

CONTRIBUTIONS FROM THE MUSEUM OF PALEONTOLOGY

THE UNIVERSITY OF MICHIGAN

VOL. 26, No. 7, p. 117-139

December 31, 1983

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PROBOSCIDEA) WITH A NEW GENUS AND SPECIES, *JOZARIA
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(PAKISTAN)**

BY

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REVIEW OF EOCENE ANTHRACOBUNIDAE (MAMMALIA, PROBOSCIDEA)
WITH A NEW GENUS AND SPECIES, *JOZARIA PALUSTRIS*, FROM THE
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Neil A. Wells and Philip D. Gingerich

Abstract.—*Anthracobune* and its primitive bunodont-bilophodont herbivorous allies from the Eocene of Indo-Pakistan are grouped together in a new family, Anthracobunidae. Anthracobunids are interpreted as basal “tethytheres” that are probably broadly ancestral to proboscideans, sirenians, and desmostylians. The family includes five genera and species: *Anthracobune pinfoldi* Pilgrim, 1940; *Lammidhania wardi* (Pilgrim, 1940); *Pilgrimella pilgrimi* Dehm and Oettingen-Spielberg, 1958; *Ishatherium subathuensis* Sahni and Kumar, 1980; and *Jozaria palustris* (new genus and species). Anthracobunidae may be ancestral to Moeritheriidae among primitive proboscideans and Prorastomidae/Protosirenidae among primitive sirenians; they resemble both groups in size and general cheek tooth morphology, and they appear earlier in the fossil record. Anthracobunids are primitive in having four premolars and in lacking the tusks and specialized rostra seen in moeritheriids and protosirenids. Desmostylia may also be derived from Anthracobunidae.

Jozaria appears to have fed on soft aquatic vegetation in brackish to freshwater marshes. Some *Pilgrimella* and *Ishatherium* specimens have been found in marine deposits. These observations are consistent with the postulated amphibious habits of moeritheres and the shallow-water littoral-marine habitats of sirenians and desmostylians.

INTRODUCTION

The most common large mammals in early-middle Eocene faunas of Pakistan are a distinctive group of primitive bunodont and moderately lophodont herbivores. Three genera are commonly recognized: *Anthracobune* (described by Pilgrim, 1940), *Pilgrimella* (described by Dehm and Oettingen-Spielberg, 1958), and *Lammidhania* (described by Gingerich, 1977). Judging from tooth size, *Lammidhania*, the smallest, was about the size of a babirussa (perhaps 1.2 m long and 100 kg in weight), *Pilgrimella* was about the size of an African river hog (ca. 120 kg), and *Anthracobune* was about the size of a small tapir or a giant forest hog (ca. 275 kg). A fourth genus, *Jozaria palustris*, described here, was intermediate in size and may have resembled a pigmy hippopotamus (ca. 1.6 m and 180 kg). *Lammidhania*, *Pilgrimella*, *Jozaria*, and *Anthracobune* are all similar in dental morphology, and they are undoubtedly closely related. The type species of *Lammidhania* was originally described as “Aff. *Anthracobune*,” and *Pilgrimella* is regarded as a synonym of *Anthracobune* by some authors (e.g., West, 1980). One additional genus, *Ishatherium*, is known from a partial upper molar (Sahni and Kumar, 1980). The molar is very similar to those of *Pilgrimella*, but little can be said about the systematic position of *Ishatherium* until more complete remains are discovered.

Anthracobune and its allies have a complex taxonomic history. They have been assigned or compared to six families and five or six orders of mammals: Anthracotheriidae (Artiodactyla—Pilgrim, 1940; Gingerich, 1977; West, 1980); Dichobunidae (Artiodactyla—Dehm and Oettingen-Spielberg, 1958); Perissodactyla *incertae sedis* (Coombs and Coombs, 1979); Dugongidae (Sirenia—Sahni and Kumar, 1980); Phenacolo-phidae (Embrithopoda or Order *incertae sedis*; McKenna and Manning, 1977; Gingerich and Russell, 1981); and Moeritheriidae (Proboscidea—West, 1980). Coombs and Coombs (1979) also noted some similarities to phenacodontid Condylarthra.

In this paper we describe a new genus and species, *Jozaria palustris*, and place all *Anthracobune*-like forms in a new family, Anthracobunidae. This group shares important similarities with late Eocene moeritheriids and primitive sirenians but its mandibular morphology and dental structure are more generalized than either. Anthracobunids are plausibly regarded as the stem group that gave rise to "Tethytheria" (*sensu* McKenna, 1975), including the extant orders Proboscidea and Sirenia and the extinct order Desmostylia.

A map showing the fossil localities discussed in this paper is given in Figure 1 of Gingerich and Russell (1981). Institutional abbreviations used here are as follows: BMNH, British Museum of Natural History (London); GSP-UM, Geological Survey of Pakistan-University of Michigan (Quetta and Islamabad); H-GSP, Howard University-Geological Survey of Pakistan (Quetta and Islamabad); IVPP, Institute of Vertebrate Paleontology and Paleoanthropology (Peking); LUV, Lucknow University Vertebrate Paleontology collection, Department of Geology (Lucknow); IPHG, Institut für Paläontologie und Historische Geologie, Universität München (Munich); and USNM, U.S. National Museum of Natural History (Washington).

SYSTEMATIC PALEONTOLOGY

Important morphological characteristics of *Anthracobune* and its relatives are compared and contrasted in Table 1. On the basis of similarities in the talonid cusps on P₃ and P₄, trigonid cusps (especially paraconids) on P₄, point of origin of the cristid obliqua, occlusal outline of M₂, and conformation of the hypoconulid on M₃, *Jozaria* and *Lammidhania* seem to be closely related. *Anthracobune* is like *Pilgrimella* in having a twinned hypoconulid, but it resembles other anthracobunid genera in the shape of M₂ and position of the cristid obliqua. Stratigraphic resolution within the fossiliferous formations yielding Anthracobunidae is not at present sufficient to provide any reliable evidence of phylogeny or character polarity based on relative ages of the fossils themselves.

Class MAMMALIA
Order PROBOSCIDEA Illiger, 1811
Anthracobunidae, new family

Type genus.—*Anthracobune* Pilgrim, 1940.

Referred Genera.—*Lammidhania*, *Pilgrimella*, *Ishatherium*, *Jozaria*, and *Anthracobune* (from smallest to largest, in the order of discussion below).

Age and Distribution.—Early to middle Eocene in the northwestern part of the Indo-Pakistan subcontinent.

TABLE 1— Distribution of dental characteristics among genera and species of Anthracobunidae. To facilitate comparison, genera are arranged according to their morphological similarity (i.e., *Anthracobune* is more similar to *Jozaria* and *Pilgrimella* than to *Lammidhanian*; *Jozaria* is more similar to *Lammidhanian* than to *Pilgrimella*, etc.). *Ishatherium* is not included because it is known only from a partial upper molar. Asterisk indicates estimate.

Dental characters	<i>Pilgrimella pilgrimi</i>	<i>Anthracobune pinfoldi</i>	<i>Jozaria palustris</i>	<i>Lammidhanian wardi</i>
UPPER DENTITION				
P ³ Transverse crests	Two	One, anterior	-	One, anterior
LOWER DENTITION				
P ₃ Shape	Broad front	-	Broad front	Narrow front
P ₃ Metaconid size relative to protoconid	Equal	-	Less than or equal	Less than or equal
P ₃ Paraconid size relative to protoconid	One-half	-	One-quarter	One-third
P ₃₋₄ Talonid cusps	Two	-	One	One
P ₄ Presence of paraconid	Yes	-	No	No
M ₁ Crests from metaconid to protoconid	One, posterior	-	Two	Two
M ₂ Length/width ratio	1.0	1.5	1.2	-
M ₂ Cristid obliqua height	Low	High	High	Intermediate
M ₂ Cristid obliqua arises from:	Metaconid	Lingual edge of metaconid	Mid-protolophid	Mid-protolophid
M ₃ Relative sizes of hypoconulid cusps	1 to 1	1 to 1	1 to 5*	1 to 15*

Diagnosis.—Three molars and four premolars (five premolars are present in the earliest sirenians, three in moeritheriids); teeth lophodont, with high, conical cusps; enamel finely crenulated or rugose. P₃ and P₄ are usually larger than M₁. Molars become larger posteriorly. Molars lack paraconids; hypoconulids are well developed, particularly on M₃; and the other four cusps form squares that are highest in front, with lingual cusps slightly higher and narrower than buccal equivalents. Twinning of cusps is common. The cristid obliqua and the crest connecting the hypoconulid to the hypoconid-endoconid ridge are best developed on M₁ and least developed on M₃, making M₃ very lophodont. Known upper molars have six cusps in two transverse rows. Upper molars lack an ectoloph.

Discussion.—The history of discovery and changing taxonomy in this group can be summarized as follows: In 1940, Pilgrim described one genus and three species, *Anthracobune pinfoldi*, *A. (?) daviesi*, and "Genus indet. (aff. *Anthracobune*)" *wardi*, from Lammidhan and Jhalar in the Kala Chitta Hills of northwestern Punjab Province, India (now Pakistan). In 1958, Dehm and Oettingen-Spielberg described a new genus and species, *Pilgrimella pilgrimi*, together with additional *A. pinfoldi* material from Ganda Kas, two kilometers east of Lammidhan, and they transferred "Genus indet. (aff. *A.*)" *wardi* to *Pilgrimella*. At this point, *P. pilgrimi* and *A. (?) daviesi* were known only from a few isolated, poorly preserved upper cheek teeth, *A. pinfoldi* from badly worn lower molars, and *P. wardi* from the posterior half of a broken lower molar. In 1977, Gingerich improved the type material of *A. pinfoldi* by fitting a referred partial crown onto the holotype, identified additional specimens, and noted that *A. daviesi* is probably a partial upper dentition of *A. pinfoldi* (based on their apparent association in the field, equivalence in size and preservation, and similar adhering matrix). He also referred an isolated M₃ to "*Pilgrimella*" *wardi* and renamed it *Lammidhanian*. Later discoveries demonstrate that the M₃ was incorrectly allocated to *Lammidhanian* (it belongs to a more advanced Anthracothere, and may have come

from the overlying Murree Formation at Lammidhan). Later discoveries also confirm that *L. wardi* differs from both *Anthracobune* and *Pilgrimella* at the generic level.

In 1980, West described new specimens, the best found to date, from a site near Lammidhan (West, 1980). He referred a left M_3 and a right dP_3-M_1 with underlying crowns of P_{2-4} to *Lammidhanian wardi*, which was previously represented solely by the broken holotype molar. West also described a remarkably complete pair of dentaries that he identified as *A. pinfoldi*. Meanwhile, Sahni and Khare (1973), working in approximately equivalent beds in northwestern India, had described a right maxilla with P^3-M^2 of *Pilgrimella pilgrimi*. West (1980) occluded the upper teeth of *P. pilgrimi* and the new lower teeth of "*A. pinfoldi*", and therefore synonymized them as *A. pinfoldi*. In our opinion, however, West's dentaries are not *A. pinfoldi* but rather *P. pilgrimi*. The teeth of *A. pinfoldi* are much larger and disproportionately longer than those of *P. pilgrimi*, and these two taxa are distinct at the specific if not generic level (Gingerich and Russell, 1981).

Anthracobune is the first-named and most familiar member of the group of genera and species placed in Anthracobunidae. *Pilgrimella* is represented by better material at present, but West (1980) considers it to be a synonym of *Anthracobune*. Genera and species of Anthracobunidae are discussed in order of increasing tooth and body size in the following systematic review.

Lammidhanian Gingerich, 1977
Lammidhanian wardi (Pilgrim, 1940)
Figures 1A,B and 2A,B

- Genus indet. (aff. *Anthracobune*) *wardi* Pilgrim, 1940, p. 138, Pl. 1, fig. 3 and 3a.
Pilgrimella wardi, Dehm and Oettingen-Spielberg, 1958, p. 36.
Lammidhanian wardi (in part), Gingerich, 1977, p. 199.
Lammidhanian wardi, West, 1980, p. 529, Pl. 4, fig. 4 and 5, Pl. 5, fig. 1-4.

Holotype.—BMNH 15799, talonid of left M_2 .

Hypodigm.—GSP-UM 103, probably a right M_3 ; GSP-UM 474, left P_2 ; GSP-UM 519, left M_1 or M_2 trigonid; possibly GSP-UM 549, a left M_3 ; H-GSP 982, partial teeth; H-GSP 1000, right P_{2-4} and dP_3-M_1 ; and H-GSP 1633, left M_3 . BMNH 32168 is excluded.

Age and distribution.—Late early to middle Eocene: Chorlakki locality, Kohat District, North-West Frontier Province, and Kala Chitta Hills (Lammidhan and vicinity), Attock District, Punjab Province, Pakistan. Chorlakki is located across the River Indus to the west of the Kala Chitta Hills.

Diagnosis.—Most similar to *Jozaria palustris*, but differs in being smaller (Tables 2 and 3). Other differences are: (1) metaconids are more prominently twinned on all molars, (2) the metaconid is smaller and the paraconid larger on P_3 , and (3) P_3 is semimolariform (with a narrow anterior and a square back) rather than massive and rectangular. Molars have small, low, and anterior paracristids that are nevertheless better developed in *Lammidhanian* than in any other anthracobunid. Hypoconulid on M_3 has an exceedingly small accessory cusp on its lingual flank. Like *Jozaria*, *Lammidhanian* differs from *Pilgrimella* (as defined below) and *Anthracobune* (restricted to *A. pinfoldi* of Pilgrim, 1940, and Gingerich, 1977) in lacking two equal hypoconulid cusps on M_3 . Also differs from *Pilgrimella* in having much longer and narrower molars, and in having a single central talonid cusp (probably a hypoconid) on P_3 and P_4 (lower premolars of *Anthracobune* are not known). Lastly, the posterior cingulum is markedly asymmetrical about

the hypoconulid, being much lower on the buccal side; the two sides are equally elevated in *Pilgrimella* and *Anthracobune*.

Description.—The diagnosis, description, and referral of new material in this paper pertain to *L. wardi* as exemplified principally by H-GSP 1000 (as well as the type specimen).

P_1 is not known. West (1980) inferred that *L. wardi* had no P_1 on the basis of extensive excavation of H-GSP 1000 without finding it. This conclusion seems unsupported, however, because H-GSP 1000 does not appear to extend far enough forward to preserve dP_2 , let alone P_1 . P_1 , not normally being replaced, should already have erupted and taken its place in front of dP_2 . By comparison, P_1 is known in both *Pilgrimella* and *Jozaria*.

The remaining teeth are described fully in West (1980, p. 530). P_2 is narrow and quite linear, with a high and flat protoconid, a subsidiary paraconid on its anterior flank, an attached small metaconid, and a smaller but more detached hypoconid behind. P_3 is wedge-shaped, narrowing anteriorly, and has a twinned protoconid, a slightly smaller appressed metaconid, a low and semi-detached paraconid, and a low, medial, semi-detached hypoconid with wide flanking cingula. P_4 is less wedge-shaped, has a similar hypoconid, and lacks a paraconid. Its protoconid and metaconid are high, equal, and twinned, and have descending anterior ridges that form the front of the tooth.

Each molar appears to have had a twinned metaconid and a slightly anterior and lower protoconid, which, particularly on M_2 , are joined by a double ridge. A small low paracristid curves around the base of the trigonid from the protoconid. On each, the hypoconid is anterior to the endoconid, giving the teeth parallel and slightly diagonal lophes. The hypoconulid is small and central, even on M_3 . The cristid obliqua is evident, but it is of low relief. M_1 is smaller than either P_3 or P_4 , as in other anthracobunid genera.

GSP-UM 549 is tentatively identified as a right P^3 of *Lammidhanian* (Figure 1A, B). It is more similar in outline to P^3 than to P^2 or P^4 of *Pilgrimella*, given the 14% larger size of P^3 in *Pilgrimella*, and it occludes reasonably well with the talonid of P_3 on H-GSP 1000. It has three main cusps and a small anteriorly situated paraconule with crests extending to the protocone and paracone. The protocone is mostly isolated, and the metacone and paracone are large and appressed. In form, GSP-UM 549 is more similar to P^3 in *Anthracobune* than it is to P^3 in *Pilgrimella*—there is a single anterior transverse crest (preprotocrista) in *Anthracobune*, like that of GSP-UM 549, whereas *Pilgrimella* has two large conules and two transverse crests (pre- and postprotocristae). However, GSP-UM 549 differs from *Anthracobune* in being much smaller in size and in having a lower and more curved preprotocrista.

Discussion.—The holotype (BMNH 15799) is the isolated and broken talonid of a left M_1 or M_2 . Pilgrim (1940) thought that it might represent *Anthracobune*, Dehm and Oettingen-Spielberg (1958) reassigned it to *Pilgrimella*, and Gingerich (1977) compared it to a long selenodont M_3 (BMNH 32168), renamed it *Lammidhanian wardi*, and placed it in Anthracotheriidae. Comparison with the anthracotherine M_3 was later recognized to be in error. West (1980) clarified the morphological distinctiveness of *Lammidhanian wardi* when he described a right dentary (H-GSP 1000) that is complete from dP_3 to the trigonid of M_2 , with unerupted P_2 - P_4 beneath. West also allocated a different and more likely M_3 (H-GSP 1633) to *Lammidhanian*.

West (1980) tentatively assigned *Lammidhanian* to Anthracotheriidae because of the supposed artiodactyl-like loss of P_1 and widened spacing of the premolars. As mentioned above, P_1 may well have been present. Since the teeth are not erupted, their spacing can not be determined. The dental similarities shared by *Lammidhanian* and other genera included here in Anthracobunidae are much more impressive than any resemblance to Anthracotheriidae.

Pilgrimella Dehm and Oettingen-Spielberg, 1958
Pilgrimella pilgrimi Dehm and Oettingen-Spielberg, 1958
 Figures 1C,D, and 2C,D

Pilgrimella pilgrimi Dehm and Oettingen-Spielberg, 1958, p. 33, Fig. 6, Pl.3, figs. 6a, b, 7. Sahni and Khare, 1973, p. 46, Pl. 6, fig. 3, Pl. 7, fig. 12.

Anthracobune pinfoldi (in part), West, 1980, p. 518, Pl. 2, fig. 5.

Holotype.—IPHG 1956-II-20; right M^1 .

Hypodigm.—GSP-UM 615, a left M^2 . GSP-UM 687, right M^3 ; GSP-UM 860, right M^3 ; H-GSP 568, left $M^{3?}$; H-GSP 1975, right $M^{3?}$; H-GSP 1981, left P_1-M_3 and right P_4-M_3 ; and LUVF 15006, right P^2-M^2 .

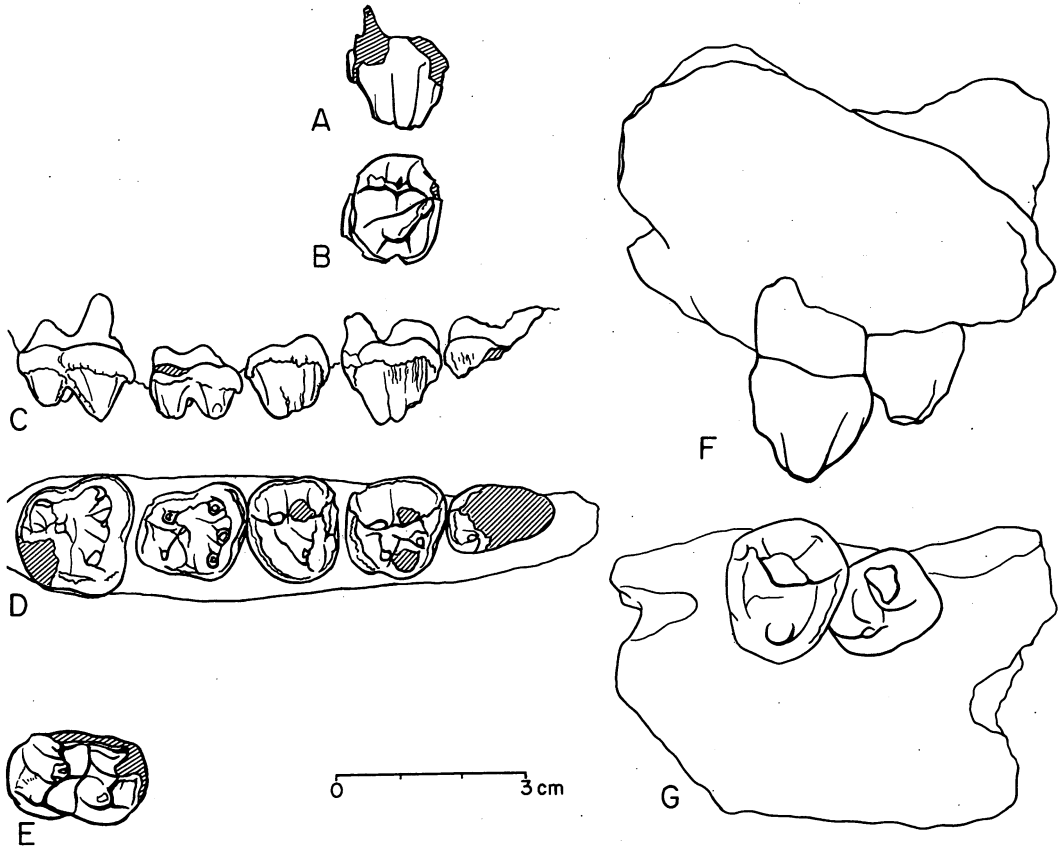


FIG. 1.—Upper dentition of Anthracobunidae, all drawn to the same scale. A,B: GSP-UM 549 from Chorlakki, tentatively identified as a right P^3 of *Lammidhaniania wardi*, buccal and occlusal views. C,D: LUVF 15006 from Kalakot, Kashmir, right P^2-M^2 of *Pilgrimella pilgrimi*, buccal and occlusal views. E: LUVF 1 from Subathu, Himachal Pradesh, lingual half of right M^1 or M^2 of *Ishatherium subathuensis*, occlusal view. F,G: BMNH 15795 from Lammidhan, left P^{2-3} (reversed) of *Anthracobune pinfoldi*, buccal and occlusal views.

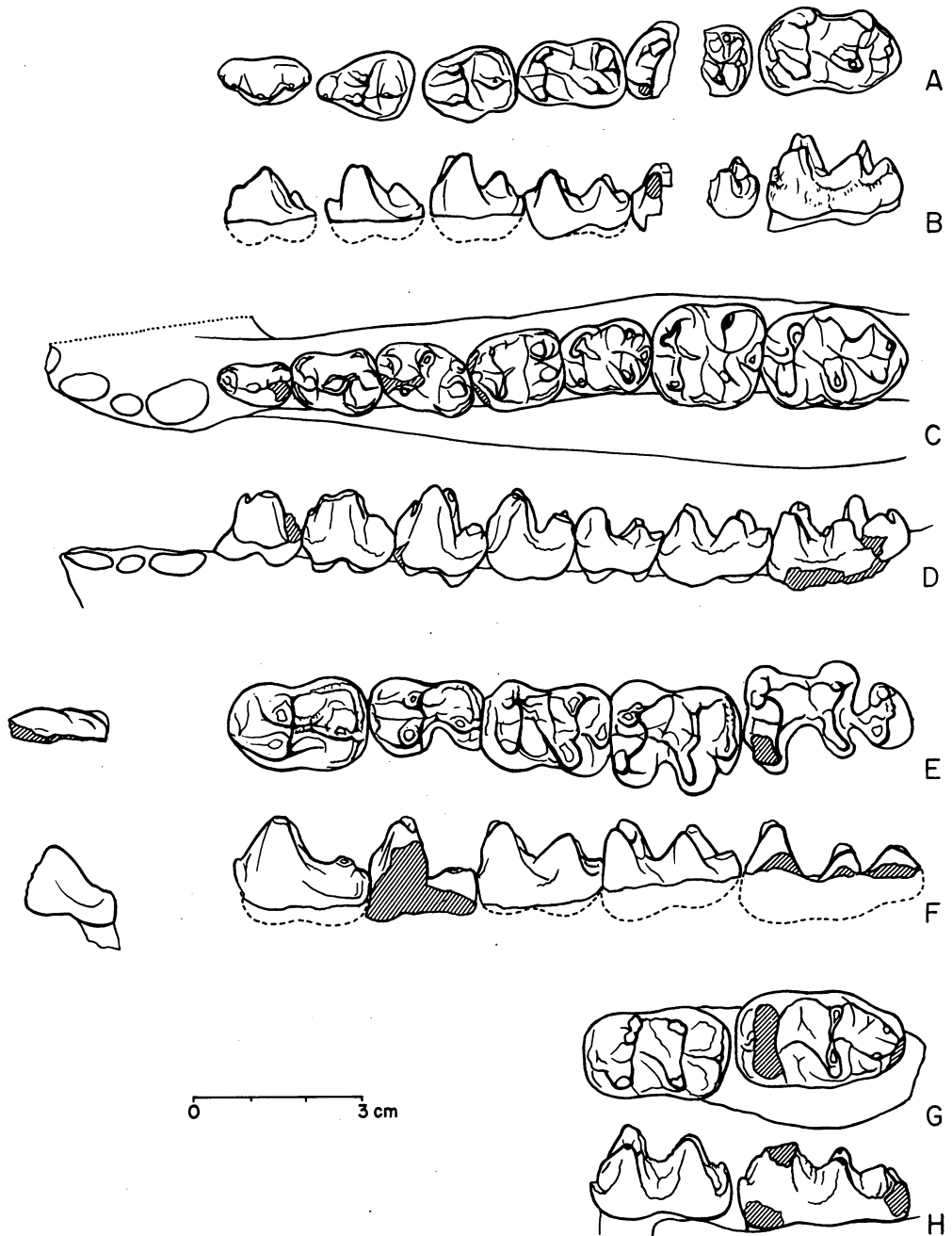


FIG. 2— Lower dentition of Anthracobunidae, all drawn to the same scale. *A, B*: composite right P_2 - M_3 of *Lammidhania wardi*, occlusal and buccal views H-GSP 1000 from Lammidhan, right P_2 - M_2 (reversed); BMNH 15799 from Lammidhan, trigonid of left M_2 (holotype); and H-GSP 1633 from Ganda Kas, left M_3 . *C, D*: H-GSP 1981 from Ganda Kas, left P_1 - M_3 of *Pilgrimella pilgrimi*, occlusal and buccal views. *E, F*: GSP-UM 738 from Jozara, left P_1 - M_3 of *Jozaria palustris* (P_3 reversed), occlusal and buccal views. *G, H*: BMNH 15792 from Lammidhan, left M_{2-3} of *Anthracobune pinfoldi* (M_2 rev.), occlusal and buccal views.

Age and distribution.—Late early to middle Eocene: Chorlakkı locality, Kohat District, North-West Frontier Province, and Kala Chitta Hills, Punjab Province, Pakistan. Also Subathu Formation, Kalakot, Jammu and Kashmir State, India.

Diagnosis.—Two talonid cusps on P_3 and P_4 , small paraconid on P_4 , M_2 more squared than in other anthracobunid genera, hypoconulid fully twinned on M_3 , lower molars relatively low, with a poorly developed cristid obliqua that joins the metaconid rather than the center of the protolophid (Figure 2C,D).

Description.—The most complete specimens of *Pilgrimella pilgrimi* are H-GSP 1981 (including left dentary with P_1 - M_3 , Fig. 2C,D) and LUVF 15006 (right mandible with P^2 - M^2 , Fig. 1C,D).

P^2 is relatively long and narrow. P^3 has three cusps in a triangle with both pre- and post-protocristae connecting the protocone to the appressed metacone and paracone. A distinct paraconule and metaconule are present as well. P^4 is similar, but it lacks the paraconule and a metaconule.

Upper molars are moderately lophodont, relatively square but broader in front, with six cusps and connecting crests forming two loph-like transverse rows. There is no ectoloph (Figure 1C,D). The median valley is curved, and it is split into two basins by a low saddle between the metaconule and the protocone. Both lophs bend slightly forward at their centers, due to the anterior positions of the metaconule and paraconule relative to laterally adjacent cusps.

Alveoli in front of P_1 suggest a very short diastema, a relatively large upright canine, and at least two smaller incisors, one vertical and the one in front more procumbent. There are four lower premolars. P_1 has a high and narrow protoconid with a high anterior paraconid joined to it and a lower posterior cusp. P_2 is similar but larger and broader, particularly in back. P_3 has a high trigonid with a large protoconid and an adjoined metaconid. A distinct lower and smaller anterior paraconid is also present. The broad talonid on P_3 has two cusps, unlike the single cusp seen in *Jozaria palustris* and *Lammidhanıa wardi*. P_4 is square, with high, equal, and adjoined protoconid and metaconid cusps and smaller, equal, and close (but separate) endoconid and hypoconid cusps. A small paraconid is incorporated at the base of the paracristid ridge descending the protoconid.

M_1 and M_2 are relatively square, with high and partly adjoined protoconids and metaconids and no paraconids. The anterior cusps are farther apart than anterior cusps in the premolars. The hypoconulids are small, central, and symmetrical. The hypoconulid on M_3 consists of two cusps of equal size.

Discussion.—*Pilgrimella pilgrimi* was known only from two isolated molars until Sahni and Khare (1973) described a well preserved maxilla (LUVF 15006). West (1980) found an excellent pair of dentaries (H-GSP 1981) that occlude with LUVF 15006 and he correctly referred them to the same species. Identification of the dentaries as *Anthracobune pinfoldi* (see below) led West to synonymize *Pilgrimella pilgrimi* with *Anthracobune pinfoldi* and, incidentally, to remove *A. daviesi* from synonymy with *A. pinfoldi*.

Specimen IPHG 1956-II-21 was described by Dehm and Oettingen-Spielberg (1958) as a left M^2 of *Pilgrimella*, but it is much smaller and disproportionately shorter than the M^2 of LUVF 15006, and its central transverse valley is straighter. It may represent a very small upper molar of *Pilgrimella*, or possibly an upper molar of *Lammidhanıa*.

Ishatherium Sahni and Kumar, 1980

Ishatherium subathuensis Sahni and Kumar, 1980

Fig. 1E

Ishatherium subathuensis Sahni and Kumar, 1980, p.133-134, fig. 2

Holotype.—LUVP 1.

Age and distribution.—Early Eocene, Subathu Formation, Subathu, Himachal Pradesh state, India.

Discussion.—Careful reconstruction by Mr. W. Ryan of the extremely fragmented holotype and sole representative of *I. subathuensis* shows it to be the lingual half of a right M^1 or M^2 that differs from *P. pilgrimi* only in its greater size (Figure 1). Its protocone and hypocone cusps are 11.0 mm apart: comparative values for *Pilgrimella* in GSP-UM 615 M^2 , the holotype M^1 , and LUVP 15006 M^1 are 9.2 mm, 7.9 mm, and 7.8 mm respectively. Apart from size, LUVP 1 appears to be identical to an upper molar of *P. pilgrimi*. Both have low, rounded upper molars; the upper molars of *Jozaria* would necessarily have higher cusps than are present in *Ishatherium* and *Pilgrimella*.

Jozaria, new genus

Type.—*Jozaria palustris*, new species.

Included species.—Type species only.

Age and distribution.—Early middle Eocene, Upper Member of the Kuldana Formation, Kohat District, Pakistan (see below).

Diagnosis.—*Jozaria* differs from other anthracobunids in its relatively massive P_3 , its relatively short P_4 , and its small lingual accessory hypoconulid cusp on M_3 . *Jozaria palustris* is most similar to *Lammidhania wardi* but differs in being much larger (comparable linear measurements of the teeth are 22% to 44% larger), in having slightly less prominent twinning of metaconids, and in having a more massive and rectangular P_3 with a smaller paraconid and a larger metaconid. Cheek tooth crests are generally extremely wrinkled. Paraconids are missing except for a much reduced one on P_3 . Hypoconulids are central and tend to be worn asymmetrically.

Etymology.—*Jozaria* (fem.), named for Jozara Rest House, located just east of the type locality.

Jozaria palustris, new species

Figures 2E,F and 3A-D

Holotype.—GSP-UM 738, partial P_1 , right P_3 and trigonid of P_4 , left P_4 to M_3 ; collected by one of us (N.A.W.) in 1980.

Type locality.—North bank of gully just upstream from the first bridge on the Kohat-Thal road west of Jozara Rest House, Ibrahimzai area, about midway between Kohat and Hangu, North-West Frontier Province, Pakistan (Figure 4).

Diagnosis.—As for the genus (see above).

Etymology.—From *palustris* (L.), of a marsh; in reference to the inferred coastal marsh habitat of this species; marshes link land and water and *J. palustris* may link land mammals with more amphibious to fully marine subungulates.

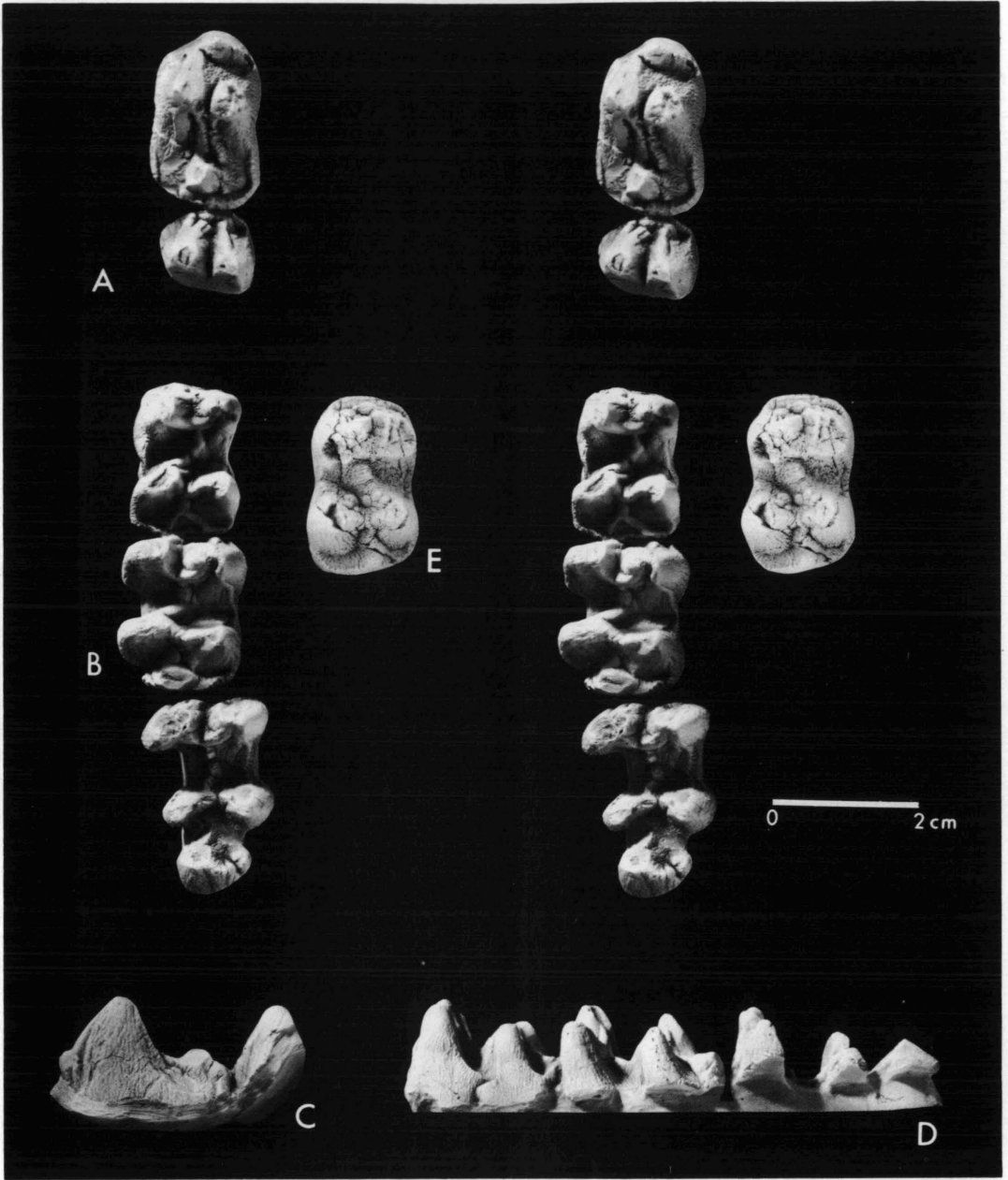


FIG. 3— Holotype of *Jozaria palustris*, GSP-UM 738 (A-D) compared to *Anthracobune pinfoldi* (E). A: right P₃ and trigonid of P₄ (reversed), occlusal view. B: left M₁₋₃, occlusal view. C: right P₃₋₄, lingual view. D: left M₁₋₃, buccal view. E: BMNH 32169, right M₃ of *Anthracobune pinfoldi*, occlusal view.

Description.—Identification of P_1 is confirmed by comparison with P_1 of *Pilgrimella* in H-GSP 1981. It is a flat, linear, two-rooted tooth with a single, simple, high and narrow crown, and an extremely small posterior cingulum. P_2 is not known. P_3 is large, slightly longer and wider than M_1 , and rectangular in occlusal outline. The protoconid and metaconid are high and very close together, and their posterior surfaces are wrinkled. One of the wrinkles weakly connects the trigonid cusps to a single posterior cusp, which is small and central, bordered by large cingula on both sides. The protoconid is slightly larger than the metaconid and it has a long broad anterior paracristid with a broad anterior wear facet incorporating a small paraconid near its base. P_4 has no paraconid. The metaconid and protoconid are separated by a deep fissure and both have steep anterior ridges with wear facets. As in P_3 , there is a single central talonid cusp.

M_1 has four major cusps (protoconid, metaconid, hypoconid, and entoconid) and a relatively small, single, central hypoconulid. There is no paraconid. The four major cusps form a square. Trigonid cusps are higher than talonid cusps, and lingual cusps are higher than their buccal equivalents. The metaconid and protoconid are joined by a double ridge that encloses a small basin. There are some slight, narrow, and complex cristae and cingula across the base of the front of the tooth, but there are no descending anterior ridges in front of the main cusps as on P_4 . The cristid obliqua is wrinkled, and the hypoconid and the entoconid are joined by a transverse crest (hypolophid). The hypoconulid is joined to the middle of the hypolophid by a small crest of its own. M_2 is similar to M_1 , but it is slightly larger. It differs in that the anterior of the two protoconid-metaconid crests on the trigonid is not fully developed and the cristid obliqua is a little lower. The hypoconulid is larger and it is made asymmetrical by a lingually sloping wear facet. M_3 is larger and considerably longer than M_2 , and its crests are less developed. The cristid obliqua is almost absent, which, with a broadening of the hypoconulid, produces strong lophodonty. Measurements of the lower cheek teeth are given in Table 2.

The upper dentition of *Jozaria* is unknown, but it might be expected to resemble *Pilgrimella pilgrimi*, as described by Dehm and Oettingen-Spielberg (1958) and Sahni and Khare (1973), differing principally in having longer, narrower, and higher crowned upper molars with higher cusps.

Discussion.—An extended account of the taphonomy and paleoecology of the *Jozaria* site is included in the following section of this paper.

Anthracobune Pilgrim, 1940
Anthracobune pinfoldi Pilgrim, 1940
Figures 1F,G, 2G,H, and 3E

Anthracobune pinfoldi Pilgrim, 1940, p. 129, Pl. 1, figs. 5, 5a, 6, 7. Gingerich, 1977, p. 199, Pl. 2, figs. 1, 2, 3, and 4.
Anthracobune daviesi Pilgrim, 1940, p. 135, Fig. 1.

Holotype.—BMNH 15792, right and left M_{2-3} , Pilgrim, 1940. BMNH 15794 was added to the holotype by Gingerich (1977).

Hypodigm.—BMNH 15793, left M_3 ; BMNH 15795, left P^{2-3} ; BMNH 32169, left M_2 .

Age and distribution.—Middle Eocene, Upper Kuldana Formation, Kala Chitta Hills, Attock District, Punjab Province, Pakistan.

Diagnosis.—Largest of the species included in Anthracobunidae. P^4 has a single and anterior transverse ridge. Well-developed cristid obliqua joins the metaconid on lower molars; two equal hypoconulid cusps on M_3 .

Discussion.—Pilgrim originally described two mandible fragments with M_{2-3} and an isolated left M_3 . Gingerich (1977) later identified an isolated right lower molar as a probable M_2 , and suggested that the holotype of *A. daviesi* (BMNH 15795) may represent part of the holotype of *A. pinfoldi*. The *A. daviesi* holotype is identified as a maxilla with P^{2-3} because of the elongated shape of the anterior premolar, which compares well with P^2 in *Pilgrimella pilgrimi* (LUVF 15006, Fig. 1C,D). Dehm and Oettingen-Spielberg (1958, p.36-38) have also assigned some fragmentary and isolated premolars and incisors to *Anthracobune*.

As explained in discussing *Pilgrimella*, West (1980) placed the dentaries of H-GSP 1981 in the same species as the upper tooth row of *P. pilgrimi* (LUVF 15006). In our opinion, West's identification of H-GSP 1981 as *Anthracobune pinfoldi* is not likely to be correct. H-GSP 1981 resembles *A. pinfoldi* in its doubled hypoconulid, but otherwise it is 20-30% smaller and its M_2 is considerably more square (Tables 2 and 3). The cristid obliqua of *Pilgrimella* is less well developed and arises directly from the metaconid, not beside it, and its P^3 has two transverse ridges, not just a single anterior one. Therefore the genus and species *Anthracobune pinfoldi* is maintained here in the sense used by Gingerich (1977), and the distinctly different dentaries described by West are referred to *Pilgrimella pilgrimi* on the basis of occlusion with the maxillary dentition of *Pilgrimella* demonstrated by West.

TABLE 2— Measurements of lower cheek teeth of *Jozaria palustris* and other Anthracobunidae compared to those of a possibly ancestral form *Minchenella grandis* and two probable descendants *Moeritherium gracilis* (order Proboscidea) and *Protosiren* (Sirenia). L = crown length, W = crown width, all measurements in mm.

Genus and species	P ₁		P ₂		P ₃		P ₄		M ₁		M ₂		M ₃	
	L	W	L	W	L	W	L	W	L	W	L	W	L	W
ANTHRACOBUNIDAE														
<i>Pilgrimella pilgrimi</i>														
H-GSP 1981(l)	13.2	8.5	12.5	12.3	18.3	12.7	16.6	14.4	15.7	13.5	18.8	18.9	25.9	18.7
H-GSP 1981(r)	-	-	-	-	-	-	-	-	-	-	18.9	18.1	26.2	17.6
<i>Anthracobune pinfoldi</i>														
BMNH 32169	-	-	-	-	-	-	-	-	25.6	16.5?	-	-	-	-
BMNH 15792	-	-	-	-	-	-	-	-	-	-	26.7	18.3	31.6	18.9
BMNH 15792	-	-	-	-	-	-	-	-	-	-	-	-	31.7	19.1
BMNH 15793	-	-	-	-	-	-	-	-	-	-	-	-	31.2	17.5
<i>Jozaria palustris</i>														
GSP-UM 738	15.9	10.0?	-	-	24.5	16.3	20.6	15.2	22.2	15.9	23.0	18.5	29.0	19.3
<i>Lammidhanian wardi</i>														
H-GSP 1000	-	-	16.3	8.6	17.2	11.3	16.6	12.5	16.3	11.6	-	-	-	-
H-GSP 1633	-	-	-	-	-	-	-	-	-	-	-	-	23.5	14.1
PHENACOLOPHIDAE (Upper Paleocene, China)														
<i>Minchinella grandis</i>														
IVPP 5600	-	-	11.0	7.3	12.2	10.0	11.8	12.3	14.0	12.4	14.8	12.6	25.3	13.3
MOERITHERIIDAE (Upper Eocene, Egypt)														
<i>Moeritherium gracilis</i>														
Osborn ¹	-	-	-	-	22.0	15.0	21.0	18.0	22.5	20.5	28.5	23.5	34.5	24.0
PROTOSIRENIDAE (Middle Eocene, America)														
<i>Protosiren sp.</i>														
Domning ²	-	-	9.0	7.4	9.7	8.4	12.1	9.0	13.4	10.0	14.5	11.6	18.6	11.8

¹ Measurements from Osborn (1936, p. 73); some values are averages of two measurements.

² Measurements from Domning et al. (1982, p. 47); some values are averages of two measurements, P_4 above is equivalent to dP_5 , P_3 above is equivalent to P_4 , etc.

TABLE 3— Tooth crown areas and crown shape indices for Anthracobunidae and possible relatives. Crown area (LxW) is expressed in mm^2 , shape (L/W) is a dimensionless scalar. Data from Table 2.

ANTHRACOBUNIDAE								
Tooth	<i>Pilgrimella pilgrimi</i>		<i>Anthracobune pinfoldi</i>		<i>Jozaria palustris</i>		<i>Lammidhanja wardi</i>	
	LxW	L/W	LxW	L/W	LxW	L/W	LxW	L/W
P ₁	112	1.6	-	-	159?	1.6?	-	-
P ₂	215	1.4	-	-	-	-	-	-
P ₃	232	1.4	-	-	399	1.5	194	1.5
P ₄	239	1.2	-	-	313?	1.4	208	1.3
M ₁	212	1.2	422?	1.6?	353	1.4	189	1.4
M ₂	348	1.0	489	1.5	426	1.2	-	-
M ₃	473	1.4	587	1.7	560	1.5	331	1.7

POSSIBLE RELATIVES							
Tooth	<i>Minchenella grandis</i>		<i>Moeritherium gracile</i>		<i>Protosiren sp.</i>		
	LxW	L/W	LxW	L/W	LxW	L/W	
P ₂	80	1.5	-	-	67	1.2	
P ₃	122	1.2	330	1.5	81	1.2	
P ₄	145	1.0	378	1.2	109	1.3	
M ₁	174	1.1	439	1.2	134	1.3	
M ₂	186	1.2	619	1.2	168	1.3	
M ₃	339	1.9	804	1.4	219	1.6	

TAPHONOMY AND PALEOECOLOGICAL INTERPRETATION OF JOZARIA LOCALITY

The type and only known specimen of *Jozaria palustris* was found in a loose block of grey marl in a gully less than a kilometer west of the Jozara rest house. The source bed is a very small lens of bone-filled argillaceous micrite in the Upper Member of the Kuldana Formation. Its position in the outcrop is marked with an *x* in Figure 4.

At Jozara, as elsewhere in the Kohat District, the Upper Kuldana is a thin sequence of diverse lithofacies that separates uniform brick-red clays of the Lower Member of the Kuldana Formation from foraminiferal limestones of the overlying Kohat Formation. The brick-red clays of the Lower Kuldana are believed to be terrestrial deposits on the basis of their color, their position above a regressive shoreline complex comprising sabkhas, evaporitic and non-evaporitic lagoons, deltas, and streamfed cobble beaches (Wells, 1980, and in prep.), and their predominantly terrestrial biota (including typically terrestrial land mammals of the orders Insectivora, Primates, Rodentia, Artiodactyla, and Perissodactyla; Gingerich et al., 1983; Wells, 1983). The Kohat Formation, dominated by benthic foraminiferans with echinoids, marine molluscs, and rarely corals and bryozoa, is clearly marine. In the Kohat District, the intervening Upper Kuldana Formation is typically about 10 m thick and represents a variety of coastal environments including low-lying coastal plains, fresh-water ponds, marshes, saline-alkaline lakes, lagoons, and bays (Wells, in prep.).

The Upper Kuldana section exposed at Jozara is described in Figure 5. Resistant beds are numbered to facilitate comparison of Figures 4 and 5, and for ease of reference in the following



FIG. 4— Jozara locality, showing the source bed (marked x) of the isolated block of marl containing the holotype of *Jozaria palustris*. Numbers 1-4 refer to beds listed in Figure 5 and discussed in the text.

discussion. The Upper Kuldana section here is at least two-thirds clay, and most of the lenticular and laterally variable limestone beds represent a simple local change from calcareous mudstone to argillaceous mudstone. Features of the section that are important for its interpretation are: (a) color changes from red through "maroon" (here greyish red) and brown to green near the base of the section; (b) a *Pinna* shell in Bed 3, which is a shelly marl; (c) fossil *Chara* in Bed 4, a locally burrowed, olive, ostracodal, calcareous shale; and (d) abundant rootlets and freshwater snails (*Planorbis*) in the nodular marls of the *Jozaria* bed itself.

In the Kohat District, where there was a single progressive marine advance, the change in clay color from brick red to off-red (maroon and brown) occurs at the base of almost every Upper Kuldana section. East of the River Indus, where Upper Kuldana continental and marine facies are extensively interbedded, the same color change demarcates nearly all red beds. Consequently, it seems to be the first indication of initiation of a marine transgression. Red clays indicate oxidation in the soil zone and off-red clays suggest decreased oxidation, so the color change is reasonably attributed to a rise in the water table and decreased drainage. The overlying transition from brown to green clays probably represents submergence.

Beds 1, 2, and 3 are tentatively interpreted as marine bay deposits. Bed 3 is identified as marine because *Pinna* is a very fragile marine pelecypod that lives today standing vertically on small shells or stones buried in mud, some in very shallow subtidal environments. Bed 2, a clayey ostracodal biomicrite with gastropods and fragmentary pelecypods, is probably also marine. Bed 1 is a calcareous claystone with 1-cm thick beds consisting of a basal 1-3 mm thick clay-free quartz

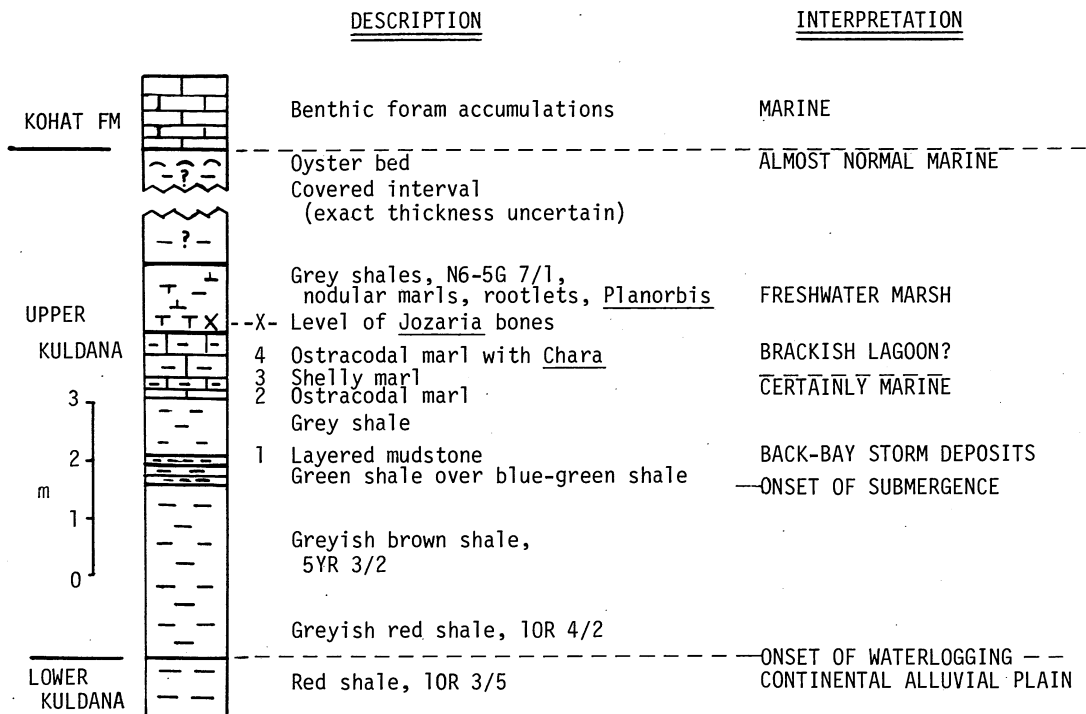


FIG. 5— Jozara rest house section, with a description of the Upper Member of the Kuldana Formation and its interpretation as a quiet, muddy, and marshy shoreline transitional between well-drained alluvial redbeds below and marine foraminiferal limestones above. Positions of Beds 1-4 in outcrop at Jozara is shown in Figure 4.

and skeletal calcite sand fining upward into clay. It is tentatively interpreted as some kind of back-bay storm deposit because it is layered (like many storm deposits) and because it necessarily represents a low-energy facies that intervenes between continental and marine environments.

The thin marine section comprising Beds 1 to 3 is followed by several meters of freshwater marsh beds. Bed 4 is an olive colored calcareous ostracodal shale, locally burrowed, with rare *Chara*. The *Chara*, a freshwater alga, could have been washed into a bay or a brackish lagoon, but the marl beds in the succeeding 1.4 m, including the lens yielding *Jozaria*, are completely bioturbated, riddled with rootlets, contain many freshwater snails (*Planorbis*), and locally show evidence of repeated wetting and drying, thereby demonstrating the presence of a freshwater marsh at this point in the section. Extensive bioturbation and remains of freshwater snails can be seen in association with fragmentary remains of *Jozaria* in Figure 6A,B. No additional *Chara* were found, but they are abundant in similar rootlet-ridden rocks in nearby Upper Kuldana sections. The Jozara section is consistent with a transgressive model if the bay (Beds 1 to 3) is considered to have been a short-lived feature that was cut off (i.e., turned into a lagoon) and filled in Bed 4 time. It is unlikely to have been a landward equivalent of the freshwater marsh.

The section succeeding the marsh beds is partially covered, but it seems to be mostly clay. An oyster bed occurs near the top of the covered interval; oyster beds typically cap the Upper Kuldana facies and lie beneath the first benthic foraminiferal limestones, and they therefore seem to mark the change to relatively normal marine conditions. This is followed by "Nummulitic

Shales" of the Kohat Formation - here a relatively well-sorted concentration of small (young) *Nummulites uronensis* and *Assilina papillata* in a sparse and fine sand matrix.

The remains of *Jozaria* occur as a jumbled mixture of several large bones and bone fragments surrounded by a multitude of small and rotted bone chips (Figure 6A,B). Accumulation of loose bones by currents can be ruled out due to the hydraulic non-equivalence of some bones and bone fragments relative to each other and to the very fine enclosing sediment. Loss of bones from a floating carcass also seems unlikely, because the preserved bones, although not precisely identifiable, seem to represent both distal and central parts of the body (dentaries and a podial element vs. a clavicle-like long bone and several large, massive bone fragments, probably including part of the pelvis). Flotation seems relatively unlikely after rupture of a carcass, and loss of the dentaries is likely to be a very early event in decomposition (see Schafer, 1972, p.20 ff.), so it seems likely that much or all decomposition of the body occurred at the fossil site. In fact, given quiet and vegetation-choked waters in the marsh, the animal is likely to have decomposed essentially where it died.

Although the loose block yielding *Jozaria* and the source lens itself are rich in bone, they are very small and the total amount of bone preserved makes up only a small proportion of a complete skeleton. Many of the bone fragments are in poor condition and there are many rotted bone chips. The rock is thoroughly bioturbated and contains a multitude of tiny borings or burrows that are probably rootlets and/or fungal hyphae growing down to the bones (Figure 6B). The intense root and/or hyphae activity around the bones suggests, in turn, that the bones were buried with flesh still on them. Bioturbation could easily have reduced a large part of the skeleton to small and dispersed bone chips during burial (some, of course, were undoubtedly eroded and destroyed in recent years).

The very high-cusped, lophodont cheek teeth of *Jozaria* are the only intrinsic evidence that it was marsh-dwelling. Molars of *Jozaria* seem poorly suited for either grinding or shearing resistant vegetation, but one can more easily imagine that they were used to mash soft aquatic vegetation such as water hyacinths, water lilies, seagrasses, or seaweed. Discovery of more skeletal elements of *Jozaria*, particularly ribs and long bones, could potentially be very interesting because mammals with amphibious habits are usually characterized by dense and pachyostotic bone (Wall, 1983). In sum, *Jozaria* appears to have been buried on the landward and freshwater side of a quiet and muddy coastal marsh, where it probably lived and died. Burial was rapid, but considerable destruction of the skeleton followed.

EVOLUTIONARY RELATIONSHIPS OF ANTHRACOBUNIDAE

Origin of Anthracobunidae

Minchenella (Zhang, 1978, 1980) from the late Paleocene of China is the most plausible ancestor of Anthracobunidae, given present knowledge of the Paleocene faunas of Asia. Morphological similarities include a full eutherian tooth formula (with four premolars), posterior increase in size of the molars, transverse alignment of the hypoconid and endoconid and of the metaconid and protoconid on the molars, weak development of a metalophid crest with a weaker crest between the hypoconid and endoconid, presence of a low but noteworthy cristid obliqua, and presence of a small hypoconulid that is connected to the middle of the hypoconid-endoconid crest, becoming more important on posterior molars. *Minchenella* is most like *Pilgrimella* in that P_3 and P_4 have small endoconids, and the hypoconulid on M_3 is doubled (although the lingual cusp is much smaller than the buccal one). *Lammidhanian wardi* is the anthracobunid closest to *Minchenella* in retaining at least a rudimentary paracristid on the

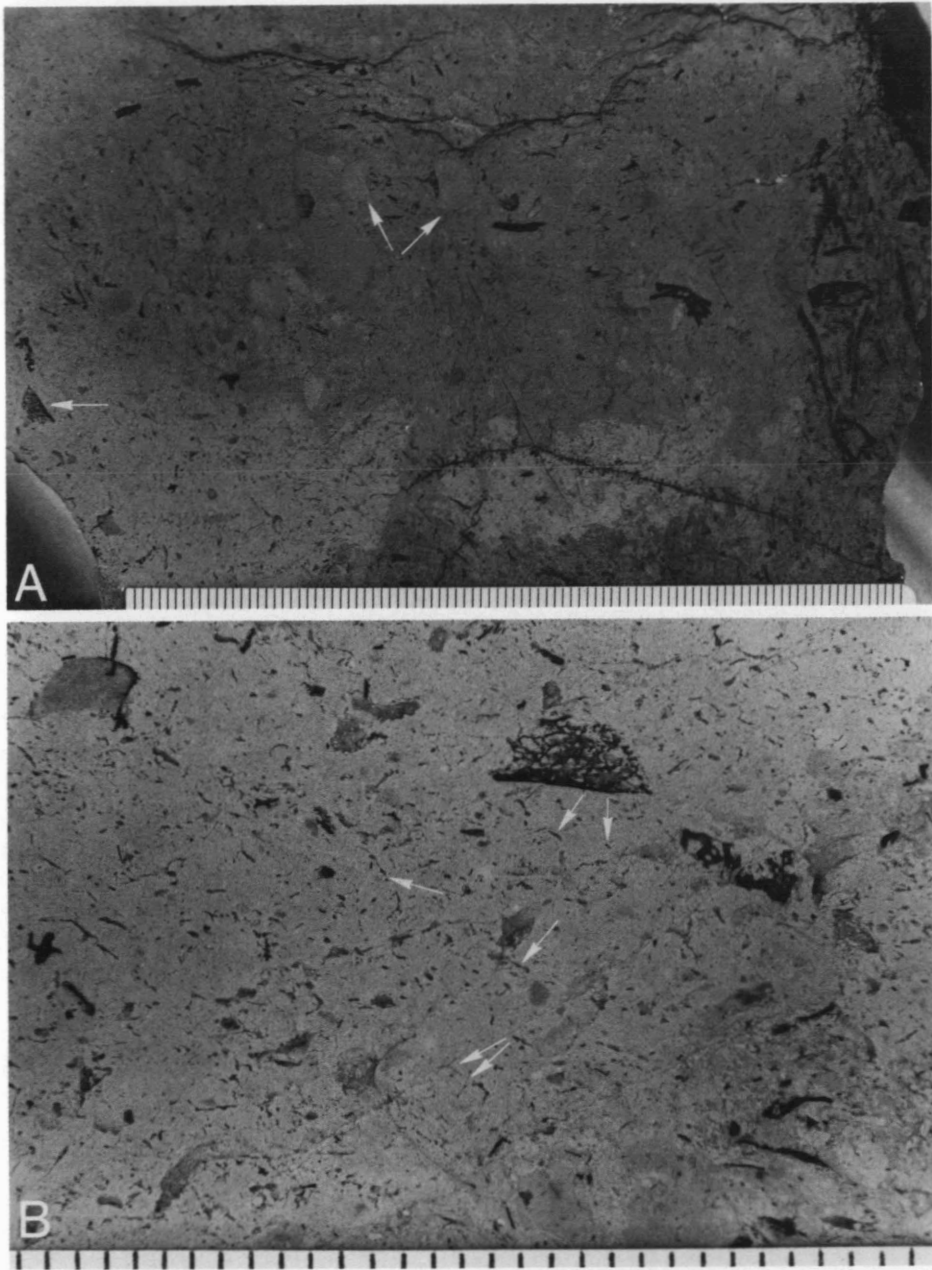


FIG. 6— Photographs of lightly etched slab cut from loose boulder containing the *Jozaria palustris* holotype. Orientation using geopetal structures is impossible due to excessive bioturbation. Both scales are in millimeters. *A*: Dark material is nearly all rotted chips of bone (the solitary arrow points to a bone fragment that is enlarged in Fig. 6B). Two arrows point to the sides of the freshwater snail *Planorbis*, the center of which has been dissolved away. The outermost whorl is preserved because it was filled with mud prior to compaction and dissolution. Other effects of solution are visible at top. Fabric is clearly disturbed by bioturbation. *B*: Ubiquity of small rootlets and/or fungal hyphae between bone fragments is best seen at higher magnification than that in Figure 6A. Arrows show range in morphology of some of the smallest branched and sinuous rootlets seen in longitudinal and transverse section.

molars, in having cingulids of markedly different height on either side of the hypoconulid of M_1 and M_2 , and in its size.

Minchenella differs from anthracobunids in possessing a much better developed paracristid (although without a paraconid), and corresponding broad trigonids, broad lingual faces of metaconids and hypoconids, poor development of transverse lophs, off-center placement of hypoconulids on molars and hypoconids on premolars, and the slightly more pronounced waisting of the occlusal outline of molars and posterior premolars. The trigonid of M_3 is particularly large and unlike that of anthracobunids. *Minchenella* is even smaller than *Lammidhania*: for comparison, P_2 - P_4 length is 33.7 mm in *Minchenella*, 49.8 mm in *Lammidhania*, and 48.8 mm in *Pilgrimella*; M_1 - M_2 length is 28.2 mm in *Minchenella*, 34.9 mm in *Pilgrimella*, and 45.0 mm in *Jozaria*. Zhang (1978) classified *Minchenella* in Phenacolophidae, in the order Condylarthra. McKenna and Manning (1977) placed Phenacolophidae in Embrithopoda, and Chow and Wang (1979) placed it in Pantodonta. We would retain *Minchenella* and Phenacolophidae questionably in Condylarthra, noting that both may be related to the origin of Anthracobunidae as well.

Proboscidea

Anthracobunidae are similar dentally to moeritheriid proboscideans (West, 1980), and for this reason we have classified Anthracobunidae in the order Proboscidea. They are most like the oldest (late Eocene) species, *Moeritherium lyonsi*, as redefined by Coppens and Beden (1978). Both have bilophodont upper and lower molars without ectolophs and paraconids. Lower molars of *Moeritherium* have the same relative proportions as the molars of *Anthracobune* and *Jozaria*, and they increase in size posteriorly. The hypoconulids are closely comparable. The hypoconulid of M_1 in moeritheriids is a small cuspid on the back of the hypolophid. On M_2 it is larger, more distinct, single, and central. On M_3 it is double, with the lingual cusp being slightly smaller, so M_3 is rectangular, six-cusped, and trilophodont, as in *Anthracobune*. Moeritheriid premolars are also similar to those of anthracobunids. P_2 is a narrow tooth with a large protoconid, a small paraconid sitting high on its anterior side, and a lower, single, central talonid cusp (Osborn, 1936: figs. 27 and 37). P_3 is rectangular with a rounded front, like *Jozaria*, and it has a slightly larger anterior paraconid and a twinned lingual metaconid adjoined to its large protoconid. P_4 seems similar but broader. Paraconids are lost on the molars, but not entirely on P_4 .

Upper molars of Moeritheriidae are also comparable to those of Anthracobunidae. P^2 is long and widens posteriorly, as in *Anthracobune* and *Pilgrimella*. P^3 and P^4 are three-cusped, with a weak preprotocrista and a broad shelf in place of the hypocone, much like *Lammidhania* and *Anthracobune*, but not like *Pilgrimella*. The upper molars of moeritheriids have better-developed transverse lophs than do anthracobunids; the conules can no longer be distinguished but medial inflections in the lophs suggest their former presence. M^3 in moeritheriids has a small metaloph basin and crest that are not present in anthracobunids. H-GSP 538, with its post-metaconule shelf and a small posterior circular ridge, is the most *Moeritherium*-like upper molar of an anthracobunid. *Anthracobune pinfoldi* is most similar to *Moeritherium* overall, given its large size, tritubercular upper premolars and trilophodont M_{3s} .

Nevertheless, moeritheriids and anthracobunids are also significantly different. Moeritheriid dentaries were massive, with parallel tooth rows posterior to P_2 , no P_1 or canine, a diastema, and large I_2 tusks bordering smaller I_{1s} . Judging from H-GSP 1981 (West, 1980, plate 2, fig. 5), the dentaries of *Pilgrimella pilgrimi* were more slender, V-shaped, retained a P_1 and a canine, and lacked all but the most rudimentary diastemata and tusks. These differences indicate that moeritheres were significantly more like later Proboscidea in their massive jaws, well-developed

tusks, and snout shape, and that Anthracobunidae cannot be included in Moeritherioidea as defined in Osborn (1921, and 1936, p.69). Nevertheless, anthracobunids could represent a more primitive stock broadly ancestral to moeritheriids. Most students have concluded that moeritheriids were ancestral to other Proboscidea (e.g., Matsumoto, 1923; Romer, 1966; Tassy, 1979, 1981; *contra* Coppens and Beden, 1978).

Sirenia

Anthracobunids are also very similar to the earliest sirenians. Lower cheek teeth of middle Eocene *Protosiren* (cf. USNM 214596, described from North Carolina by Domning et al., 1982) are barely distinguishable from anthracobunid molars. Cheek teeth of *Protosiren* resemble those of *Pilgrimella* except in being smaller. Specific similarities include the shape and placement of the cristid obliqua, presence of two talonid cusps on P₃ and P₄, and presence of a paraconid on P₃. Differences include the much smaller size of *Protosiren* and the presence of a single hypoconulid cusp on M₃ (making it resemble *Lammidhanina* more than *Pilgrimella*). Domning et al. (1982) described an isolated, six-cusped, bilophodont, left M²⁷ of *Protosiren* (USNM 214597), which is also very similar to M² of *Pilgrimella pilgrimi*. It differs in having straighter lophs and a slightly straighter central valley. It differs also in lacking lateral cingula (anterior and posterior cingula are well developed). Other specimens of *Protosiren* have more sinuous troughs (e.g., Domning et al., 1982, figs. 15 and 16). The Munich molar of *Pilgrimella* or *Lammidhanina*? (IPHG 1956-II-21) is probably closest to *Protosiren* because of its unobstructed and relatively straight medial valley.

In spite of the similarities described above, even the earliest sirenians had lengthened rostra with anterior diastemata and five or even six premolars. This is true for *Prorastomus* (Prorastomidae) from the middle Eocene of Jamaica and both *Protosiren* (Protosirenidae) and *Eotheroides* (Dugongidae) from the middle Eocene of Egypt (Owen, 1855; Andrews, 1906, fig. 67; Abel, 1912; Reinhart, 1959; Savage, 1976; Domning, 1978a, Domning et al., 1982). These features are lacking in *Pilgrimella*, so although it may be considered to be broadly ancestral to Sirenia, it does not have enough of the distinguishing characteristics to warrant inclusion in this order.

Prorastomus is notably more primitive and anthracobunid-like than other sirenian genera in that it lacks enlarged tusks and its dentaries and rostrum were straight and not down-turned as in *Protosiren* and *Eotheroides* (Owen, 1875; Abel, 1914, fig. 175; Simpson, 1932a). Domning et al. (1982) view the possession of five premolars by sirenians as a primitive condition linking them to early mammals of pre-metatherian/ eutherian grade, which would make their evolution from anthracobunids impossible. However, manatees, like whales, have added even more supernumerary cheek teeth that are certainly not primitive, so a fifth premolar seems to be of little special significance in determining the ancestry of Sirenia.

Sereno (1982; following McKenna, 1981) refers *Florentinoameghinia mystica* Simpson (1932b), from the lower Eocene *Notostylops* beds (Casamayoran) of Argentina, to the order Sirenia, a conclusion that might appear to contradict the link between primitive anthracobunid Proboscidea and Sirenia suggested here. However, there are a number of difficulties with Sereno's hypothesis that make inclusion of *Florentinoameghinia* in Sirenia unlikely: (1) The fossil specimen includes three cheek teeth of uncertain homology. Sereno regards these as permanent cheek teeth in spite of previous suggestions that they may be deciduous (crypts, apparently for permanent premolars, are preserved in bone above the cheek teeth; see Simpson, 1932b, McKenna, 1981). (2) The principal derived characteristic shared by *Florentinoameghinia* and primitive Sirenia, upper molariform teeth with unobstructed transverse valleys between the protoloph and hypoloph, is contradicted by the form of the anterior tooth identified as an upper molar (which may actually be dP⁴). The protocone and hypocone on this tooth are joined,

obstructing the transverse valley. The degree of obstruction of the transverse valley cannot be determined on the posterior tooth identified as an upper molar because of breakage. (3) There is no stratigraphic evidence suggesting proximity of marine habitats and there is no evidence of marine affinities in the associated mammalian fauna from the *Notostylops* beds (Simpson, 1948, 1967). Given these problems and the greater resemblance of early sirenians to Anthracobunidae, it appears that *Florentinoameghinia* has little bearing on the ancestry of Sirenia.

Other Orders

It is possible that an anthracobunid gave rise to Desmostylia, given trends toward serial tooth replacement and progressive addition of cusps seen in most early subungulate lineages. Desmostylians were amphibious kelp- or mussel-eating animals that lived along the northern Pacific coastline during Miocene times (Vanderhoof, 1937; Domning, 1978b). They had very unusual cheek teeth with thick, high, cylindrical cones of enamel, somewhat like extremely high-crowned mastodon molars. The teeth erupted sequentially, as in later proboscideans, and they had elephantine bodies with strong and heavy limbs (Romer, 1966, p.254). Their jaws were elongated and down-turned and they had upper and lower incisor tusks (like some proboscideans such as gomphotheres), but some apparently had an extra pair of tusks in their upper and/or lower jaws and their foreheads were flat instead of highly domed (Vanderhoof, 1937). Presumably desmostylians were not simply unusual proboscideans, but rather showed a remarkably long and complex parallel evolutionary history that in some ways anticipated characteristics of later mastodons. M_2 in desmostylians has six cusps that are arranged like the cusps on M_3 of *Pilgrimella* and moeritheriids. A seventh cusp is present on M_3 behind the doubled hypoconulid cusps, just as mastodons exhibit one or more extra posterior lophes. Desmostylian upper molars have eight cusps in an unusual pattern that is similar to, for example, *Pliomastodon* among proboscideans (fig. 89 in Osborn, 1936). An intermediate between Anthracobunidae and a typical desmostylian might have had very high and (initially) free-standing cusps with no remaining interconnecting crests.

Coombs and Coombs (1979) suggested that *Pilgrimella* was an extremely primitive perissodactyl. However, their argument relies considerably on *Pilgrimella* having an ectoloph on upper molars, which it lacks. Coombs and Coombs also discuss the many ways *Pilgrimella* differs from artiodactyls.

It is interesting that moeritheriids were amphibious and estuarine, living beside the central part of the Eocene Tethys seaway in Egypt. Early sirenians were fully aquatic and, like the seagrass on which some of them may have fed, had a para-Tethyan distribution. Primitive desmostylians may have resembled moeritheriids morphologically, and they had a pan-Pacific (east Tethyan?) distribution (Osborn, 1936; Reinhart, 1959, McCoy and Heck, 1976; Domning, 1976, 1978b; and Coppens and Beden, 1978). The early to middle Eocene age of Anthracobunidae and their morphological resemblances to moeritheriid proboscideans, primitive sirenians, and possibly desmostylians imply that anthracobunids are probably among the most primitive members of a Tethyan radiation of subungulates. The anthracobunid fossils shed no light, however, on the evolutionary position of Hyracoidea and Embrithopoda.

CONCLUSIONS

Jozaria palustris, a new bilophodont herbivore, is recorded from the early middle Eocene of Pakistan. It seems to have been amphibious, feeding on soft aquatic vegetation, and it probably lived in or near coastal marshes behind quiet embayments.

Jozaria is closely related to *Anthracobune pinfoldi*, *Pilgrimella pilgrimi*, and *Lammidhania wardi*, which are also recorded from the middle Eocene of Pakistan. *Pilgrimella pilgrimi* is also known from the lower Eocene of northern India. *Ishatherium subathuensis* from the early Eocene of India is apparently closely related to (if not synonymous with) *Pilgrimella*. The most obvious shared characteristics of all these species are high-cusped and bilophodont lower molars that lack paraconids. Upper molars have two transverse lophs that incorporate distinct central conules and lack ectolophs, producing an unobstructed transverse central valley.

Anthracobune, *Pilgrimella*, *Lammidhania*, *Ishatherium*, and *Jozaria* are grouped together in the new family Anthracobunidae. *Pilgrimella* seems to be the most distinct form, because it has two talonid cusps on P₃ and P₄, a short and broad M₂, and a double hypoconulid on M₃. Whether this morphology is primitive or derived can not yet be determined.

Anthracobunidae may have evolved from Asian phenacolephid Condylarthra(?). They appear plausibly to have given rise to Proboscidea and to Sirenia, and possibly to Desmostylia as well. Anthracobunids differ from these groups principally in lacking characteristic rostral specializations (elongated and/or downturned snouts, tusks, and supernumerary or lost premolars). They are therefore likely to be basal "tethytheres" (*sensu* McKenna, 1975). The initial stages of this radiation appear to have taken place along the Asian shores of central Tethys.

ACKNOWLEDGMENTS

We gratefully acknowledge officials of the Geological Survey of Pakistan for cooperation in making field research possible: in particular, we thank Dr. S.M.I. Shah, Director, and Mr. M. Asif Jah, Deputy Director, of the Paleontology and Stratigraphy Branch. Field research was funded by the Foreign Currency Program of the Smithsonian Institution and by a grant from the National Science Foundation (EAR 82-07256). Additional funds were awarded to N.A.W. by the Geological Society of America and Society of Sigma Xi. GSP-UM specimens were prepared by William J. Ryan, and the photographs in Figure 3 are by George Junne. Figures 1, 2 and 7 were drawn by Karen Klitz.

LITERATURE CITED

- ABEL, O. 1912. Die Eozänen Sirenen der Mittelmeerregion: I, *Eotherium aegypticum*. Paläontographica, 59: 289-358.
_____. 1914. Die vorzeitlichen Säugetiere. Fischer, Jena, 309 pp.
ANDREWS, C. W. 1906. A descriptive catalogue of the Tertiary Vertebrata of the Fayum, Egypt. British Museum of Natural History, London, 342 pp.
CHOW, M. and B. WANG. 1979. Relationship between the pantodonts and tillodonts and classification of the order Pantodonta. Vertebrata Palasiatica, 17: 37-48.
COOMBS, W. P. and M. C. COOMBS. 1979. *Pilgrimella*, a primitive Asiatic perissodactyl. Zoological Journal of the Linnean Society, 65: 185-192.

- COPPENS, Y. and M. BEDEN. 1978. Moeritherioidea, p. 333-335. *In* V. J. Maglio and H. B. S. Cooke (eds.), Evolution of African Mammals. Harvard University Press, Cambridge.
- DEHM, R. and T. zu OETTINGEN-SPIELBERG. 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, Mathematische-Naturwissenschaftliche Klasse, Abhandlungen, n.f., 91: 1-54.
- DOMNING, D. P. 1976. An ecological model for late Tertiary sirenian evolution in the North Pacific Ocean. *Systematic Zoology*, 25: 352-362.
- . 1978a. Sirenia, p. 573-581. *In* V. J. Maglio and H. B. S. Cooke (eds.), Evolution of African Mammals. Harvard University Press, Cambridge.
- . 1978b. Sirenian evolution in the North Pacific Ocean. *University of California Publications in Geological Science*, 118: 1-177.
- , G. S. MORGAN, and C. E. RAY. 1982. North American Eocene sea cows (Mammalia: Sirenia). *Smithsonian Contributions to Paleobiology*, 52: 1-69.
- GINGERICH, P. D. 1977. A small collection of fossil vertebrates from the middle Eocene Kuldana and Kohat Formations of Punjab (Pakistan). *Contributions from the Museum of Paleontology, University of Michigan*, 24(18): 190-203.
- , and D. E. RUSSELL. 1981. *Pakictus 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(11): 235-246.
- , N. A. WELLS, D. E. RUSSELL, and S. M. I. SHAH. 1983. Origin of whales in epicontinental remnant seas: new evidence from the early Eocene of Pakistan. *Science*, 220: 403-406.
- MATSUMOTO, H. 1923. A contribution to the knowledge of *Moeritherium*. *Bulletin of the American Museum of Natural History*, 48(4): 97-140.
- MCCOY, E. D. and K. L. HECK. 1976. Biogeography of corals, seagrass, and mangroves: an alternative to the center of origin concept. *Systematic Zoology*, 25: 201-210.
- McKENNA, M. C. 1975. Toward a phylogenetic classification of the Mammalia, p. 21-46. *In* W. P. Luckett and F. S. Szalay (eds.), *Phylogeny of the Primates: A Multidisciplinary Approach*. Plenum, New York, pp. 21-46.
- . 1981. Early history and biogeography of South America's extinct land mammals. *In* R. L. Ciochon and A. B. Chiarelli (eds.), *Evolutionary Biology of the New World Monkeys and Continental Drift*. Plenum, New York, pp. 43-77.
- , and E. MANNING. 1977. Affinities and paleobiogeographic significance of the Mongolian Paleogene genus *Phenacolophus*. *Geobios, Memoire Speciale*, 1: 61-85.
- OSBORN, H. F. 1921. The evolution, phylogeny, and classification of the Proboscidea. *American Museum Novitates*, 1: 1-10.
- . 1936. Proboscidea. I. *American Museum of Natural History*, New York, 802 pp.
- OWEN, R. 1855. On the skull of a mammal (*Prorastomus sirenioides*, Owen) from the island of Jamaica. *Quarterly Journal of the Geological Society of London*, 11: 541-543.
- . 1875. On *Prorastomus sirenioides* (Ow.), part II. *Quarterly Journal of the Geological Society of London*, 31: 559-567.
- PILGRIM, G. E. 1940. Middle Eocene mammals from north-west Pakistan. *Proceedings of the Zoological Society, London, Series B*, 110: 127-152.
- REINHART, R. H. 1959. A review of the Sirenia and Desmostylia. *University of California Publications in Geological Science*, 36(1): 1-146.
- ROMER, A. S. 1966. *Vertebrate Paleontology* (3d. Ed.). University of Chicago Press, Chicago, 468 pp.
- SAHNI, A. and S. K. KHARE. 1973. Additional Eocene mammals from the Subathu Formation of Jammu and Kashmir. *Journal of the Palaontological Society of India*, 17: 31-49.
- , 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 Paleontological Society of India*, 23: 132-135.
- SAVAGE, R. J. G. 1976. Review of early Sirenia. *Systematic Zoology*, 25: 344-351.
- SCHAFFER, W. 1972. *Ecology and Paleocology of Marine Environments*. (Translated by I. Oertel; G. Y. Craig, ed.) Oliver and Boyd, Edinburgh.
- SERENO, P. C. 1982. An early Eocene sirenian from Patagonia (Mammalia, Sirenia). *American Museum Novitates*, 2729: 1-10.
- SIMPSON, G. G. 1932a. Fossil Sirenia of Florida and the evolution of the Sirenia. *Bulletin of the American Museum of Natural History*, 9: 419-504.
- . 1932b. The supposed association of dinosaurs with mammals of Tertiary type in Patagonia. *American Museum Novitates*, 566: 1-21.

- _____. 1948. The beginning of the age of mammals in South America, Part 1. Bulletin of the American Museum of Natural History, 137: 1-232.
- _____. 1967. The beginning of the age of mammals in South America, Part 2. Bulletin of the American Museum of Natural History, 137: 1-259.
- TASSY, P. 1979. Relations phylogénétiques du genre *Moeritherium* Andrews, 1901 (Mammalia). Comptes Rendus de l'Académie des Sciences, Paris, 289D: 85-87.
- _____. 1981. Le crâne de *Moeritherium* (Proboscidea, Mammalia) de l'Éocène de Dor el Talha (Libye) et le problème de la classification phylogénétique du genre dans les Tethytheria McKenna, 1975. Bulletin du Museum National d'Histoire Naturelle, ser. 4, 3, sec. C, no. 1, p. 87-147.
- VANDERHOOF, V. L. 1937. A study of the Miocene sirenian *Desmostylus*. Bulletin of the Department of Geological Sciences, University of California Publications, 24(8): 169-262.
- WALL, W. P. 1983. The correlation between high limb-bone density and aquatic habitats in recent mammals. Journal of Paleontology, 7(2): 197-207.
- WELLS, N. A. 1980. Nearshore marine and continental facies in the Eocene of north-central Pakistan (Abstract). American Association of Petroleum Geologists Bulletin, 64(7): 537.
- _____. 1983. Transient streams in sand-poor redbeds: early/middle Eocene Kuldana Formation of north-central Pakistan. Special Publication of the International Association of Sedimentologists, 6: 393-403.
- _____. In prep. Geological history of the youngest (Eocene) seas in pre-Himalayan north-central Pakistan. Ph.D. dissertation, University of Michigan.
- WEST, R. M. 1980. Middle Eocene large-mammal assemblage with Tethyan affinities, Ganda Kas region, Pakistan. Journal of Paleontology, 4: 508-533.
- ZHANG, Y. 1978. Two new genera of condylarthran phenacolophids from the Paleocene of Nanxiong Basin, Guangdong. Vertebrata Palasiatica, 16: 267-274.
- _____. 1980. *Minchenella*, new name for *Conolophus* Zhang, 1978. Vertebrata Palasiatica, 18: 257.

