SKULL OF A NEW MESONYCHID (MAMMALIA, MESONYCHIA) FROM THE LATE PALEOCENE OF CHINA

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ABSTRACT—Cranial remains of Mesonychidae are poorly known from the Paleocene of Asia. A well-preserved late Paleocene mesonychid skull from Anhui Province in China is described here as a new genus and species, *Sinonyx jiashanensis*. The new species has a primitive dental formula of 3.1.4.3/ 3.1.4.3 and distinctive cheek teeth; P3 is three-rooted, P4 lacks a metacone, the buccal cingula are distinct on P4–M3, M3 lacks a metastyle, the talonid of p3–4 is trenchant and square-shaped, and m1 and m3 lack a metaconid. Resemblances of the new genus to *Ankalagon*, together with the common presence of *Dissacus* on both continents, suggest that North America and Asia shared a common mesonychid fauna during the late Paleocene. Comparison of the new skull to *Hapalodectes* supports removal of Hapalodectinae from Mesonychidae, and suggests that mesonychids are closer to archaeocetes than either is to hapalodectids.

INTRODUCTION

Mesonychia is a group of archaic hoofed mammals present in the Paleocene and Eocene of Asia, Europe, and North America. They are generally considered to be cursorial *Hyaena*-like carrion feeders (Boule, 1903; Zhou et al., 1992). Mesonychids are important as a group because of their distinctive morphological and functional specializations, because of their broad geographic distribution, and because they may be related to whales (Van Valen, 1966; Szalay, 1969; Gingerich et al., 1983; Prothero et al., 1988). Mesonychia were grouped in Condylarthra as a suborder (Van Valen, 1966) because they are hoofed mammals and because early mesonychids resemble early arctocyonids, but Van Valen (1966) also suggested that they could be separated from Condylarthra as a distinct order.

Szalay and Gould (1966) divided Mesonychidae into three subfamilies: Mesonychinae, Hapalodectinae, and Andrewsarchinae. According to Ting and Li (1987), *Hapalodectes* should be placed in its own family, Hapalodectidae, which is supported by our study. Hapalodectidae includes only one genus, *Hapalodectes*, with four species (reviewed in Zhou and Gingerich, 1991).

Mesonychinae include *Dissacusium* (Chow et al., 1973, 1977), *Honanodon* (Chow, 1965), *Hukoutherium* (Chow et al., 1973, 1977; Qi and Huang, 1982), *Lohoodon* (Chow, 1965; Chow et al., 1973a), *Mongolestes* (Szalay and Gould, 1966), *Mongolonyx* (Szalay and Gould, 1966; Dashzeveg, 1976), and *Yantanglestes* (Yan and Tang, 1976; Ideker and Yan, 1980) from Asia; *Harpagolestes* (Wortman, 1901; Szalay and Gould, 1966) from both Asia and North America; *Dissacus* (Cope, 1881; Matthew, 1915, 1937; Russell, 1964;

Chow et al., 1977) and *Pachyaena* (Boule, 1903; Cope, 1874; Matthew, 1909, 1915; Osborn and Wortman, 1892) from Asia, Europe, and North America; and *Ankalagon* (Matthew, 1897, 1937; Osborn and Earle, 1895; Van Valen, 1978, 1980), *Synoplotherium*, and the type genus *Mesonyx* (Cope, 1872; Wortman, 1902; Matthew, 1909) from North America. Andrewsarchinae includes a single genus and species, *Andrewsarchus mongoliensis* (Osborn, 1924), based on a single cranium with worn teeth from the Irdin Manha beds in Inner Mongolia (a late Bridgerian equivalent; Qi, 1987).

The specimen described here is the best preserved skull of a mesonychid known from the Paleocene of Asia. It provides important information on the anatomy, evolution, and systematics of mesonychids. The skull was found and collected in 1978 from a Paleocene locality, Tujinshan, in Jiashan County, Anhui Province, China. It is from the middle part of the Tujinshan Formation. The middle and upper parts of the Tujinshan Formation also yield *Sinostylops*, several kinds of anagalids, and a primitive eurymylid; based on faunal comparisons, the beds are probably equivalent to the Doumu Formation of Qianshan County, Anhui, China, which is earlier than the Gashato Formation of Mongolia (Tang and Yan, 1976; Russell and Zhai, 1987).

ABBREVIATIONS

Institutional—AMNH, American Museum of Natural History, New York; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; PIN, Paleontological Institute, Moscow, Russia; UM,

University of Michigan Museum of Paleontology, Ann Arbor.

Anatomical — A. P., angular process; Al. Or., alisphenoid and orbitosphenoid; Bo., basioccipital; C. P., condyloid process; E. A. M., external auditory meatus; E. F., ethmoid foramen; E. F. C., external frontal crest; E. R., epitympanic recess; E. T., eustachian tube; E-t., ectotympanic; E-t. B., ectotympanic bulla; F., frontal; F. O., foramen ovale; G. F., glenoid fossa; H. F., hypoglossal foramen; I. F., incisive foramen; I-o. F., infraorbital foramen; J, jugal; J. F., jugular foramen; La., lacrimal; La. F., lacrimal foramen; La. T., lacrimal tubercle; M. C., mandibular condyle; M-f., mandibular foramen; Mas., mastoid part of the petrosal; Max., maxilla; Max. F., maxillary foramen; Na., nasal; O., occipital; P., parietal; Pal., palatine; P-m., premaxilla; P. O. A. C., posterior opening of the alisphenoid canal; P. O. C., posterior orbital crest; P-o. P., postorbital process; P. P., paroccipital process; Pt., pterygoid; S-e. G., supra-ethmoid groove; S-m. F., stylomastoid foramen; Sp., sphenoid; Sq., squamosal; Sym., symphysis; T-h., tympanohyal; Z. P. S., zygomatic process of squamosal.

SYSTEMATIC PALEONTOLOGY

Order MESONYCHIA Van Valen, 1966
Family MESONYCHIDAE Cope, 1875

SINONYX, gen. nov.

Type Species — *Sinonyx jiashanensis*.
Included Species — Type species only.
Age and Distribution — Tujinshan Formation (late Paleocene), China.

Diagnosis — *Sinonyx* differs from all described mesonychids in having a dental formula of 3.1.4.3/3.1.4.3, combined with the following cranial and dental characters: a maxilla–frontal contact is present in the facial region, separating the nasal from the lacrimal. The mastoid is relatively large, while the paroccipital process is weak and considerably smaller than the mastoid. The angular process of the dentary is distinct. P3 is three-rooted. P4 lacks a metacone. There are distinct buccal cingula on P4–M3. The paracone is distinctly larger than the metacone on M1–2. M3 is reduced and small, its metastyle is absent. The paraconid is small on p4, the talonid of p3–4 is trenchant and square-shaped; m1 and m3 lack a metaconid.

Etymology — *Sino-*, Chinese; *onyx* (Gr., masc.), claw or hoof.

Discussion — *Dissacusium, Hukoutherium,* and *Yantanglestes* are known from the middle Paleocene of China. *Hukoutherium* is the best known among the three genera; its differences from *Sinonyx* are discussed in detail here. *Hukoutherium* includes two species, the type species *H. ambigum* (Chow et al., 1973) and *H. shimemensis* (Qi and Huang, 1982).

H. ambigum was based on broken dentaries with incisors, canines, p1–4, and m2–3 (IVPP V4233) from the Luofuzhai Formation, Nanxiong County, Guang-

dong, China (Chow et al., 1977). Chow et al. (1977) described the following characteristics: it has a lower dental formula of 3.1.4.3.; it lacks a diastema between p1 and p2, p4 is larger than m1, lower molars have a small metaconid; and the lingual cingulum is strongly developed on m3. Other important characters are: the talonid of p3–4 is rounded and narrower than the trigonid (Chow et al., 1977:fig. 11); a diastema between p2 and p3 is lacking; m2–3 are stout (Chow et al., 1977: table 10). *Sinonyx* differs from *H. ambigum* in that it has diastemata between p1 and p2 and between p2 and p3, the talonid of p3–4 is square-shaped and wider than the trigonid, m1 is larger than p4, m2–3 are more slender, and the lingual cingulum is lacking on m3. Additionally, the horizontal ramus of the dentary of *H. ambigum* is much thicker (25.4 mm at m3; Chow et al., 1977:table 10) than that of *Sinonyx* (14.4 mm at m3), which is surprising given that p2–3 and m2 of the latter are longer than those of the former.

H. shimemensis was based on a crushed and broken skull with lower jaws (IVPP V6260) from Shimen, Luonan County, Shanxi, China. The diagnosis (Qi and Huang, 1982:25) includes: a mesonychid somewhat smaller than *H. ambigum,* lower premolars are simple and have apices pointing straight upward, m3 has a long talonid, and the lingual cingulum is undeveloped. Other important characteristics are: M2 is much wider than long, lacking a metastyle; the upper canine is very robust and high; p3–4 have a very small talonid (Qi and Huang, 1982:22); p2–4 and m2–3 are stout; the lower molars have a metaconid; and m1 seems to have a basin-like talonid (Qi and Huang, 1982:22). The unique characters of *H. shimemensis,* such as a small talonid of p3–4, stout p2–4 and m2–3, a basin-shaped talonid on m1, and loss of a metastyle on M2, are not found in other mesonychine genera, but are found in the triisodontine genera like *Eoconodon* and *Triisodon.* This indicates that *H. shimemensis* may be different from *H. ambigum* at the generic level. *H. ambigum* is more mesonychine-like than "*H.*" *shimemensis* in that the protoconid of its p3–4 is inclined posteriorly and the talonid of its p3–4 is more developed. Ting and Li (1987:185) raised the possibility that "*Yantanglestes,* as well as *Hukoutherium* and *Dissacusium,* may represent a group different from the mesonychines at the subfamily level." Our analysis partly corroborates that idea because "*H.*" *shimemensis* is very different from other mesonychines.

Sinonyx differs from "*H.*" *shimemensis* in that it has more slender p2–4 and m2–3, the talonid of p3–4 is square-shaped and wider than the trigonid, the protoconid of p3–4 is inclined posteriorly, the talonid of m1–2 is trenchant, the metaconid is absent on m3, diastemata are present between p2 and p3 and between P2 and P3, and a metastyle is present on M2. Additionally, even though the skull of *Sinonyx* is about 313 mm long, the maximum breadth across the jugals is only 160 mm, the skull of "*H.*" *shimemensis* is only 231 mm long, but the maximum breadth across the jugals is 240 mm (Qi and Huang, 1982:21); the hori-

zontal ramus of the dentary of "*H.*" *shimenensis* is much thicker (22 mm at m3; Qi and Huang, 1982:21) than that of *Sinonyx* (14.4 mm at m3), while the dentary of the latter is distinctly longer (255.4 mm) than that of the former (221 mm).

SINONYX JIASHANENSIS, sp. nov.
(Figs. 1–6; Table 1)

Holotype—IVPP V10760, cranium and dentaries.

Horizon and Locality—Late Paleocene, Tujinshan Formation, Tujinshan, Jiashan County, Anhui Province, China.

Diagnosis—As for the genus.

Etymology—Named for Jiashan County, Anhui Province, China.

DESCRIPTION

The new skull, IVPP V10760 (Figs. 1–3) is preserved in very good condition. The right side of the skull is relatively undistorted, but the left side is compressed medially; the left maxilla is displaced slightly mediodorsally. The orbital and temporal fossae and the basicranium are well preserved. Areas of minor damage include the palatines, the pterygoids, ventral part of the left squamosal, and the right auditory bulla. Condylobasal skull length (from the front of the premaxilla to the posterior side of the occipital condyle) is 313 mm, and the skull measures 160 mm in maximum breadth across the jugals. The maximum frontal chord distance across the postorbital process is 67 mm. The distance from the foramen magnum to the top of the sagittal crest is 82 mm. The dental formula is 3.1.4.3/3.1.4.3.

Nasal (Figs. 1, 3)—The nasal contacts the premaxilla anteriorly, the maxilla laterally, and the frontal posteriorly; it does not contact the lacrimal. The nasal is shovel-shaped, narrow in the middle, slightly wider at the anterior end, and expanded in the posterior part where it meets the frontal; the widest part is across the triple junction where the nasal, frontal, and maxilla meet.

Frontal (Figs. 1, 3)—The anterior border of the frontal is in front of the orbit, and its posterior border is at the postorbital constriction. In dorsal view, the frontal is divided by the external frontal crest into an anterior facial part and a posterior temporal part. Anteriorly, the facial part contacts the nasal broadly; moderate contacts with the maxilla and the lacrimal are present. The postorbital process is weakly developed, blunt, and low. In lateral view, the frontal meets the lacrimal anteriorly, palatine ventrally, and alisphenoid posteriorly. It does not contact the maxilla within the orbit. Starting from the postorbital process, there is a posterior orbital crest extending downward, backward, and medially until it reaches two small ethmoid foramina in the posterior part of the orbit. The more anteromedial of the two ethmoid foramina is much larger than the more posterolateral, both are within the frontal and directed anteroventrally. Above these two

foramina, a distinctive supra-ethmoid groove starts, which extends backward and slightly downward.

Parietal (Figs. 1, 3)—The anterior portion of the parietal marks the postorbital constriction, the narrowest region of the skull. The sagittal crest starts on the parietal at the posterior end of the frontal and continues posteriorly to the high, narrow, overhanging occiput. The sagittal crest is prominent and dorsoventrally high. The parietal forms only a small part of the cranial roof. The sutures with the frontal, alisphenoid, and squamosal are preserved along fractures on the skull.

Premaxilla (Figs. 1, 3)—In dorsal view, the body bearing incisors is strong and curved; the dorsal process tapers posteriorly and inserts between the nasal and the maxilla for about half of the length of the snout to above P2. The incisive foramen is single on each side.

Maxilla (Figs. 1, 3)—In dorsal view, the maxilla contacts both the frontal and nasal. The maxilla is penetrated by a long infraorbital canal that opens anteriorly above the posterior border of P3. The infraorbital foramen is elliptical and about 11 mm in dorsoventral diameter. The distance from the infraorbital foramen to the anterior rim of the orbit is about 45 mm, which is approximately the length of the infraorbital canal. The maxilla-lacrimal contact is broad, and the suture is clearly preserved near the zygomatic arch. Behind the posterior opening of the infraorbital canal (maxillary foramen of Miller et al., 1964), the floor of the orbit is smooth and formed by the maxilla. Anteromedially, the lacrimal forms part of the floor of the orbit. Posteromedially, the frontal and the palatine (?) form the posterior floor of the orbit. The palatine contacts the lacrimal, and therefore separates the frontal from the maxilla. In ventral view, most of the right palatal process of the maxilla is preserved. The surface of the palatal process is concave between the protocone lobes of P4–M3, but not perforated as in *Hapalodectes*. The palatine–maxilla suture starts at the posteromedial side of M3 and runs along the lingual side of the tooth row. The suture on the right side in front of M1 is not preserved, nor is the part where the sutures of both sides meet.

Lacrimal (Figs. 1, 3)—The lacrimal has an orbital plate and a facial expansion. The facial expansion is wide, and the medial part is bordered by a moderate lacrimal tubercle. There is an elliptical lacrimal foramen posterior to the tubercle within the orbit, and a slightly smaller one below the tubercle, on the rim of the orbit. In the orbit, the lacrimal is bounded by the lacrimal–maxilla suture ventrally, by the lacrimal–palatine suture posteriorly, and by the lacrimal–frontal suture dorsally. The lacrimal forms part of the posterolateral wall of the posterior opening of the infraorbital canal.

Palatine (Fig. 1)—In the orbit, the palatine is a large element. There are two broken pieces in the orbit that are provisionally identified as parts of the palatine. The palatine contacts the maxilla anteroventrally, the lacrimal anteriorly, and the frontal posterodorsally. Pos-
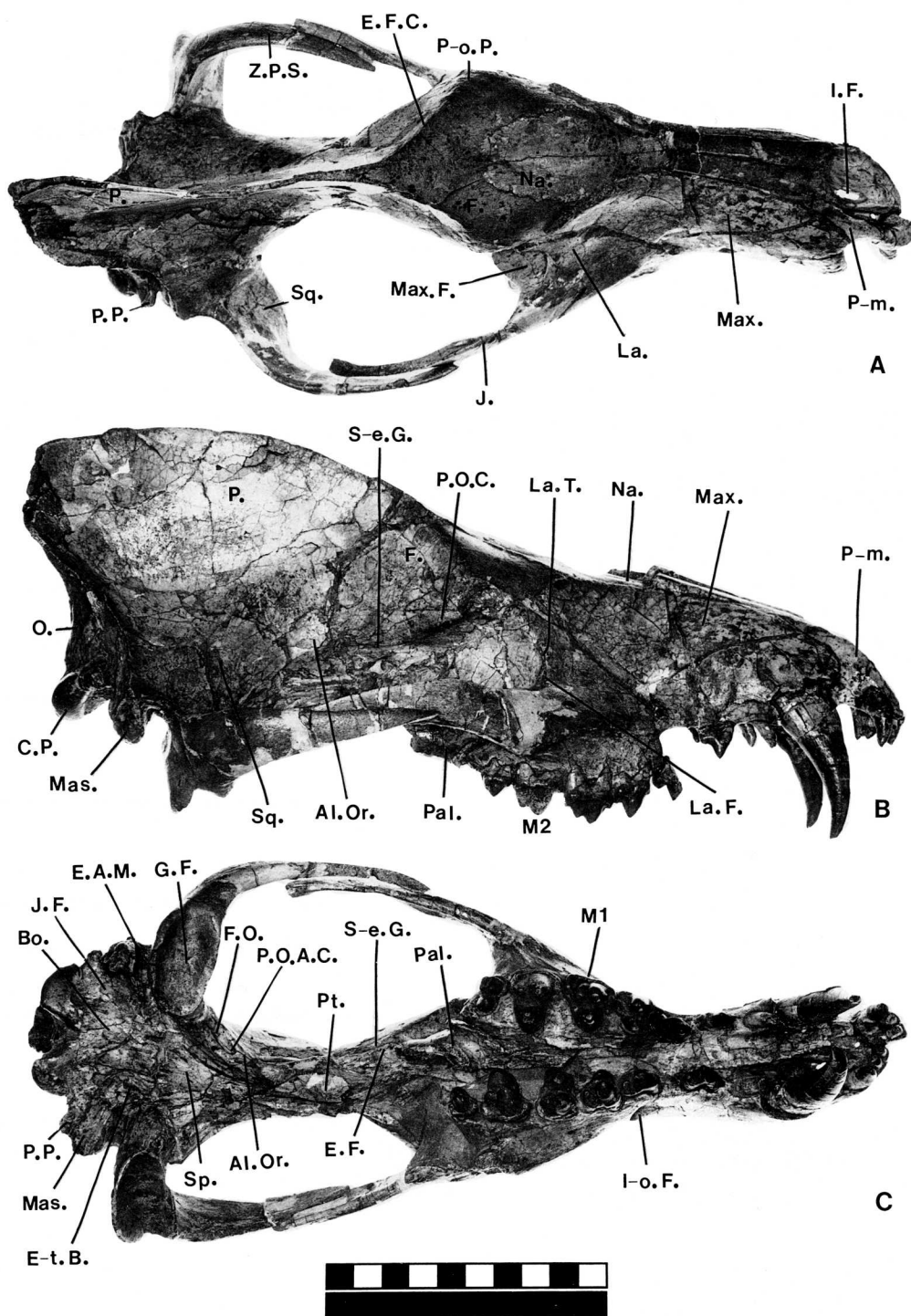
FIGURE 1.   Skull of *Sinonyx jiashanensis* gen. et sp. nov. (IVPP V10760, holotype). **A**, dorsal view; **B**, lateral view; **C**, ventral view. See text for abbreviations. Scale in cm.

teriorly, the palatine probably has a moderate contact with the orbitosphenoid, but the area for the orbitosphenoid is badly damaged. Medial to the palatine–maxilla suture, there is a slit-like posterior palatine foramen (Miller et al., 1964) posterior to the posterior

opening of the infraorbital canal, and about 1 cm away from the posterior notch of the palatine. Medial to the posterior palatine foramen is the sphenopalatine foramen. The posterior edges of the palatal processes are prominently thickened and ridged; there is a deep
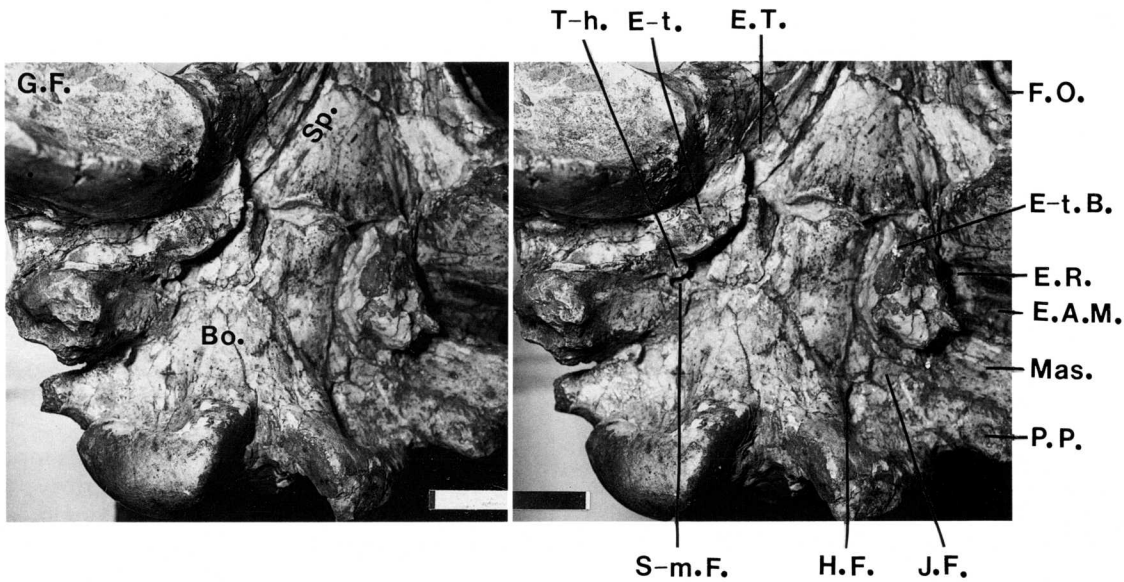
FIGURE 2.   Stereophotograph of the basicranial region of *Sinonyx jiashanensis* gen. et sp. nov. (IVPP V10760, holotype). See text for abbreviations. Scale in cm.

groove passing in front of the ridge and proceeding through the notch between the posterior end of the maxilla and the vertical wing of the palatine.

Pterygoid (Fig. 1)—The pterygoids are crushed. They were probably close to and parallel to each other. They appear to have had strong ridges for attachment of m. pterygoideus medialis on the lateral side.

Jugal (Figs. 1, 3)—The jugal tapers posteriorly and articulates freely with the zygomatic process of the squamosal. There is no postorbital process on the jugal. The jugal begins to taper at a depression where the narrow and flat surface articulating with the squamosal starts. Contact with the maxilla reaches anteriorly above M1.
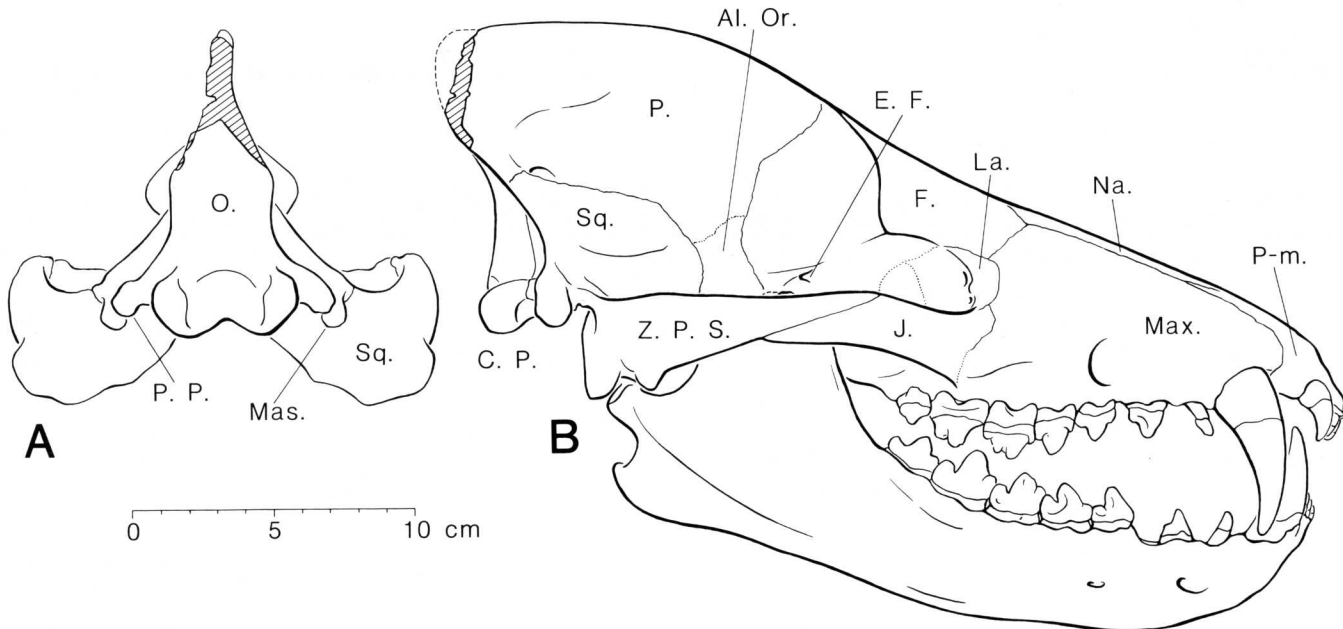

FIGURE 3.   Reconstruction of the skull of *Sinonyx jiashanensis* gen. et sp. nov. (IVPP V10760, holotype). **A**, occipital view; **B**, lateral view. See text for abbreviations. Scale in cm.

Squamosal (Figs. 1–3)—In dorsal view, the squamosal is bounded medially by the squamosal-parietal suture; the foramen for the ramus temporalis from the ramus superior of the stapedial artery (Wible, 1987) is present at the posterior part of the squamosal-parietal suture. The zygomatic process of the squamosal is long and articulates with the jugal, with the squamosal lying dorsal to the jugal. In ventral view, the glenoid fossa is concave, transverse, and notched laterally. There is a prominent ridge extending anteromedially from the medial side of the glenoid fossa towards the alisphenoid. The glenoid fossa measures 39.0 mm transversely and 22.0 mm anteroposteriorly. The preglenoid and postglenoid processes are well developed. A postglenoid foramen is lacking. Medial to the external auditory meatus, a moderate epitympanic recess is present on the squamosal. The most posterior part of the squamosal probably forms the posterior part of the external auditory meatus. In lateral view, the squamosal forms the dorsal, anterior, and probably the posterior wall of the external auditory canal.

Sphenoid (Figs. 1, 2)—In ventral view, the presphenoid is not exposed; the basisphenoid is trapezoidal. The basisphenoid is bounded laterally by the alisphenoid and the anterior part of the bulla, and posteriorly by the basioccipital. As preserved, the basisphenoid is displaced from the basioccipital on the skull. The basisphenoid is separated from the alisphenoid by sutures that now correspond to fractures on the skull.

Alisphenoid and Orbitosphenoid (Figs. 1–3)—The orbitosphenoid is not well preserved and its sutures with other nearby bones are not determinable. Both alisphenoids are present. In lateral view, the alisphenoid, with a large dorsal process, forms a small part of the side wall of the braincase. Anteriorly from top to bottom, the alisphenoid contacts the frontal, orbitosphenoid, and palatine, but the sutures are unclear due to poor preservation. Posteriorly, the alisphenoid has a broad contact with the squamosal. In ventral view, the alisphenoid–squamosal suture goes along the ridge that marks the border between the side wall and the floor of the braincase in the temporal region. The relationship of alisphenoid to palatine and pterygoid is not clear.

The posterior orbital region is distorted, and the walls of several canals leading to foramina are broken, but it is possible to recognize these canals and assess the position of relevant foramina on the left side. The optic foramen is located about 1 cm below the supraethmoid groove extending posteriorly from above the two ethmoid foramina. The superior orbital fissure (for the oculomotor nerve, the trochlear nerve, the profundus ramus of the trigeminal nerve, and the abducens nerve) is posteroventral to the optic foramen; it is single and anteroposteriorly extended; it is laterally separated by a bony wall from the canal (leading to the foramen rotundum) for the maxillary ramus of the trigeminal nerve. Judging from bone fractures, the foramen rotundum is located posterolateral to the superior orbital fissure and is probably not confluent with

the latter. The canal for the maxillary ramus of the trigeminal nerve is laterally separated from the alisphenoid canal. The anterior part of the alisphenoid canal is broken, the anterior opening of the alisphenoid canal is probably located posterolateral to the foramen rotundum and it transmits the maxillary artery (ramus infraorbitalis of Wible, 1987). There is a single long, narrow, and elliptical opening that leads to the foramen ovale (for the mandibular ramus of the trigeminal nerve) and the posterior opening of the alisphenoid canal on the ventral side of the alisphenoid ridge leading forward from the glenoid fossa. In front of the bulla and on the ventral surface of the alisphenoid, there is a distinct groove indicating the presence of the eustachian tube.

Ectotympanic (Figs. 1, 2)—The ectotympanic forms the bulla and the tubular external auditory meatus. The bony bulla is bulb-shaped, and its major axis is directed anteromedially. It is well preserved on the left side, with most of the bulla and a small piece of the tubular external auditory meatus at the posterolateral corner of the bulla. The bulla on the right side is relatively broken, but the tubular external auditory meatus is shown by a remaining piece. The left bulla measures about 19 mm anteroposteriorly, 13 mm mediolaterally. The bulla is bounded by the alisphenoid anteriorly, the squamosal laterally, the mastoid posterolaterally, and the basioccipital medially and posteromedially. The surface of the bulla is irregular. The external auditory meatus is tubular and is placed between the postglenoid process and the most posterior part of the squamosal which contacts the mastoid. At the posterior side of the bulla, there is a distinct rectangular indentation on the occipital which is the jugular foramen, through which the glossopharyngeal nerve, the vagus nerve, the accessory nerve, and the internal jugular vein draining the braincase make their exit.

Petrosal (Figs. 1, 2)—The promontorium is slightly visible in the tympanic cavity on the right side, covered by a piece of basioccipital. The exposed surface faces ventrolaterally, and it appears to be convex. The epitympanic recess is moderate. It is formed laterally by the squamosal.

The mastoid forms a distinct process laterally in the basicranial region, bounded by the squamosal anteriorly, the bulla anteromedially, and the occipital posteriorly. It is directed slightly posteriorly, as well as laterally. In lateral view, the mastoid is wide and uneven ventrally, and it tapers dorsally; it forms part of the lateral border of the basicranium. The squamosal–mastoid suture is transversely straight and is separated from the external auditory meatus by a thin sheet of squamosal, which is the most posterior part of the squamosal. The stylomastoid foramen, for the facial nerve, is located at the connection of the medial side of the mastoid process with the posterolateral angle of the auditory bulla. The suture between the mastoid and the bulla probably starts from the triple junction of the squamosal, mastoid and ectotympanic in front

of the stylomastoid foramen, and it terminates at the triple junction of the mastoid, ectotympanic, and occipital about 3–4 mm lateral to the jugular foramen. In front of the stylomastoid foramen is an elevated rounded surface with a concavity, the tympanohyal. Lateral to the stylomastoid foramen, the ventral surface of the mastoid is uneven, and there is a distinct groove on the anterior part leading to the stylomastoid foramen. In occipital view, the mastoid is weakly exposed and forms an irregular surface; it meets the squamosal dorsally and the exoccipital ventromedially. The mastoid process is better developed than the paroccipital process of the exoccipital.

Occipital (Figs. 1, 2)—In occipital view, the supraoccipital above the foramen magnum is high; the ventral part is rectangular, and the dorsal part is triangular. The exoccipital is extended to form a distinct paroccipital process which has more of a backward and outward than downward orientation. The occipital–petrosal suture is straight laterally and curved medially, and directed ventrolaterally. A depression is formed on the occipital near the medial and curved part of the suture. In ventral view, the occipital is bounded by the basisphenoid anteriorly and by the ectotympanic and the mastoid laterally. The condyles are large; the foramen magnum faces posteroventrally. There are three small hypoglossal foramina on each side, although they are arranged differently. The jugular foramen is rectangular and located anterolateral to the hypoglossal foramina, between the occipital and the ectotympanic bulla.

Dentary (Figs. 3–4)—The unfused mandibular symphysis reaches posteriorly to the level of p3. The horizontal ramus is highest behind the m3 and lowest at the p1. The coronoid process is strongly developed and has a thickened anterior border. The mandibular condyle is robust and at the same level as the occlusal surface; it is hinge-like and transversely elongate. The angular process is a salient, curved, and pointed process directed posteromedially. The fossa on the medial side of the angle for insertion of m. pterygoideus medialis is well defined.

There are two mental foramina; the larger of the two is below the anterior root of p2 and the smaller is below the posterior root of p3. An additional foramen, subequal in size to the posterior mental foramen, is present below the posterior root of p2 on the left mandible. The masseteric fossa on the lateral surface of the ascending ramus is wide and shallow. The medial surface of the ramus for insertion of the temporalis muscle is wide and very shallow. The mandibular foramen is located below the line connecting the mandibular condyle to the occlusal surface; it is 20 mm away from the ventral border of the dentary and 38 mm away from the condyloid crest.

Upper Dentition (Figs. 1, 5)—The tooth crowns of all cheek teeth except the right P1 are well preserved. Diastemata are present between I3 and C1, P1 and P2, and P2 and P3. Buccal cingula are developed on P4–M3.

I1–2 are small and slightly compressed laterally; I2 is slightly larger than I1. I3 is pointed and significantly larger than I1 or I2. The canine is long, slender, and sharp; the crown is curved posteriorly. P1 is small, peg-like, single-rooted, and single-cusped. P2 is two-rooted, with a prominent paracone and a tiny tubercle-like metastyle, but no parastyle. P3 is three-rooted, with a distinct paracone, a small parastyle, and a low metastyle; a metacone is lacking and there is a tiny cusp on the lingual side. P4 is three-rooted; it bears a distinct protocone, a high paracone (larger than the protocone), a small parastyle, and a distinct metastyle but it lacks a metacone. M1–3 are three-rooted. M1–2 have a well developed protocone, paracone, and metacone. The metacone is smaller than the paracone. M1 has a well developed parastyle and metastyle. M2 has a well developed parastyle but a weak metastyle. M3 has a distinct and stout protocone and paracone, a weak and narrow parastyle, and a small cusp-like metacone; it lacks a metastyle. See Table 1 for dental measurements.

Lower Dentition (Figs. 4, 6)—The crowns of all lower cheek teeth are well preserved. All the cheek teeth are double-rooted except p1; diastemata are present between p1 and p2, and between p2 and p3.

The incisors are small, transversely compressed, and peg-like. The canine is high and slender, its base is longer than wide. The first lower premolar is small, single-rooted, and single-cusped; p2 is also single-cusped but double-rooted, it has a protoconid pointed slightly posteriorly and a tiny, cusp-like talonid. The third lower premolar has a posteriorly inclined protoconid, a tiny pointed tubercle on the lingual side of the anterior border of the trigonid, and a trenchant talonid. The trigonid of p4 is narrower than the talonid; p4 has a distinct paraconid, a trenchant and square-shaped talonid, and a protoconid that is posteriorly inclined. The first lower molar differs from p4 in having a stouter and more vertically oriented protoconid, and from m2 in having a lower trigonid and a less vertically oriented protoconid; m1 has a stout protoconid with a distinct paraconid and a trenchant and square-shaped talonid but no metaconid. The second lower molar is the largest lower cheek tooth. It has a distinct paraconid, a strong, tall, and vertically oriented protoconid, and a distinct metaconid; the talonid is trenchant and square-shaped. There is a distinct re-entrant groove on the posterior surface of the talonid on p4–m2. The last lower molar has a distinct paraconid and a vertically oriented protoconid, but there is no metaconid. The talonid is simple, trenchant, and narrower than the trigonid. The posterior surface of the talonid is rounded and lacks a re-entrant groove. See Table 1 for dental measurements.

PHYLOGENETIC RELATIONSHIPS OF *SINONYX*

A cladistic analysis was undertaken in order to better understand the relationships of *Sinonyx* to other me-
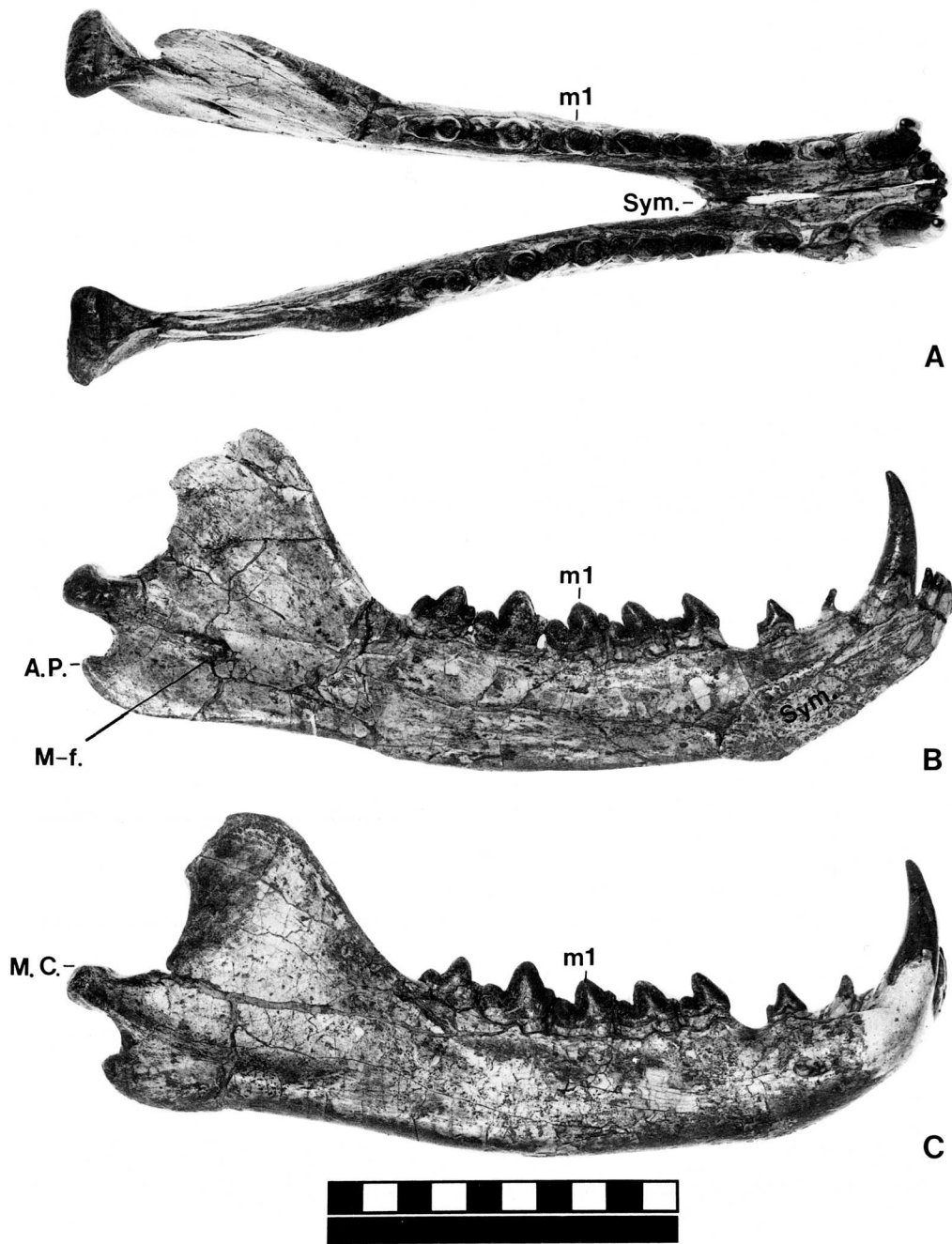
FIGURE 4. The dentaries of *Sinonyx jiashanensis* gen. et sp. nov. (IVPP V10760, holotype). **A**, occlusal view; **B**, medial view of the left dentary; **C**, lateral view of the right dentary. See text for abbreviations. Scale in cm.

sonychid genera. Triisodontinae are similar to meso-nychids and usually considered to be closely related (Matthew, 1909, 1937; Van Valen, 1966; Szalay, 1969). Four triisodontine genera, *Goniacodon, Eoconodon, Triisodon,* and *Paratriisodon,* are most like *Hapalo-dectes* and *Dissacus,* mesonychids, *Andrewsarchus,* and cetaceans among all ungulates (Prothero et al., 1988). *Eoconodon* (AMNH 766, 3181, 3187, 4764, and 16329) and *Triisodon* (AMNH 3174, 3175, and 3352), are well

represented by dental materials and were chosen as outgroups to polarize character states. The ingroup taxa (Fig. 7) included in this study are mesonychine genera *Sinonyx, Ankalagon, Dissacus, Harpagolestes, Meso-nyx, Mongolestes, Mongolonyx,* and *Pachyaena*. Six of these, *Dissacus, Harpagolestes, Mesonyx, Mongolestes, Mongolonyx,* and *Pachyaena,* were also analyzed by Prothero et al. (1988). When a genus has multiple spe-cies, the characters coded are primarily based on the
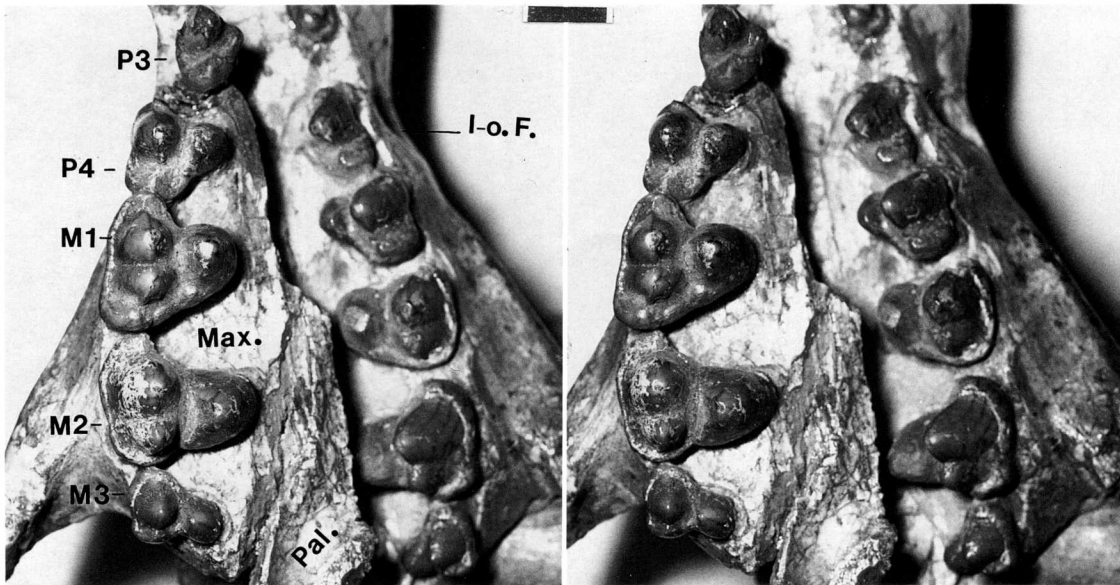
FIGURE 5. Stereophotograph of upper cheek teeth of *Sinonyx jiashanensis* gen. et sp. nov. (IVPP V10760, holotype), occlusal view. See text for abbreviations. Scale in cm.

type species. We have omitted *Andrewsarchus* and focused on the Mesonychinae (sensu Szalay and Gould, 1966). Among the Mesonychinae, *Synoplotherium* from North America is omitted because cheek teeth of its holotype are highly worn and tooth morphology is poorly preserved; *Dissacusium, Honanodon,* and *Yantanglestes* from Asia are omitted because they are poorly known. *Hukoutherium ambigum* and *"H."* shimemensis were included in a preliminary analysis (Table 2).

The present cladistic analysis is based on 17 characters (Table 2). All characters are dental because the dentition of all the taxa is well documented while cranial features are poorly documented in most genera. Characters are as follows:

1. P1 present (0); absent (1).
2. P3 three-rooted (0); two-rooted (1).
3. P4 metacone absent (0); present (1).
4. M1 metacone subequal to paracone (0); metacone greatly reduced (1).
5. M2 paracone subequal to protocone (0); paracone significantly larger (1).
6. M2 metacone subequal to paracone (0); metacone greatly reduced (1).
7. M3 present (0); absent (1).
8. P4–M3 buccal cingula developed (0); reduced or absent (1).
9. p1 well developed (0); greatly reduced or absent (1).
10. p4 paraconid small or moderate (0); large (1).

TABLE 1. Dental measurements (mm) of *Sinonyx jiashanensis* (IVPP V10760, holotype). L, length of the canine and cheekteeth is the maximum anteroposterior dimension of the crown; that of incisor is the labial–lingual diameter of the crown. W, width of the canine and cheekteeth is the maximum lingual–buccal dimension of the crown; that of incisor is the medial–lateral diameter of the crown. H, maximum height of the preserved crown, measured from the labial side.

Dentition	Left			Right		
	L	W	H	L	W	H
I1	4.4	3.4	5.5	4.1	3.7	—
I2	4.4	4.1	5.0	4.6	3.9	6.1
I3	6.8	5.5	—	7.2	5.4	12.4
C1	17.3	11.0	38.6	17.2	10.8	37.7
P1	5.4	5.0	6.9	—	—	—
P2	12.1	5.8	9.5	12.6	5.9	9.6
P3	15.0	10.2	9.6	—	9.9	—
P4	14.1	13.7	13.1	14.2	13.0	12.9
M1	—	18.8	13.2	18.9	17.9	13.0
M2	18.2	—	13.9	18.3	20.2	14.6
M3	11.4	12.6	8.9	10.0	12.5	8.7
i1	3.9	2.4	5.3	4.0	2.6	5.2
i2	5.0	3.3	6.8	4.9	3.7	4.8
i3	5.2	3.5	8.7	5.0	3.8	8.6
c1	15.2	12.4	38.1	15.1	11.7	38.6
p1	6.1	4.8	8.7	6.2	4.8	7.9
p2	11.4	5.5	9.3	12.0	5.5	9.2
p3	15.1	7.1	13.3	15.2	7.3	12.6
p4	17.1	7.8	14.1	18.2	8.1	14.6
m1	18.7	8.0	14.1	19.2	8.4	14.7
m2	21.8	8.5	17.7	21.4	8.9	17.1
m3	17.4	7.6	12.0	18.2	7.1	11.9

FIGURE 6. Stereophotograph of lower cheek teeth of *Sinonyx jiashanensis* gen. et sp. nov. (IVPP V10760, holotype), occlusal view. See text for abbreviations. Scale in cm.

11. m1 metaconid well developed (0); reduced or absent (1).
12. m2 metaconid well developed (0); reduced or absent (1).
13. m3 present (0); absent (1).
14. m3 metaconid well developed (0); reduced or absent (1).
15. p4 talonid small and not trenchant (0); trenchant and square-shaped (1).
16. p3–4 protoconids straight or slightly inclined posteriorly (0); distinctly inclined posteriorly (1).
17. M1–2 parastyle weak or absent (0); moderate to strong (1).

Characters were analyzed using the exhaustive search algorithm of PAUP, version 3.1.1 (Swofford, 1993). All characters are binary. The analysis generated a single most-parsimonious tree (Fig. 7) with a length of 22 steps, a consistency index (CI) of 0.77, and a retention index (RI) of 0.84. The relationships among the eight ingroup taxa are fully resolved. Stratigraphic distribution of the ten taxa (Fig. 7) is in good agreement with the cladogram. Relationships hypothesized for Eocene mesonychine *Harpagolestes, Mesonyx, Mongolestes, Mongolonyx,* and *Pachyaena* are the same as those in Prothero et al. (1988:fig. 8.1) and are better supported here. *Sinonyx* is important as it is closer to Eocene mesonychines than other Paleocene taxa. Outside the Eocene mesonychines, *Sinonyx* appears to be

most closely related to *Ankalagon* (Fig. 7, character 11).

Inclusion of *H. ambigum* as an ingroup taxon in the analysis yields one most parsimonious and fully resolved cladogram; the relationships of other eight ingroup taxa do not change and *H. ambigum* is placed as the sister taxon to the other eight taxa in the cladogram. Inclusion of "*H.*" *shimemensis* as an ingroup taxon in the analysis yields two most parsimonious cladograms; in both cladograms, the relationships of other eight ingroup taxa are the same as shown in Figure 7, but the relationships of "*H.*" *shimemensis* to the outgroups cannot be resolved. Most of the available characters (Table 2) for *H. ambigum* and "*H.*" *shimemensis* are missing or primitive and do not add phylogenetically important information to the analysis.

COMPARATIVE ANATOMY OF THE CRANIUM IN MESONYCHIDAE AND HAPALODECTIDAE

The Hapalodectidae (sensu Ting and Li, 1987) includes one unambiguously assigned genus, *Hapalodectes,* which appeared in the early Eocene of North America and the early to middle Eocene of Asia (Zhou and Gingerich, 1991). Hapalodectids are characterized by being small, having highly compressed teeth, retaining a hypocone on the upper molars, having a re-entrant groove on the anterior surface of the lower

FIGURE 7. The single most-parsimonious cladogram (L = 22, CI = 0.77, RI = 0.84) resulting from analysis of seventeen characters using the exhaustive search algorithm of PAUP, showing the distribution of the eleven homologous characters, the stratigraphic ranges and the geographic distributions of all the taxa. A, Asia; E, Europe; NA, North America. Character-state distributions are listed in Table 2.

molars, and having vascularized embrasure pits between the upper molars on the maxilla. Differences in the teeth of hapalodectids and mesonychids have been discussed extensively elsewhere (Szalay and Gould, 1966; Szalay, 1969).

Prothero et al. (1988) placed *Hapalodectes* as the sister taxon of *Dissacus* and included the two genera in Hapalodectini less closely related to cetaceans than mesonychids in their cladogram. The synapomorphies for Hapalodectini that they cited are: lower cheek teeth are narrow; parastyle on M1–2 is long; and diastema is present between P2 and P3. Based on our observations, all mesonychid lower cheek teeth are narrow, *Hapalodectes* has narrower lower cheek teeth simply because it is much smaller than mesonychids (Szalay and Gould, 1966); the parastyle on M1–2 is equally developed on *Dissacus, Ankalagon, Sinonyx,* and

Pachyaena; and diastema is also present between P2 and P3 on *Sinonyx*. In sum, the characters given by Prothero et al. (1988) are homoplastic and do not support the holophyly of their Hapalodectini. *Dissacus* is well represented by UM 69305, which includes cranial, dental, and postcranial materials; our study shows that *Dissacus* is closer to other mesonychids than it is to *Hapalodectes* in both dental and cranial characters. The type species of *Hapalodectes, H. leptognathus,* was identified as a new species of *Dissacus* when it was first found (Osborn and Wortman, 1892); this emphasizes how closely *Hapalodectes* resembles mesonychids in dental morphology, and it is not surprising that Prothero et al. (1988) placed *Hapalodectes* and *Dissacus* in a separate group; however, *Dissacus* is much more similar to other mesonychids.

The discovery of good cranial materials of *Hapa-*

TABLE 2. Data matrix showing the distribution of seventeen dental characters among twelve taxa. Character-state codes: "0" primitive; "1" derived; "?" missing or uncertain.

Taxa/Characters	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Outgroup
Eoconodon	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Triisodon	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ingroup
Sinonyx	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	1	1
Dissacus	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1
Ankalagon	0	0	1	0	0	0	0	0	0	1	1	0	0	0	1	1	1
Pachyaena	0	1	1	0	0	0	0	0	0	1	1	1	0	1	1	1	1
Mesonyx	0	1	0	0	0	0	1	1	0	0	1	1	0	1	1	1	1
Harpagolestes	0	1	1	1	0	1	1	1	1	?	1	1	0	1	1	1	1
Mongolonyx	0	1	1	?	1	1	1	1	0	1	1	1	0	1	1	0	1
Mongolestes	1	1	1	1	0	1	1	1	1	0	1	1	1	?	1	1	1
Other taxa for comparison (see text for discussion)
Hukoutherium ambigum	?	?	?	?	?	?	?	?	0	0	?	?	0	?	0	1	?
"*Hukoutherium*" *shimemensis*	0	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0

lodectes hetangensis from the early Eocene of China led Ting and Li (1987) to propose removal of *Hapalodectes* from the Mesonychidae (sensu Szalay and Gould, 1966). Cranial character analysis has important implications for superfamilial relationships of mesonychids, and contributes to knowledge of their possible relationships to cetaceans. In polarizing cranial characters, we have relied on outgroup comparison (Maddison et al., 1984). An arctocyonid genus, *Arctocyon* (Russell, 1964), and a phenacodontid genus, *Phenacodus* (Thewissen, 1990), are used as outgroups in our comparisons.

Cranial differences of *Hapalodectes* from mesonychines (sensu Szalay and Gould, 1966) are discussed by Ting and Li (1987). They noted that hapalodectids have a closed and more anterior orbit, a lacrimal without facial expansion, a large braincase with an expanded parietal, and a relatively longer basicranium. These characters are different from those of mesonychines (which is supported by the present study). The presence of a postorbital bar in *Hapalodectes* is a derived feature not found in mesonychines (including *Dissacus*), *Andrewsarchus*, archaeocetes, *Arctocyon*, and *Phenacodus*. A lacrimal without facial expansion in *Hapalodectes* is a derived feature not found in all mesonychids, *Arctocyon*, and *Phenacodus*. A sagittal crest is distinct in *Arctocyon,* mesonychines, and *Pakicetus* (Gingerich et al., 1983), moderate in *Andrewsarchus*, and weak in *Hapalodectes* and *Phenacodus*. A short basicranium in mesonychines is a derived character shared with *Andrewsarchus* and cetaceans; the basicranium is relatively long in *Hapalodectes*, *Arctocyon*, and *Phenacodus*.

Ting and Li (1987:183) mentioned that "the frontal is in contact with the maxilla in Hapalodectidae; it is excluded, or nearly so, from contact with the maxilla in Mesonychidae," which we found not true. Frontal–maxilla facial contact is absent in *Harpagolestes* (Szalay and Gould, 1966); but it is clearly present outside the orbit in *Sinonyx* and *Synoplotherium* (Wortman, 1901). Another difference between *Sinonyx* and *Hapalodectes* is that the nasal of *Sinonyx* and other known mesonychines is posteriorly expanded as in *Arctocyon* and *Phenacodus*, while in *Hapalodectes* it is not posteriorly expanded and represents a derived feature.

Ting and Li (1987) listed some characters in the ear region of hapalodectids that are different from those of mesonychines. They (1987:183–184) noted that, in Hapalodectidae, "the postglenoid foramen is still present; three arteries are preserved; a foramen in the tympanic wall for the superior ramus of the stapedial artery is probably present." Ting and Li (1987) also considered the tympanic bulla in *Hapalodectes hetangensis* to be absent even though they did not exclude the possibility that it contacted the petrosal loosely during life. More fossil evidence is needed to resolve the question of whether or not there is a bulla in *Hapalodectes*. The statement by Ting and Li (1987:184) that three arteries are preserved in Hapalodectidae and not in Mesonychidae is questionable. Ting and Li (1987:181)

interpreted three grooves on the ventral side of the petrosal of *Hapalodectes* to represent the presence of three vessels, the medial internal carotid, the promontory, and the stapedial arteries. The three grooves on the ventral side of the petrosal in eutherians have been proved to represent the single internal carotid artery in the lateral groove and a venous channel (inferior petrosal sinus) in the medial one, the last groove (usually transverse in position, if present on the ventral side of the petrosal) is for the internal carotid artery before it gives off the stapedial artery (Presley, 1979; Wible, 1983, 1986).

Loss of a postglenoid foramen in mesonychine genera, in *Andrewsarchus*, and in cetaceans is a derived feature not found in *Arctocyon* and *Phenacodus*. The presence of a foramen for the ramus temporalis above the squamosal in *Sinonyx* indicates the presence of the ramus superior of the stapedial artery (Wible, 1987), as in *Hapalodectes*, even though a separate foramen for the ramus superior of the stapedial artery may be lacking in *Sinonyx* and other mesonychines. The external auditory meatus is short in *Hapalodectes* but long in *Sinonyx*, *Dissacus*, other mesonychines, and *Pakicetus*; a short external auditory meatus in *Hapalodectes* is a primitive character because it is also present in *Arctocyon* and *Phenacodus*. Other differences exist between *Sinonyx* and *Hapalodectes* in the configuration of cranial foramina. The foramen for the ramus temporalis (Wible, 1987) is present in *Sinonyx*; it is absent in *Hapalodectes*. In *Hapalodectes*, the optic foramen is said to be confluent between the orbits (Ting and Li, 1987); there is no evidence for this in *Sinonyx*. The superior orbital fissure, the foramen rotundum, and the anterior opening or the alisphenoid canal are said to be confluent in *Hapalodectes*; this is not so in *Sinonyx*.

In *Dissacus* and *Sinonyx*, the foramen ovale is anteromedial to the glenoid fossa and confluent with the distinct posterior opening of the alisphenoid canal on the prominent ridge of the alisphenoid; in *Hapalodectes*, the foramen ovale is immediately medial to the glenoid fossa and not confluent with the tiny posterior opening of the alisphenoid canal. The jugular foramen is at the posterior end of the narrow and fissure-like basicapsular fenestra, and it is not differentiated clearly from the latter in *Hapalodectes*. This is a well defined, enlarged, and rectangular indentation on the basioccipital near the posterior part of the basicapsular fenestra and posterior to the auditory bulla, and it is clearly differentiated from the basicapsular fenestra in *Dissacus* and *Sinonyx*. A foramen ovale located immediately medial to the glenoid fossa and a jugular foramen not clearly differentiated from the basicapsular fenestra in *Hapalodectes* are primitive because similar patterns appear in *Arctocyon* and *Phenacodus*.

RELATIONSHIPS TO CETACEA

Van Valen (1966) proposed that mesonychids, not hyaenodontids, are ancestral to archaeocetes and there-

fore to recent whales. Van Valen's analysis was based on comparisons of tooth morphology, tooth wear pattern, and cranial anatomy. Among the characters he gave are basicranial features that are partially listed here (Van Valen, 1966:92): "The basicranium of *Protocetus* is specialized in many respects, but there appears to be a broad space between the petrosal and basioccipital bones as in mesonychids. The bony bulla in whales is wholly formed by the tympanic bone, as is probably that of mesonychids. The external auditory meatus in mesonychids and archaeocetes is rather long and appressed closely against the base of the postglenoid process. A postglenoid foramen is absent from *Protocetus,* as also from Eocene and later mesonychids. In both mesonychids and whales the venous drainage is mainly through an enlarged jugular foramen and the foramen lacerum medium. The posterior position of the glenoid fossa in *Protocetus* is characteristic of all mesonychids." Discovery of the earliest archaeocete *Pakicetus* (Gingerich et al., 1983) offers more evidence to support a mesonychid-archaeocete relationship.

McKenna (1975) placed the Mesonychidae as the sister group of cetaceans, based on Van Valen's hypothesis and a similar one by Szalay (1969). Szalay's tentative phylogenetic diagram (1969:24) implied that *Hapalodectes* is closer to archaeocetes than *Andrewsarchus* and mesonychines. Ting and Li (1987) suggested that archaeocetes are more similar to mesonychids than hapalodectids in teeth and skull morphology, but they did not specify the characters that support their inference. Prothero et al. (1988) placed *Andrewsarchus* as the sister group of cetaceans, and placed mesonychids (excluding *Dissacus* and *Hapalodectes*) as the sister group of *Andrewsarchus* and cetaceans. But as discussed in the above paragraphs, Hapalodectini (sensu Prothero et al., 1988) is based on three homoplastic dental characters and it is not a holophyletic group. This necessitates a new analysis regarding to the relationships of *Hapalodectes, Andrewsarchus,* mesonychines (sensu Szalay and Gould, 1966), and archaeocetes. It is difficult to assess the relationships of *Andrewsarchus* and mesonychines to archaeocetes without more information about *Andrewsarchus*; the synapomorphies (Prothero et al., 1988; node 36: medial portion of lambdoid crest high, I2–3 aligned with cheek teeth, and elongated premaxilla) of *Andrewsarchus* and Cetacea only weakly support a closer relationship between them.

Regarding the relationships of mesonychines and *Hapalodectes* to archaeocetes, our analysis of cranial features supports the idea that mesonychines and archaeocetes are closer to each other than either is to *Hapalodectes,* as they share the following derived characters: loss of the postglenoid foramen (absent in archaeocetes, *Sinonyx,* and Eocene and later mesonychids); enlarged jugular foramen (it is small and undifferentiated from the basicapsular fenestra in *Hapalodectes*); glenoid fossa posteriorly located relative to the foramen ovale (*Pakicetus* and mesonychines); short basicranium; and large size. Similarly, *Andrews-*

archus is closer to archaeocetes than either is to *Hapalodectes,* as *Andrewsarchus* shares the following derived characters with mesonychines and archaeocetes: loss of the postglenoid foramen; short basicranium; and large size. In sum, Mesonychidae (mesonychines and *Andrewsarchus*) is still the most likely candidate group for the ancestry of whales.

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