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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, Guangdong, 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 horizontal 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-

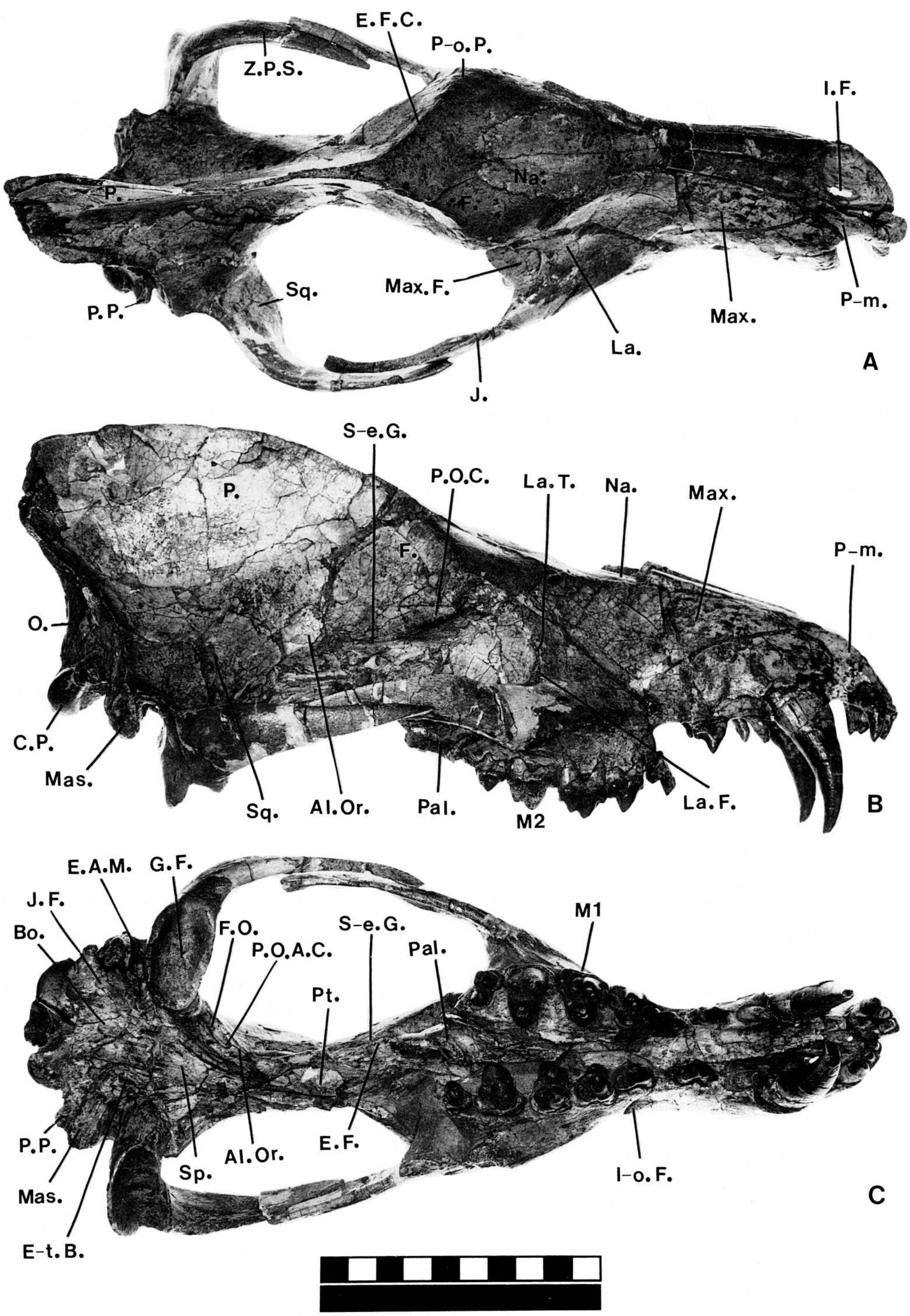

FIGURE 1. Skull of *Sinonyx jiashanensis* gen. et sp. nov. (IVPP V10760, holotype). **A**, dorsal view; **B**, lateral view; **C**, ventral view. See text for abbreviations. Scale in cm.

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