colombia. Left lower jaw fragment bearing P_4 and M_1. A., lingual; B., occlusal; and C., labial views. × 1.

At least two lineages may be discerned within the group of genera now formalized as the family Didolodontidae. In the lineage exemplified by *Didolodus, Lamegoia, Paulogervaisia, Proectocion,* and their less well known allies and synonyms a rather litoptern- and notoungulate-like specialization was attained in some structures, but in so far as is known, there was no tendency toward molarization in P_4. In the lineage exemplified by *Megadolodus, Ernestokokenia,* and *Asmithwoodwardia* an essentially arctocyonid-like morphology was retained, but a tendency toward molarization in the fourth premolars developed. The molar paraconids became lost and a *Hyopsodus*-like paralophid developed.

This interpretation is in opposition to that of de Paula Couto (1952b), who proposed the novel and exciting view that *Asmithwoodwardia* is actually a hyopsodont and not a didolodont at all. His viewpoint is not to be passed over lightly. It has such important implications for protungulate classification and zoogeography that his principal conclusions are summarized below.

1. "*Asmithwoodwardia* is so similar to the North American Paleocene-Eocene Hyopsodontinae, in its general characters, and especially in the dental structure, that, in my opinion, the classification of this genus in this group is in complete accordance with its real affinities."

2. "The size of *A. scotti* is close to that of *Hyopsodus lepidus,* from the Bridger beds. . . . "

3. "If [the remains of *A. scotti*] were accidentally found in North America, they would probably be considered as representing a new species of this small North American . . . Eocene relative."

4. " . . . The differences between *Asmithwoodwardia* and the Paleocene-Eocene North American forms classified in the subfamily Hyopsodontinae are merely of generic rank. . . . "

5. *Ernestokokenia* is more closely allied with the most primitive Phenacodontidae than with the Hyopsodontidae. *Asmithwoodwardia* is a hyopsodont. Ergo, the two genera are not related.

6. *Ernestokokenia* is much larger than *Asmithwoodwardia* but agrees well in size with the most primitive Phenacodontidae.

7. *Ernestokokenia* resembles the phenacodonts in the structure of $P\frac{3-4}{3-4}$ more closely than does *Didolodus* but is retained in the Didolodontidae.

De Paula Couto's first point is over-generalized. The only members of the Hyopsodontinae that *Asmithwoodwardia* resembles are *Haplaletes* and the type genus *Hyopsodus* itself. This resemblance is not closer than that of *Asmithwoodwardia* to *Ernestokokenia.* In particular, the arctocyonid-like aspect of the molars, the projecting hypoconulid of M_3, the size of the canine, the shape of the incisor crowns, the heel of P_4, and the structure of P^3 in *Asmithwoodwardia* are not at all suggestive of hyopsodont relationships.

With regard to the second point, it might be pointed out that at least one species of *Hyopsodus, H. powellianus,* is actually larger than *Ernestoko-*

kenia parayirunhor, let alone *Asmithwoodwardia*. Size is an important character, but it should not be over-emphasized.

The accuracy of point 3 is a matter of opinion and should be decided for himself by each worker. Personally, I would give *Asmithwoodwardia* generic rank if it were found in North America, and would give serious consideration to the thought that it might be an arctocyonid rather than a hyopsodont. This argument applies to point 4 as well.

While de Paulo Couto does not explicitly state point 5, its conclusion is implied. The conclusion is a non sequitur based on the a priori premise that *Asmithwoodwardia* actually is a hyopsodont.

With regard to de Paula Couto's sixth point, while it is admitted that *Ernestokokenia* compares favorably in size with such primitive phenacodonts as *Tetraclaenodon minor* and other small forms, the size difference between *Asmithwoodwardia* and *Ernestokokenia parayirunhor* is only about 40 percent. De Paula Couto himself has created two new species of *Ernestokokenia* which differ in size by more than this.

In addition to de Paula Couto's statement in point 7, it should be pointed out that there is a strong arctocyonid resemblance in the morphology of *Ernestokokenia*, e.g., compare with *Thryptacodon* and its allies.

Discovery of the gigantic new Miocene genus *Megadolodus* sheds important new light on the question of the interrelationships of *Ernestokokenia* and *Asmithwoodwardia*. Now a third South American genus is known in which the anterior portion of the molar trigonids has assumed an *Hyopsodus*-like aspect. All three South American forms are believed to be closely related. Either all three are advanced hyopsodonts and a drastic re-evaluation of that group is necessary or all three are didolodonts of an essentially primitive sort that have converged to a degree with a particular genus of a distant North American family.

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