CARNILESTES, A NEW PRIMITIVE LIPTOTYPHAL (INSECTIVORA: MAMMALIA) FROM THE EARLY AND MIDDLE PALEOCENE, NANXIONG BASIN, CHINA

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ABSTRACT—Well-preserved dentitions of a new genus and two species of basal liptotyphal insectivoran, Carnilestes, are described from the early(?)–middle Paleocene Shanghu Formation, Nanxiong Basin, Guangdong Province, China. As the earliest east Asian record of a liptotyphal, Carnilestes is distinct from primitive eutherians and leptictids in its rectangular upper molars with reduced stylar shelves, and transversely oriented, crestiform paraconid on the lower molars. Carnilestes differs from east Asian micropterodontid palaearctoids in its lack of transversely elongated upper molars, its isolated paracone and metacone on the upper molars, and its low trigonids. Carnilestes is peculiar in lacking the last molar (an autapomorphy), paralleling the condition of such Asiatic forms as the micropterodontid palaearctoids Prosarcodon and Sarcodon, and the erinaceid erinaceomorph Exallierix.

INTRODUCTION

Exploration in recent decades in what are known as the redbeds of southern China has resulted in extensive collections of fossil vertebrates. Among half a dozen early Tertiary basins, the Late Cretaceous–Paleocene Nanxiong (Nan-hsiung) Basin, Guangdong (Kwangtung) Province, stands out as the most fossiliferous of the entire region and contains one of the best Paleocene mammal records of east Asia. Containing the Late Cretaceous and possibly the Early Paleocene, the Nanxiong strata promise to be important for the studies of terrestrial vertebrates across the Cretaceous–Tertiary (K/T) boundary (Zhao et al., 1991).

Besides its apparent geologic importance, the Nanxiong Basin offers a wealth of fossil mammals not found in other parts of the world. Materials described so far have been mostly large vertebrates (e.g., Ting, 1987; Ting and Tong, 1979; Wang, 1978; Zhou et al., 1973, 1977) and little is known about small mammals. During the IVPP 1974 field season and the subsequent Nanxiong Field Conference two years later, a collection of excellently preserved small mammals was assembled. Some of the specimens are within or only a few meters above a basal nodular layer that is immediately above the putative K/T boundary (Zhao et al., 1991). The collection includes a diverse small mammal assemblage, currently under study; the present report is part of this larger effort. For practical reasons, we describe only the dentition of Carnilestes. While the present paper is being readied for publication, the cranium and basicranium regions are being prepared and will be the subject of a separate paper. The small size and fragile nature of these specimens do not allow for rapid preparation.

Only a handful of primitive insectivorans are presently known from the Paleogene of Asia, most belonging to various groups of palaearctoids: Sarcodon pygmaeus Matthew and Granger (1925) from the Paleocene Gashato Formation in Mongolia; Sinosinopa sinensis Qi (1979; formally described in Qi, 1987) of the Eocene Arshanto Formation in Nei Mongol (Inner Mongolia, China); Prosarcodon lonanensis McKenna et al. (1984) of the Paleocene Fangou Formation in Shaanxi Province; Naranius infrequens Russell and Dashzeveg (1986) and Tsaganiuus ambiguus Russell and Dashzeveg (1986) of the early Eocene Naran Bulak Formation at Tsagan-Khusu of The People's Republic of Mongolia. Also found at the latter locality are two species of nyctitheriid soricomorphs, Bumbanianus rarus Russell and Dashzeveg (1986) and Oedolius perexiguus Russell and Dashzeveg (1986). East Asian records of erinaceomorphs are unknown prior to the middle Eocene; the Paleogene records include (all nominal names without critical evaluations): Eochenus Wang and Li (1990) from the middle Eocene Huanian Formation in Huanian Basin, Jilin Province; Ictopidium Zdansky (1930) from the Eocene of Shaxi and Shandong provinces; Exallierix McKenna and Holton (1967) from the early Oligocene Hsanda Gol (Shand-Gol) Formation of Mongolia; Palaeoscoptor Matthew and Granger (1924) (=Amphypical Aymard) from the Hsanda Gol Formation; and Tupaiodon Matthew and Granger (1924) from the middle Eocene to early Oligocene of Jilin Province and Mongolia. Two genera of Paleogene soricomorphs in China have been described: Ernoserex Wang and Li (1990) from the Huanian Formation and Changlestes Tong and Wang (1993) from the early Eocene Wutu Formation in Wutu Basin, Shandong Province. All are quite advanced in morphology,
and found in rocks of relatively young ages. The present description of a very primitive lipotyphlan from possibly the early Paleocene is thus of both phylogenetic and biogeographic significance.

**Institutional Abbreviations**—IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Academia Sinica, Beijing.

**MATERIALS AND METHODS**

Small mammals from the Nanxiong Formation are usually embedded in red or purplish-red mudstones having a rather high calcareous content. The matrices are harder than the bones and teeth, making preparation of the specimens extremely difficult and arduous. Bony elements are subject to limited cracking but the overall shape of the skulls and mandibles is often intact. Teeth are excellently preserved in most specimens and damage is mostly incurred during preparation. Some specimens are tightly articulated skull-and-jaws, making it necessary to sacrifice some elements in order to fully expose the teeth.

Taxonomic nomenclature of higher level insectivorans is adopted from Novacek (1986a) and Butler (1988). We follow Van Valen (1966) for dental cusp terminologies. The traditional dental formula (in the case of *Carnilestes*, 11–3 C1 P1–4 M1–2 and ii–3 c1 p1–4 m1–2) is adopted here, which is still the most commonly used in the fossil insectivoran literature (see Luckett, 1993, for a recent ontogenetic assessment of the dental homologies) although an alternative interpretation of the number of premolars in primitive eutherians, in the sequence of P1 P2 P4 P5 and p1 p2 p4 p5, has been proposed based mainly on fossil evidences (McKenna, 1975; Novacek, 1986b). By convention, molar numbers are designated according to their sequential positions rather than their morphology. Therefore, the second (last) upper and lower molars of *Carnilestes* are here labeled as M2/m2 despite their morphological similarities to M3/m3 of primitive eutherians. Measurements follow those of Novacek (1976:fig. 2).

Stratigraphic nomenclature and correlations of the Paleogene of Asia follow Russell and Zhai (1987). Geographic and personal names, the official Chinese Pinyin system is adopted throughout the text and followed, where appropriate, by the traditional Wade-Giles spelling.

**SYSTEMATIC PALEONTOLOGY**

**Superorder INSECTIVORA Illiger, 1811**

**Order LIPOTYPHA Haecikel, 1866**

**Remarks**—We follow Novacek (1986a) and Butler (1988) in their definitions of Lipotypha, which is divided into two major dichotomous clades, Erinaceomorpha and Soricomorpha, although a third clade, Chrysochloromorpha, was maintained by MacPhee and Novacek (1993). Such archaic insectivoran groups as palaecorycids and leptictids, generally of the dubious “Proteutheria” grade, are here included in a broadly construed superorder Insectivora.

Earliest fossil records of lipotyphlas, *Mckennatherium* and *Leptacodon* (Archibald et al., 1987), are well established in the middle Paleocene (late Torrejonian) of North America, although isolated teeth of nyctitherelike forms can be traced to as early as the Late Cretaceous of Alberta (Fox, 1970, 1979, 1984). As will be discussed below, the North American lipotyphlas are also the most primitive known in the World. The European late Paleocene (Cernaysian of Paris Basin) *Adapisorex* is not only younger (Savage and Russell, 1983; Archibald et al., 1987) but also significantly more derived in morphology (Krishtalka, 1976a; Bown and Schankler, 1982; Novacek et al., 1985). The earliest east Asian lipotyphlas, *Bumbanius, Oedolius*, and *Changilestes*, and found in the early Eocene Naran Bulak Formation of Mongolia or the Wu Tu Formation of Shandong Province. As discussed below, evidence suggests that basal sediments of the Shanghu Formation, from immediately above the putative K/T boundary, may be very close to the beginning of the Tertiary, i.e., the earliest Paleocene, and *Carnilestes* may thus represent the earliest record of the Lipotypha in Asia.

**LIPOTYPHA incertae sedis**

*Carnilestes*, gen. nov.

**Type Species**—*Carnilestes palaeasianicus*, sp. nov.

**Included Species**—*Carnilestes major*, sp. nov.

**Diagnosis**—More derived than *Prokennalestes, Kennalestes, Zalambdalestes*, and *Asioryctes* in having simple, single-rooted incisors; long, caniniform canines, transversely shortened M1–2 with reduced stylar shelf; trenchant talonid of lower last premolar; and in lacking a distinct metacone on P4; differs from Asiatic palaecorycoids (e.g., *Sarcodon, Prosarcodon, Sinostopha*) in shortened upper molars, paracone and metacone not appressed together, low trigonid on lower molars, and lack of a large hypocone on upper molars; more primitive than didymoconids in the presence of i3 and P1/p1 and a fully-formed talonid on lower molars; distinct from the Mongolian nyctitheres *Bumbanius* and *Oedolius* in more closely spaced paracone and metacone of upper molars and loss of M3/m3; distinguishable from more advanced lipotyphlas such as *Changilestes, Tupaiodon*, and *Ictopidium* in slender, less crowded premolars, semi-molariform P4, and higher trigonids of lower molars; and differs from most of the above taxa in P4 having a carnassial-like metastylar crest.

**Geologic Age**—All specimens were collected from the Shanghu Formation (Shanghu section of Lofochai Formation in Zhou et al., 1973), which has a thickness of 470–600 m, and is underlain by the Late Cretaceous Nanxiong Group (Nanxiong Formation) and overlain by the late Paleocene Nongshan Formation (Nongshan section of Lofochai Formation in Zhou et al., 1973). Paleomagnetic studies by Zhao et al. (1991) in a section
south of Datang indicated four normal magnetic zones. Based on two K-Ar dates of 67.04 ± 2.34 and 67.37 ± 1.49 m.y. on the uppermost basalt layer, the Nanxiong Basin sequence was calibrated to extend over chron 28N–31N. The K/T boundary was postulated to be within the upper part of a 203 m section of a reversed zone, chron 29R (Zhao et al., 1991; see Russell et al., 1993, for an alternative interpretation). This putative K/T boundary (no iridium anomaly has been found), at the lower and upper limits of the Shanghu Formation/Nanxiong Group, is marked by color changes (from purplish red below to dark red above), calcareous nodules (immediately above and below), and faunal changes (dinosaurs and their eggs replaced by mammals) (Zhao et al., 1991). A critical issue is thus the contact relationship between the Tertiary Shanghu Formation and the Cretaceous Nanxiong Group, a hotly debated question, for which existing opinions range from disconformity (Zheng et al., 1973; Tong et al., 1976; Zhou et al., 1977; Li and Ting, 1983; Russell et al., 1993) to continuous deposition (Zhao et al., 1991).

Although a rich mammalian fauna is available from the Shanghu Formation, its rather endemic nature makes faunal correlations difficult. The early Tertiary fauna from the Nanxiong Basin was earlier compared to the late Paleocene Gashato fauna of Mongolia (e.g., Zhou et al., 1973, 1977; South China “Redbeds” Research Group, 1977). A review of the fossil plants and invertebrates from the South China Redbeds by Yang et al. (1979) placed the Shanghu Formation in the Paleocene without further restriction. Here, we do not wish to challenge the conventional wisdom that most of the Shanghu Formation belongs to the middle Paleocene, but we recognize an early Paleocene component as equally likely. We thus tentatively assign Carnilestes to early(?)–middle Paleocene, as did Li and Ting (1983).

Etymology—Carnis, Latin, flesh, meat, in allusion to its carnassial-like upper last premolars; lestes, Greek,
robbor, pirate, commonly used as endings for insec
tivornans.

Discussion—Carnilestes can be distinguished from
the Cretaceous central Asian eutherians (Prokennale-
stes, Kannalestes, Zalambdalestes, Asiorctes, etc.) in
several of its derived dental characteristics: single-rooted
canines and first premolars; long, caniniform can-
nine; lack of a distinct metacone in P4; transversely
shortened M1–2; better developed hypocone; and pre-
and postcingula on upper molars, trenchant talonid of
lower last premolar, and low trigonid of lower molars.

The Chinese and Mongolian Paleocene micropteron-
dontid palaeoerycoids Prosercadon lonanesis and
Sarcodon pygmaeus, but not Sinosinopia sinensis, share
with the Nannoxion insectivorans the loss of the last
upper and lower molars. Their North American rela-
tive, Micropteronodus (=Kentrogonphios White, 1954:
fig. 43 and Cryptryctes Reed, 1954; Reed and Turn-
bull, 1965:108), still retains its last molars. Other than
this reduction of dentitions, however, there are con-
siderable differences between Carnilestes and the Asi-
atic micropteronodontids. Chief among them are the
possession in micropteronodontids of transversely elong-
ate upper molars, the tendency toward zalambdodont
upper molars (i.e., higher-crowned and closely com-
pressed paracanines and metacones), and the develop-
ment of an enlarged hypocone (not enlarged in Pro-
sarcodon). The trigonids in the lower molars of these
micropteronodontids are also distinctly more upright
and sectorial (less so in Sarcodon; Szalay and McKen-
da, 1971:figs. 5–7) than in Carnilestes. The tendencies
toward zalambdodonty (excluding the large hypocone)
can also be used to distinguish palaeoerycoids from the
Naran Buluk Formation of Mongolia, Naranius and
Tsaganius.

Another group of early Tertiary archaic insectivorns
from east Asia which has lost its last molars is the
family Didymocoridae (excluding Wyolestes, see Phy-
genetic Position below). Carnilestes is distinct from
didymocorids in its primitive retention of a basined
talonid on the lower molars, in contrast to a trenchant
talonid on lower molars of all didymocorids. Didymo-
corids also have lost i3 and P1/p1, which are still
present in Carnilestes.

Of the few known early Tertiary east Asian lipo-
typhlans, morphologically and chronologically closest
to Carnilestes are the early Eocene Bumbnaius and
Oedolius from Tsgan-Khusu of Mongolia. From the
figures and descriptions in Russell and Dashzevez
(1986), these nyctitherid soricomorphs are
quite similar to Carnilestes. Chief among distinctions
between Carnilestes and the Mongolian nyctitheres are
more separate paracine and metacone on the upper
molars of the latter, and their primitive possession of
both M3 and m3. Such distinctions can also be ob-
served between Carnilestes and Changlelestes, from
Wutu of Shandong Province. In addition, the latter has
a very large, nearly single-cusped p4, in contrast to a
small trigonid on p4 of the former.

Carnilestes differs from the North American late Pa-
leocene Litocherus, Cedrocherus, and Diaococherus (see
Gingerich, 1983) in having more sectorial teeth (high
trigonid cusps) and lacking M3/m3. In addition, these
North American forms (except in Diaococherus) tend
to have progressively smaller posterior lower molars,
in contrast to large m2 (relative to m1) in Carnilestes.

Carnilestes is easily distinguishable from the Hsanda
Gol Tupaiodon (also from Jilin Province) and Ictopi-
dium (Tupaiodontinae of Butler, 1988), and from the
Eocene Eochoenus of northeastern China in its slender,
far less closely spaced cheek-teeth; higher, more sec-
torial trigonid of the lower molars; shorter and less
anteroposteriorly oriented trigonid shearing blade;
narrower talonid; lower entocone; and absence of the
last upper and lower molars. These characters can also
be used to differentiate Carnilestes from more derived
erinaceoids such as Ampechinus and Palaeoscoptes
(possibly congeneric according to Sulimski, 1970) in
addition to the latter’s elongated trigonid shearing blade.
Carnilestes is more primitive than the middle Eocene
Ernosorex in its lack of multi-cusped incisors in addi-
tion to most of above characters.

Ting and Zhang (1979) described as “Insectivora
gen. et sp. indet.” two ramal fragments with the left
posteromost two molars (IVPP V5032) and an in-
complete right last molar (IVPP V5032.1) from the late
Paleocene Chijiag Formation, Chijiag Basin (just
north of Nanxiong), Jiangxi (Kiangsi) Province.
As noted by the authors, the Jiangxi form is characterized
by its open trigonid, i.e., a conical paracone well sepa-
ratated from the protoconid, a feature present in Carni-
lestes major. In addition, part of an upper molar is
still articulated with the last lower molar in IVPP V5032
and indicates the presence of a very large hypocone
(Ting and Zhang, 1979:fig. 1). If this it true, the
hypocone in the Jiangxi taxon is significantly larger
than that in Carnilestes. Further determination of the
identity of the Jiangxi insectivoran must await better ma-
terials than are presently available.

Russell and Gingerich (1981) described as a member of the “?Erinaceomorpha” Seia shahi, from the Eocene
Kuldana formation of Pakistan. This taxon was based
on two isolated upper molars (M1 and M2). From the
published figures and descriptions (Russell and Gin-
gerich, 1981:figs. 1–5), Seia shahi differs from Carni-
lestes in its development of crests on the anterior, pos-
terior, and to a lesser extent, lingual faces of the paracone
and metacone, and its lack of a hypocone.

CARNILESTES PALLAEOSASIATICUS, sp. nov.

Fig. 2

Holotype—IVPP V10488, incomplete skull and right
ramus with nearly complete upper left and lower right
dentinion.

Type Locality—IVPP Locality 73170, at a small hill
approximately 100 m northwest of the Nanxiong Nor-
mal School, approximately 3 km southwest of Nanxi-
ong County seat, in northern Guangdong (Kwangtung)
Province (Russell and Zhai, 1987:fig. 7; Fig. 1). Lower part of the Shanghu Formation, early(?)-middle Paleocene.

**Referred Specimens** (see Fig. 1 for locations)—IVPP V10489, complete skull, from the Datang section in the northeastern part of the Nanxiong Basin, 100 m (surface measurement, representing just a few meters of thickness of strata) above the basal nodular layer of the Shanghu Formation.

IVPP V10490, incomplete, articulated skull and mandible with isolated limb bones, Locality No. 74009, from between two isolated houses, 800 m northeast of Liren, northeast of Zhuji (Commune), upper part of Shanghu Formation.

IVPP V10491, articulated, nearly complete skull and mandible, from Yetangwei, Locality No. 74015, approximately 5 km north of Gushi, in Shanghu Formation.

**Diagnosis**—Distinct from *Carnilestes major* in a number of characters: smaller size; triple-rooted P2 without a posterior cusplet; P3 with well-developed protocone; P4 protocone relatively closer to paracone; p1 less procumbent; and m2 having relatively wide talonid.
Etymology—Palaeo, Greek, palaio, ancient, old; asiaticus, from Asia.

Distribution—Carnilestes palaeasiaticus is only known from the Shanghu Formation of the Nanxiong Basin, Guangdong Province.

Description—Unless otherwise noted, descriptions of teeth are mainly based on the type, IVPP V10488, which not only has a nearly complete dentition but is the best preserved specimen. The referred specimens are in various stages of preparation and are included in this species based, to some extent, on size.

I1 on IVPP V10488 is mostly broken but that on IVPP V10489 is well preserved. In IVPP V10489, there is a long diastema of nearly 2 mm between the medial bases of left and right I1. I1 is a slender, simple tooth with an oval cross-section. Its crown is the highest among the three incisors. It is slightly recurved and also tilts medially; thus the tip-to-tip distance between left and right I1 is reduced to 1 mm. There is a sharp edge on both anterior and posterior margins of the I1. On both IVPP V10488 and V10489, only the labial surface of the I1 is exposed and the matrix on the lingual side was left intact.

I2–3 are similar to I1, but are progressively lower-crowned from front to back. I2 is slightly recurved, whereas I3 has a nearly vertical orientation. Diastemata are present between the upper incisors, which interdigitate with the lowers.

A large upper canine is preserved in all specimens except IVPP V10490, but is well exposed only in IVPP V10488. C1 is single-rooted, curves slightly backward, and is mediolaterally compressed.

P1 is double-rooted in IVPP V10488, in contrast to the single-rooted P1 in Carnilestes major. It has a single principal cusp and is mediolaterally compressed, although the lingual face is slightly more swollen. A lingually located root (third root) appears to be present on P2 of IVPP V10488, instead of the double-rooted P2 seen in C. major. The P2 is composed of a single main cusp.

P3 is triangular in occlusal outline and has three roots. The principal cusp (paracone) is large and trailed behind by a thin cusp reminiscent of a metastyle of carnivorans, contrasting with the more conical cusp in the North American Eocene Diacodon alticuspis (Novacek, 1982:fig. 3). Anterior to the paracone is a small metastyle. A distinct protocone is almost certainly present although its tip is broken near its base on IVPP V10488 (Fig. 2B–C).

P4 is intermediate, both in size and shape, between P3 and M1, in contrast to the considerable size difference in corresponding teeth of Prosorcanodon longanensis. The P4 does not have a discrete, conical metacone. Instead, a thin crest continues behind the large paracone to form a metastyle. In IVPP V10491, the metastylar crest appears even more pronounced in buccal view and there is an incipient stylar shelf along the posterolabial corner. As an anteriorly projecting spur, the parastyle is larger than that on P3 and forms a small but distinct cusp (worn flat in IVPP V10488).

The protocone is high and, together with a low preprotoprotocrista and postprotoprotocrista, encloses a broad basin lingual to the paracone. There is, at the base of the paracone, a slight indication of a paraconule (protoconule). No hypocone is present on P4.

M1 begins to take on the rectangular outline of primitive lipothyphlans as opposed to transversely elongated upper molars in most primitive eutherians from the Cretaceous. The parastyle and metastyle in IVPP V10488 are reduced and the labial cingulum is narrow. The protocone is located close to the paracone/metacone, further contributing to the transversely shortened appearance. On IVPP V10491, however, M1 primitively still has a relatively long parastyle as an extension of a ridge on the anterior face of paracone; the parastyle extends forward beyond the posterior border of the P4. Corresponding to this long parastyle is the more buccally expanded cingulum labial to the paracone and metacone, resulting in a rather prominent indentation in the mesostyle area instead of the rather straight buccal border as in IVPP V10488. The paracone and metacone have nearly circular cross-sections and are not appressed together as in palaeoryctids. The paracone is slightly higher than the metacone (seen in IVPP V10491; the metacone in IVPP V10488 is broken). A large protocone dominates the lingual half of the M1. There is moderate development of a paraconule (protoconule) and a metacone; both were heavily worn in IVPP V10488. Anterior to the protocone is a low and narrow precingulum. The postcingulum is slightly stronger than the precingulum, not only for its greater width but for its development of a hypocone on the lingual tip of the postcingulum; this small hypocone is best developed (highest) on IVPP V10489. The hypocone lacks any trace of an anterolabially directed crest running toward the lingual side of metaconule, which is common in living erinaceids (Butler, 1948).

M2 is smaller than M1, instead of the larger M2s commonly seen among primitive eutherians. Compared to that of M1, the M2 parastyle shows more prominent buccal and anterior expansions. In IVPP V10491, the parastyle is particularly long and slender, and forms a sharp ridge surrounding the posterolabial corner of the M1. Other than this relatively larger parastyle, the general outline of the M2 is similar to that of the M1, i.e., with a rather rectangular outline. The paracone is higher than the metacone; both are rounded in occlusal view. The M2 protocone is almost as large as that of M1, and is subequal to the M2 paracone in height. The paraconule is weaker than on M1, and the metaconule is indicated by a widened wear facet along the postprotoprotocrista. There is no hypocone. Only a low and narrow pre- and postcingulae are present; the latter is much smaller than on M1 and is hidden in lingual view (Fig. 2C) because of the large protocone.

Three right lower incisors are well preserved in IVPP V10488 and the tips of i2–3 of the left side remain in their articulating position with the corresponding upper incisors. All of the lower incisors are procumbent,
with slightly curved tips, and have a single, chisel-shaped cusp. The cross-sections are labiolingually compressed; the lingual surfaces tend to be straight or slightly concave as opposed to the more arched labial surfaces.

An incomplete lower right canine is preserved in IVPP V10488; it is large, single-rooted, and oval in cross-section. Although broken in the middle, c1 is judged to be long and truly caniniform instead of the small, procumbent, incisiform lower canine seen in leptictids (Novacek, 1986a).

The p1 is single-rooted and oval in cross-section. The crown consists only of a mediolaterally compressed principal cusp. The p2 is double-rooted and is dominated by a main cusp. There is a ridge on both anterior and posterior surfaces of the main cusp. A low, talonid heel is rather posteriorly located away from the main cusp. The p3 shows an incipient development of an anterior cingular cusp. This cusp is separated from the anterior ridge of the main cusp (protoconid) by a shallow notch and is slightly bent lingually to assume the position of a paraconid. The posterior ridge of the protoconid also bends lingually but is only minutely swollen at its base, i.e., no metaconid is present. The p3 also has a small talonid, which is made up of a low central ridge (a trenchant talonid).

The p4 has a fully formed trigonid, which is more elongated, due to a more anteriorly located paraconid, than those on m1–2. The paraconid is separated from the protoconid by a deep and broad valley on the lingual side (far deeper than the notch between protoconid and metaconid). The trigonid is thus more "open" than on m1–2. The trigonid of p4 is also more upright and sectorial than on m1–2. The metaconid is significantly lower than the protoconid, in contrast to the much higher metaconid on m1–2. The talonid is basically trenchant and is made up of a central, anteroposteriorly directed ridge (cristitid obliqua) running the entire length of the talonid. A low, lingual ridge is present to enclose, together with the central ridge, a shallow, longitudinal basin.

The trigonid of m1 is low and more procumbent than that on p4, a derived character in lipotyphlans relative to Late Cretaceous and early Tertiary eutherians. The paraconid is slightly higher than on p4 and closer to the protoconid, so that the valley between these two cusps is narrow and high relative to that of p4. This more closed trigonid is brought about by a more transversely oriented paraconid crest (paralophid or paracristid), which is beginning to assume the compressed, crestiform shape as in more derived erinaceomorphs. Below the paracristid blade, there is a narrow anterolabial cingulum (precingular). The protoconid and metaconid are nearly equal in height and size, and form a transverse ridge that shears against the crest formed by preprotocrista-paraconule-paracone of M1. The width of the talonid is almost identical to that of the trigonid, and is narrower than in advanced erinaceomorphs. The length of the talonid, however, is not shortened as in many lipotyphlans.

The hypoconid is slightly higher than the entoconid, which is about the same height as the hypoconulid, in contrast to a much higher entoconid in Diacodon, Tupaiodon, Palaeoscaptor, etc. Together with a high cristic obliqua, the hypoconid forms a dominant ridge on the buccal side. A modest-sized talonid basin is enclosed by the hypoconid, hypoconulid, and entoconid, although anterior to the entoconid the basin is open lingually.

The trigonid of m2 is slightly more compressed (closed) anteroposteriorly than that of m1. The most striking difference between m2 and m1 is the much longer m2 talonid due to a prominent, posteriorly expanded hypoconulid. This elongated talonid of the last molar (in this case m2) is unusual among most lipoptyhans, which tend to have progressively shorter molars toward the posterior end (see more discussion in Phylogenetic Position). The talonid is slightly narrower than the trigonid (more so in C. major). The large hypoconulid is slightly procumbent. The entoconid is relatively small compared to that on m1.

**Wear Facets**—All individuals in the present sample have sustained little (IVPP V10491) or moderate wear (IVPP V10488), such that discrete wear facets can easily be identified yet are not obscured by extensive wear. Observations of the wear facets, however, are mainly derived from IVPP V10488 because of its nearly complete dentition.

The main mode of occlusion of the cheek teeth in Carnilestes palaeasiaticus is the shear of the transverse ridge formed by protoconid and metaconid in lower cheek teeth against the anterior edge of the upper teeth (Fig. 3, horizontal hatched lines). A nearly vertical wear facet is clearly seen on the posterior face of the protoconid and metaconid of p4–m2 and protoconid of p3. These facets press against the anterior border of the upper teeth formed by the continuous edge of preprotocrista-paraconule-paracone-parastyl; the wear is most extensive on the paracone.

A less conspicuous shearing facet resembles that in
carnivores, although it is not confined to the carnassial teeth (P4/m1) only; the shear involves three pairs of teeth: P3/p4, P4/m1, and to a lesser extent, M1/m2 (Fig. 3, diagonal hatched lines). The lingual surfaces of the P3–4 protocenes are flat and are extended posteriorly by the metastylar crest (there is no carnassial notch). The resultant large, straight blade shears against the anterolabial face of the trigonid on p4–m1; this wear facet is vertical. Butler (1988) regarded this carnassial-like shear as a main dental characteristic of the Erinaceidae.

On the talonid, the main wear is between the posterolabial surface of the hypoconid of the lower molars against the anterolingual surface of the metacone on the upper molars (Fig. 3, stippled areas).

**Carnilestes major**, sp. nov.

Fig. 4

**Holotype**—IVPP V10492, incomplete left palate with P2–M2 and roots of C1–P1, left and right rami with left i2–c1, p3–m2, and right c1–m2; the only known specimen.

**Type Locality**—From IVPP Locality 73065 (Fig. 1), southwest of Fengmenao, which is approximately 2 km southwest of Nanxiong County seat, at a small hill in the north side of the road between Nanxiong and Gushi, lower part of Shanghu Formation, early(?)-middle Paleocene.

**Diagnosis**—Distinguished from *C. palaeoasiaticus* by: approximately 55% larger in individual teeth; double-rooted P2; presence of an incipient posterior cingular cusplet in P2; lack of a salient protocone in P3; more lingually positioned protocenes of P4–M2; more procumbent p1; higher trigonid of m1–2; stronger and more procumbent paraconid of p4–m2; and narrower talonid of m2.

**Etymology**—Major, Latin, greater; in allusion to its larger size.

**Distribution**—Type locality only.

**Description**—Regrettably, teeth of the type specimen have sustained considerable damage during preparation, particularly the upper molars and lower premolars. To minimize redundancy, the description below will mostly contrast the differences between *Carnilestes major* and the type species, *C. palaeoasiaticus*.

There are three mental foramina (more distinct on the left side), one below each of the p1–3. C1–P1 are broken at the base. Both are single-rooted and show an oval cross-section, as in *C. palaeoasiaticus*. P2 is double-rooted, in contrast to the triple-rooted P2 in *C. palaeoasiaticus*. It has a small posterior cingular cusplet that is not present in *C. palaeoasiaticus*. Corresponding to that of the P2, the P3 protocone is less distinct than in *C. palaeoasiaticus*; on the lingual side of the main cusp is a swelling supported by a lingual root, but no discrete protocone is formed. The protocone of P4, however, is more distinct and lingually positioned than in *C. palaeoasiaticus*. The lingual border of the P4 protocone extends almost as far lingually as that of M1, in contrast to the more labially positioned P4 protocone in *C. palaeoasiaticus*. The metastylar blades posterior to the paracones of P3–4 seem slightly shorter than those in *C. palaeoasiaticus*. M1–2 are extensively damaged and only the lingual halves are preserved. Although the M1 protocone is relatively intact, much of the enamel surrounding the pre- and postcingulae has unfortunately been trimmed off during preparation and their outlines are no longer original. The remaining dentine leaves no doubt that there was a well-developed postcingulum which is raised to form a hypcone at its lingual end. From what is left on the lingual halves of the two cusps, the paracone and metacone seem to be rather closely appressed judging from the lack of an apparent notch between them, although such can be cause by wearing on the lingual face of the cusps. Only the protocone of M2 remains, which seems to be slightly more lingually positioned than that in *C. palaeoasiaticus*. Presence of pre- and postcingulae cannot be confirmed because of damage in these areas.

The i1–3 are single-rooted. Much of the crowns of the i1–3 are broken off and little of their morphology can be learned from the remaining fragments. The canines are broken in the middle, but are large, single-rooted, and oval in cross-section. The p1, single-rooted, is more procumbent than in *C. palaeoasiaticus*. The p2–3, both double-rooted, are badly damaged. The metaconid of p4 is slightly smaller than in *C. palaeoasiaticus*, and the p4 is otherwise quite similar to that of the latter. The main difference of m1–2 between *C. major* and *C. palaeoasiaticus* is the relatively narrower talonids of the former. In particular, the m2 talonid of *C. major* is markedly narrower than the trigonid, in contrast to their nearly equal widths in *C. palaeoasiaticus* (Table 1). Another difference between the two species is the stronger, more procumbent paraconid of p4–m2 in *C. major*.

**Discussion**—The lower postcanine toothrow (p1–m2) in IVPP V10492 is 72% longer than that in *C. palaeoasiaticus* (IVPP V10488 in Table 1). Measurements of individual teeth have a similarly large difference of 55% (an average of all comparable measurements in Table 1 except the above tooth row data) between the two species. In addition to this considerable difference in size, other morphological differences—for example, the double-rooted P2, the more transversely elongated P4, the higher trigonids of m1–2, the more procumbent paraconids of m1–2, and the narrower talonid of m2 in *C. major*—may even suggest that these two species belong to quite different lineages. Some of these features are reminiscent of palaecoryctids (transverse P4–M2 and high trigonids), although they are not as fully expressed as in *Palaecoryctes, Eoryctes, Aapteryctes, Naranius, or Prosarccodon*. The more transverse upper cheek teeth and higher trigonids, however, are likely to be primitive characters because many Late Cretaceous eutherians tend to have them (e.g., *Kennalestes, Cimolestes, Procerberus*, etc.). If the metacone and paracone in M1 are indeed appressed together, as is sug-
FIGURE 4. Upper and lower teeth of *Carnilestes major*, IVPP V10492, holotype, from Nanxiong Formation. A, stereo photograph of occlusal view of upper left teeth; B, stereo photograph of occlusal view lower left teeth; C, buccal view of left mandible. Scales = 5 mm.
<table>
<thead>
<tr>
<th>TABLE 1. Dental measurements (mm) of <em>Carnilestes</em>.</th>
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<td>C. palaeoasiaticus (IVPP V10488: holotype)</td>
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<tr>
<td>C1 length</td>
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<td>m2 trigonid width</td>
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<td>m2 talonid width</td>
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<td>p1–m2</td>
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*Measurements estimated.

inference about its phylogeny, based on the dental morphology only, is necessarily provisional.

Comparisons with Primitive, Insectivore-like Eutherians

Although perhaps not immediately ancestral to *Carnilestes*, such well known primitive eutherians from the Cretaceous of Mongolia as *Asiaurocytes*, *Kenneales*, *Prokenneales*, and *Zalambdalestes* naturally come to mind as good candidates for outgroups. *Carnilestes* has acquired the following (most probably derived) dental features as compared to these taxa (as described in Kielan-Jaworowska, 1968; Kielan-Jaworowska et al., 1979; Kielan-Jaworowska and Dashzeveg, 1989): 1, single-rooted C1, P1 (double-rooted in *C. major*), and p1; 2, long, caniniform incisors; 3, simple anterior premolars dominated by one main cusps; 4, lack of a distinct P4 metacone and development of a large metastylar crest (i.e., carnassial-like shearing blade); 5, reduced stylar shelf in M1–2; 6, better developed pre- and postcingulae of M1; 7, presence of a hypocone on M1; 8, tranchant talonid of p4; and 9, low, less sectorial trigonid in lower molars. Of these traits, several (1, 3, 6, 7, 9) have been cited as possible synapomorphies of Erinaceomorpha (Novacek, 1982, 1986a; Novacek et al., 1985) and will be further discussed below. Some of the above features (e.g., 5–9) can also be used to distinguish *Carnilestes* from North American Cretaceous eutherians such as *Cimolestes* and *Procerberus* (as described by Lillegarden, 1969; and summarized by Kielan-Jaworowska et al., 1979). The carnassial-like P4 (4) and tranchant p4 (8), however, could be primitive for the Cretaceous eutherians; for example, the carnassial-like P4 is present in *Prokenneales*, *Cimolestes*, and *Procerberus*, whereas the tranchant p4 occurs in *Kenneales*, *Prokenneales*, and *Cimolestes*.

The intriguing loss of the M3/m3 may seem to suggest common ancestry between some early Paleogene east Asian micropterodontid palaeoerycoids (*Prosarcoodon* and *Sarcodon*) and *Carnilestes*. This loss of last molars, however, is here interpreted as independent developments for the following reasons. The North American and Asian palaeoerycoids (such as *Palaeoerycetes*, *Pararycetes*, *Aapteryctes*, *Sarcodon*, *Prosarcoodon*, *Sinosinopar*) share a derived character complex in having high, closely appressed paracone and metacone (or complete suppression of the metacone), well-developed metastyles (and correspondingly high trigonids in the lower molars), and a tendency toward zalambdodonty, which is not seen in *Carnilestes*. Furthermore, the Asiatic micropterodontid palaeoerycoids (*Sarcodon*, *Prosarcoodon*, *Sinosinopar*) have a large hypocone on the upper molars, another derived feature not present in *Carnilestes*. On the other hand, *Carnilestes* possesses derived characters present in lipotyphlans but absent or poorly-developed in the Asiatic palaeoerycoids: presence of a precingulum on upper molars and more labially positioned protocone (features combining to give the upper molars a more
rectangular appearance). In contrast, most palaeoercydoid, except the extremely derived North American Micropterostephus, have transversely elongated upper molars. Given this divergent morphology, the common loss of M3/m3 in Sarcodon and Prosarcodon on the one hand and Carnilestes on the other probably represents independent events since the primitive Asian palaeoercydoid Sinosinopha still has well developed third molars but otherwise exhibits dental patterns typical of the group. For the loss of M3/m3 to become a synapomorphy among Carnilestes, Sarcodon, and Prosar- 
codon, several reversals of zalambdalont characters (from Sinosinopha which has them but retains M3/m3) would have to be invoked to explain the primitiveness of Carnilestes. One possible link between Carnilestes and palaeoercydoids is the trentanch (crest-like) p4 talonid, a character whose polarity is uncertain among Cretaceous eutherians: basined talonids are present in Zalambdalolestes, Procerberus, and Gypsonictops, while Kennalestes, Prokennalestes, and Cimolestes have trentanch talonids.

Another group of insectivoran-like mammals, the Asiatic Paleogene didymocons, also lacks the third upper and lower molars (excluding Wyolestes, which still has M3/m3 but does not seem to be closely related to the Old World didymocons [Novacek et al., 1991; Meng, 1992], despite the alleged similarities to the latter as enumerated by Gingerich [1981]). In fact, the only dental synapomorphy listed by Meng (1992) for the family Didymoconidae is the reduced dental formula, a character seen even in the most primitive genus Archaeorctes (Zheng, 1979; Meng, 1990). An insectivoran affinity for the didymocons is indicated by a recent analysis of cranial morphology, which suggests a sister-group relationship with the Lipotyphla (Meng, 1992; Meng et al., 1994). The notion that didymocons are derived from an insectivoran ancestry is further supported by the transversely shortened upper molars and the initial development of a cingulum surrounding the protocone in Archaeorctes (more derived didymocons, however, may have transversely elongated upper molars without a cingulum on the lingual side). A dental character (probably an autapomorphy for the Didymoconidae) that distinguishes 
didymocons from primitive eutherians, leptictids, and lipotyphlans is the very reduced (trentanch) talonids on the lower molars and last premolars, without or with only a weak entoconid (e.g., Archaeorctes and Ardynictis; Zheng, 1979; Meng, 1990). Bicuspid talonids are probably secondarily developed in the more derived Didymoconus because the lingual cusp of the talonid may be homologous with the hypoconulid instead of the entoconid (Meng, 1992). Although Carnilestes lacks the high, sectorial twin-cusps of protoconid-metaconid, a highly derived character typical of most didymocons, the possibility exists that Carnilestes is related to didymocons, in which case the lack of the third molars would be a synapomorphy between Carnilestes and didymocons, a hypothesis to be tested by cranial characters.

Novacek (1986a) considered the leptictids (including Prodiacodon, Lepticus, and Palaeictops) a basal stock of Insectivora and the closest sister-group of Lipotyphla. Carnilestes is distinct from leptictids (using Gypsonictops and Prodiacodon as morphotypes) in having I1 (loss of I1 in leptictids is an autapomorphy for leptictids according to Novacek, 1986a), a large incisor, a less molariform P3-4 (lack of a metacone), transversely shortened upper molars, a trentanch talonid of p4, and a low trigonid of lower molars.

Comparisons with Primitive Lipotyphls

The phylogenetic relationships of primitive lipo-
typhls have proven to be resistant to resolution al-
though the group is divided by most authors into two 
major clades, erinaceomorphs and soricomorphs. Besi-
de the common frustration over fragmentary pres-
ervation of fossils, the more serious problem seems to be the profound uncertainty about character polarities. While consensus remains distant, recent attempts to identify cranial and basicranial synapomorphies for such fundamental taxa as Insectivora, Lipotyphla, Er-
inaceomorpha, and Soricomorpha help to define these 
taxa in a more rigorous manner (McDowell, 1958; Mc-
Kenna et al., 1984; Novacek, 1986a; Novacek et al., 
1983; Butler, 1956, 1972, 1988; MacPhee et al., 1988; 
MacPhee and Novacek, 1993). Unique dental syna-
poromorphies, however, remain elusive and consequent-
ly opinions proliferate.

Despite their different opinions concerning the phy-
ologeny of erinaceomorphs, Novacek and his co-authors (1982; Novacek et al., 1985) and Butler (1988) agree that 
primitive taxa such as Diacodon and Adunator stand at the base of the erinaceomorph radiation. On 
the soricomorph side, there also seems to be general 
agreement that the late Paleocene Leptacodon (sensu 
stricto), a primitive member of the European and North 
American family Nytchiderii, is one of the most 
primitive soricomorphs (McKenna, 1968; Robinson, 
1968; Butler, 1972, 1988; Krishitaka, 1976b). Rob-
inson (1968) further suggested that its generalized char-
acteristics could have given rise to both erinaceom-
orpha and soricomorphs. Indeed, various authors had 
named species of “Leptacodon” which can be referred to 
various groups of primitive insectivorans: leptictids, 
dormaialid (adapisoricid) erinaceomorphs, and nyt-
chiderid soricomorphs (see Krishitaka, 1976b, for a review). Furthermore, the type species, L. tener, may 
still retain the primitive eutherian complement of five 
premolars (McKenna, 1968; Krishitaka, 1976b; but see 
Luckett, 1993).

The presumed dichotomy between erinaceomorphs and soricomorphs is difficult to recognize at the base of the emerging clades, the monophyly of which are still in need of justification. Primitive taxa such as Diacodon, Adunator, McKenneratherium, and Leptaco-
don are so close to one another that assignments to 
one clade or another are heavily dependent on individual preferences. On the other hand, the primitive-
ness of these taxa allows the construction of a dental morphotype of lipothyphlans from a combined picture of the most primitive erinaceomorphs (Adjutator and Diacodon) and soricomorphs (Leptacodon): single-rooted canine; four or five premolars; widely spaced premolars; essentially single-cusped P1–2 and p1–2; a metacone or metastylar crest on last upper premolar; rectangular upper molars with reduced stylar shelves; pre- and postcingulae on upper molars; small hypocone on M1–2; last lower premolar with trigonid; small, basined talonid of last lower premolar; and nearly transversely oriented crestiform paraconid in lower molars.

Carnilcestes fits well in this lipothyphan morphotype except for the loss of M3/m3. Further allocation within the Lipothypha, however, proves difficult.

On the erinaceomorph side, 11 dental characters were listed by Novacek (1982:table 2, node 1; combined into nine functional units in his discussion) as an approximation of its morphotype (not in original sequence): 1, reduced P4 metacone; 2, P4 with a large metastylar crest; 3, narrow stylar shelves in upper molars; 4, distinct hypocones in M1–2; 5, single-rooted p1; 6, simple p2–3 with a main cusp; 7, semimolariform p4 with basined talonid; 8, lower molar trigonid modestly closed, with crestiform paracronids; 9, slightly canted trigonid; 10, wide talonid on m1–2; and 11,entoconid higher than hypoconid. Novacek (1982:143) acknowledged that polarities for most of these characters were “largely speculative,” although he did recognize characters 3, 8, 9, 10, 11 as derived for the Erinaceomorpha. In light of the preceding discussion of the lipothyphan morphotype, many of the erinaceomorph features in Novacek (1982) would seem to be primitive retentions of lipothyphan characters (3, 7, 8, 10, 11)—we failed to see substantial differences between Diacodon and Leptacodon in these five characters. Therefore, most of what Novacek considered to be derived erinaceomorph conditions (3, 8, 10, 11) may have been primitive for lipothyphans if Diacodon and Leptacodon were sufficiently close to the initial erinaceomorph–soricomorph dichotomy. This leaves the canted trigonid (9) as one possible synapomorphy for erinaceomorphs, a character that Carnilcestes has slight development of.

Although a carnassial-like shearing blade on P4 seems likely to be a synapomorphy for erinaceomorphs at some stage of their phylogeny, it, too, can be found in a few primitive eutherians, Cimolestes, Prokennesolestes, Procerberus, and in soricid insectivorans, in addition to creodonts and carnivorans. Since both the primitive leptictid Prodiodacon and the primitive soricomorph Leptacodon have a distinct metacone, a long metastylar crest on P4 in Carnilcestes and Diacodon, the latter being the earliest and most primitive erinaceomorph (Novacek, 1982; Novacek et al., 1983), clearly indicates a synapomorphy for the erinaceomorphs.

The polarity of basined vs. trhecent talonid in p4 is difficult to assess; Novacek (1986a) changed his earlier (1982) polarity assignment, i.e., trhecent talonid became primitive in Erinaceomorpha. A basined talonid is found in Procerberus, Zalambdalestes, Gypsonictops, Prodiodacon, Diacodon, and Leptacodon, in contrast to a trhecent talonid in Prokennesolestes, Kenkallestes, Cimolestes, and derived erinaceomorphs.

Gingerich (1983) described three insectivoran genera, Litocherus, Cedrocherus, and Diacocherus, from the late Paleocene (Tiffanian) of North America. All three were included by him in an exclusively North American subfamily Litocherinae (family Adapisoricae), along with such known taxa as Litolesstes, Leipsanosolestes, and Mckennatherium. Some of these taxa (e.g., Litocherus notissimus, L. lacunatus) had previously been confused with hypsodontid condylars and the validity of this subfamily was seriously questioned by Novacek et al. (1985). Most of above genera (except Mckennatherium) are more derived than Carnilcestes in their low, more bunodont molar cusps. In fact, Novacek et al. (1985) went so far as to include Leipsanosolestes, Litolesstes, and Cedrocherus into the family Erinaceidae. Diacocherus, on the other hand, appears to be more similar to Carnilcestes. The p4 trigonid in Diacocherus is more or less in the same developmental stage as in Carnilcestes. In addition, Diacocherus has a large m2 relative to m1, a feature also shared by Carnilcestes. Diacocherus, however, still retains the M3/m3.

On the soricomorph side, Carnilcestes differs from Leptacodon tener, a primitive member of the soricomorph clade, in its loss of one premolar (presumably P3 of L. tener), loss of the metacone and presence of an elongated metastylar crest in the last upper premolar (P5 of L. tener, P4 in the present usage), low entoconids on m1–2, anteriorly canted trigonids on m1–2, and loss of M3/m3 in Carnilcestes. While nearly all of these characters (except the low entoconids) are most likely apomorphic relative to the primitive states in Leptacodon, none is uniquely derived within the soricomorph clade only and most are also seen in the erinaceomorph clade.

Finally, we take the opportunity to comment on the peculiar loss of molars in Carnilcestes. The last molars in Carnilcestes are very similar to the M3/m3 morphology in most primitive eutherians. This is particularly so in its last lower molar, which has a narrow but long talonid and a large hypoconulid. Such an arrangement presents an interesting question of tooth homologies: did Carnilcestes lose the M1/m1 or M2/m2 while retaining M3/m3? Luckett (1983) suggested, however, that ontogeny (i.e., developmental sequence), not morphology, is a better criterion for tooth homologies. Since the absence of M1/m1 or M2/m2 cannot be demonstrated without ontogenetic evidence, we designate the last molars in Carnilcestes as M2/m2 following normal conventions.

Reductions of dentitions are rather frequent phenomena among Asiatic insectivorans. The Paleogene records include such examples as, among a handful of known fossil genera, two micropterodontids, Prosarcodon and Sacrocodon, one erinaceid, Exallarix, and all
of the didymoconids (the loss of M3/m3 in Prosarcodon and Sarcoodon apparently represents a single event, i.e., the two are sister-taxa). The absence of M3/m3 in Carnilestes is unrelated to those in Prosarcodon and Sarcoodon because they seem to be in different clades (see above discussion). The lost molars in Carnilestes also probably represent an event independent from the reduction of last molars in derived erinaceomorphs, particularly erinaceids, for the following reasons. First, the molar reduction in erinaceids is accomplished through gradual reduction of the posterior molars, i.e., the posterior molars are progressively smaller than the anterior ones, in contrast to the large m2 vs. small m1 in Carnilestes. Second, this gradual reduction can be observed to happen within the phylogeny of erinaceids (McKenna and Holton, 1967; Rich, 1981; Novacek, 1982, 1985; Frost et al., 1991) and Carnilestes is too primitive to fit into that derived clade. Third, the shortening of the tooth row in most insectivorans is accomplished by compression, which involves shortening (relative to the width) of the individual teeth and imbrication between adjacent teeth. The cheek teeth of Carnilestes, on the other hand, are individually elongated and widely spaced.

ACKNOWLEDGMENTS

Discussions with Gina Gould, Ye Jie, Jason Lillegraven, Malcolm C. McKenna, Jin Meng, Michael J. Novacek, and Su-yin Ting helped to clarify various questions about lipotyphlan phylogeny and the stratigraphy of Nanxiong Basin. We have benefitted from comments by M. McKenna, J. Meng, and M. Novacek on earlier versions of this manuscript. We are particularly indebted to McKenna, whose incisive criticisms and detailed comments have prevented many errors. The manuscript was critically reviewed by Richard C. Fox and Thomas M. Bown, whose helpful comments are gratefully acknowledged. M. Novacek and M. McKenna permitted access to specimens under their care. We thank Li Gongzhuo and Wang Jingwen for their effort in collecting some of the excellently preserved specimens during the 1974 field season. Zhang Hong prepared one of the specimens described herein (IVPP V10492). Robert Evander and Alexander Kellner of the American Museum of Natural History (AMNH) in the acid preparation of some specimens.

Funding for this study was supported by IVPP, Academia Sinica, and the Frick Postdoctoral Fellowship Fund of the AMNH. Travel was provided by the Carter Fund, Department of Vertebrate Paleontology, AMNH.

LITERATURE CITED


Received 27 August 1993; accepted 8 November 1993.