CONTRIBUTIONS FROM THE MUSEUM OF PALEONTOLOGY

THE UNIVERSITY OF MICHIGAN

VOL. 28, NO. 3, PP. 71-77 December 14, 1990

ASTRAGALUS OF *ANTHRACOBUNE* (MAMMALIA, PROBOSCIDEA) FROM THE EARLY-MIDDLE EOCENE OF KASHMIR

BY

PHILIP D. GINGERICH, DONALD E. RUSSELL, and NEIL A. WELLS

MUSEUM OF PALEONTOLOGY
THE UNIVERSITY OF MICHIGAN
ANN ARBOR

CONTRIBUTIONS FROM THE MUSEUM OF PALEONTOLOGY

Philip D. Gingerich, Director

This series of contributions from the Museum of Paleontology is a medium for publication of papers based chiefly on collections in the Museum. When the number of pages issued is sufficient to make a volume, a title page and a table of contents will be sent to libraries on the mailing list, and to individuals on request. A list of the separate issues may also be obtained by request. Correspondence should be directed to the Museum of Paleontology, The University of Michigan, Ann Arbor, Michigan 48109-1079.

VOLS. 2-27. Parts of volumes may be obtained if available. Price lists are available upon inquiry.

ASTRAGALUS OF *ANTHRACOBUNE* (MAMMALIA, PROBOSCIDEA) FROM THE EARLY-MIDDLE EOCENE OF KASHMIR

By

PHILIP D. GINGERICH, DONALD E. RUSSELL[1], and NEIL A. WELLS[2]

Abstract.— Field work in 1980 and 1981 yielded the first substantial collection of early-middle Eocene mammals from the Subathu Formation of Pakistan Kashmir. This collection includes a well preserved astragalus referable to *Anthracobune*. The new astragalus has a prominent medial process, which is characteristic and diagnostic of proboscideans, and it corroborates placement of *Anthracobune* and Anthracobunidae in Proboscidea. While classified as proboscidean, nothing in the morphology of known Anthracobunidae precludes derivation of Sirenia and Desmostylia from this family as well.

INTRODUCTION

The family Anthracobunidae includes five genera and species from the early and middle Eocene of India and Pakistan. These are, in the order described: *Anthracobune pinfoldi* Pilgrim 1940 (including *A. daviesi* Pilgrim 1940); *Lammidhania wardi* (Pilgrim 1940); *Pilgrimella pilgrimi* Dehm and Oettingen-Spielberg 1958; *Ishatherium subathuensis* Sahni and Kumar 1980; and *Jozaria palustris* Wells and Gingerich 1983. All are based on dental remains that differ in size and shape but share a common distinctive bunolophodont cusp pattern.

These genera and species have been classified in various ways: as Anthracotheriidae (Pilgrim, 1940) or Dichobunidae (Dehm and Oettingen-Spielberg, 1958) in the order Artiodactyla; as family *incertae sedis* in the order Perissodactyla (Coombs and Coombs, 1979); as Dugongidae in the order Sirenia (Sahni and Kumar, 1980); and as Moeritheriidae (West, 1980, 1983, 1984; Gingerich and Russell, 1981) or Anthracobunidae (Wells and Gingerich, 1983) in the order Proboscidea. Domning et al. (1986) included *Anthracobune* as a plesion-without-a-family in Proboscidea, while Tassy and Shoshani (1988) placed it in Desmostylia. There is general agreement that *Anthracobune* and its allies lie at or near the base of Tethytheria (the mirorder or superorder encompassing Proboscidea, Sirenia, and Desmostylia; McKenna, 1975), a stem position consistent with its early-to-middle Eocene age.

[1]Institut de Paléontologie (UA 12, CNRS), Muséum National d'Histoire Naturelle, 8 rue Buffon, 75005 Paris FRANCE

[2]Department of Geology, Kent State University, Kent, Ohio 44242, U.S.A.

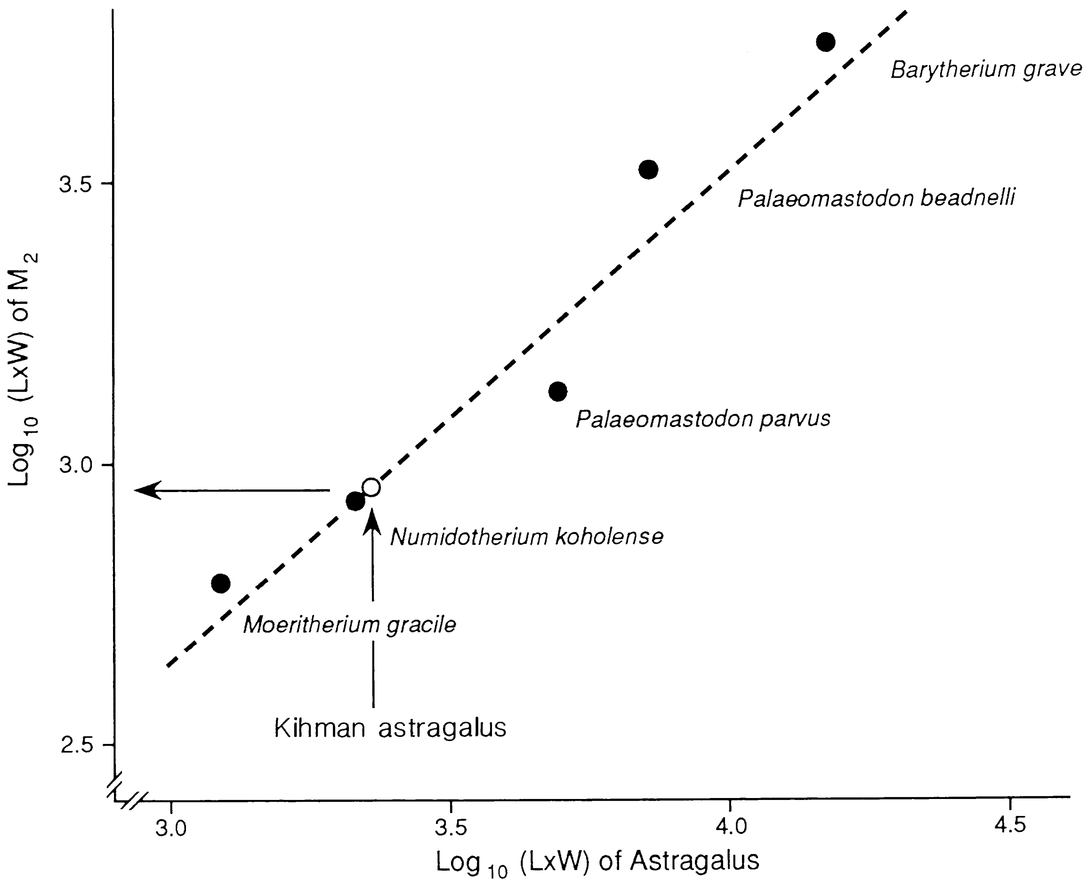

FIG. 1— Relationship of tooth size to astragalus size in Eocene and Oligocene Proboscidea. Abscissa is $\log_{10}$ length x width of astragalus, and ordinate is $\log_{10}$ length x width of M_2. Size of *Moeritherium gracile* astragalus and M_2 from Tassy (1982) and Tobien (1971), respectively, size of *Numidotherium koholense* from Jaeger (in Mahboubi et al., 1986), size of *Palaeomastodon parvus* and *P. beadnelli* from Andrews (1906), and size of *Barytherium grave* from Tassy (1982) and Andrews (1906). All areas are in mm^2. Size of anthracobunid astragalus described here yields estimated $\log_{10}$ (L x W) of M_2 of 2.95, corresponding to an M_2 length and width of about 25-35 mm, larger than all anthracobunids except *Anthracobune pinfoldi*.

Anthracobune and its allies are grouped together in the family Anthracobunidae because of their similarity in dental morphology. Dental similarity is the basis for postulated relationships of Anthracobunidae to later Proboscidea, Sirenia, and Desmostylia, but a poor understanding of the early evolution of each leaves relationships among tethythere orders ambiguously multichotomous.

We here describe the astragalus of a proboscidean referable to *Anthracobune* that supports inclusion of Anthracobunidae in Proboscidea while leaving open the possibility that Sirenia and Desmostylia were derived from Anthracobunidae as well.

KIHMAN FAUNA

Wadia (1928) reported an "ossiferous pseudoconglomerate" bearing bones of mammals in purple shales near the village of Nikial in Kashmir. None of the bones were ever described, but we followed up on Wadia's report in the field in 1980 and 1981. We were unable to locate Wadia's original bone bed, but found several other Eocene bone beds including one at Kihman Hill along the road from Kotli to Kamroti (Wells and Gingerich, 1987). Fossils here occur in the transitional Subathu-Murree purple shale at the top of the Subathu Formation (Russell and Zhai, 1987, p. 136), also known as Subathu "Unit J" (Wells and Gingerich, 1987, p. 31).

In 1981, two fossiliferous sites were found 100 meters apart at the same stratigraphic level. These were designated Kihman A and Kihman B. The large astragalus described here, University of Michigan-Geological Survey of Pakistan [UM-GSP] 1745, comes from Kihman A. The only identifiable dental remains come from Kihman B. These include the complete crown of a right P_4 of *Kalakotia simplicidentata* (UM-GSP 1772), and a molar fragment of *Pilgrimella* or *Anthracobune* (UM-GSP 1774).

The *Kalakotia* premolar is important in showing that mammals from unit J are early-to-middle Eocene in age like the rest of the upper Subathu fauna, and not Oligocene or Miocene in age like the overlying Murree Formation. The *Pilgrimella-Anthracobune* fragment is important in showing that Anthracobunidae are present in Subathu-J, but the tooth is not complete enough to identify to genus. The upper Subathu mammalian fauna is usually regarded as middle Eocene in age (Russell and Zhai, 1987), although it could possibly be late early Eocene as well.

The Kihman astragalus, UM-GSP 1745, measures 47 mm in maximum length anteroposteriorly, 34 mm in width of the body excluding medial and lateral processes, 49 mm in maximum width overall, and about 32 mm in height. These measurements depend critically on orientation of the specimen and must be viewed as approximations, but they nevertheless permit some comparison with other early proboscideans. Astragali have been described for large and small species of *Palaeomastodon* by Andrews (1906), for *Moeritherium gracile* by Schlosser (1911) and Tassy (1982), for *Barytherium grave* by Tassy (1982), and for *Numidotherium koholense* by Jaeger (in Mahboubi et al., 1986). The Kihman anthracobunid astragalus is very similar in size to that of *Numidotherium koholense* and it is almost exactly intermediate in size (on a proportional scale) between *Moeritherium gracile* and *Palaeomastodon parvus*. Scaling of tooth size relative to astragalus size in Figure 1 can be used to estimate tooth size for the Kihman proboscidean. The $\log_{10}$ of the product of length and width of the Kihman astragalus, projected on the general trend for early proboscideans, yields an estimate of ca. $10^{2.95}$ mm^2 for M_2 crown area, or an estimate of some 25-35 mm for M_2 crown length. The largest described anthracobunid species, *Anthracobune pinfoldi*, has M_2 length in the range 25-30 mm, which is close enough to the Kihman estimate to suggest reference to *Anthracobune*. The molar fragment from Kihman B, mentioned above, could be either *Pilgrimella* or *Anthracobune*, but the Kihman astragalus appears too large to belong to *Pilgrimella*.

ASTRAGALUS OF *MOERITHERIUM*

As noted above, astragali have been described for large and small species of *Palaeomastodon* by Andrews (1906), for *Moeritherium gracile* by Schlosser (1911) and Tassy (1982), for *Barytherium grave* by Tassy (1982), and for *Numidotherium koholense* by Jaeger (in Mahboubi et al., 1986). *Moeritherium* is the genus most closely resembling anthracobunids in size and form, and it is consequently the most useful for comparison. Well preserved tarsal elements of this genus described and illustrated by Schlosser (1911, p. 133, Pl. 8, figs. 4 and 8) are no longer in the Stuttgart collection, and the only astragalus of *Moeritherium* known at present is YPM 24186, a specimen illustrated in outline by Tassy (1982, fig. 2B) and identified as *Moeritherium gracile* on the basis of size. YPM 24186, illustrated here in Figure 2, is not well preserved. It suffers from the erosive gypsification characteristic of many vertebrates from the Qasr el Sagha Formation in Egypt. Nevertheless, it does show clearly, in

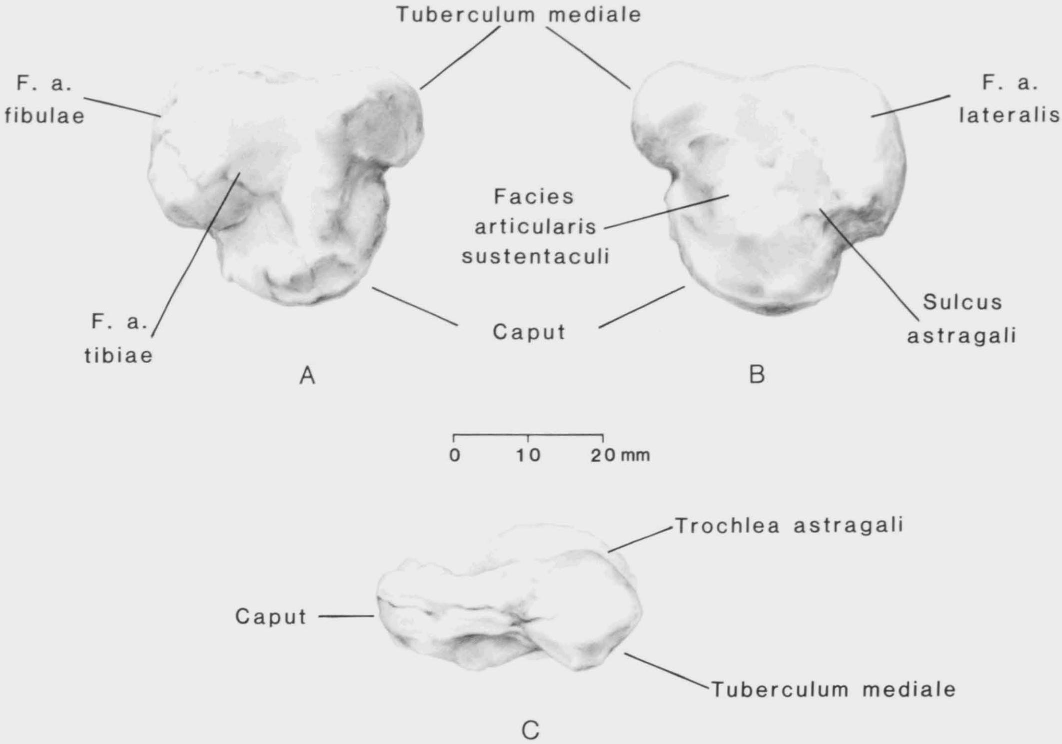

FIG. 2— Right astragalus of late Eocene *Moeritherium gracile* (YPM 24186) from Quarry H, Qasr el Sagha Formation, Fayum, Egypt. A, dorsomedial view. B, ventrolateral view. C, ventromedial view. Specimen is shown natural size. It was first described by Tassy (1982).

a way Schlosser's illustrations do not, the salient posteromedially developed *tuberculum mediale* cited by Tassy (1982) as characteristic and diagnostic of Proboscidea.

ASTRAGALUS OF *ANTHRACOBUNE*

The Kihman astragalus is illustrated in Figure 3 for comparison with that of *Moeritherium gracile*. The two differ somewhat in size, but both reflect a common structural plan. The tibial facet (*facies articularis tibiae*) occupies most of the dorsomedial surface of the Kihman astragalus. It extends posteromedially and ventrally onto a prominent *tuberculum mediale* like that of *Moeritherium*. There is a substantial fibular facet (*facies articularis fibulae*) parallel and lateral to the tibial facet. The most important difference between the Kihman astragalus and that of *Moeritherium* is retention of a substantial astragalar foramen (*foramen astragali*) piercing the posterior astragalar body. YPM 24186 appears to lack this foramen, and Schlosser's specimen of *Moeritherium* also lacked it (Schlosser, 1911, p. 133). The Kihman astragalus has a distinct posterior trochlear groove for a large *flexor hallucis longus* tendon. The orientation of this groove and the course of the astragalar foramen indicate that the Kihman astragalus had the prominent anteroposterior ridge separating tibial and fibular facets, rather than the tibial facet, positioned upward in life. This is the orientation shown by Schlosser (1911, Pl. 8, fig. 4a) for *Moeritherium*.

The neck of the Kihman astragalus is a little longer, relative to the size of the body, than is seen in later proboscideans, and the head (*caput*) is broad and smoothly curved. The head measures 30 mm in breadth and 19 mm in maximum height. A navicular facet occupies the

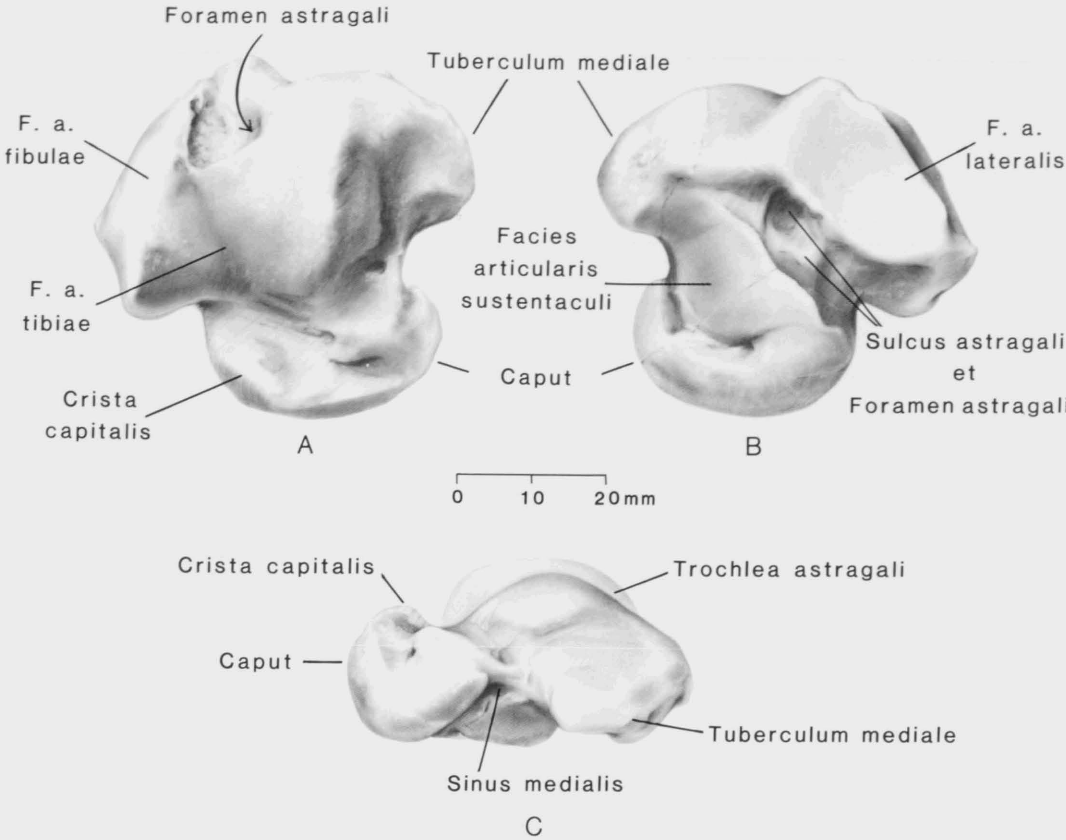

FIG. 3— Right astragalus of early-middle Eocene *Anthracobune* sp. (UM-GSP 1745) from Kihman A, Subathu Formation (unit J), Kashmir, Pakistan. A, dorsomedial view. B, ventrolateral view. C, ventromedial view. Specimen is shown natural size.

entire anterior surface of the head. There is no indication of articulation between the astragalus and cuboid. The navicular facet is oriented at about 90° to the tibial facet (best seen in Fig. 3C). The dorsal surface of the head is distinctive in carrying a sharp crest (*crista capitalis*) limiting anterior excursion of the tibia and dorsiflexion at the tibioastragalar joint. This anterior stop on the head, the position of the astragalar foramen well forward on the trochlea, and the 90° angle between navicular and tibial facets combine to indicate a plantigrade foot posture, with the foot habitually dorsiflexed and a limited range of plantar flexion.

In dorsomedial view (Fig. 3A), there is a distinct inflection in the medial margin of the astragalus between the head and the medial tuberosity. This inflection is the site of a small sinus (*sinus medialis*; Fig. 3C) with three distinct foramina opening on the dorsomedial surface of the astragalar body and head, and two foramina opening on the ventral surface of the head. These foramina possibly presage more extensive perforation of the astragalus of later proboscideans that have highly vascularized plantigrade feet.

The ventrolateral surface of the Kihman astragalus (Fig. 3B) is dominated by a central sulcus (*sulcus astragali*) with a large sustentacular facet (*facies articularis sustentaculi*) bordering it anteromedially and a large ectal facet (*facies articularis lateralis*) bordering it posterolaterally. The central sulcus has two parts: a broad open anterior part, and a narrower and deeper posterior part including the ventral opening of the astragalar foramen.

The sustentacular facet of the Kihman astragalus is a relatively large, complexly curved, oval facet. It is convex over most of its surface, but concave where it joins the medial tubercle. It is broadly confluent anteriorly with the navicular facet of the astragalar head. The central functional part of the sustentacular facet is a circular convex surface measuring about 18 mm in diameter. To the extent that differing preservation allows them to be compared, the sustentacular facet of the Kihman astragalus resembles that of YPM 24186 *Moeritherium gracile*. Schlosser (1911) shows a much more extensive, anteroposteriorly aligned, hourglass-shaped sustentacular facet for *Moeritherium*. Andrews (1906) illustrates smaller, narrower, and anteroposteriorly aligned sustentacular facets in *Palaeomastodon beadnelli* and *P. parvus*. Tassy (1982) shows an extensive sustentacular facet for *Barytherium grave*, but this is obliquely oriented relative to an anteroposterior axis and it extends well onto the medial tubercle. Jaeger (in Mahboubi et al., 1986) describes the sustentacular facet of *Numidotherium koholense* as strongly concave anteroposteriorly, extending well onto the medial tubercle and only narrowly connected to the navicular facet.

The ectal facet in the Kihman astragalus is concavely curved and more elongated than the sustentacular facet, measuring 27.5 mm in length and 15.5 in breadth. It is oriented oblique to the anteroposterior axis of the astragalus. *Moeritherium*, *Palaeomastodon*, *Barytherium*, and *Numidotherium* all differ in having a more circular oval or teardrop-shaped ectal facet. Articulation with corresponding calcanea will be required to determine the functional meaning of these differences, but the more elongated, obliquely oriented, concave ectal facet on the Kihman astragalus probably indicates a greater range of inversion-eversion at the astragalocalcaneal joint than was possible in later Eocene and Oligocene proboscideans.

DISCUSSION

Anthracobune and Anthracobunidae have been placed in Proboscidea in recent years because of dental and gnathic similarities to *Moeritherium* and other early proboscideans (West, 1980; Gingerich and Russell, 1981; Wells and Gingerich, 1983). The Kihman astragalus is important in corroborating this relationship based on new and independent evidence from the hind limb. Tassy (1982) cited the presence of a salient medial tubercle (*tuberculum mediale*) as a key character distinguishing *Moeritherium*, *Barytherium*, and other Proboscidea from mammals of other orders, and the medial tubercle is well developed in *Anthracobune*.

An astragalar foramen is present in many Paleocene and Eocene mammals, and its presence in *Anthracobune* is undoubtedly a primitive tethythere characteristic. Most later proboscideans (including *Moeritherium* and *Numidotherium*) lack an astragalar foramen. Similarly, all desmostylians for which the astragalus is known lack an astragalar foramen. This loss probably occurred independently in the two orders. Presence of a distinct crest on the head of the astragalus (*crista capitalis*) in *Anthracobune* is probably also a primitive tethythere characteristic, in this instance a characteristic lost in later proboscideans but retained in desmostylians.

Anthracobunidae are classified in Proboscidea because of their overall similarity in known dental characteristics and because of shared specializations like the salient medial tubercle of the astragalus described here. However, classification in Proboscidea does not preclude Anthracobunidae from ancestry of aquatic Desmostylia and possibly also Sirenia. There is little question that early tethytheres were terrestrial mammals. Proboscidea is the only tethytherian order that remains terrestrial, and consequently stem tethytheres are, a priori, more likely to resemble Proboscidea than they are to resemble aquatic orders Desmostylia or Sirenia.

ACKNOWLEDGMENTS

Paleontological research in Pakistan was funded by the Geological Survey of Pakistan [GSP] and a series of grants from the Smithsonian Foreign Currency Program. We thank Dr.

S. M. I. Shah of the GSP for facilitating this cooperation. M. Hussan, A. Jah, H. Shaheed, and R. Ullah of the GSP and H. Dineur, Dr. J.-L. Hartenberger, and A. Phelizon helped in the field. Dr. N. Court, Université de Montpellier, provided a cast of the *Numidotherium* astragalus; Dr. E. P. J. Heizmann provided access to Fayum collections in the Staatliches Museum für Naturkunde, Stuttgart; and Dr. J. H. Ostrom, Yale University, loaned the *Moeritherium* astragalus illustrated in Figure 2. We thank Drs. D. P. Domning, D. C. Fisher, J. Shoshani and P. Tassy for discussion. W. J. Ryan prepared the *Anthracobune* astragalus and B. Miljour drew the illustrations.

LITERATURE CITED

ANDREWS, C. W. 1906. A Descriptive Catalogue of the Tertiary Vertebrata of the Fayum, Egypt. British Museum (Natural History), London, 324 pp.

DEHM, R. and OETTINGEN-SPIELBERG, T. 1958. Paläontologische und geologische Untersuchungen im Tertiär von Pakistan. 2. Die mitteleocänen Säugetiere von Ganda Kas bei Basal in Nordwest-Pakistan. Bayerische Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse, Abhandlungen (n.F.), 91: 1-54.

DOMNING, D. P., C. E. RAY, and M. C. McKENNA. 1986. Two new Oligocene desmostylians and a discussion of tethytherian systematics. Smithsonian Contributions to Paleobiology, 59: 1-56.

GINGERICH, P. D. and D. E. RUSSELL. 1981. *Pakicetus inachus*, a new archaeocete (Mammalia, Cetacea) from the early-middle Eocene Kuldana Formation of Kohat (Pakistan). Contributions from the Museum of Paleontology, University of Michigan, 25: 235-246.

MAHBOUBI, M., R. AMEUR, J.-Y. CROCHET, and J. J. JAEGER. 1984. Earliest known proboscidean from early Eocene of north-west Africa. Nature, 308: 543-544.

———. 1986. El Kohol (Saharan Atlas, Algeria): a new Eocene mammal locality in northwestern Africa. Stratigraphical, phylogenetic and paleobiogeographical data. Paläontographica, Abteilung A, 192: 15-49.

McKENNA, M. C. 1975. Toward a phylogenetic classification of the Mammalia. *In* W. P. Luckett and F. S. Szalay (eds.), Phylogeny of the Primates, Plenum Publishing Corporation, New York, pp. 21-46.

PILGRIM, G. E. 1940. Middle Eocene mammals from north-west India. Proceedings of the Zoological Society, London, Series B, 110: 127-152.

RUSSELL, D. E. and R.-J. ZHAI. 1987. The Paleogene of Asia: mammals and stratigraphy. Mémoires du Muséum National d'Histoire Naturelle, Série C, Sciences de la Terre, 52: 1-488.

SAHNI, A. and K. KUMAR. 1980. Lower Eocene Sirenia, *Ishatherium subathuensis*, gen. et sp. nov. from the type area, Subathu Formation, Subathu, Simla, Himalayas, H.P. Journal of the Palaeontological Society of India, Lucknow, 23-24: 132-135.

TASSY, P. 1982. Les principales dochotomies dans l'histoire des Proboscidea (Mammalia): une approche phylogénetique. *In* E. Buffetaut, P. Janvier, J.-C. Rage, and P. Tassy (eds.), Phylogénie et Paléobiogéographie, Livre Jubilaire en l'Honneur de Robert Hoffstetter. Géobios, Mémoire Spécial, 6: 225-245.

TASSY, P. and J. SHOSHANI. 1988. The Tethytheria: elephants and their relatives. *In* M. J. Benton (ed.), The Phylogeny and Classification of the Tetrapods, Volume 2: Mammals. Clarendon Press, Oxford. Systematics Association Special Volume 35B: 283-315.

TOBIEN, H. 1971. *Moeritherium*, *Palaeomastodon*, *Phiomia* aus dem Paläogen Nordafrikas und die Abstammung der Mastodonten (Proboscidea, Mammalia). Mitteilungen aus dem Geologischen Institut der Technischen Universität Hannover, 10: 141-163.

WADIA, D. N. 1928. The geology of Poonch State (Kashmir) and adjacent portions of the Punjab. Memoirs of the Geological Survey of India, Calcutta, 51: 185-370.

WELLS, N. A. and P. D. GINGERICH. 1983. Review of Eocene Anthracobunidae (Mammalia, Proboscidea) with a new genus and species, *Jozaria palustris*, from the Kuldana Formation of Kohat (Pakistan). Contributions from the Museum of Paleontology, University of Michigan, 26: 117-139.

———. 1987. Paleoenvironmental interpretation of Paleogene strata near Kotli, Azad Kashmir, northeastern Pakistan. Kashmir Journal of Geology, Muzaffarabad, 5: 23-41.

WEST, R. M. 1980. Middle Eocene large mammal assemblage with Tethyan affinities, Ganda Kas region, Pakistan. Journal of Paleontology, 54: 508-533.

———. 1983. South Asian middle Eocene moeritheres (Mammalia, Tethytheria). Annals of Carnegie Museum, 52: 359-373.

———. 1984. A review of the South Asian middle Eocene Moeritheriidae (Mammalia, Tethytheria). Mémoires du Société Géologique de France, N.S., 147: 183-190.