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Prosarcodon lonanensis, a New Paleocene Micropternodontid Palaeoryctoid Insectivore from Asia

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ABSTRACT

A new genus and species of primitive micropternodontid soricomorph insectivores, *Prosarcodon lonanensis*, is described from the Paleocene Fangou Formation, Shaanxi Province, People's Republic of China. *Prosarcodon lonanensis* sheds new light on the origin of the mammalian family Micropternodontidae, linking them to the Palaeoryctoidea and demonstrating an early Asian oc-

currence of the micropternodontids prior to their apparent restriction to North America. The petrosal bone of *Prosarcodon* is similar to that of *Palaeoryctes puercensis* from the North American Paleocene. *Prosarcodon* and *Sarcodon* were both specialized in the loss of a molar, unlike the younger genus *Sinosinopa* from Inner Mongolia (Nei Mongol), PRC.

INTRODUCTION

Among collections of Chinese Paleogene mammalian fossils there are 17 species of insectivores (*sensu lato*) from various stratigraphic levels at more than a dozen major localities. Most of them are erinaceids from the Oligocene. Thus far, Cretaceous insectivores and insectivore-like animals such as *Prokennalestes*, *Kennalestes*, *Asioryctes*, *Zalambdalestes*, *Barunlestes*, *Deltatheridium*, *Deltatheroides*, and *Hyotheridium* have not been found in China although they occur nearby to the north in the Mongolian People's Republic (MPR). Except *Endotherium* from the Chinese Lower Cretaceous and var-

ious anagalids from the Chinese Paleogene, the earliest previous records of Chinese fossil insectivores are *Sarcodon* from the upper Paleocene or lower Eocene of North China and the MPR and *Hyracolestes* from the upper Paleocene or lower Eocene of the MPR and the upper Paleocene of Anhui Province, PRC. The affinities of most of the early non-erinaceoid insectivores of Asia have been disputed in one way or another. *Sarcodon* is no exception. With the description of *Prosarcodon*, presented here, we hope to throw some much-needed light on the relationships of *Sarcodon*, *Sinosinopa*, *Palaeoryctes*, and the

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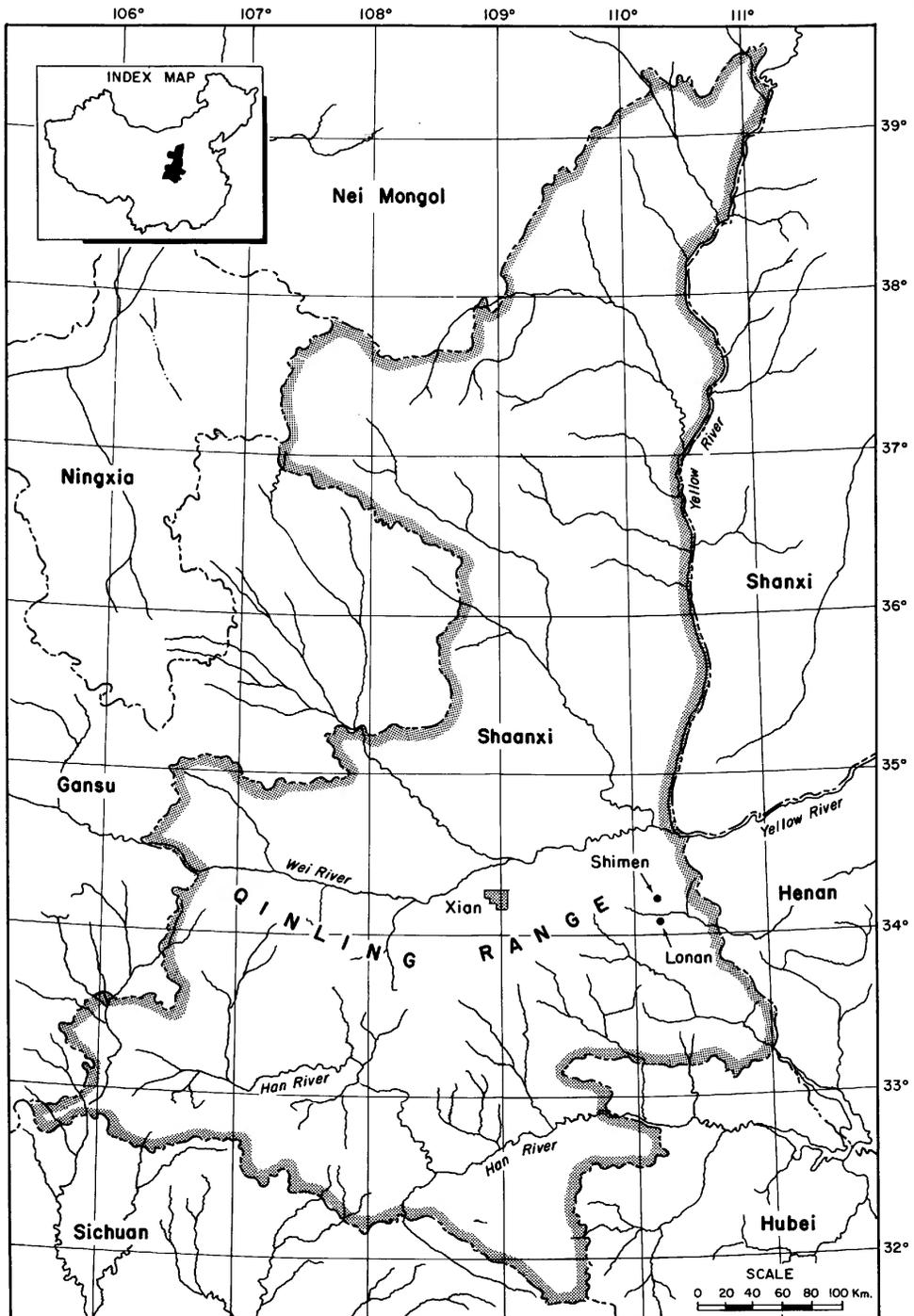


FIG. 1. Map of Shaanxi Province, PRC, showing location of Xian, Lonan, and Shimen.

peculiar "American" insectivore family Micropternodontidae.

In 1977 fossil mammals were found (Xue, 1978) and in 1978 a small skull with artic-

ulated jaws of a *Sarcodon*-like insectivoran was discovered by Xue and technician Zhao Jufa in deposits of early or middle Paleocene age in the lower part of the Fangou Forma-

tion, Fangou Valley, near Shimen Commune, Lonan County, Shaanxi Province, PRC (fig. 1). The Shimen Basin is small, fault-bounded, and was formed in Sinian (Precambrian) quartzites and marbles during the early Tertiary. The basin is only about 52 km.² in area and is about 110 km. east of Xian (170 km. by road), about 15 km. north from Lonan, capital city of Lonan County, in the northern part of the Qinling Range at its boundary with the North China Platform. Many other small fault-controlled basins exist in the Qinling Range.

The Shimen Basin contains three Cenozoic rock units above its Sinian basement (Xue and Jufa, 1982):

Pleistocene		Alluvium and talus
Upper Miocene or Pliocene	Gedamiao Fm. (68 m.)	Red clay, conglomerate, with <i>Hipparion</i> , etc.
Lower or middle Paleocene	Fangou Fm. (165 m.)	Brown-red, sandy mudstone
Precambrian	Gaushanhe Fm.	Quartzite and marble

The Fangou Formation is about 165 m. thick (fig. 2) and is unconformable both with the underlying Precambrian basement and with the overlying Neogene Gedamiao Formation. The Fangou Formation is distributed widely in the Shimen Basin and consists of brown-red, dense, sandy mudstones. These mudstones contain green deoxidation spheres and are cut by a network of inclined fractures filled with gypsiferous material. The Fangou Formation can be divided informally into upper and lower parts: the mudstones of the upper part (41 m.) of the Fangou Formation are interlayered with several gray-green conglomeratic sandy mudstones and silty sandstones containing many calcareous concretions about 2 cm. in diameter. The lower part (124 m.) of the Fangou Formation contains several thin conglomeratic layers in the middle and a thick one at the base.

There are two fossil-bearing beds in the Fangou Formation. One specimen of a bema-lambdid pantodont has been collected from the upper fossil-bearing beds about 6 m. above

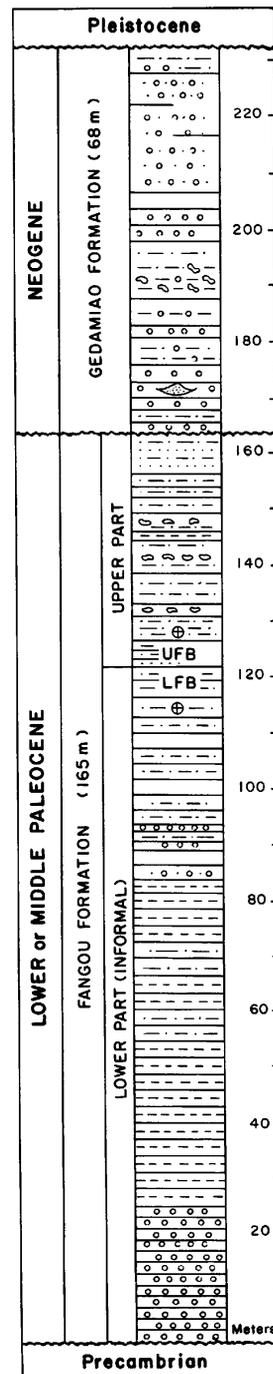


FIG. 2. Generalized geological section of Tertiary deposits of the Shimen Basin, Shaanxi, PRC. LFB—lower fossiliferous beds where *Prosarcodon lonanensis* and other Paleocene mammals were found (lower circle with cross). UFB—upper fossiliferous beds where one specimen of a bema-lambdid pantodont has been recovered (upper circle with cross). Scale in meters.

the base of the upper part of the Fangou Formation, but the remaining fossils collected thus far were found about 6 m. below the top of the lower part of the Fangou Formation, where specimens of the anagalid genus *Linnania*, bemalambdid pantodonts, and the mesonychid *Hukoutherium* occur in addition to the palaeoryctoid *Prosarcodon lonanensis*. In both lithostratigraphy and fauna, as well as geological structure, the Shimen Basin is very similar to the Nanxiong Basin of Guangdong Province in South China. The Fangou Formation can be compared favorably with the Shanghu Formation of the Nanxiong Basin. The two fossiliferous beds in the Fangou Formation are older than the dated parts of the Taizichun Formation of Xinjian or of the Loumugeng Formation of Nei Mongol, PRC (Inner Mongolia).

The specimen from the Fangou Formation, here made the type of *Prosarcodon lonanensis*, is poorly preserved and dorsally incomplete, but the jaws and dentition remain generally in excellent condition and part of the basicranium is still present. The animal is, as would be expected, somewhat more primitive than *Sarcodon*.

INSTITUTIONAL ABBREVIATIONS AND ORTHOGRAPHY

AMNH, American Museum of Natural History, New York, New York.

CMNH, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania.

IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Academia Sinica, Beijing, PRC.

MPR, Mongolian People's Republic.

PRC, People's Republic of China.

UM, University of Michigan Museum of Paleontology, Ann Arbor, Michigan.

USA, United States of America.

USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

WNUG, Department of Geology, Northwest University, Xian, Shaanxi, PRC.

Except where quoted from previous usage, all names from the Chinese language (Mandarin, Beijing Dialect) are rendered here in English in the current version of Pinyin. Thus, "Fan-gou" becomes "Fangou," "Chow Min-

chen" becomes "Zhou Mingzhen," etc. Also, unless quoted from previous usage, Chinese family names of authors are listed before given names and are not separated by a comma from given names.

ACKNOWLEDGMENTS

We thank Drs. Zhai Renjie of the IVPP, and M. R. Dawson, M. J. Novacek, P. V. Rich, and L. Van Valen for advice and other aid, Mr. Zhao Jufa for aid in the field, and the IVPP staff for a cast of the type specimen of *Sinosinopa sinensis*. Dr. R. J. Emry permitted us to study the type specimen of *Kentrogomphios strophensis* and Dr. Dawson gave us access to various specimens in her care. Preparation of the type specimen of *Prosarcodon lonanensis* was skillfully executed by Zhao Jufa and Otto Simonis. The illustrations were prepared by Messrs. Chester Tarka and Raymond Gooris. This project was supported in large part by a grant to Xue from the Geological Academia Sinica for fieldwork and travel, partly by the American Museum of Natural History, partly by the Carnegie Museum of Natural History, and, with regard to travel expenses, partly by a U.S. National Science Foundation grant to Dr. R. M. Hunt at the University of Nebraska.

ORDER SORICOMORPHA GREGORY, 1910;
MCKENNA, 1975

SUPERFAMILY PALAEORYCTOIDEA WINGE,
1917; VAN VALEN, 1963

FAMILY MICROPTERNODONTIDAE STIRTON
AND RENSBERGER, 1964

(=MICROPTERNODIDAE STIRTON
AND RENSBERGER, 1964;

MICROPTERNODONTIDAE VAN VALEN, 1965;
MICROPTERNODONTINAE VAN VALEN, 1966)

PROSARCODON MCKENNA, XUE,
AND ZHOU, NEW GENUS

TYPE: *Prosarcodon lonanensis* McKenna, Xue, and Zhou, new species.

LOCALITY, ASSOCIATED FAUNA, AGE, AND DISTRIBUTION: As for the type species.

ETYMOLOGY: Pro, first, early, in allusion to the supposed ancestral position of this genus with regard to *Sarcodon*. *Sarcodon*, name of a latest Paleocene or earliest Eocene genus of

Mongolian and Chinese fossil soricomorph insectivores.

DIAGNOSIS: As for the type species.

***Prosarcodon lonanensis* McKenna,
Xue, and Zhou, new species**

Figures 3–7

TYPE: WNUG specimen no. 78Sh001, fragmentary skull and jaws.

LOCALITY: Fangou Formation, Fangou Valley, Qinling Mountains, Shimen Commune, Lonan County, Shaanxi Province, PRC.

ASSOCIATED FAUNA: *Bemalambdidae*, new genus and species; *Hukoutherium*, new species; and *Linnania*, new species.

AGE: Early or middle Paleocene, *Bemalambda* Zone.

DISTRIBUTION: Type locality only.

ETYMOLOGY: *lonanensis*—from Lonan City and County, Shaanxi Province, PRC.

DIAGNOSIS: Smaller than *Sarcodon pygmaeus* from the Gashato and Naran Bulak localities of the MPR and from the Nomogen locality of Nei Mongol, PRC. As in *Sarcodon pygmaeus* (Szalay and McKenna, 1971, fig. 11), P⁴ of *Prosarcodon lonanensis* does not have its hypoconal shelf so well-developed as in *Sinosinopa sinensis* from the Arshanto Formation of Nei Mongol and on the shelf lacks the small hypoconal eminence of P⁴ of *Sinosinopa sinensis*. Only M¹ possesses a hypoconal shelf with a distinct hypocone. Hypocone of M¹ less posterolingually expanded and paracone and metacone less closely associated than in *Sarcodon pygmaeus*. M¹ of *Prosarcodon lonanensis* differs from M¹ of *Sarcodon pygmaeus* by possessing a faint anterior cingulum at the base of the protocone. *Prosarcodon lonanensis* (as well as *Sarcodon pygmaeus*) differs from *Sinosinopa sinensis* by loss of both M³ and M₃.

DESCRIPTION: There are three upper incisors per premaxilla (however, one incisor is not preserved in the present specimen). The anteriormost upper incisor is the largest. All upper incisors are rounded in cross-section and possess bluntly conical apexes. We arbitrarily regard the upper incisors as permanent ones.

The upper canine (presumably a permanent tooth) is a conical, curved, projecting

tooth, but it lacks any sort of a cutting crest on its posterior side and is therefore oval rather than triangular in cross-section.

P¹ (or dP¹) is a small, single-rooted, piercing tooth that tilts forward slightly. Its rear slope is crested, as in *Sinosinopa sinensis*.

Following a short diastema behind P¹, the upper dentition (figs. 3, 4) is continuous through M². P² is a double-rooted, piercing tooth about twice the size of P¹. It too has a posterior crest, which curves to join the parastyle of P³. There is a faint heel at the rear and just a trace of a lingual cingulum running forward from it.

P³ is three-rooted and serves as a cutting blade as in *Sinosinopa sinensis* and the three valid species of *Micropternodus*. The roots lie dorsal to the parastyle, protocone, and posterior cutting edge, respectively. The parastyle is low, but it projects far anteriorly. From the parastyle to the paracone apex the anterior crest is dull, but from the paracone apex to the metastyle a concave and "hollow ground" crest is present. No trace of a metacone is seen. The protocone, although worn, projects abruptly linguad at the lingual base of the tooth. A tiny apex was present before wear.

P⁴ is broken across the lingual base of the paracone, but can be seen in its entirety and reconstructed in spite of a gap separating the protocone from the rest of the tooth. P⁴ lacks a metacone and is three-rooted and transverse. In contrast to P³, P⁴ is a large tooth, with the paracone towering above the cusps of all other teeth. An external cingulum runs along the labial base of the paracone from the anterior-projecting parastyle posteriad to just behind the middle of the paracone base, where a suggestion of a styler cusp deflects the cingulum ventrad. The cingulum then continues more or less straight back to the metastyle but supports faint swellings that again suggest styler cusps. In the metastylar area the cingulum swings linguad to join the posterior cutting crest of the paracone. This last is steep, sharp, and "hollow-ground" as in P³. No trace of a metacone appears. The protocone is a high cusp, although it is not so high as on M¹. It is larger than that of M², however. The protocone bears no anterior cingulum, but a faint posterior cingulum begins at the posterolingual base of the protocone and then

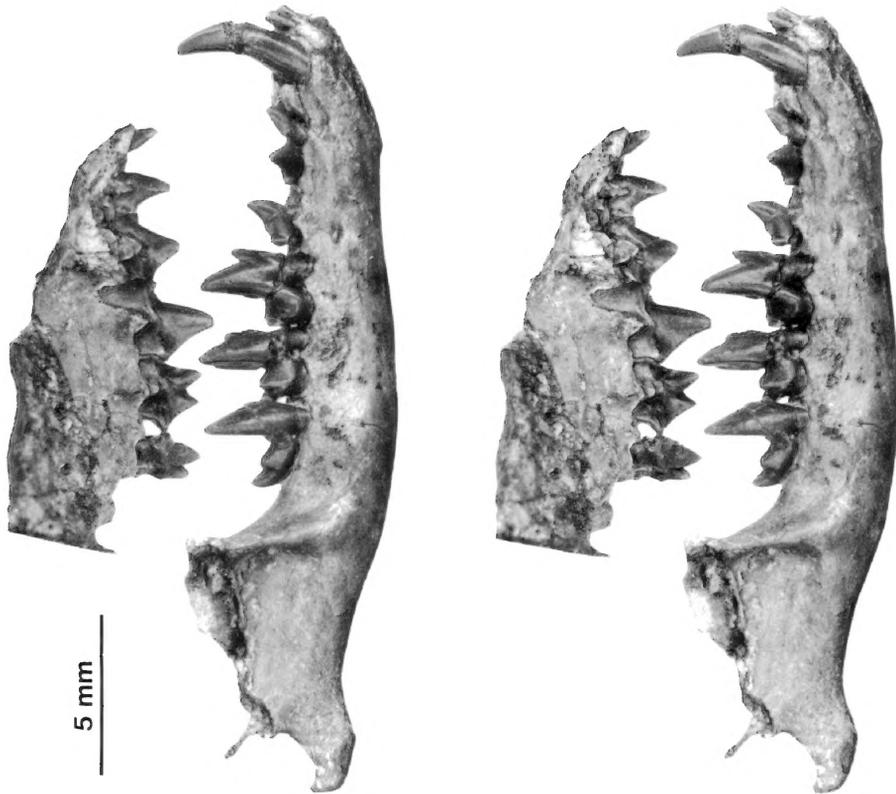


FIG. 3. *Prosarcodon lonanensis* McKenna, Xue, and Zhou, new genus and species. Northwest University, Xian, PRC, specimen no. 78Sh001, lower or middle Paleocene, Fangou Formation, Shimen Basin, Shaanxi Province, PRC. Buccal view of right maxilla and lower jaw. Stereoscopic pair. See 5 mm. bar for scale.

merges with the posterior shelf between the protocone apex and the paracone base. In contrast to the derived condition exhibited by *Micropternodus*, there is no hypocone or posterolingual swelling of the protocone root.

M¹ is clearly *Sarcodon*-like, but has a less well-developed hypocone, more widely separated paracone and metacone, and a slightly smaller metastylar wing. The metastylar wing has a steeply inclined, posterolingually-facing wear facet as in the type specimen of *Sarcodon pygmaeus*, AMNH 20427.

M² is a transverse, three-rooted tooth and has a reduced metacone. From the parastyle the buccal border of the tooth is aligned posterolingual. The paracone overtops the

metacone, but the paracone is broken and its apex may not be properly attached. The protocone has a faint anterior basal cingulum and a weak posterior basal cingulum that fails to reach as far as the metaconule. No hypocone is present and the protoconal root is not posterolingually swollen.

M³ has been suppressed.

At the posterior end of the lower jaw a hooklike angular process occurs (fig. 3). The jaw is not inflected, however. The anterior end of the lower jaw possesses an unfused symphysis, but the symphysis is not prolonged past P₁. Mental foramina occur beneath P₁ and P₃, about halfway between the ventral and alveolar borders as in *Sarcodon*

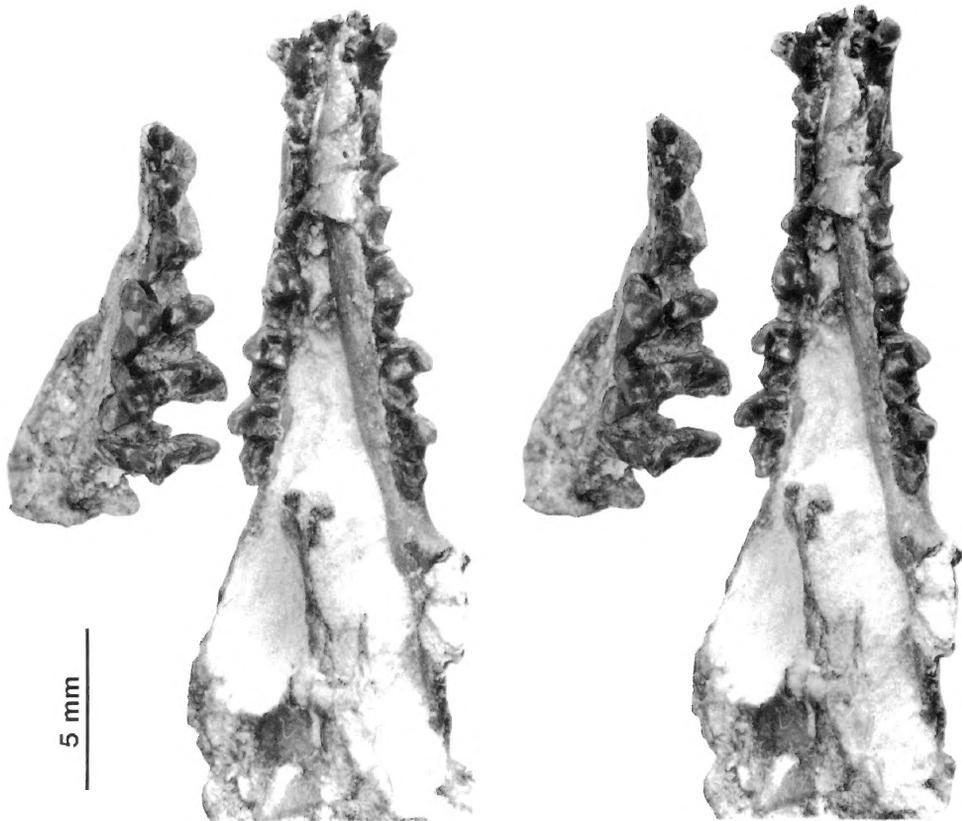


FIG. 4. *Prosarcodon lonanensis* McKenna, Xue, and Zhou, new genus and species. Northwest University, Xian, PRC, specimen no. 78Sh001, lower or middle Paleocene, Fangou Formation, Shimen Basin, Shaanxi Province, PRC. Occlusal views of upper right maxillary dentition (at left) and lower right and left dentitions (at right). Stereoscopic pair. See 5 mm. bar for scale.

pygmaeus (see Szalay and McKenna, 1971). In general, the jaw is quite shallow, each ramus being very little deeper than necessary to accommodate the tips of the cheek-tooth roots (figs. 3, 5, 7). The coronoid process rises gradually behind the last molar, with a flattened anterior surface that borders a deeply excavated masseteric fossa. Lingually, the coronoid process is also very slightly excavated. In lateral aspect, the top of the coronoid process is squared, the length of the process being maintained to the gently curved top, which abruptly terminates the dorsal end of the process. This part of the coronoid is preserved on the piece of the specimen that bears the upper dentition.

There are a total of five lower incisors preserved, of which three are in the left jaw and two are in the right one (figs. 4, 6). Like the upper incisors, we arbitrarily regard the lower ones as permanent teeth. The second lower incisor is the largest. I_1 is not spatulate, but I_2 and I_3 appear to be so (or to have been so in early wear).

The incisors are followed by a high, curved canine (presumably permanent), which lacks a posterior cutting crest but does possess a flattened lingual surface that meets the anterior surface at an angle. The canine is single-rooted.

Following a short diastema, a small, single-rooted P_1 (or dP_1) juts forward. The tooth

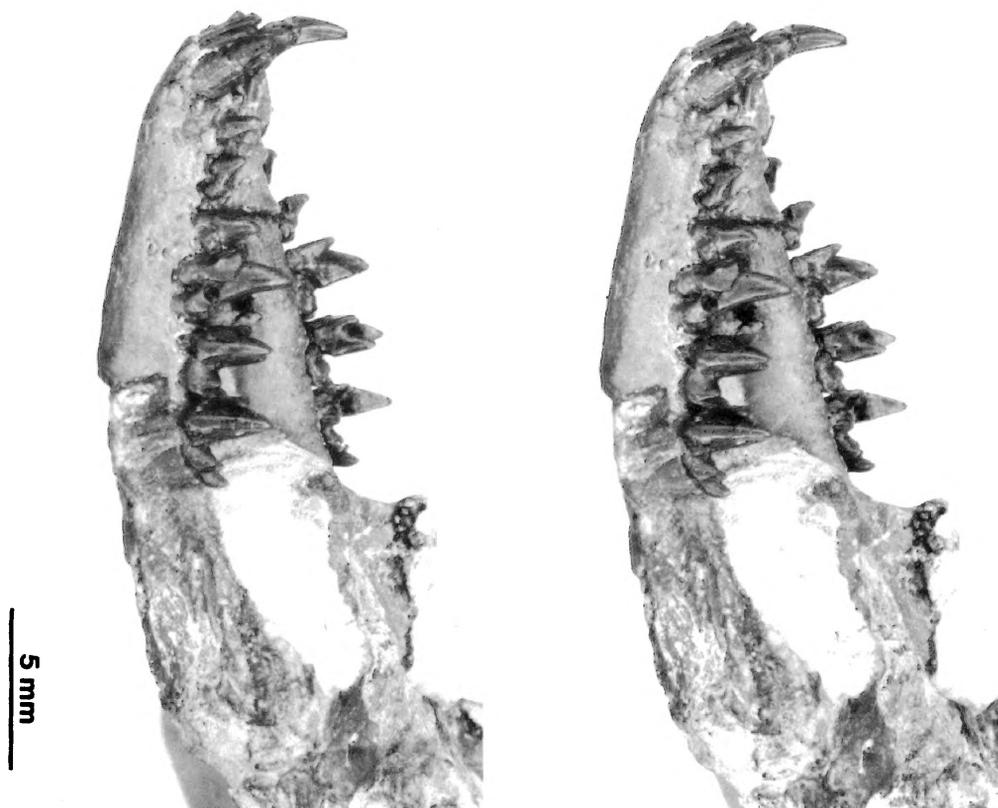


FIG. 5. *Prosarcodon lonanensis* McKenna, Xue, and Zhou, new genus and species. Northwest University, Xian, PRC, specimen no. 78Sh001, lower or middle Paleocene, Fangou Formation, Shimen Basin, Shaanxi Province, PRC. Buccal view of left lower jaw and lingual view of right lower jaw. Stereoscopic pair. See 5 mm. bar for scale.

bears a single cusp. It is followed by another short diastema.

P_2 is double-rooted and leans forward. The apex of its protoconid lies over its anterior root. A tiny anterior basal cusp is present on the anterior base of the protoconid. From the apex of the protoconid a concave crest curves downward and then to the rear, where it ends in a heel cuspule above the posterior root.

Following another, very brief, diastema that was presumably once the site of an additional premolar in the remote ancestry of *Prosarcodon* (contra McKenna, 1975), P_3 rises erectly on its two roots, in contrast to the "heeled-over" aspect of P_1 and P_2 . The protoconid is located a bit anterior to the midpoint of the tooth and bears an anterolingual

basal cusp (paraconid) and a small heel cusp.

P_4 is abruptly larger than P_3 and is in fact a larger tooth than the lower molars, as in *Sarcodon pygmaeus*. The trigonid of P_4 bears a high protoconid, a low, centrally located and forward-projecting paraconid, and a low metaconid that is closely appressed to the lingual side of the protoconid and not so widely separated from it as in M_1 . Both P_4 s are damaged, so that details of the heel are obscured by breakage, but the heel appears to have consisted of a single, rather lingually shifted crest, against which the paracone of P^4 would have lain in occlusion. The posterior cusp of the heel is shifted to the posterolingual corner of the tooth.

M_1 is an elongate tooth with a well-devel-

oped heel. The trigonid bears the usual three cusps, of which the protoconid is easily the highest and most important. The paraconid is bladelike and projects linguad from the anterior base of the protoconid. The anterior base of the paraconid is very slightly indented, presumably for the reception of the heel of dP_4 during the eruption of M_1 . The indentation lies well above the heel of P_4 . The metaconid is widely separated from the protoconid and is lower than the latter. The posterior surfaces of both cusps are flat and joined. A hypoconid, entoconid, and hypoconulid complete the tooth, enclosing an elongate talonid basin that is broadly open anterolingually. A low cristid obliqua crosses the heel to join the base of the trigonid about midway across the tooth. Otherwise, the morphology of the tooth is closely similar to that of *Sarcodon*.

M_2 is an elongate tooth, principally because of the extreme length of its talonid. The trigonid is wide and larger, as well as more transverse, than its counterpart in M_1 . The angle between the apices of the paraconid, protoconid, and metaconid is more acute than in M_1 . The size relationships of these cusps

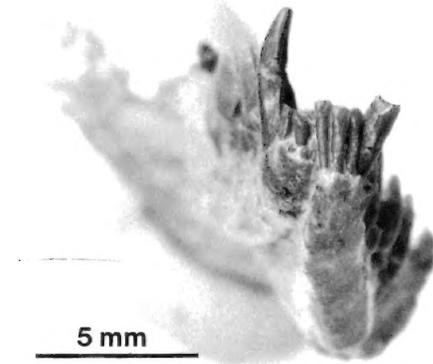


FIG. 6. *Prosarcodon lonanensis* McKenna, Xue, and Zhou, new genus and species. Northwest University, Xian, PRC, specimen no. 78Sh001, lower or middle Paleocene, Fangou Formation, Shimen Basin, Shaanxi Province, PRC. Anterior view of lower incisors and canines. See 5 mm. bar for scale.

are maintained as in M_1 , with the protoconid being the largest and the paraconid the smallest trigonid cusps. The elongate heel bears the usual cusps, but the structure is narrow and the hypoconulid projects as a sharp cusp

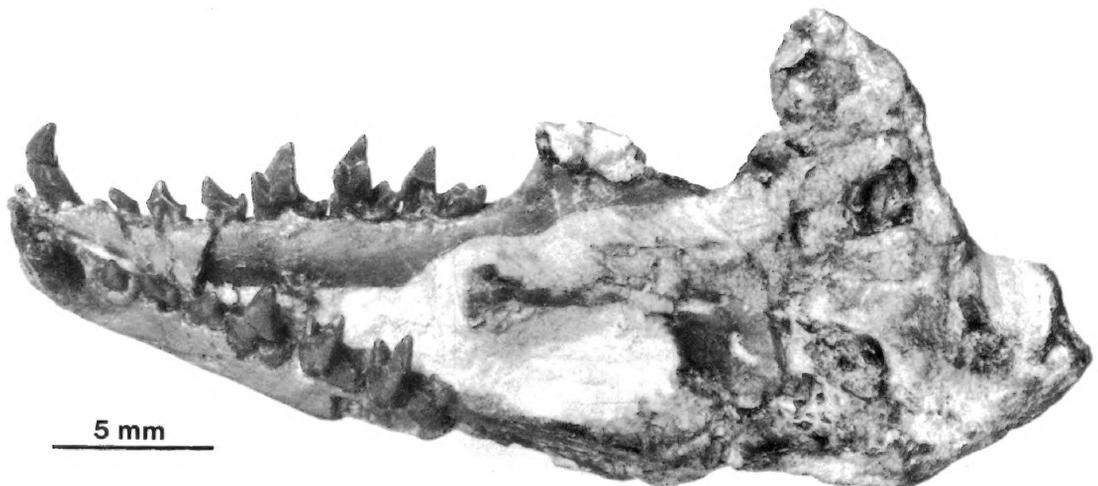


FIG. 7. *Prosarcodon lonanensis* McKenna, Xue, and Zhou, new genus and species. Northwest University, Xian, PRC, specimen no. 78Sh001, lower or middle Paleocene, Fangou Formation, Shimen Basin, Shaanxi Province, PRC. Oblique view of lower jaws and traces of dorsal part of basicranium. See 5 mm. bar for scale.

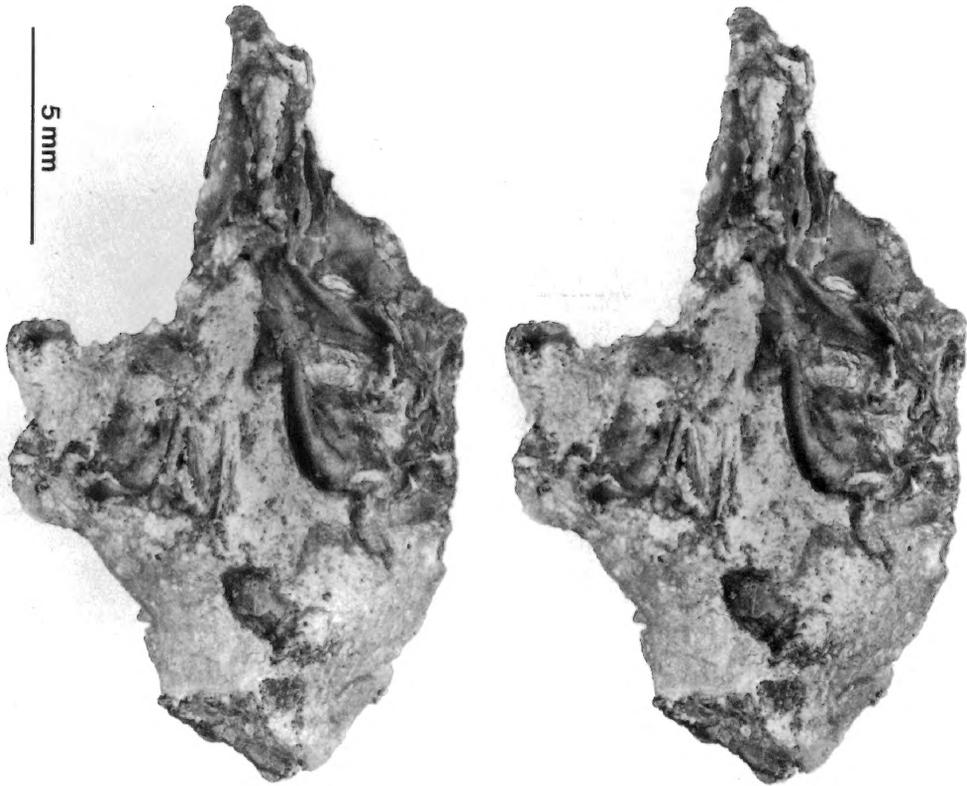


FIG. 8. *Prosarcodon lonanensis* McKenna, Xue, and Zhou, new genus and species. Northwest University, Xian, PRC, specimen no. 78Sh001, lower or middle Paleocene, Fangou Formation, Shimen Basin, Shaanxi Province, PRC. Ventral view of basicranium. Stereoscopic view (at left) and interpretive drawing (at right). See 5 mm. bar for scale. Abbreviations: bo, basioccipital bone; dmw, descending medial wing (crista promentorii medio-ventralis) of petrosal bone; fc, fenestra cochleae; fo, foramen ovale; pgf, site of postglenoid foramen; pi, piriform fenestra; s, sphenoid bone.

far to the rear. The entoconid and hypoconid have a rearward tilt. At the anterior base of the entoconid, a small secondary cuspule helps to delimit the lingual wall of the talonid basin. The cristid obliqua meets the rear of the trigonid wall about halfway across, as in M_1 . A faint anterior basal cingulum can be seen on the front of M_2 , keyed to the talonid of M_1 .

M_3 has been suppressed.

When originally discovered, the maxillary teeth and the lower dentition of the type specimen of *Prosarcodon lonanensis* were in occlusion. The anterior end of a thin zygomatic arch is preserved above the last molar, but

this is terminated by breakage at the anterior end of the top of the coronoid process, which is still attached to the part of the specimen that bears the upper dentition. Between the two rami of the mandible and extending to the rear is part of the basicranium of the skull. Breakage has left the ventral parts of the petrosal bones and a considerable extent of the alisphenoid and basisphenoid bones (figs. 7, 8). Traces of the pterygoids are also present.

BASICRANIUM: Breakage through the basicranium and ear region has resulted in the loss of most of the cranium in the type specimen of *Prosarcodon lonanensis*, but a few features of the basicranium are preserved. In

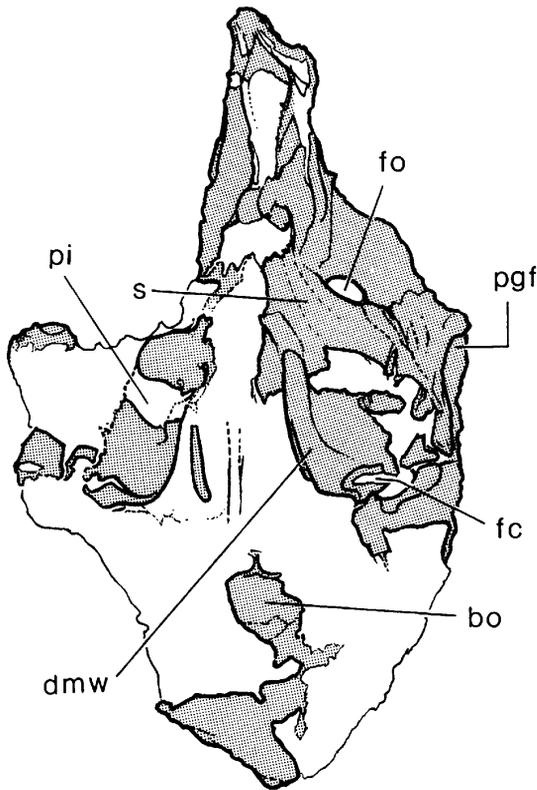


FIG. 8. Continued.

the laboratory at the American Museum of Natural History, transparent epoxy resin was applied to the dorsal surface of the remaining bone. Preparation of the ventral aspect of the glenoid and basicranial region was then accomplished with safety, revealing a ventral morphology remarkably similar to that of *Palaeoryctes* (Matthew, 1913; McDowell, 1958) and, in lesser degree, to that of the recently recognized early erinaceomorph genus *Diacodon* (Novacek et al., in press). Features deemed to be important are as follows:

1. The glenoid fossa (anterior, articular surface of entoglenoid process of McDowell, 1958) of the squamosal faces forward as in soricoids and palaeoryctoids.
2. A large foramen ovale is present.
3. A piriform fenestra (McDowell, 1958, p. 128; MacPhee, 1981, p. 59) is present,

separating the basisphenoid bone from the petrosal bone as in shrews, *Nesophontes*, *Solenodon*, *Apternodus* (contra McDowell, 1958), and various other lipotyphlans. The piriform fenestra is proportionally larger than that of *Palaeoryctes*, about the same size as that of *Apternodus*.

4. The petrosal bone possesses a rudimentary descending medial wing (crista promontorii medio-ventralis of Kielan-Jaworowska, 1981), similar to that of leptictids and *Diacodon* and virtually identical with that of *Palaeoryctes puericensis*.
5. There is no bulla. The tympanic bone is presumably a free ring oriented nearly horizontally.
6. There is no trace of a groove crossing the ventral surface of the petrosal bone (to house either a promontory artery, a nerve, or both).
7. The fenestra rotunda (fenestra cochleae) is overlapped somewhat posteriorly by a flap of bone so that it appears to open directly ventrad (cochlear fossula of MacPhee, 1981, p. 51; recessus fenestra cochleae of Kielan-Jaworowska, 1981).
8. A large postglenoid foramen for the external jugular vein can be seen in the left squamosal bone, far to the side and anterior to an anteroposterior groove in the roof of the external auditory meatus.
9. There is no pronounced sella turcica on the dorsal surface of the sphenoid bone. The area is flat, as in Lipotyphla generally.

MEASUREMENTS (table 1): Measurements were taken from the right dentition unless otherwise noted, with the same equipment and in the same manner as elucidated in Lillegraven, McKenna, and Krishtalka, 1981. AP: upper and lower premolars—longest axis of crown, generally parallel to buccal side of tooth; upper molars—greatest measurement at right angle to “width axis” dividing tooth into anterior and posterior halves; lower molars—greatest length of crown parallel to long axis of tooth and exclusive of anterior cingulum. ANW and POW: greatest anterior and posterior widths, respectively, at right angle to AP measurements. LTRI: length of trigonid, parallel to AP axis and exclusive of anterior cingulum.

TABLE 1
Measurements (in Millimeters) of
Prosarcodon lonanensis

P ¹ : AP 0.76, ANW 0.47
Diastema between P ¹ and P ² : 0.62
P ² : AP 1.21, ANW 0.59
P ³ : AP 2.36, ANW 1.34
P ⁴ : AP 2.56, ANW 2.63 (breakage corrected), POW 2.48 (breakage corrected)
M ¹ : AP 2.40, ANW 3.26 (approximate), POW 3.85
M ² : AP 1.49, ANW 3.89, POW 2.11
P ¹ -M ² length: 10.91
P ₁ : AP 0.96
P ₂ : AP 1.25
P ₃ : AP 1.55 (approximate)
P ₄ : AP 2.57 (approximate), LTRI 1.46, ANW 1.18, POW 1.18 (approximate)
M ₁ : AP 2.18, LTRI 1.24, ANW 1.70, POW 1.27
M ₂ : AP 2.74, LTRI 1.22, ANW (left) 1.74, POW 1.19
I ₁ -M ₂ length in lower jaw: 15.47
Approximate skull length (originally): 30.0
Approximate skull width (originally, at orbit, zygoma to zygoma): 21.0

DISCUSSION: *Prosarcodon* is a small, primitive relative of *Sarcodon*. As in *Sarcodon*, *Prosarcodon* has lost both an upper and a lower molar, presumed to be M³ and M₃.

For a long time after its initial description by Matthew and Granger (1925), *Sarcodon* was an enigma. The genus is now known from the latest Paleocene or earliest Eocene (Clark-forkian equivalent) Gashato and Naran Bulak sediments of the MPR (Dashzeveg and McKenna, 1977) and from the earliest Eocene or latest Paleocene Nomogen fauna of Nei Mongol (Inner Mongolia), PRC (Zhou, Qi, and Li, 1976; Chow (Zhou) and Qi, 1978; Qi, 1979). On the basis of the type specimen of *Sarcodon pygmaeus*, Van Valen (1966) believed *Sarcodon* to be closely related to the palaeoryctid genus *Pararyctes*, but stated that *Sarcodon* is intermediate between palaeoryctids and *Micropternodus*. In his classification published the next year, Van Valen (1967) placed *Sarcodon* in the Micropternodontidae and placed the Micropternodontidae in the Superfamily Palaeoryctoidea, in turn in the Hyaenodonta, a suborder of Van Valen's order Deltatheridia. Several years later, *Opisthopsalis vetus* Matthew and Granger, 1925,

originally described from the same locality and in the same paper as was *Sarcodon*, was shown to be a synonym of the latter by Szalay and McKenna (1971), who discussed what was then known of the animal, including the previously unrecognized lower jaw and dentition and additional features of the upper dentition. On the basis of the type and newly referred material, Szalay and McKenna concluded that *Sarcodon* was a member of the Deltatheridiidae, which in 1971 they regarded as a family of palaeoryctoid insectivores. However, they denied special relationship of *Sarcodon* to *Micropternodus*, holding that there was no special similarity of the newly recognized lower dentition of *Sarcodon* (i.e., that of its synonym *Opisthopsalis*) to that of *Micropternodus*. Szalay and McKenna (1971) therefore believed mutual similarities of the upper dentitions of *Sarcodon* and *Micropternodus* to be the results of convergence.

With the collection of *Sinosinopa sinensis* from the early to middle Eocene Arshanto Formation southwest of Erlian [Erhlien, etc.], Nei Mongol, a second, more primitive, Asian line of *Sarcodon*-like insectivores was made known (at least by name) by Qi (1979). Casts of the dentition of this specimen are available to the authors. *Sinosinopa* differs from *Sarcodon* and *Prosarcodon* in that it retains all three molars. In *Sinosinopa* both M¹ and M² possess a hypocone that juts strongly posterolinguad; in *Prosarcodon* M², the last molar, possesses a narrow cingulum-like hypocone. P₄ of *Sinosinopa* is more elongate than in either *Sarcodon* or *Prosarcodon*.

AFFINITIES: *Prosarcodon*, *Sarcodon*, and *Sinosinopa* seem to be palaeoryctoid insectivores, but palaeoryctoids are no longer believed to be especially related to the Asian and possibly American Cretaceous family Deltatheridiidae (Butler and Kielan-Jaworowska, 1973; Fox, 1974, 1975, 1976). Rather, *Palaeoryctes* and its closest palaeoryctoid allies appear to be related to lipotyphlan insectivores (Lillegraven, McKenna, and Krishtalka, 1981) as well as to the Ferae. That *Prosarcodon*, *Sarcodon*, and *Sinosinopa* are lipotyphlan insectivores is suggested by the presence of a piriform fenestra in *Prosarcodon*. None of these Asiatic genera is zalambodont, as *Palaeoryctes* and *Pararyctes* had

nearly become, but a trend toward zalambdodonty was under way. *Prosarcodon* and *Sarcodon* became specialized in the loss of a molar, but the latest-occurring member of the group in Asia, *Sinosinopa*, is less specialized in that particular regard, although it is more specialized in having jutting hypocones on several upper molars.

Among palaeoryctoids and palaeoryctoid-like derivatives similar to *Sinosinopa*, *Prosarcodon*, and *Sarcodon*, the American genus *Micropternodus* Matthew, 1903 (= *Kentrogomphios* White, 1954) immediately comes to mind, as it did to Van Valen (1966, 1967) before us. *Micropternodus* is an Eocene (Robinson, Black, and Dawson, 1964; Novacek, 1976), Oligocene (Matthew, 1903, 1909; White, 1954; Russell, 1960), and Oligo-Miocene (Stirton and Rensberger, 1964) American insectivore, in which *Sarcodon*-like hypocones are present on P⁴-M², but in which P¹ was lost by the Oligocene and P² by the Oligo-Miocene. I¹ was enlarged in *Micropternodus* (CM 8674), as was the upper canine tooth, which ultimately came to have a triangular cross-section. The snout of *Micropternodus* is highly specialized (Russell, 1960) and the infraorbital foramen of *Micropternodus* is far to the rear (White, 1954, fig. 43) rather than over P³ as it still was in *Sinosinopa* or over the anterior root of P⁴ as it was in several undescribed American early Eocene palaeoryctid skulls (UM 68074, 72624) currently under study by McKenna. In another palaeoryctid skull (UM 80855) from the Paleocene of Montana, the infraorbital foramen is above the rear of P⁴. As is suggested by the cheek-teeth, if *Sinosinopa* lies close to the ancestry of *Micropternodus* then much of the specialization of the snout and reduction of the zygomatic arch and its base near the infraorbital canal would have taken place during the middle and late Eocene prior to the known appearance of specialized skull morphology in *Micropternodus*, as exemplified by specimens from the early Oligocene of Montana (White, 1954; Russell, 1960). These autapomorphies separate *Micropternodus* from other genera by considerable morphologic distance, but they do not alter cladistic relationships based upon postulated shared-derived cheek-tooth patterns.

The taxonomic history of *Micropternodus* is, like that of many other fossil insectivorans, checkered. In 1903 Matthew described two new genera and species of insectivorans, *Apternodus mediaevus* and *Micropternodus borealis*, from Chadronian (approximately lower Oligocene) deposits at Pipestone Springs, Montana. Matthew regarded both genera to be descriptively as well as taxonomically zalambdodont insectivores, although at that time only the lower jaws of each were known and therefore the nature of the upper dentitions could only be estimated. Matthew also stated (1903, p. 199) that *Micropternodus* might be allied to *Centetodon pulcher* Marsh, 1872, now recognized to be a geolabidid insectivoran but which was then known only from the Bridgerian (See Lillegraven, McKenna, and Krishtalka, 1981, for a review of the taxonomic history of *Centetodon*). In a semipopular paper, Matthew (1905, p. 49) placed both *Centetodon* and *Micropternodus* in the Centetidae (Tenrecidae). Two years later, Leche (1907, p. 54) regarded both *Micropternodus* and *Apternodus* as leptictids differing in talonid structure from centetids (tenrecids). Matthew (1909a) next placed *Micropternodus* in "Fam. indet." among the Insectivora, but in his monograph on Bridgerian (approximately middle Eocene) mammals Matthew (1909b, p. 543) considered *Micropternodus* as effectively a genus *incertae sedis* among the Zalambdodonta. Excellent photographs of the type specimen of *Micropternodus borealis* appear on plate 51 of Matthew's monograph. Moreover, Matthew (1909b, p. 543; 1928, p. 975) was of the opinion that Marsh's *Centetodon* is not a zalambdodont. This was eventually confirmed when the upper dentition of *Centetodon* was recognized (Lillegraven, McKenna, and Krishtalka, 1981).

Matthew's early insight about the descriptive zalambdodonty of the upper molars of *Apternodus* was soon proven correct (Matthew, 1910). However, when the upper molars of *Micropternodus* finally became known a half-century after the animal's debut, they were found to possess well-developed metacones in addition to paracones (White, 1954; Russell, 1960), although the bases of the paracone and metacone are fusing on each

molar and suggest the beginning stages of zalambdodonty as in *Palaeoryctes* and *Pararyctes*.

Broom (1909, p. 133) remarked that the (lower) molars of both *Apternodus* and *Micropternodus* are essentially similar to those of Cenozoic chrysochlorids and Jurassic *Phascolestes* and *Amphitherium*, but, with his usual perspicacity, he also noted a similarity to Eocene *Palaeosinopa* and *Palaeonyctis*. Gregory (1910, pp. 558, 559) regarded *Micropternodus* as an American fossil chrysochlorid but also suggested that it might be a primitive centetid (tenrecid). Schlosser (1911, p. 166) placed *Micropternodus* as an intermediate between centetids (tenrecids) and *Potamogale* on the one hand, and the leptictids on the other. Osborn (1910, p. 520), Matthew (1913, p. 308; 1919, p. 174), Hay (1930, p. 427), Schlaikjer (1933, p. 20), and Scott and Jepsen (1936, p. 12) all believed that *Micropternodus* is allied with the Solenodontidae of the West Indies. In each case the conclusions of all these authors about *Micropternodus* were based solely on the lower jaw and its dentition. The upper dentition was not to be made known until 1954.

White (1954) described the first known rostrum of *Micropternodus* (as that of a supposedly new genus, *Kentrogomphios*) and figured for the first time the upper dentition of *Micropternodus strophensis*. Without stating his reasoning, White placed "*Kentrogomphios*" *strophensis* in the Nyctitheriidae. Presumably, relegation to this family of insectivorans resulted from White's conclusions that the animal was not a soricid and not definitely a talpid. Thus, the Nyctitheriidae as then understood represented a stem "soricoid" scrap basket into which White's "new genus" could be tossed.

Examination of USNM 18870, type of "*Kentrogomphios*" *strophensis* White, 1954, has revealed several features not adequately illustrated by White (1954, fig. 43). We take the opportunity to correct or comment on them here:

1. The roots of the molars are not visible because they are remarkably closely held in the maxilla, as in several other kinds of lipotyphlans.
2. The anterior part of the orbit is somewhat crushed.
3. There was probably a small lacrimal foramen.
4. Foramina for the palatine nerve and artery penetrate the postpalatine torus in the usual places.
5. Although most of the sutures of the rostrum are fused, those separating the palatine bones from the maxillaries on the rear of the palate are faintly visible. The palatines extended forward to the level of the hypocone of M¹.
6. M³ has a mesostyle.

McDowell (1958) rescued *Micropternodus borealis* from the Solenodontidae but reincarcerated it as a nyctitheriid without, however, recognizing that its cell mate, "*Kentrogomphios*," is synonymous with it at the generic level. Robinson, Black, and Dawson (1964), without comment, also placed *Micropternodus* in the Nyctitheriidae.

Russell (1960), following a personal communication to McKenna from John Clark of the Carnegie Museum, recognized that White's "*Kentrogomphios*" *strophensis* is congeneric with Matthew's *Micropternodus borealis*, described a half-century earlier. Russell reviewed the history of study of *Micropternodus* and concluded that the genus is an insectivoran (lipotyphlan), but that it cannot be placed in the Talpidae, Solenodontidae, Apternodontidae, or Nyctitheriidae. Presumably, he did not consider it necessary to mention other, less closely related families. Russell left *Micropternodus* as a genus *incertae sedis* within the Insectivora, the latter being considered identical with Lipotyphla in content.

Stirton and Rensberger (1964) described *Micropternodus morgani*, an advanced species from the Oligo-Miocene John Day beds of Oregon. They placed *Micropternodus* in a monotypic family within the Erinaceoidea.

Recently, Ostrander (1983, p. 129) has commented upon *Micropternodus* and has named a new species, *Micropternodus montrosensis*, from the Chadronian (approximately lower Oligocene) of Nebraska. However, the new species appears to belong to a true genus of Erinaceoidea and is not an ally

of *Micropternodus*. Among other reasons, the lower teeth of "*M.*" *montrosensis* are too low-crowned to belong to *Micropternodus*. Ostrander's conclusion that his new species may have descended from Eocene erinaceoids is logical, but this has no bearing on the taxonomic fate of *Micropternodus* if "*M.*" *montrosensis* is unrelated to it.

Since 1956 *Cryptoryctes* Reed (1954) has come to be regarded with increasing conviction as a second synonym of *Micropternodus*. *Cryptoryctes kayi* was based upon a humerus somewhat like that of proscalopine talpids, not upon a dentition. To date, no *Cryptoryctes* humerus has ever been found in an articulated specimen that includes a dentition; thus its reference to *Micropternodus* is based on provenience, size, frequency of occurrence, and subjective estimate. But if Reed (1956), Russell (1960), and Reed and Turnbull (1965) have correctly inferred that the material upon which *Cryptoryctes* is based actually represents the humerus of *Micropternodus*, then by the Oligocene *Micropternodus* had departed from the primitive condition and had acquired a peculiarly modified humerus, adapted to talpid-like rather than terrier-like digging. Van Valen (1966) described a fragmentary humerus of *Palaeoryctes punctatus*, implying that it is somewhat talpid-like but nevertheless adapted to terrier-like digging. A palaeoryctoid relationship of micropternodontines is thus not precluded by the morphology of the humerus.

A remote linkage with the soricoid genus *Centetodon* (Matthew, 1903; Novacek, 1976; Lillegraven, McKenna, and Krishtalka, 1981) is also indicated, but in that subfamily of soricoid insectivores P_1 remained double-rooted, whereas in *Prosarcodon* P_1 was already single-rooted and in *Micropternodus* presumably was lost. Russell (1960) suggested (echoing Matthew, 1903, p. 199) that *Micropternodus* and Oligocene species of *Centetodon* (i.e., its junior subjective synonyms *Geolabis*, *Embassis*, and *Metacodon*) might be specially related. If so, the relationship must be a distant one.

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