CONTRIBUTIONS FROM THE MUSEUM OF PALEONTOLOGY

THE UNIVERSITY OF MICHIGAN

VOL. 27, NO. 7, p. 151-193 (3 plates) March 15, 1987

LOWER VERTEBRATES FROM THE EARLY-MIDDLE EOCENE KULDANA FORMATION OF KOHAT (PAKISTAN):

HOLOSTEI AND TELEOSTEI

BY

MIREILLE GAYET

CHELONIA

BY

FRANCE DE BROIN

SQUAMATA

BY

J. C. RAGE

MUSEUM OF PALEONTOLOGY
THE UNIVERSITY OF MICHIGAN
ANN ARBOR

CONTRIBUTIONS FROM THE MUSEUM OF PALEONTOLOGY

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 upon 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.

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

LOWER VERTEBRATES FROM THE EARLY-MIDDLE EOCENE KULDANA FORMATION OF KOHAT (PAKISTAN): HOLOSTEI AND TELEOSTEI

by

Mireille Gayet[1]

Abstract.—At least nine families belonging to six orders of holostean and teleostean fishes have been identified in the Kuldana Formation (early-middle Eocene) of Pakistan. Their association characterizes a freshwater deposit. The presence of some families on the Indian plate early in the Eocene could provide supplementary evidence for the paleogeographic relationships of India, on one hand with Southeast Asia and Australia (Gondwana), and on the other, with Laurasia (probably during Paleocene time).

Résumé. - Neuf familles, au moins, appartenant à six ordres d'Holostéens et ont été identifiées dans la Formation Kuldana (Eocène inférieur-moyen) du Pakistan. Leur association définit un milieu d'eau douce. La présence de certaines familles sur la plaque indienne à l'Eocène inférieur permet d'apporter des renseignements quant aux relations paléogéographiques de l'Inde, d'une part avec le sud-est asiatique et l'Australie et d'autre part avec l'Europe (probablement dès le Paléocène).

INTRODUCTION

Early Cenozoic fishes of the Indo-Pakistan subcontinent are still poorly known. Most of the remains described here were collected from the Kuldana Formation at Chorlakki, Kohat District, Pakistan. A few were collected from the Kuldana Formation at Shekhan Nala, another locality in Kohat District, Pakistan. Taxa found at Shekhan Nala are always found also at Chorlakki, but the opposite is not true. In spite of their fragmentary character, the affinities of most can be approximately determined. A minimum of six, and possibly seven, orders are represented (Table 1).

---

[1] Centre National de la Recherche Scientifique (UA 12), Institut de Paléontologie, Muséum National d'Histoire Naturelle, 8 rue Buffon, Paris 75005 FRANCE.

TABLE 1 — Faunal list of early-middle Eocene actinopterigian (Holostei and Teleostei) fish remains from Chorlakki (*C*) and Shekhan Nala (*S*), Kohat District, Pakistan.

- Perciformes
  - Percichthyidae
    - *Macquaria antiquus* (Hills) 1934 (*C*)
- Siluriformes
  - Bagridae
    - Genus and species indet. (*C*)
  - Clariidae
    - Genus and species indet. (*C*, *S*)
  - Ariidae
    - Genus and species indet. (*C*)
  - Family *incertae sedis*
    - Genus and species indet. (*C*)
- Cypriniformes
  - Cyprinidae
    - Genus and species indet. (*C*)
    - Cf. *Varohstichthys* sp. (*C*)
- Cyprinodontiformes
  - Cyprinodontidae
    - Genus and species indet. (*C*)

- Osteoglossiformes
  - Osteoglossidae
    - Genus and species indet. (*C*, *S*)
- Lepisosteiformes
  - Lepisosteidae
    - *Lepisosteus* sp. (*C*)
- Order indet.
  - Acanthopterygii *incertae sedis* (*C*, *S*)

ABBREVIATIONS

The following abbreviations are used in the text and figures:

art.cav.Cl	articular cavity of the cleithrum
art.cav.Q-md	cavity of the mandible for articulation of the quadrate
art.fa.exoc	facet of the first vertebra for articulation with exoccipital
axial.pr	axial process of the pectoral spine
cond	condyle of the pectoral spine for articulation with the cleithrum
cor.pr	coronoid process
dep.ar	depressed area
dist.pr	distal process of pectoral spine
epi.pr.Pt	process of the posttemporal for the epiotic
gr.s	grinding surface
int.pr.Pt	process of the posttemporal for the intercalar
int.pr.Q	internal process of the quadrate
i.o.c	infraorbital sensory canal
h	hook

la.ethm.pr	process of the lateral ethmoid
lat.op	lateral opening of the tubular basal part of the tooth
lat.pr.Bocc	lateral process of the basioccipital for articulation with cleithrum
lo.pr	locking process of the dorsal spine
md.c	mandibular sensory canal
med.pad	medial pad of abdominal vertebra
n.a	neural arch
par	parapophysis
prox.pr	proximal process of pectoral spine
pzyg	postzygapophysis
ret.pr	retroarticular process of the angular
S.gr	groove on the quadrate for the symplectic
trab	longitudinal trabecula
tub	squamule internal tubercula

SYSTEMATIC PALEONTOLOGY

Order PERCIFORMES
Family Percichthyidae
Genus *Macquaria** Cuv. & Val.

Macquaria antiquus (Hills) 1934
Figs. 1-5

Referred specimens.—The following specimens from Chorlakki are referred to *Macquaria antiquus*: GSP-UM 450, left lachrymal; GSP-UM 451-452, preopercular spine fragments; GSP-UM 453, left posttemporal; GSP-UM 454, anteriormost abdominal vertebra; GSP-UM 455, posterior abdominal vertebra; GSP-UM 456, hemaxanal complex; GSP-UM 457, spine of dorsal fin; and several fragments of dorsal and anal spines.

Description.—The lachrymal or first interorbital (Fig. 1) is a bone of crescent shape, enlarged anteriorly. Its lower border, smooth along the anterior third of its length, is ornamented along the posterior two-thirds with eleven spines; the first three project anteriorly, the next five project ventrally, and the last four project posteriorly. The first spine is slightly larger than the others. The upper border is of convex shape, with two corners on the first and the second third of its length. The lateral ethmoid process (*la.ethm.pr*) is low. Posteriorly, the second infraorbital extends to a deep cavity in the lachrymal. The groove of the sensory canal (*i.o.c*) is totally open posteriorly and closed anteriorly; at this level, it opens only by three pores: the largest one is situated just above the first spine and the two others, smaller, are situated more anteriorly.

Two spine fragments are thought to represent the preopercular. The spines are well individualized, thick and narrow. They compare favorably with the spines of the preopercular of *Macquaria antiquus* (Hills, 1934, fig. 11b).

**Percalates* Ramsay and Ogilby is considered to be a junior synonym of *Macquaria* Cuvier and Valencienne (MacDonald, 1978).

The posttemporal (Fig. 2) is a classical forked-bone with a short stout ventral limb articulating with the intercalar (*int.pr.Pt*), and a longer, but broken, dorsal limb articulating with the epiotic (*epi.pr.Pt*). This dorsal limb is followed on the external surface by a broad pad. The entire external surface is ornamented with thin, longitudinal ridges.

The neural arch and spine of the anteriormost vertebrae (Fig. 3) are autogenous. They join in the middle of the upper area of the centrum between the two facets for the articulation with the exoccipital (*art.fa.exoc*). The anterior face of the centrum, in front of the basioccipital, is circular, the posterior face in front of the second vertebra is higher than broad. Posteriorly, two postzygapophyses (*pzyg*) articulate by their lower face on the upper face of the prezygapophyses of the second vertebra. In lateral view, there are numerous cavities of various shapes, separated by more or less broad trabeculae of bone. A large round cavity is situated just behind and below the postzygapophysis: it may have been for the insertion of a rib, but this is not certain (a similar but broader cavity is present on the anteriormost vertebra of *Lates*, but the first rib is inserted only on the third vertebra).

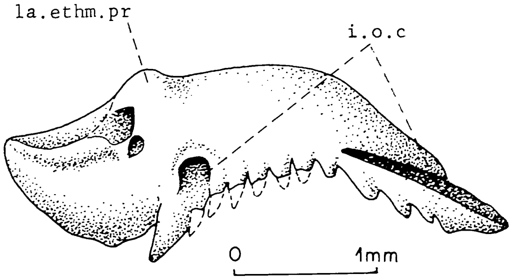
The posterior abdominal vertebra (Fig. 4) is slightly distorted. It is characterized in its median part by hour-glass shaped ornamentation with thin longitudinal trabeculae. Such trabeculae can be observed among the Centropomidae (*Lates*) and Percichthyidae (*Macquaria* and *Percichthys*). The neural arch is broad and relatively high. The neural spine is not preserved. Ventrally, there are two very small posterior parapophyses.

A fragment of a bone is thought to be an hemaxanal complex. It is characterized by two facets of articulation for two spines, separated by a median process.

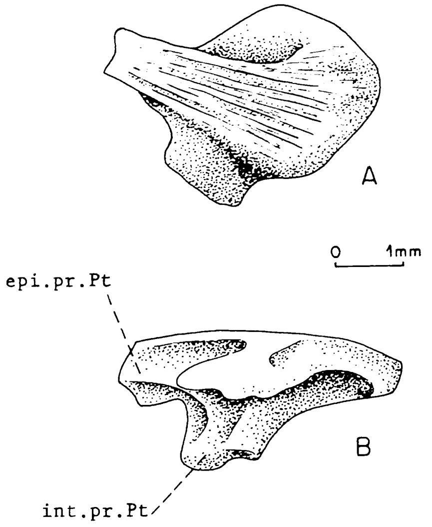
Spines of the dorsal and anal fins are known (Fig. 5). There is nothing special permitting comparison of spines among Acanthopterygii. All have one relatively narrow base and two strong locking processes (*lo.pr*).

Discussion.—The affinities of *Macquaria* and the paleobiogeography of Percichthyidae require discussion. If, as we suppose, the remains described here represent a single taxon, the association of dorsal and anal spines, an hemaxanal complex, and anteriormost vertebrae with autogenous neural arches, permits attribution of this taxon to Perciformes. Spines of unpaired fins and an hemaxanal complex are also present among Beryciformes, but no representatives of this order yet described, either fossil (Gayet, 1978a,b; 1980a,b; 1982a; Sorbini, 1979a,b), or living (Zehren, 1979), possess a first autogenous arch located between two exoccipital articular facets on the centrum. Independancy of the first neural arch was noted by Ford (1937:43) in several families of Perciformes. This feature had been observed among Serranidae (Mordant, 1965) and among Percichthyidae (Hill, 1934; pers. obs.). The latter, considered by several authors as the most generalized among Perciformes, is known since the Danian in Sweden, where it is represented by *Proserranus ludensis* (Davis). Another Paleocene serranid, *Prolates*, is known by a single species *P. heberti* Priem from the Montian of France. It is difficult to compare these two genera with the Pakistani fish because of differing modes of preservation. Several Serranidae have been recognized in Europe since the Eocene: *Properca*, *Dapalis*, *Cyclopoma*, *Anthrocoperca*, *Amphiperca*, and *Bilina*. Only *Dapalis* (Mordant, 1965) and *Cyclopoma* (Sorbini-Frigo & Sorbini 1975) are sufficiently well studied to provide valuable comparison with the Pakistani remains. Specimens described here differ from *Dapalis* in having an anteriormost vertebra characterized by a fully reticulated system of trabeculae, and from *Cyclopoma* in the configuration of the lachrymal and infraorbital sensory canal.

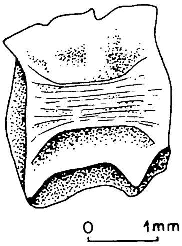
Three fossil fishes, *Eoserranus*, *Macquaria* and *Percichthys* are of particular interest. *Eoserranus* was described by Woodward (1908) based on remains discovered in the early Eocene of Dongargaon (India). Unfortunately, the lachrymal is not preserved, and it is not possible to observe the anteriormost vertebra. Comparison with *Serranus*, a genus close to *Macquaria*, shows that the lachrymal of all its species is smooth or slightly denticulated. Also, none of the



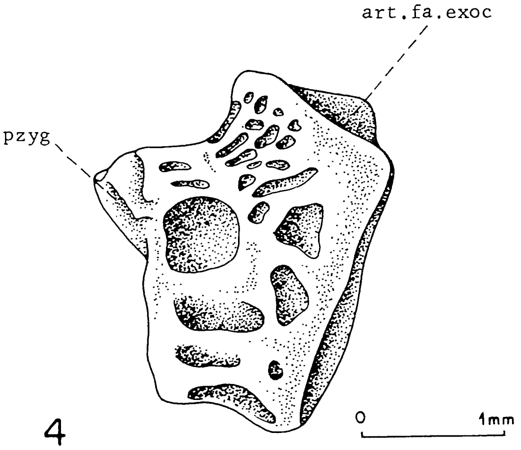
1



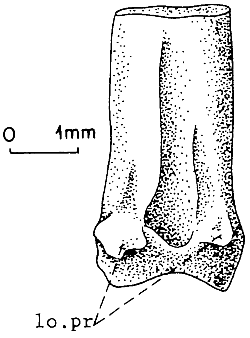
2



3



4



5

FIGS. 1 - 5— Perciform percichthyid *Macquaria antiquus* (Hills) from Chorlakki. FIG. 1: First left infraorbital in lateral view (GSP-UM 450). FIG. 2: Left posttemporal in dorsal view (A) and lateral view (B) (GSP-UM 453). FIG. 3: Anteriormost vertebra in lateral view (GSP- UM 454). FIG. 4: Posterior abdominal vertebra in lateral view (GSP-UM 455). FIG. 5: Dorsal spine in posterior view (GSP-UM 457).

abdominal vertebrae have longitudinal trabeculae. The living genus *Percichthys* is known in the Eocene of Patagonia (Schaeffer 1947a, b) and seems to be limited to this landmass. Its comparison with the Pakistani specimens is difficult, but it is possible to observe that it does not possess an hemaxanal complex and that the two first proximal axonostes would be completely separated (Schaeffer, 1947b, text-fig. 3).

Comparison of the lachrymals of *Macquaria* and the Pakistani remains described here shows that in these two forms the groove of the sensory canal has an identical configuration, with a long gutter opening posteriorly and a broad pore opening anteriorly. The ethmoidian process, also, is not very high. The principal difference is that the lower border, concave in the Pakistani remains, is convex in *Macquaria*. The vertebrae of *Macquaria* show a nearly perfect similarity to those from Pakistan: longitudinal trabeculae are present, and reticulated trabeculae are absent.

All of the pharyngeal teeth of *Macquaria* are narrow and sharp [personal observation on *M. colonorum*, and observation by Hills, 1934, on *Macquaria* (= *Percalates*) *antiquus*]. Fish teeth have been found at both Chorlakki and Shekhan Nala, and some may prove referrable to *Macquaria* (although teeth of this genus have not yet been confidently identified). In any event, despite the small number of remains discovered in Chorlakki, the fish described here does appear to be related to *Macquaria*, as determined by the configuration of both the abdominal vertebrae and the lachrymal. It is assigned to the species *M. antiquus* (Hills) because of similarity in structure of the preopercular spines.

The distribution of living Percichthyidae is discontinuous, including southern South America, eastern North America, southeastern Australia, and northeastern Asia (Fig. 6). This distribution was undoubtedly more extensive in the past: Percichthyidae have recently been discovered in the late Tertiary of Brazil (Arratio, 1982), the late Cretaceous (Maestrichtian) El Molino Formation of Bolivia (de Muizon *et al.,* 1983, 1984), the Vilquichico Formation of Peru (pers. obs.), and in several Tertiary localities in Europe. Consequently, the origin of Percichthyidae as freshwater forms (percichthyids were previously supposed to have evolved from a generalized marine group like Serranidae) is likely to have been Gondwanan.

The Indian subcontinent was separated from the rest of Gondwana by the early Cretaceous. Thus the phylogenetic origin of Percichthyidae may be even older. Colonisation of northeastern Asia and Australia could have been realized in two ways: (1) Discovery of supposed Percichthyidae in the Paleogene of Europe (Obrhelova 1970; Gaudant, 1981) could be explained by the theory of intermediate landmasses between Laurasia and India (Sahni *et al.*, 1982) in Paleocene times. Then dispersal of Percichthyidae could be from Laurasia through eastern Asia and, at the end of the Miocene, to Australia. (2) Alternatively, taking into account the theory (Ridd, 1971) that southeastern Asia, India, and Australia were joined together and constituted a separate part of Gondwana, dispersion into northeastern Asia and Australia becomes simplified and extremely easy.

Order SILURIFORMES

Detailed study of separate bones of the African and Asiatic siluriform genera and species has never been completed, and thus it is difficult to confidently assign isolated bones (or fragments of bones) to particular genera. Consequently, identification of the siluroid remains found at Chorlakki and at Shekhan Nala is tentative, and assignment is made only to family.

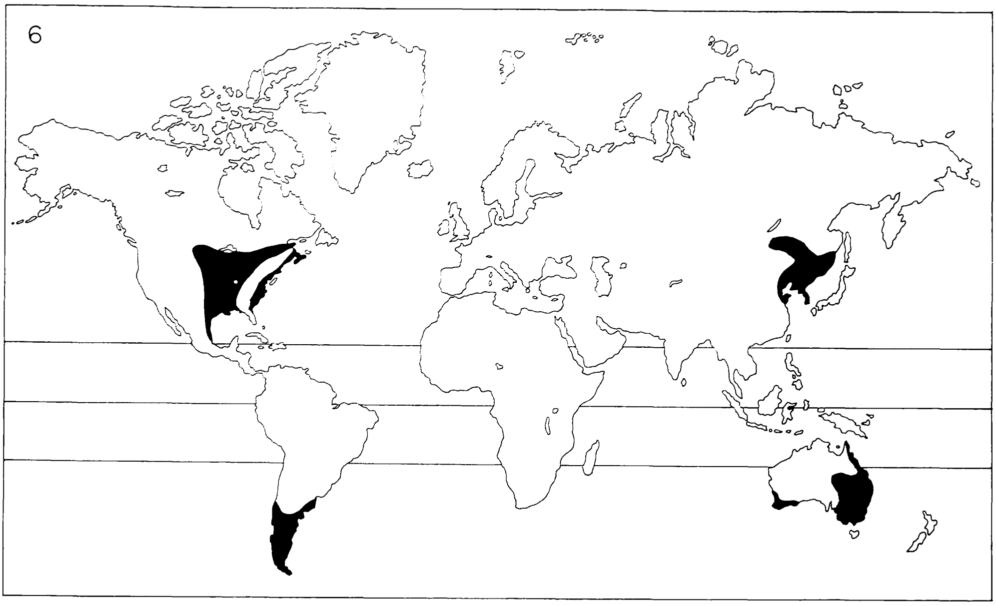


FIG. 6— Worldwide geographic distribution of Percichthyidae (from Berra, 1981).

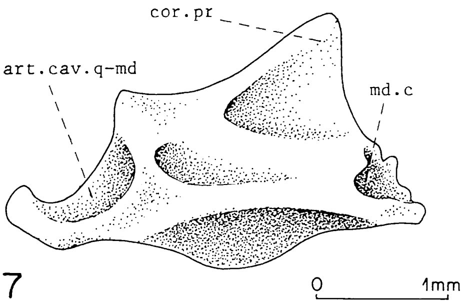
Family Bagridae
Figs. 7-10

Referred specimens.—The following specimens from Chorlakki are referred to Bagridae: GSP-UM 458, angular; GSP-UM 459, cleithrum; and GSP-UM 460-461, pectoral spines.

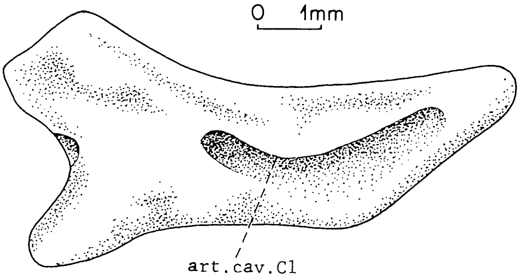
Description.—The angular (Fig. 7) is characterized by a well developed articular cavity for the quadrate (*art.cav.Q.md.*), which is deep and situated in an oblique position relative to a horizontal line. It is limited posteriorly by a well developed retroarticular process. At this level, the mandible is very low. In front of the articular cavity for the quadrate, the angular border rises swiftly, and then makes a curved concave line before the coronoid process (*cor.pr*) which is triangular, relatively narrow but high. The sensory canal (*md.c*) runs in a closed groove, opening posteriorly as a round pore just in front of the articular cavity.

Only one fragment of a left cleithrum is known (Fig. 8). It is approximately triangular in shape with curved lines, and it possesses a short strong spine oriented backward. In medial view, a long deep bean-shaped cavity matches the articulation of the pectoral spine (*art.cav.Cl*). The external surface is smooth, without ornamentation.

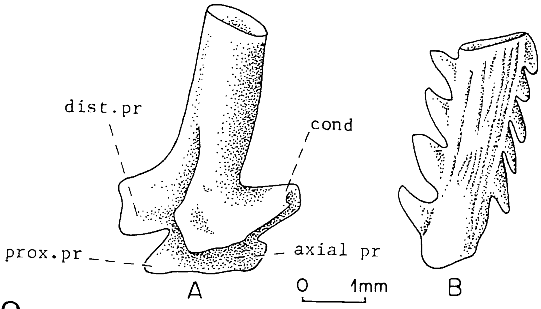
Several pectoral spines (e.g., Fig. 9) are thought to belong to this family, owing to the morphology of their articular base. The three articular processes have a special configuration, consisting of: (1) a lower proximal process (*prox.pr*), used for locking the spine towards the cleithral cavity (when the spine is extended from the body); (2) a lower distal process (*dist.pr*), used for locking the spine backward (when the spine is pressed against the body); and (3) an upper axial process (*axial.pr*), used both as a pivot for the spine during movement and in locking it backward. Both lower processes are subparallel and close together, while the axial process is well separated and more vertical in comparison to the proximal process. The condyle (*cond*) is nearly semicircular in shape. It is probable, but not certain, that the fragments of pectoral spines



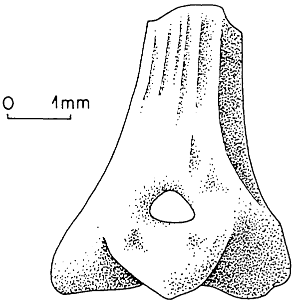
7



8



9



10

FIGS. 7 - 10— Siluriform Bagridae from Chorlakki. FIG. 7: Left angular of Bagridae *incertae sedis* in medial view (GSP-UM 458). FIG. 8: Left cleithrum of Bagridae *incertae sedis* in lateral view (GSP-UM 459). FIG. 9: Left pectoral spine of Bagridae *incertae sedis*; base (A), and fragment of shaft (B) (GSP-UM 460). FIG. 10: Base of dorsal spine of Bagridae *incertae sedis* in frontal view (GSP-UM 461).

with tooth-like serrated and medial faces belong to this family. None of the two other families present at Chorlakki, Arridae and Clariidae, appear to have had such sharp pectoral spines.

Dorsal spines with parallel longitudinal lines like the one illustrated here (Fig. 10) are assigned to Bagridae. Clariidae do not possess dorsal spines, and Ariidae have a dorsal spine with very special granulous ornamentation.

Family Clariidae
Figs. 11-12

Referred specimens.—The following specimens from Chorlakki are referred to Clariidae: GSP-UM 463, articular; and GSP-UM 464, pectoral spines. GSP-UM 771, pectoral spines, are from Shekhan Nala.

Description.—An angular is referred to Clariidae (Fig. 11). It is low, and the cavity or articulation for the quadrate is elongated and situated in a quasi-horizontal position. There is no marked retroarticular process. In front of this cavity, the upper border of the angular is nearly horizontal and parallel with the lower border. A deep elongate cavity occurs on the lateral surface just in front of the articular cavity for the quadrate, becoming less distinct anteriorly.

Several pectoral spines (Fig. 12) are thought to belong to this family for the following reasons: (1) the distal process (*dist.pr*) is very narrow and not square-shaped as in Bagridae; (2) the proximal process (*prox.pr*) is more central; (3) the axial process (*axial.pr*) is nearly non-existent; and (4) the condyle (*cond*) represents only a quarter of a circle and is therefore more reduced than in Bagridae.

Discussion.—Clariidae are representated today by eight living genera. The family is known by only two fossil genera, *Clarias* Gronow and *Heterobranchus* Geoffroy St-Hilaire, which are not clearly different osteologically. The two extinct genera (especially *Heterobranchus*) are characterized by a very low angular like that seen here.

Family Ariidae

Fig. 13

Referred specimens.—The following specimen from Chorlakki is referred to Ariidae: GSP-UM 465, abdominal vertebra.

Description.—Several abdominal vertebrae (including GSP-UM 465) are thought to belong to this family (Fig. 13). They are characterized in lateral view by their "double" aspect, caused by a median pad (*med. pad*) that becomes indistinct towards the distal extremity of the parapophyses (*par*). The latter enlarged, terminates with a quadrate shape. The border of the centrum is always very thick.

Discussion.—The same type of vertebra was discovered in the late Cretaceous of Bolivia (Gayet, in preparation) and may belong to the Ariidae. This is a marine family of tropical and subtropical areas and some may enter estuaries and coastal rivers, explaining their presence in the South American and Pakistani localities, both otherwise regarded as freshwater deposits.

Siluriformes *incertae sedis*

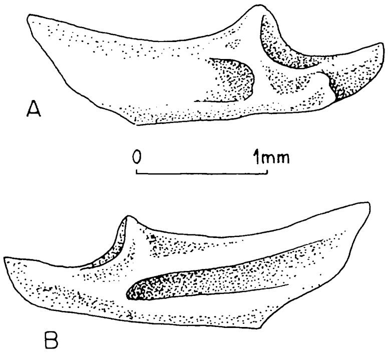
Fig. 14

Referred specimens.—The following specimen is referred to Siluriformes *incertae sedis*: GSP-UM 466, basioccipital.

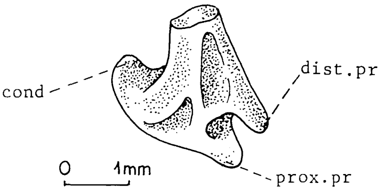
Description.—One basioccipital (Fig. 14) unquestionably represents a siluriform fish. It is characterized by the presence on its lower face of two lateral processes (*lat.proc.Bocc*) for articulation of the lower branches of the cleithrum. There is a round cavity at the lower and posterior part of the bone.

Discussion.—This basioccipital differs in detail from those of all families of Siluriformes with which it was compared, and it differs distinctly from basioccipitals of the three families recognized above. The only positive comparison is with the Ictaluridae, a North American family known from the Eocene (living records of this family in other parts of the world, principally those in China, are likely to be a result of recent introduction; Berra 1981:70). I prefer to assign this basioccipital to Siluriformes *incertae sedis*.

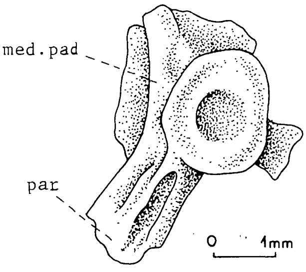
Siluriformes are represented at Chorlakki and at Shekhan Nala by at least three families. The present distribution of Clariidae and Bagridae is nearly identical: Africa, India, and Asia (Fig. 15; Bagridae have a more extended distribution in Asia), suggesting a Gondwanan origin for these two families.



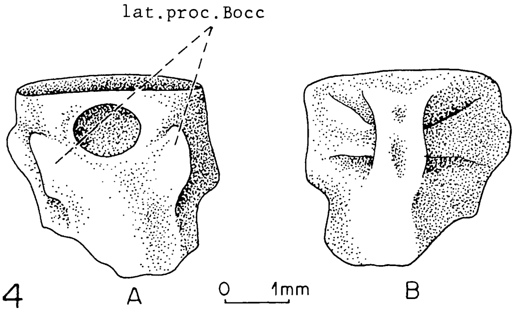
11



12



13



14

FIGS. 11 - 14— Siluriform Clariidae and Ariidae from Chorlakki. FIG. 11: Right angular of Clariidae *incertae sedis* in medial view (A), and lateral view (B) (GSP-UM 463). FIG. 12: Base of left pectoral spine of Clariidae *incertae sedis* (GSP-UM 464). FIG. 13: Abdominal vertebra of Ariidae *incertae sedis* in frontal view (GSP-UM 465). FIG. 14.- Basioccipital of Siluriformes *incertae sedis* in ventral view (A) and dorsal view (B) (GSP-UM 466).

Ariidae have a worldwide marine distribution along coasts and sometimes enter freshwater river systems (Fig. 16). They are the oldest family of Siluriformes known anywhere in the world, coming from the late Cretaceous (Maastrichtian) of Bolivia (de Muizon *et al.*, 1983, 1984).

Order CYPRINIFORMES
Family Cyprinidae
Figs. 17-18

Referred specimens.—Two teeth from Chorlakki, GSP-UM 479 and GSP-UM 480, appear to belong to the fifth pharyngeal of a cyprinid.

Description.—One pharyngeal tooth is a small and globular in shape (Fig. 17), oval in cross-section, with a slightly blunt hook (*h*) whose height is about one-third of total crown height. The hook is slightly bent above a narrow, moderately developed grinding surface (*gr.s*). Because of the variability of teeth in different rows on the fifth pharyngeal, it is very difficult to assign any isolated tooth to a particular genus. This particular tooth seems more globular and lower crowned than all teeth compared. Brittan (1961: 20) notes that primitive teeth of Cyprinidae are "basically conical, moderately compressed, pointed but slightly recurved, with the grinding

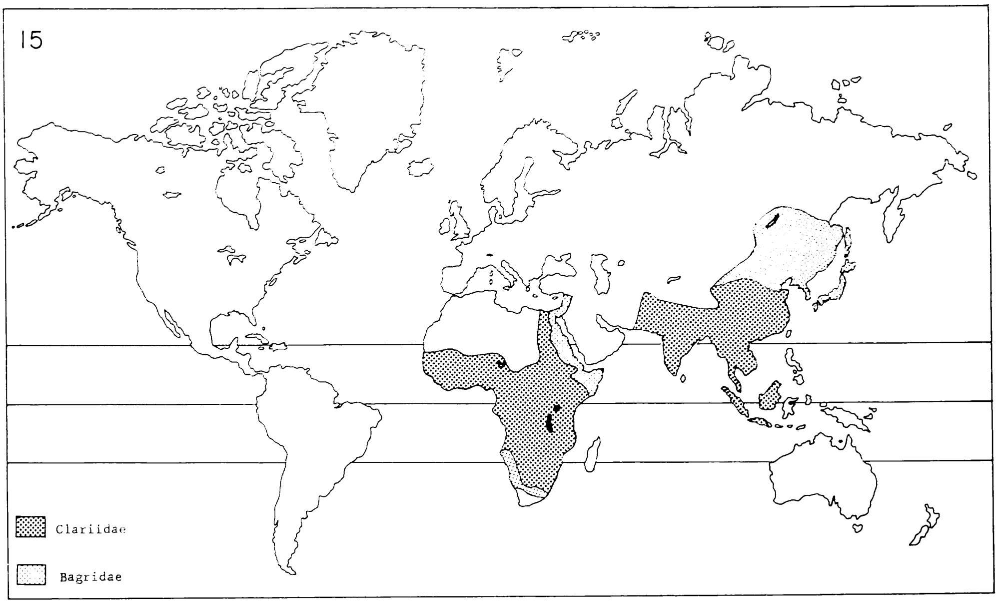


FIG. 15— Worldwide geographic distribution of siluriform Bagridae and Clariidae (from Berra, 1981).

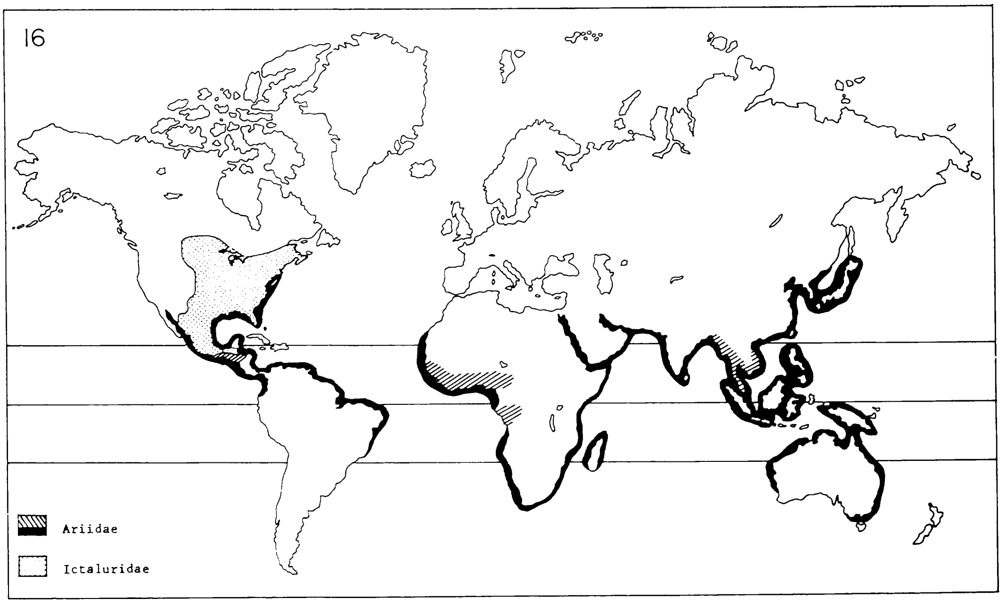
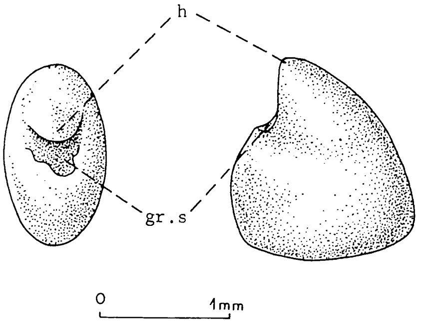
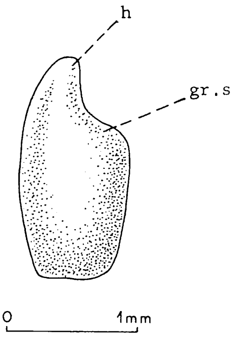


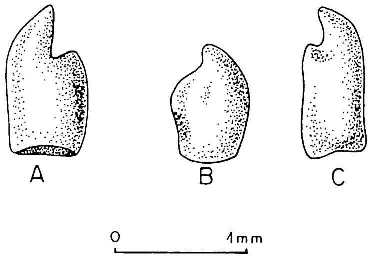
FIG. 16— Worldwide geographic distribution of siluriform Ariidae and Ictaluridae (from Berra, 1981).



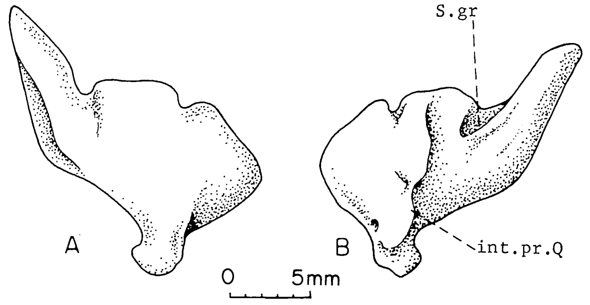
17



18



19



20

FIGS. 17 - 20— Cypriniform Cyprinidae and cyprinodontiform Cyprinodontidae from Chorlakki. FIG. 17: Fifth pharyngeal tooth of Cyprinidae *incertae sedis* (GSP-UM 479). FIG. 18: Fifth pharyngeal tooth of cyprinid Cf. *Varohstichthys* (GSP-UM 480). FIG. 19: Pharyngeal teeth of Cyprinodontidae *incertae sedis* (GSP-UM 467-469). FIG. 20: Right quadrate of Cyprinodontidae *incertae sedis* in lateral view (A) and medial view (B) (GSP-UM 472).

surfaces narrow and only moderately developed." The Pakistani tooth fits this description. However, it seems that this tooth is shorter and broader than those of generalized pharyngeals. This tooth probably belongs to an outer row of a fifth pharyngeal, where the teeth are generally more globular.

The second tooth (Fig. 18) is more elongated. The hook (*h*) is scarcely formed and slightly bent over a depressed area (*dep.ar*) not differentiated into grinding surface. This tooth may be referable to *Varhostichthys* as it compares closely to one figured by Obrhelova (1970, fig. 8), but this is not certain.

Discussion.—The oldest cypriniform fishes known from the Asiatic and African landmasses are Miocene in age. In Europe the genus *Blicca* is known from the Paleocene. One genus, *Chanoides*, from the Eocene of Monte Bolca, is marine (Patterson, 1984). The oldest cyprinid known to date is from the late Cretaceous (Maastrichtian) of Bolivia (Gayet, 1982b). Taking into account the theory of intermediate landmasses between Laurasia and India in Paleocene times, the Pakistani cyprinid could be derived from a Paleocene European form.

It is also possible to consider Tethyan origin for cyprinids, as suggested by discovery in the Cenomanian of Isreal of *Ramallichthys* possessing a rudimentary Weberian apparatus (Gayet, 1982c, 1983, 1986). In this case, rapid dispersion into freshwater of all circum-Tethyan landmasses would be required.

Order CYPRINODONTIFORMES

Family Cyprinodontidae

Fig. 19-20

Referred specimens.—The following specimens from Chorlakki are referred to cyprinodontidae: GSP-UM 467-469, a large number of teeth, and GSP-UM 472, quadrate.

Description.—These teeth are small and characterized by an oval shaped body, more or less bulbous, surmounted on one side by a blunt point somewhat recurved on the body of the tooth (Fig. 19). In front of the hook, which may be well or poorly developed, the basal part of the tooth has either a poorly defined globular process (Fig. 19A,B) or a small well defined one (Fig. 19C). All forms of the process occur between these two extremes, and all are generally laterally compressed.

The quadrate (Fig. 20) is thought to be referable to an undetermined cyprinodontiform. Despite its unusually large dimensions for this family (the same observation could be made also about the dimensions of the teeth), it is characterized on its medial face by a well developed internal process (*int.pr.Q*) which exists in some representatives of this order. The sympletic groove (*S.gr*), very short on its medial face, does not indent the upper border of the quadrate. The posterior border of the quadrate is very long (twice as long as the anterior one) and forms a well developed process located along the posterior border of the symplectic, as found in some cyprinid genera. However, in cyprinids there is nearly always an anterior process just under the insertion of the ectopterygoid.

Discussion.—The teeth described here are similar to the pharyngeal teeth of some Cyprinodontidae, such as *Aphanius*, but they are not referable to that genus. No mandibular or maxillary teeth have yet been found. Cyprinodontidae are known from the Oligocene of Europe (*Prolebias*) and North America (*Parafundulus*). The genus *Lithopoecilus* Beaufort is known from the Tertiary of India. It is still not possible to know if the Pakistani teeth described here are related to *Lithopoecilus*, or if they may represent one or more of the 45 genera living in Asia today. For this reason, all are identified only to family Cyprinodontidae, whose modern distribution includes Pakistan (Berra 1981:111).

Order OSTEOGLOSSIFORMES

Family Osteoglossidae

Fig. 21

Referred specimens.—The following specimens from Chorlakki are referred to Osteoglossidae: GSP-UM 474-477, more than 100 small plates of various shapes. GSP-UM 768, about 20 squamules.

Description.—A large sample of small plates (Fig. 21) have been found at Chorlakki. These represent the squamules of scales typical of Osteoglossiformes. Scales of representatives of this order are characterized by the absence of circuli and the presence of ridges delimiting small plates called squamules (Meunier, 1982). When sediment containing these scales is washed in an acid solution, the plates become detached and separate from one another. The plates are angular and have a uniform thickness. On the lower face each plate is excavated and encircled with a flattened ridge. On most plates the internal surface is smooth (Fig. 21B,D), while others have tubercles which sometimes seem to be included in an outgrowth of the crest (Fig. 21D). The external surface shows an ornamentation made of very small tubercles, well separated and sometimes arranged linearly (Fig. 21A,C).

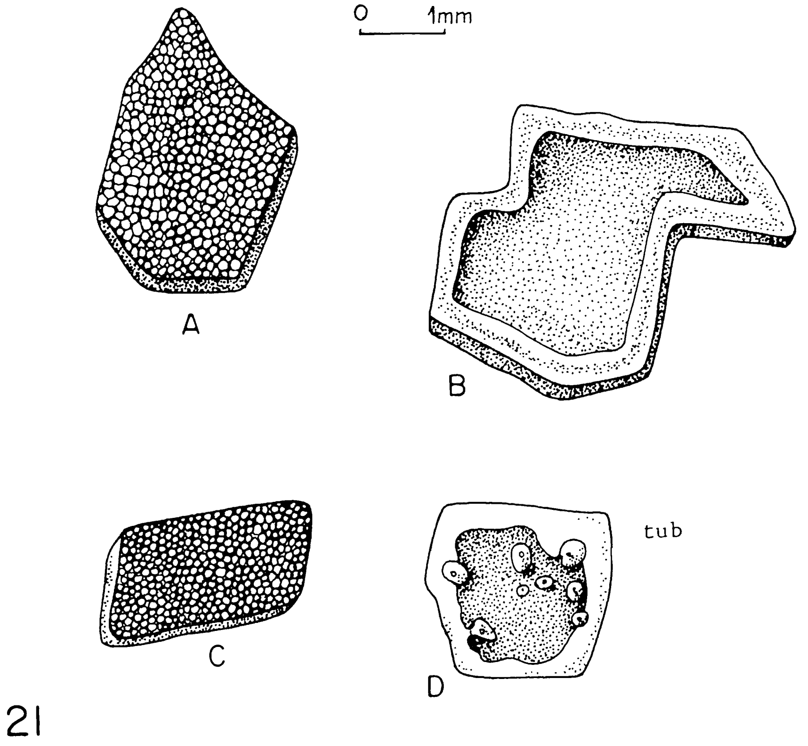


FIG. 21— Squamules of scales of Osteoglossidae *incertae sedis* from Chorlakki. (A) (GSP-UM 474) in dorsal view. (B) (GSP-UM 475) in ventral view. (C) (GSP-UM 476) in dorsal view. (D) (GSP-UM 477) in ventral views.

Discussion.—The relationships and paleobiogeography of the Osteoglossidae are discussed in detail in Gayet and Meunier (1983). Comparison of the squamules found in Pakistan with those found in Bolivia shows that the two are very similar. In Bolivia, two families have been recognized (de Muizon *et al.,* 1983, 1984): Osteoglossidae and Hiodontidae. Among the Osteoglossiformes, it seems that only Osteoglossidae and the fossil *Brychaetus* have reticulated scales. In the other families, the scales have only circuli (Taverne, 1977, 1978). These observations agree with relationships suggested by Patterson (1975), where *Brychaetus* is placed as a sister-group of the Osteoglossidae.

Order LEPISOSTEIFORMES
Family Lepisosteidae
Genus *Lepisosteus*
Lepisosteus sp.

Referred specimens.—GSP-UM 772, an isolated tooth, and GSP-UM 773, a scale, both from Chorlakki, are referred to *Lepisosteus indicus.*

Description.—GSP-UM 772 can be referred without doubt to the genus *Lepisosteus.* It is a large conical tooth, slender, vertical and tipped with a sharply pointed cap of smooth nearly translucent enamel.

Discussion.—Woodward (1908) described and figured *Lepisosteus indicus* from the late Cretaceous-early Eocene Lameta Beds of Dongargoan (India). It is the most eastern *Lepisosteus* found in the world (Wiley, 1976). At the present time, Lepisosteidae are limited to North America, but their distribution was much larger in the past as demonstrated by their discovery in Pakistan, India, Zaire (Casier, 1961), and Bolivia (de Muizon *et al.*, 1983, 1984; Marshall *et al.*, 1985).

Comparative morphological study of the ganoine of the scales in Lepisosteidae, Polypteridae, and Semionotidae, using a scanning electron microscope, shows tubercles located on its surface (Gayet and Meunier, 1986). These tubercules can be used to distinguish different fossil taxa. Study of the ganoid surface of nearly all fossil and living Lepisosteidae demonstrates (Gayet *et al.*, in preparation) that the Pakistani lepisosteid is a *Lepisosteus* very close (identical?) to living *L. osseus* from North America, but different in this character from *Lepisosteus indicus* from India.

ACANTHOPTERYGII *incertae sedis*

Figs. 22-23

Referred specimens.—The following teeth from Chorlakki are referred to Acanthopterygii *incertae sedis*: GSP-UM 481-483. Several teeth from Shekhan Nala are similarly referred: GSP-UM 769-770.

Description.—Some teeth are acuminate incisiform teeth, more or less globular, with the two parts, base and crown, of similar development (Fig. 22). If these are oral teeth, one may speak of labial and lingual sides. The approximately cylindrical base is more globular on its labial side. The crown is lingually convex and labially concave. The latter seems to be more developed and extends into the lingual side, making two inferior pads. The limit between the two sides is sharp. Alternatively, these teeth may be pharyngeal teeth.

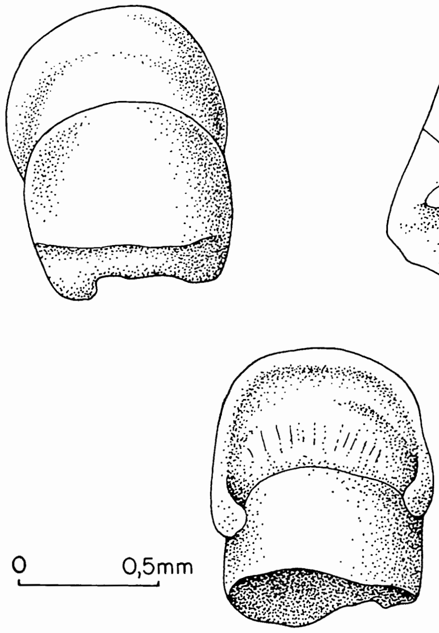
Many acuminate teeth cannot be attributed either to a genus or to a family (Fig. 23). These teeth are probably from pharyngeal plates. The crowns are of two shapes: some are quandrangular with soft angles, while others are conical. The base, at least of the second type, is compressed in the middle making it x-shaped.

Many complete teeth or complete crowns are probably also from pharyngeal plates (Fig. 24). These crowns are conical. Some of them are higher than broad and straight. Others are as high as broad, and slightly curved on one side. The base of these teeth is generally very high (three or four times the height of the crown). It is possible that these teeth could be assigned to pharyngeal teeth of Osteoglossiformes.

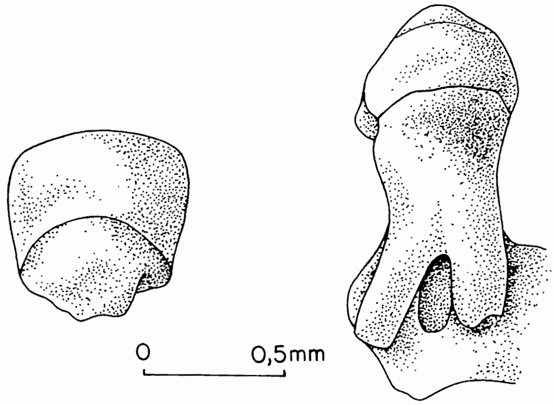
Discussion.—Because of a lack of comparative specimens, we could not assign some teeth to any taxon, family or genus. These are figured as Acanthopterygii *incertae sedis*.

DISCUSSION AND CONCLUSIONS

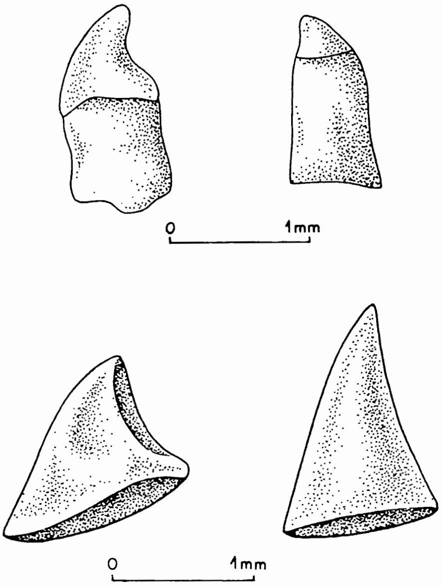
The ichthyofauna at Chorlakki and Shekhan Nala, composed of at least ten families, is well diversified, especially when we consider that it is a continental locality. Among the families recognized with certainty, only one family, Ariidae, is in part marine (but even here, ariids enter freshwater fluvial systems). Cyprinodontiformes and Osteoglossiformes are telolimnic groups (Patterson, 1975), which means that they probably had a marine origin, but are now (and were throughout the Tertiary) freshwater forms.



22



23



24

FIGS. 22 - 24— Teeth of Acanthopterygii *incertae sedis* from Chorlakki. FIG. 22: oral or pharyngeal tooth (GSP-UM 481). FIG. 23: Pharyngeal tooth (GSP-UM 482). FIG. 24: Pharyngeal tooth, possibly referable to Osteoglossidae (GSP-UM 483).

From the point of view of paleogeography, this ichthyofauna is of some interest because it gives some biogeographic support to two hypotheses: (1) Ridd's (1971) theory proposing that Southeast Asia, India, and Australia were all parts of Gondwanaland; and (2) Sahni *et al.*'s (1982) theory proposing that intermediate landmasses and/or insular arcs existed between Laurasia and Indo-Pakistan during the Paleocene.

LITERATURE CITED

ARRATIA, G. F. 1982. A review of freshwater percoids from South America (Pisces, Osteichthyes, Perciformes, Percichthyidae and Perciliidae). Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft, Frankfurt, 540:1-52.

BERRA, T. M. 1981. An atlas of distribution of the freshwater fish families of the world. University of Nebraska Press, Lincoln and London, 197 p.

BRITTAN, M. R. 1961. Adaptative radiation in Asiatic cyprinid fishes, and their comparison with forms from other areas. Proceedings of the 9th Pacific Science Congress (1957), 10:18-31.

CASIER, E. 1961. Matériaux pour la faune ichthyologique éocrétacique du Congo. Annales du Musée Royal d'Afrique Centrale, Sciences Géologiques, Tervuren, 39:1-96.

FORD, E. 1937. Vertebral variation in teleostean fishes. Journal Marine Biology Association, Cambridge, 22: 1-60.

GAUDANT, J. 1981. Contribution de la paléoichthyologie continentale à la reconstitution des paléoenvironnements cénozoiques d'Europe occidentale: approche systématique, paléoécologique, paléogéographique et paléoclimatologique. Thèse de Doctorat d'Etat, Paris, 368 pp. [Typescript].

GAYET, M. 1978a. Contribution à une révision des Poissons crétacés du Jbel Tselfat (Rides prérifaines, Maroc). Première partie : les "Acanthoptérygiens." Notes du Service Géologique du Maroc, Rabat, 39:79-124.

———. 1978b. Contribution à l'étude anatomique et systématique de la faune ichthyologique cénomanienne du Portugal. I. Les "Acanthoptérygiens." Communicaçoes dos Serviços Geológicos de Portugal, Lisboa, 63: 105-149.

———. 1980a. Contribution à l'étude anatomique et systématique des Poissons cénomaniens du Liban, anciennement placés dans les Acanthoptérygiens. Mémoires du Muséum national d'Histoire naturelle, Paris, Série C, 64:1-149.

———. 1980b. Recherches sur l'ichthyofaune cénomanienne des Monts de Judée. I. Les "Acanthoptérygiens." Annales de Paléontologie, Vertébrés, Paris, 66:75-128.

———. 1980c. Hypothèse sur l'origine des Ostariophysaires. Comptes Rendus hebdomadaires de l'Académie des Sciences, Paris, Série D, 290:1197-1199.

———. 1981a. Contribution à l'étude anatomique et systématique de l'ichthyofaune cénomanienne du Portugal. II. Les Ostariophysaires. Communicaçoes dos Serviços Geológicos de Portugal, Lisboa, 67:1-31.

———. 1981b. Considérations relatives à la paléoécologie du gisement cénomanien de Laveiras (Portugal). Bulletin du Muséum national d'Histoire naturelle, Paris, Section C, 3:311-315.

———. 1982a. Etude anatomique et systématique des Béryciformes du Sénonien de Sahel Alma (Liban). Paleontographica Italica, Pisa, 72:98-136.

———. 1982b. Cypriniformes crétacés en Amérique du Sud. Comptes Rendus hebdomadaires de l'Académie des Sciences, Paris, II, 295:1037-1040.

———. 1982c. Cypriniforme ou Gonorhynchiforme? *Ramallichthys*, nouveau genre du Cénomanien inférieur de Ramallah (Monts de Judée). Comptes Rendus hebdomadaires de l'Académie des Sciences, Paris, II, 295:405-407.

———. 1983. Considération sur la phylogénie et la paléobiogéographie des Ostariophysaires. *In*, E. Buffetaut, Ph. Janvier, J.-Cl. Rage, and P. Tassy (eds.), Phylogénie et Paléobiogéographie, Livre Jubilairee R. Hoffstetter, Géobios, Mémoire Spécial, 6:39-52.

———, V. LEVRAT-CALVIAC, AND F. J. MEUNIER. n.d. Comparative morphological and structural data on ganoid scales in some fossil and living Actinopterygian fishes with special reference to the Lepisosteidae. (in preparation).

———and F. J. MEUNIER. 1983. Ecailles actuelles et fossiles d'Ostéoglossiformes. Comptes rendus hebdomadaires de l'Académie des Sciences, Paris, II, 297:539-542.

———and ———. 1986. Apport de l'étude de l'ornementation microscopique de la ganoïne dans la détermination de l'appartenance générique et/ou spécifique des écailles isolées. Comptes rendus hebdomadaires de l'Académie des Sciences, Paris, II, 203:1259-1262.

HILLS, E. S. 1934. Tertiary freshwater fishes from southern Queensland. Memoirs of the Queensland Museum, Brisbane, 10:157-173.

MARSHALL, L. G., Ch. de MUIZON, M. GAYET, A. LAVENU, AND B. SIGE. 1985. The "Rosetta Stone" for mammalian evolution in South America. National Geographic Research, 1985 (Spring): 273-288.

McDONALD, C. M. 1978. Morphological and biochemical systematics of Australian freshwater and estuarine percichthyid fishes. Australian Journal of Marine and Freshwater Research, Melbourne, 29:667-698.

MEUNIER, F. J. 1982. Les tissus osseux des Osteichthyens. Structure, génèse, croissance et évolution. Thèse de Doctorat d'Etat, Université Paris VII, 199 pp. [Typescript].

MORDANT, D. 1965. Contribution à l'étude du genre *Smerdis*. Doctorat d'Etude supérieure, Université de Paris, 81 pp. [Typescript].

MUIZON, Ch. de, M. GAYET, A. LAVENU, L. G. MARSHALL, B. SIGE, and C. VILLARROEL. 1983. Late Cretaceous vertebrates, including mammals, from Tiupampa, southcentral Bolivia. Géobios, Lyon, 16:747-753.

MUIZON, Ch. de, M. GAYET, A. LAVENU, L. MARSHALL, AND C. VILLARROEL. 1984. Observation à la note de Muizon Ch. de et al. intitulée "Late Cretaceous vertebrates, including mammals, from Tiupampa, south-central Bolivia." Géobios, Lyon, 17:251-252.

OBRHELOVA, N. 1970. Die Osteologie der Vorläufer von *Tinca tinca* (Pisces) aus dem Süsswassertertiär der CSSR. Abhandlungen des Staatlichen Museums für Mineralogie und Geologie, Dresden, 16:99-209.

PATTERSON, C. 1975. The distribution of Mesozoic freshwater fishes. *In*, Biogéographie et liaisons intercontinentales au cours du Mésozoique, Congrès International de Zoologie, Monaco. Mémoires du Muséum national d'Histoire naturelle, Paris, Série A, 88:156-174.

______. 1984. *Chanoides*, a marine Eocene otophysan fish (Teleostei: Ostariophysi). Journal of Vertebrate Paleontology, 4:430-456.

RIDD, M. F. 1971. South-East Asia as a part of Gondwanaland. Nature, London, 234:531-533.

ROBERTS, T. R. 1975. Characoid fish teeth from Miocene deposits in the Cuenda Basin, Ecuador. Journal of Zoology, 175:259-271.

SAHNI, A., K. KUMAR, J.-L. HARTENBERGER, J.-J. JAEGER, J.-C. RAGE, J. SUDRE, and M. VIANEY-LIAUD. 1982. Microvertébrés nouveaux des Trapps du Deccan (Inde) : mise en évidence d'une voie de communication terrestre probable entre la Laurasie et l'Inde à la limite Crétacé-Tertiaire. Bulletin de la Société Géologique de France, 24:1093-1099.

SCHAEFFER, B. 1947a. Cretaceous and Tertiary Actinopterygian fishes from Brazil. Bulletin of the American Museum of Natural History, 89:1-39.

______. 1947b. An Eocene serranid from Patagonia. American Museum Novitates, 1331:1-9.

SORBINI, L. 1979a. Les Holocentridae du Monte Bolca. III. *Berybolcensis leptacanthus* (Agassiz). Studi e Richerche sui Giacimenti Terziari di Bolca, Verona, 4:19-35.

______. 1979b. Résultats de la révision des Béryciformes et des Perciformes généralisés du Monte Bolca. Studi e Ricerche sui Giacimenti Terziari di Bolca, Verona, 4:41-48.

SORBINI-FRIGO, M. and L. SORBINI. 1975. Revisione del genere fossile *Cyclopoma* Agassiz e suoi rapporti con l'attual genere *Percalates* Ramsay & Ogliby (Pisces). Studi e Richerche sui Giacimenti Terziari di Bolca, Verona, 2:55-84.

TAVERNE, L. 1977. Ostéologie, phylogénèse et systématique des Téléostéens fossiles et actuels du super-ordre des Ostéoglossomorphes. Première partie. Ostéologie des genres *Hiodon*, *Eohiodon*, *Lycoptera*, *Osteoglossum*, *Scleropages*, *Heterotis* et *Arapaima*. Mémoires de l'Académie Royale de Belgique, Classe des Sciences, Collection in-8°, Série 2, 42(3):1-235.

______. 1978. Ostéologie, phylogénèse et systématique des Téléostéens fossiles et actuels du super-ordre des Ostéoglossomorphes. Deuxième partie. Ostéologie des genres *Phareodus*, *Phareoides*, *Brychaetus*, *Musperia*, *Pantodon*, *Singida*, *Notopterus*, *Xenomystus* et *Papyrocranus*. Mémoires de l'Academie Royale de Belgique, Classe des Sciences, Collection in-8°, Série 2, 42(6):1-213.

WILEY, E. O. 1976. The phylogeny and biogeography of fossil and recent gars (Actinopterygii: Lepisosteidae). Miscellaneous Publications of the Museum of Natural History, University of Kansas, 64:1-111.

WOODWARD, A. S. 1908. On some fish remains from the Lameta beds at Dongargaon, Central Province. Paleontologica Indica, Memoirs of the Geological Survey of India, Calcutta, new series, 3:1-6.

ZEHREN, S. J. 1979. The comparative osteology and phylogeny of the Beryciformes (Pisces: Teleostei). Evolutionary Monographs, Chicago, 1:1-389.

LOWER VERTEBRATES FROM THE EARLY-MIDDLE EOCENE KULDANA FORMATION OF KOHAT (PAKISTAN): CHELONIA

By

France de Broin[1,2]

Abstract.—The early-middle Eocene chelonian fauna from Chorlakki, in the Kuldana Formation of Kohat District, Pakistan, includes two typically Laurasian forms. The first, *Chorlakkichelys shahi*, is described here as a new genus and species of carettochelyid, the second is an undetermined trionychine. Kuldana chelonians are probably more closely related to Indo-Asian forms (Paleocene-Eocene of India, Pakistan, and China) than they are to European forms.

Resumé.—La faune de tortues de Chorlakki est composée exclusivement de deux formes d'eau douce, typiquement laurasiatiques: le Carettochelyidae *Chorlakkichelys shahi*, n.g., n.sp., et un Trionychinae indéterminé. Son étude indique une parenté probablement plus étroite avec des formes indoasiatiques (Paléocène-Eocène Inde, Pakistan et Chine) qu'européennes.

INTRODUCTION

New remains of turtles found at Chorlakki, an early-middle Eocene vertebrate locality in the Kuldana Formation of Kohat District, Pakistan, are described in this paper. The specimens were found by P. D. Gingerich, D. E. Russell, and associates in 1978, 1980, and 1981. The Chorlakki specimens are compared with fragmentary material of early or middle Eocene age collected in the Kuldana Formation of the neighboring Kala Chitta Hills of the Attock District.

The geographic location, stratigraphic position, and faunal composition of localities mentioned here are discussed in diverse publications describing results of the 1977 through 1980 Geological Survey of Pakistan/ University of Michigan [GSP-UM] cooperative paleontological expeditions in the North West Frontier Province of Pakistan: Gingerich (1977, turtles in the Eocene Kuldana and Kohat formations); Gingerich et al. (1979a—turtles in the Paleocene Bara Formation, 1979b, 1979c); Gingerich and Russell (1981); Hussain et al. (1978); Russell and Gingerich (1980, 1981); and West (1980). Gingerich (1977) and Gingerich et al. (1979a) indicate the presence of turtles and locate them stratigraphically, while Gingerich et al., (1979b) and Gingerich and Russell (1981) give maps of the localities.

Other Paleogene turtles from different formations on the Indian subcontinent are listed in Table 1; the present article provides an occasion to bring questions of systematic determination, age, and geographic origin up to date.

---

[1] Centre National de la Recherche Scientifique (UA 12), Institut de Paléontologie, Muséum National d'Histoire Naturelle, 8 rue Buffon, Paris 75005 FRANCE.

[2] Manuscrit déposé en 1983.

TABLE 1 — Paleobiogeographical summary of turtles from the Indian Subcontinent (Upper Cretaceous-Recent). Note the probable area of origin of each taxon.

Age	Locality and formation	Taxon	Origin
GONDWANIAN FAUNA: Pelomedusidae, Schweboemys-Stereogenys group			
Plio-Pleistocene	Burma (Schwebo District, Irrawady beds)	*Schweboemys pilgrimi* Swinton, 1939	Indigenous
Miocene	India (Kutch)?, Burma (Pegu)	Pelomedusidae and/or Emydidae?	Indigenous
Miocene (early)	Pakistan (Bugti Hills)	*Schweboemys gaffneyi* Wood, 1970	Indigenous or from Africa (Egypt)
Oligocene	India (Kutch)?	Pelomedusidae and/or Emydidae?	Indigenous
Eocene (late)	Burma (Pondaung)?	Pelomedusidae/Emydidae? "Huge turtles"	Indigenous
Eocene (middle)	Pakistan (Bawar Nala, Domanda Fm.)?	Pelomedusidae and/or Emydidae?	Indigenous
Paleocene-Eocene	Pakistan (Salt Range)	"*Podocnemis*" *indica* Lydekker, 1887	Indigenous
Paleocene	India (Bombay, Intertrappean beds)	*Carteremys leithii* (Carter, 1852) and other pelomedusids	Indigenous
Late Cretaceous	India (Central India, Pisdura Fm.)	*Carteremys pisdurensis* Jain, 1978	Indigenous (Gondwana, Africa and India)
LAURASIAN FAUNA: 1) Trionychinae and Carettochelyidae (first wave); 2) Testudinidae, Emydidae, Cyclanorbinae (second wave)			
Recent to Miocene (late)	Pakistan and India (Siwaliks), and Burma (Irrawaddy beds)	Trionychinae	Indigenous and from Asia
		Cyclanorbinae	Indigenous (from Trionychinae?)
		Emydidae	From Asia or already present (Pelomedusidae/Emydidae?)
		Testudinidae	From Africa and Asia, and Afghanistan (recently)

TABLE 1 — Paleobiogeographical summary of turtles from the Indian Subcontinent (Upper Cretaceous-Recent). Note the probable area of origin of each taxon. (Continued)

Age	Locality and formation	Taxon	Origin
Eocene (late)	Burma (Pondaung)	"Carettochelyoidea"	
Eocene (middle)	India (Simla Hills, upper Subathu Fm. and Kutch)	"*Trionyx*" sp., and Chelonia indet. Trionychidae indet.	From Laurasia or already present on Indian subcontinent, having previously come from Laurasia
Eocene (early-middle)	India (Simla Hills, lower Subathu)	"*Trionyx*" sp.	From Laurasia or already present
	Pakistan (Kala Chittas, Kuldana Fm.)	*Chorlakkichelys*? sp., and Trionychinae indet.	From Laurasia or already present
	Pakistan (Chorlakki, Kuldana Fm.)	*Chorlakkichelys shahi* gen. et sp. nov.	From Asia (as *Hemichelys*)
		Trionychinae indet.	From Laurasia
Paleocene-Eocene	Pakistan (Salt Range)	*Hemichelys warthi* Lydekker, 1887	From Asia

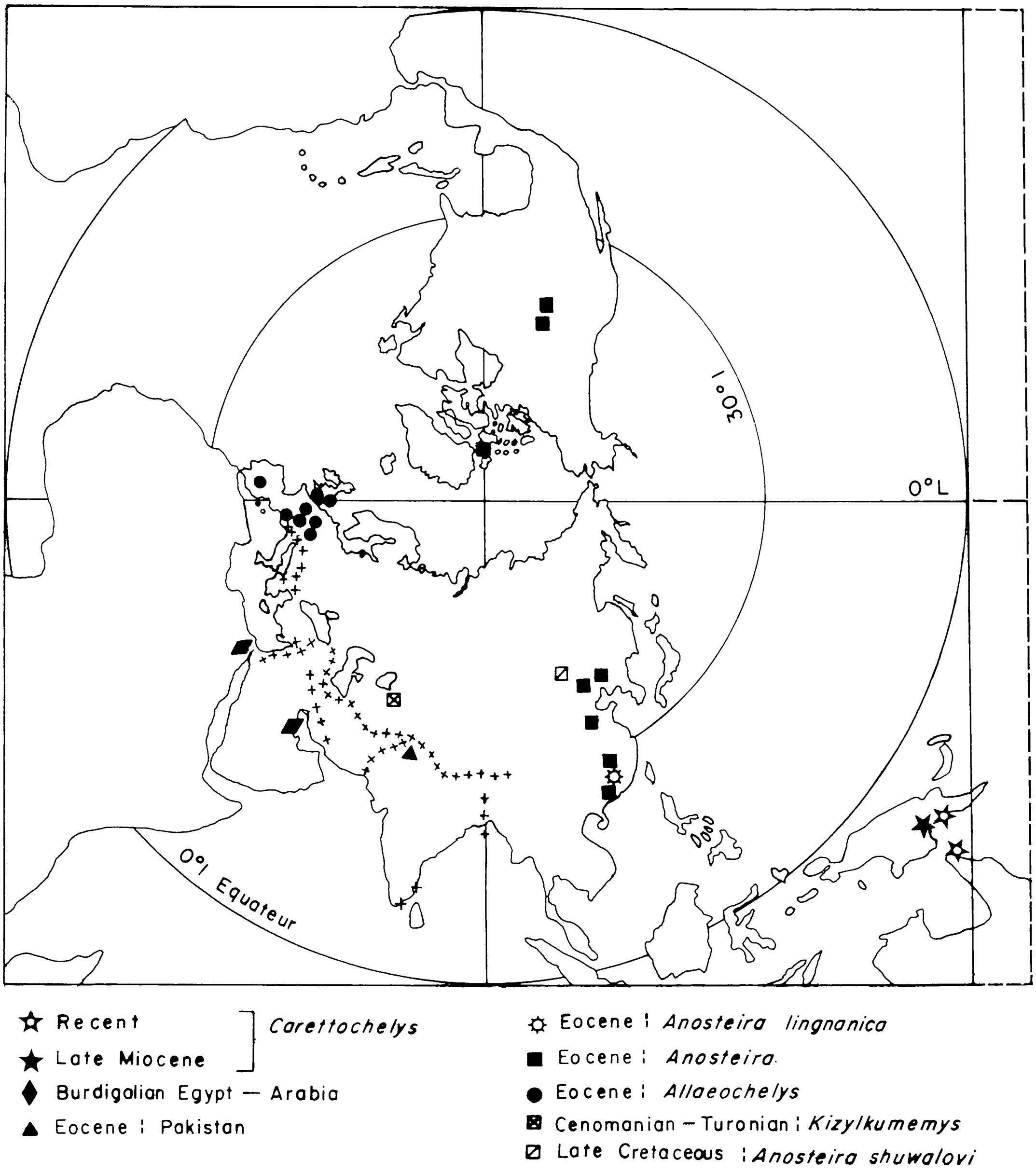


FIG. 1— Paleogeographical distribution of Carettochelyidae. Map after Smith and Briden (1977), showing present day positions of continents. Note that carettochelyids are presently confined to Australia and New Guinea.

SYSTEMATIC PALEONTOLOGY

Chelonian material from Chorlakki is restricted to several fragments belonging to two basically Laurasiatic families that are closely related phylogenetically: Trionychidae and Carettochelyidae. Nomenclature of higher taxa follows Bour and Dubois (1986).

Order Chelonii Brongniart, 1800
Suborder Casichelydia Gaffney, 1975
Infraorder Cryptodira Cope, 1868
Superfamily Trionychoidea Gray, 1870
Family Trionychidae Fitzinger, 1826
Subfamily Trionychinae Fitzinger, 1826

Trionychinae, genus and species indet.
Pl. 3, figs. 11-13

Locality.—Chorlakki, easternmost exposure of Kuldana Formation in Panoba Dome, four kilometers NNW of the village of Chorlakki (33°37′20″ N. lat.; 71°55′20″ E. long.), Kohat District, North West Frontier Province, Pakistan.

Age and distribution.—Early-middle Eocene, Kuldana Formation, in the Kohat District of Pakistan. This species may also be represented in the early to middle Eocene Kuldana Formation at Jhalar and Lammidhan in Attock District, Pakistan.

Referred specimens.—GSP-UM 535 to 538: four indeterminate pleural plate fragments. GSP-UM 535 includes the distal parts of left pleurals 7 and 8 (Pl. 3, fig. 11). This is a well developed adult, thickness 5 to 8 mm, with complete integration of the extremity of the rib in dermal bone (which extends still farther beyond it). The median length of the shell is estimated at about 30 cm. GSP-UM 536 to 538 include three small fragments of younger individuals that cannot be located precisely as to position on the shell. The thickness of these is 2 to 5 mm (Pl. 3, figs. 12-13).

Discussion.—All four fragments probably belong to the same species of Trionychinae, judging from their ornamentation: fine, narrow ridges, more or less rounded, united to form very small polygonal pits that are wider than the ridges. There are no granulations. The delicacy of this decoration is noteworthy, given the thickness and the dermic development of the pleural disk (GSP-UM 535). A more or less similar delicacy is frequent, for example, in Trionychinae of the Paleocene-early Eocene of France and Belgium, the early Eocene of North America, and also Asia—notably in the early Cretaceous of Mongolia and China, and in such living forms as *Amyda* (*Pelodiscus*) *sinensis* (southeast Asia) and *Amyda* (*Dogania*) *subplana* (from the Indian subcontinent to the Philippines). Over great distances, no phyletic or stratigraphic relations can be established on the basis of such similarity. On the other hand, between localities situated close to each other and presumed to be close in age, close similarity probably does indicate close relationship. Thus the presence of trionychine fragments in the Kuldana Formation of the Kala Chitta Hills, Attock District [at Jhalar (Pl. 3, fig. 16) and at Lammidhan (Pl. 3, fig. 14-15)], with decoration similar to that seen at Chorlakki probably does indicate close relationship.

Trionychidae have already been mentioned in the Eocene of the Indian subcontinent (Table I): in India, their presence seems certain in the middle Eocene Babia Stage at Harudi in Kutch, according to a figure of an undetermined trionychid with rather large pits (Sahni & Mishra, 1975, their Pl. 3, fig. 5). Trionychidae are also known in the lower and upper beds of the Subathu Formation of the Simla Hills in India (Sahni, et al., 1981), but this determination may perhaps require further verification as confusion between Trionychidae, Carettochelyidae, and Dermatemydidae is always possible for ornamented shells. It would be interesting to see if the ornamentation is as fine as that at Chorlakki, or coarser like that at Kutch.

Note that all three of these families, Trionychidae, Carettochelyidae, and Dermatemydidae, were exclusively Laurasian until the Miocene, residing in Laurasia since the late Jurassic or early Cretaceous. Until recently, Carettochelyidae were only known, before the Eocene, in Asia (see below). Trionychidae were exclusively Laurasian from the time of their first appearance in Asia in the Early Cretaceous, North America in the Late Cretaceous, and finally Europe in the Paleocene through Miocene (Burdigalian). In the Miocene, Trionychidae were already differentiated into Trionychinae and Cyclanorbinae, with the first group probably remaining Laurasiatic until the Pliocene (de Broin, 1983), the Indian subcontinent excepted.

Cyclanorbinae make their first appearance in the Burdigalian of Arabia (Dam Formation, de Broin *in* Thomas et al., 1982), Kenya in East Africa (de Broin, 1979, 1983), and the Siwaliks of Pakistan (upper Chinji, locality 76, ca. 10-15 m.y.B.P.) and India (Ramnagar). Cyclanorbinae remain confined to Africa and the Indian subcontinent. Logically, according to their distribution and their cranial anatomy (de Broin, 1977), one would expect that Cyclanorbinae shared a common ancestor with Trionychinae on the Indian subcontinent: some cyclanorbines have a fine decoration, granular and cupuloid at the same time, instead of the granular decoration typical for the subfamily. Cyclanorbinae are characterized by strong development of the pleural disk beyond the ribs. The trionychid species from Chorlakki, where this character is clearly visible, could possibly lie near the base of the cyclanorbine radiation.

The Trionychidae (soft-shelled turtles) are freshwater forms still living today in rivers, lakes and ponds. They are abondant in continental sediments of Laurasia. Occasionally, they are transported during life (or after death) as far as the sea where they can follow the shore and colonise distant rivers along coastlines (de Broin, 1983) (or become fossilized in nearshore marine deposits). Their geographic expansion appears, therefore, less limited than that of heavier or more terrestrial animals. However, while trionychids may follow a coast or pass from island to island, there are no examples known of colonisation across vast oceans.

The wide distribution of Trionychidae in Pakistan and India in the early-middle Eocene indicates an already solidly established geographic contiguity between the Indian subcontinent and Laurasia. This is consistent with the possibility of intermittant communication between the two blocks as early as the Cretaceous-Paleocene boundary (Sahni et al., 1982). Considering the way that trionychids live, one might expect to find their remains in Pakistan as early as the beginning of the Paleocene. The same can be said for Carettochelyidae (see below).

Given the fragmentary condition of trionychid specimens from Chorlakki, no precise geographic origin can be envisaged for the group. An origin in Asia is, however, more likely than an origin in Europe.

Family Carettochelyidae Boulenger 1887
Subfamily Carettochelyinae Boulenger, 1887

Chorlakkichelys shahi gen. et sp. nov.
Pl. 1, figs. 1-16

Holotype.—GSP-UM 500 (subnumbers 1-26, collected in 1980). An incomplete individual with a dissociated shell whose elements are mostly agglomerated and inseparable. Those determinable include fragments of a right hypoplastron (figs. 1-2); fragments of peripheral plates: right 1 (fig. 3), right 2 (fig. 4), left 2 (fig. 5), right 5 (figs. 6-7), left 7 (fig. 8), right 8 (fig. 10);

fragments of pleurals (figs. 9, 11-12); fragments of imbricated pleurals and plastron, one of which is probably a left xiphiplastron.

Type locality.—Chorlakki, easternmost exposure of Kuldana Formation in Panoba Dome, four kilometers NNW of the village of Chorlakki (33°37′20″ N. lat.; 71°55′20″ E. long.), Kohat District, North West Frontier Province, Pakistan.

Age and distribution.—Early-middle Eocene, Kuldana Formation, in the Kohat District of Pakistan.

Diagnosis.—Absence of scute sulci, large size of the carapace (attaining at least 50 cm in median length) indicates that this form belongs in Carettochelyinae, but with still (and exceptionally for this size) a juvenile ornamentation consisting of round spots, vermiculations, and wide, closely spaced granular ridges, particularly marked. Generic and specific characters (inseparable at the present time) include the notable length of the hypoplastron anterior to the base of the inguinal notch implying a long bridge as in *Carettochelys*, but with the posterior lobe definitely narrower than that of *Carettochelys*; the posterior part of the peripheral border is curved upwards.

Etymology.—Named in honor of Dr. S. M. Ibrahim Shah, Director of the Paleontology and Stratigraphy Branch, Geological Survey of Pakistan.

Description.—The holotype is a large individual, very incomplete. The shell plates are particularly ornamented. The decoration consists of vermiculations, which is usual in large individuals of Eocene Carettochelyidae, and it consists also of round spots and granular ridges that are usual only in young and small individuals of Carettochelyinae: their presence in a large individual is therefore new and can be considered as an apomorphic paedomorphosis. This ornamentation, strongly marked, covers all the preserved plates of the holotype: peripherals, pleurals, and plastral plates. The anterior peripheral plates are long, wide, and thick (Pl. 2, figs. 3-5) as is usual in Carettochelyinae. The fifth peripheral plate (Pl. 1, fig. 6) is widely open to meet the pleurals and the plastron and its borders are slightly curved upwards. The following lateral and posterior peripherals (the sixth and the eighth) are more curved (Pl. 1, figs. 8, 10). Thus all of the lateroposterior border of the carapace is notably curved upward in this species, unlike other Carettochelyidae. The hypoplastron is incomplete at its inguinal buttress, but its medial border seems complete or nearly complete: a plastral fragment of the same width seems to be a piece of xiphiplastron which fits with it. This hypoplastron is narrow with respect to its length anterior to the inguinal notch. Judging from the preserved remains, it belonged to a genus with a long bridge but with a narrow posterior lobe, and to a large species.

The other carettochelyid specimens from Chorlakki, GSP-UM 501-504, have a smoother eroded surface. In any case, most of them belonged to the medioposterior central part of the carapace (neural, suprapygal, pygal), which is always smoother than the anterior and lateral parts (Pl. 1, figs. 13-16).

Hypodigm.—From the type locality, Chorlakki: GSP-UM 500 (holotype, Pl. 1, figs. 1-12), and carapace remains with a smooth surface, including GSP-UM 501 (pygal, Pl. 1, fig. 13), GSP-UM 502 (left peripheral 6, Pl. 1, fig. 14), GSP-UM 503 (suprapygal fragment, Pl. 1, fig. 15), and GSP-UM 504 (neural, anterior part, Pl. 1, fig. 16). These fragments could belong to only one individual (or to several individuals) collected in 1980.

Material from the early to middle Eocene Kuldana Formation, Attock District, Pakistan, questionably referred to *Chorlakkichelys* includes specimens from Chharat: GSP-UM 506-507, 539, 541 (Pl. 3, figs. 7-10); Jhalar: GSP-UM 508, 511, 513, 515 (Pl. 3, figs. 1-6), 512, 514; and Lammidhan: GSP-UM 516, 518-519, 521, 523-526 (Pl. 2, figs. 1-8), 517, 520, 522, 527-534.

Discussion.—The geographic distribution of Carettochelyidae is shown in Figure 1 (see also de Broin, 1977). Two subfamilies are recognized: Anosteirinae and Carettochelyinae (see de Broin, 1977, and Nessov, 1977). Anosteirinae include *Anosteira* (including *Pseudanosteira*

Clark, 1932) from the late Cretaceous of Mongolia? and the Eocene of China, Mongolia, U.S.A., and Ellesmere Island in northern Canada (Estes & Hutchinson, 1980), and *Kizylkumemys* from the late Cretaceous of Uzbekistan, south of the Aral Sea (Nessov, 1976, 1977). Anosteirinae are characterized by a narrowing of the plastron, which is cruciform with a very narrow posterior lobe and a short bridge. Shells attain maximum lengths of about 25 cm, even 35 to 38 cm in *Kizylkumemys*. Measuring at the base of the posterior lobe of the plastron, total shell width is about 3.5 to 4.5 times the width of the plastron at this point. There are residual horny shield sulci on the shell, and the vertebral scutes are fused in a particular fashion, which is an autapomorphy of the subfamily.

Carettochelyinae include *Carettochelys*, from the late Miocene to Recent of northern Australia; *Allaeochelys*, from the Eocene of Western Europe and possibly North America ("*Anosteira*" *radulina* Cope, 1872); *Hemichelys*, from the Paleocene or Eocene of Pakistan; and some generically doubtful forms from the Eocene of China ("*Anosteira*" *lingnanica* Young and Chow, 1962) and from the Miocene (Burdigalian) of Egypt and Saudi Arabia (de Broin in Thomas et al., 1982; de Broin, 1983). Carettochelyinae are characterized by a total loss of scutes (apomorphy). They vary in size, sometimes reaching 55 cm in shell length, and even 68 cm in *Hemichelys warthi* Lydekker, 1887, from the presumed Paleocene of the Salt Range at Nila, Punjab, Pakistan. The plastron is wider than that of Anosteirinae: measuring at the base of the posterior lobe of the plastron, total shell width is only about 2.0 to 3.5 times the width of the plastron at this point. The bridge of the plastron is always long, even though it is more or less indented by the limb notches: by this fact, anterior to the inguinal notch, the hypoplastron is either: short, the posterior lobe being rather wide, as in *Allaeochelys*; relatively very short, the posterior lobe being very wide, as in *Hemichelys warthi*; rather long, the posterior lobe being rather narrow, as in "*Anosteira*" *lingnanica*; or long, the posterior lobe being wide, as in *Carettochelys insculpta* Ramsey, 1887. Note that the posterior lobe of the Carettochelyidae widens with age, the width varying according to species, but always remaining narrower in Anosteirinae.

At Chorlakki, the fragment of hypoplastron GSP-UM 500 is therefore very important for the diagnosis of *Chorlakkichelys shahi*. As preserved, the fragment indicates that the species had a narrow posterior lobe but a long bridge, longer than in any other Carettochelyidae. If the fragment is incomplete medially and if the hypoplastron was in fact wider, it would be nearer to *Carettochelys* or to *Hemichelys* (depending on whether total width attained, was greater or not than the length). Such as it is, it seems rather close to "*Anosteira*" *lingnanica*. This species is surely not referable to *Anosteira*; a relationship to *Allaeocelys* has been suggested (de Broin, 1977; Nessov, 1976), but accurate measurements are lacking and published photographs do not permit one to be sure that the length from the hypoplastron to the notch is greater than its width, as it is in *Chorlakkichelys*. Be that as it may, the species *lingnanica* is smaller, with a pronounced granulous decoration like that in *Chorlakkichelys shahi* from Chorlakki. "*Anosteira*" *lingnanica* and *Chorlakkichelys shahi* seem to be more closely related to each other than either is to species of *Alleochelys*.

Small remains of Carettochelyidae have also been collected in the Kala Chitta Hills at Lammidhan and Jhalar. I have figured some fragments in Plates 2 and 3. There is no trace of horny shields on the fragments. Some of them must be juvenile, judging from their small size and the closeness of the granulations (as in the European *Allaeochelys*): remains of a nuchal (Pl. 2, fig. 6), of peripherals (Pl. 2, fig. 3; Pl. 3, figs 5-8), of pleural 2 (Pl. 3, fig. 1); and so forth. Others are very thick for their small size and belong to more or less large adults: nuchal fragments (Pl. 2, fig. 7; 1.3 cm thick), and a pygal fragment (Pl. 2, fig. 1). The species represented at Lammidhan and Chharat, at least, was massive, as *Chorlakkichelys shahi* could be, and it is also a carettochelyine. Prudence requires that these remains be identified only as ?*Chorlakkichelys* sp. In fact the preserved elements are not parts of the carapace that exhibit diagnostic characters of *Chorlakkichelys shahi*: there are no hypoplastrons sufficiently complete to show the narrowness of the posterior lobe and the length of the bridge, no lateroposterior peripherals to show the very uplifted posterior border, no particularly large individuals with very big granulation. Therefore it is not possible to determine whether the Lammidhan and Chharat remains should be referred to the same species or only to the same genus as *Chorlakkichelys shahi*, or again, to another totally distinct carettochelyid.

The pleural fragment from Chharat (Pl. 3, fig. 9) could be attributed to a *Trionyx*, the decoration in anastomosed ridges isolating true pits dominating the vermiculated ornamentation; the thickness and the width of the rib show that it must be a large carettochelyid. This modification of the ornamentation with age and size is seen also in *Allaeochelys*. I think that it could be the same in *Hemichelys warthi*, according to Lydekker's drawing of the plastron. This species from the Salt Range had been placed in the Carettochelyidae by its author on the basis of absence of scutes, but it was said that it possessed lateral mesoplastrons; these elements, being lateral, are an apomorphy of members of the suborder Pleurodira, and mainly the Pelomedusidae, which cannot exist in a cryptodire carettochelyid. This is why Nessov (1976) referred to *Hemichelys* as a pelomedusid whose scutes had disappeared by erosion, and why de Broin (1977), because of the pitted plastral ornamentation of the plastron, unlike that of the Carettochelyidae, left it *incertae sedis*.

Examination of large remains of European Carettochelyidae and of the new fragments from Pakistan prove that this pitted ornamentation is frequent in very large Carettochelyinae. I am now certain that *Hemichelys* did not have lateral mesoplastrons nor a horny shield, and that it was a very long carettochelyine with a wide plastron; as in large *Allaeochelys* and the Chharat specimen, the granular decoration of the young adult becomes more pitted and smooth, and smoother on the carapace than on the plastron. This smoother and more pitted stage could be linked to age, but it could also be attained more rapidly (by smaller shells) within the same species for several reasons (often the male turtle is smaller than the female). That could explain why the hypodigm of *Chorlakkichelys* is smoother for a size equal to that of the type, as could be the carapace of *Hemichelys*, according to the author's description (absence of photographs), while the plastron was decorated with very shallow pits. A revision of the type of *Hemichelys* and new discoveries at Chorlakki will be necessary before the relationships between the two species will be understood.

A Paleocene age (if not early Eocene) has been proposed for the Salt Range sediments that yielded *Hemichelys*; furthermore, "Carettochelyoidea" have been reported from the late Eocene of Burma, Pondaung Sandstone (Savage & Russell, 1983). As in Trionychinae, the already vast distribution of the family Carettochelyidae in the middle Eocene, and its possible presence in the Paleocene of the Salt Range demonstrate the geographic contiguity of northern Pakistan and Laurasia before the time represented by Chorlakki.

The problem of the origin of *Chorlakkichelys* seems linked to that of *Hemichelys*, and both may have had a common ancestor arriving from Laurasia at the same time as the ancestor (or ancestors) of the Trionychinae represented at Chorlakki and in the Subathu Formation of India. At present, outside of Pakistan, only central Asia and Mongolia have produced Carettochelyidae before the Eocene. Thus one must look to central Asia and Mongolia, and not to Europe, for ancestors of the Pakistan forms. The remains of *Kizylkumemys* Nessov, 1976, from Uzbekistan are too specialized to be considered; those from Mongolia are very poor ("*Anosteira*" *shuwalovi* Chkhikvadze in Shuvalov and Chkhikvadze, 1979). However, their closest relative should be sought in the eastern part of Asia, which is probably their area of origin. The presence of "*Anosteira*" *lingnanica* in the early Eocene of northern Guangdong, and its clear resemblance to *Chorlakkichelys*, render this hypothesis likely.

DISCUSSION AND CONCLUSIONS

Pelomedusidae, an element of the Gondwana fauna, are known in the (probable) Paleocene Intertrappean Beds of India: *Carteremys leithii* (Carter, 1852) and other indeterminate Pelomedusidae (see Williams, 1953; Wood, 1970). Pelomedusids, represented by "*Podocnemis*" *indica* Lydekker, 1887, are also found in the Paleocene or Eocene of the Salt Range at Nila, Pakistan, where the latter occurs together with the carettochelyid *Hemichelys warthi* Lydekker, 1887. These Pelomedusidae all appear to belong to the *Schweboemys-Stereogenys* group of Podocnemidinae, which are common to the Indian subcontinent and eastern Africa (Fayum of Egypt in the late Eocene and Oligocene; Saudi Arabia in the Burdigalian Miocene). This group evidently began with *Carteremys pisdurensis* Jain, 1978 (Pisdura Formation, central India, late Cretaceous), and it represents a branch from the common African - South American pelomedusid trunk. This group of pelomedusids persisted until recently on the Indian subcontinent (early Miocene of Pakistan, late Irrawaddian in Burma).

There is, at present, no trace of Pelomedusidae at Chorlakki, but pelomedusids may occur in the Domanda Formation, middle Eocene, at Bawar Nala near Rakki Nala, Dera Ghazi Khan District, Punjab Province, Pakistan. The specimens in question (e.g., Pl. 3, fig. 17) are from smooth turtles with horny shields that could be either Pelomedusidae or possibly Emydidae.

Indeterminate Chelonii are mentioned in the Eocene of the upper Subathu Formation (Sahni et al., 1981) and in the late Eocene Pondaung sandstone of northern Burma (Stamp, 1922: "huge turtles"). It is not possible to tell from described material if they are Gondwanian Pelomedusidae, or Laurasiatic Emydidae, or even Laurasiatic marine Cheloniidae. Emydidae flourished in terrestrial and fresh water environments of the Indian subcontinent at the expense of Pelomedusidae. Emydids are first known in China and North America in the Paleocene, and Europe in the early Eocene (Sparnacian), but they are not known in Africa before the Pliocene. The first occurrence of emydids in India is in the late Miocene of the Siwaliks (Potwar Plateau of Pakistan and Ramnagar in India), where there is already a great diversity of forms, many of which are common to this region today and thus probably of an ancient introduction. The presence of Emydidae at Chorlakki or in the Kala Chitta Hills in the Eocene would therefore not be surprising.

The only remains of turtles found to date at Chorlakki are the carettochelyid *Chorlakkichelys shahi* gen. et sp. nov., and an indeterminate trionychine. Trionychidae, like Carettochelyidae, are not known before the late Miocene in Africa (de Broin, 1977, 1980, 1983), and Africa cannot have been the center of origin for these Laurasiatic Indo-Pakistan forms. The turtles from Chorlakki indicate, then, a clear biogeographic relationship to Laurasia and not to Africa. In fact, all of the turtle localities discussed here, Paleocene through middle and late Eocene, show such a relationship to Laurasia: Chorlakki and Kuldana Formation localities in the Kala Chitta hills, Nila in the Salt Range of Pakistan, Subathu Formation localities in the Simla Hills, Kutch in India, and finally northern Burma. Within Laurasia, the turtles of Indo-Pakistan appear to be more closely related to those of eastern Asia than to those of Europe.

Contact between the Indian subcontinent and the Eurasian continental plate (Laurasia) probably began in intermittant fashion, with regression and transgression of a shallow sea exposing and flooding shallow straits and islands in eastern Tethys, permitting first the arrival of the Trionychidae and Carettochelyidae. New discoveries will be required to tell us whether the rest of the Laurasiatic turtle fauna (Emydidae, Testudinidae) required a firmer land connection before making their passage. This requirement may explain the absence of emydids and testudinids in localities, like Chorlakki, examined here.

LITERATURE CITED

BOUR, R. and A. DUBOIS. 1986. Nomenclature ordinale et familiale des tortues (Reptilia). Note complémentaire. Bulletin mensuel de la Société Linnéenne de Lyon, 55:87-90.

BROIN, F. de. 1977. Contribution à l'étude des Chéloniens. Chéloniens continentaux du Crétacé et du Tertiaire de France. Mémoires du Muséum National d'Histoire Naturelle, Paris, Série C, 38:1-366.

———. 1979. Chéloniens du Miocène et du Plio-Pléistocène d'Afrique orientale. Bulletin de la Société Géologique de France, 21:323-327.

———. 1980. Les Tortues de Gadoufaoua (Aptien du Niger); aperçu sur la paléogéographie des Pelomedusidae (Pleurodira). Mémoires de la Société Géologique de France, 139:39-46.

———. 1983. Chéloniens. *In* N. Petit-Maire and J. Riser (eds.), Sahara ou Sahel? Quaternaire récent du Bassin de Taoudenni (Mali). Imprimerie Lamy, Marseille, 6:211-233.

CLARK, J. 1932. A new Anosteirid from the Uinta Eocene. Annals of the Carnegie Museum, 21:161-170.

ESTES, R. and J. H. HUTCHISON. 1980. Eocene lower vertebrates from Ellesmere Island, Canadian Arctic archipelago. Palaeogeography, Palaeoclimatology, and Palaeoecology, 30:325-347.

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, 24:190-203.

———, 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.

———, D. E. RUSSELL, D. SIGOGNEAU-RUSSELL, and J.-L. HARTENBERGER. 1979. *Chorlakkia hassani*, a new middle Eocene dichobunid (Mammalia, Artiodactyla) from the Kuldana Formation of Kohat (Pakistan). Contributions from the Museum of Paleontology, University of Michigan, 25:117-124.

———, E. BUFFETAUT, J.-L. HARTENBERGER, D. E. RUSSELL, and D. SIGOGNEAU- RUSSELL. 1979. Vertébrés de l'Eocène du Pakistan: premiers résultats. 7e Réunion Annuelle des Sciences de la Terre, Lyon, Société Géologique de France, p. 217.

———, D. E. RUSSELL, D. SIGOGNEAU-RUSSELL, J.-L. HARTENBERGER, S. M. I. SHAH, M. HASSAN, K. D. ROSE, and R. H. ARDREY. 1979. Reconnaissance survey and vertebrate peleontology of some Paleocene and Eocene Formations in Pakistan. Contributions from the Museum of Paleontology, University of Michigan, 25:105-116.

HUSSAIN, S. T., H. de BRUIJN, and J. M. LEINDERS. 1978. Middle Eocene rodents from the Kala Chitta Range (Punjab, Pakistan). Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, Series B, 81:74-112.

JAIN, S. L. 1978. A new fossil pelomedusid turtle from the upper Cretaceous Pisdura sediments, Central India. Journal of the Palaeontological Society of India, 20:360-365.

LYDEKKER, R. A. 1887. Eocene Chelonians from the Salt-Range. Palaeontologica Indica, 4:59-65.

NESSOV, L.A. 1976. O sistematike i filogenii dvukogotnykh cerepakh. Vestnik Leningradskogo Universiteta, 9 (Biologia):7-17. [In Russian]

———. 1977. A new genus of pitted-shelled turtle from the Upper Cretaceous of Karakalpakia. Paleontological Journal [English translation from Paleontologicheskiy Zhurnal, Akademiya Nauk SSSR], 1:96-107.

PILBEAM, D. R., A. K. BEHRENSMEYER, J. C. BARRY, and S. M. I. SHAH. 1979. Miocene sediments and faunas of Pakistan. Postilla, 179:1-45.

RUSSELL, D. E., and P. D. GINGERICH. 1980. Un nouveau Primate Omomyide dans l'Eocène du Pakistan. Comptes Rendus de l'Académie des Sciences, Paris, Série D, 291:621-624.

———, and ———. 1981. Lipotyphla, Proteutheria(?), and Chiroptera (Mammalia) from the early-middle Eocene Kuldana Formation of Kohat (Pakistan). Contributions from the Museum of Paleontology, University of Michigan, 25:277-287.

SAHNI, A., and V. P. MISHRA. 1975. Lower Tertiary vertebrates from western India. Monographs of the Paleontological Society of India, 3:1-48.

———, and V. C. SRIVASTAVA. 1976. Eocene rodents and associated reptiles from the Subathu Formation of northwestern India. Journal of Paleontology, 50:922-928.

———, and ———. 1977. Eocene rodents of India: their paleobiogeographic significance. *Géobios*, Mémoire Spécial, 1:87-95.

———, S. B. BHATIA, J.-L. HARTENBERGER, J.-J. JAEGER, K. KUMAR, J. SUDRE, and M. VIANEY-LIAUD. 1981. Vertebrates from the Subathu Formation and comments on the biogeography of Indian subcontinent during the early Paleogene. Bulletin de la Société Géologique de France, Série 7, 23:684-695.

______, K. KUMAR, J.-L. HARTENBERGER, J.-J. JAEGER, J. C. RAGE, J. SUDRE, and M. VIANEY-LIAUD. 1982. Microvertébrés nouveaux des Trappes du Deccan (Inde): mise en évidence d'une voie de communication terrestre probable entre la Laurasie et l'Inde à la limite Crétacé-Tertiaire. Bulletin de la Société Géologique de France, Série 7, 24:1093-1099.

SAVAGE, D. E., and D. E. RUSSELL. 1983. Mammalian Paleofaunas of the World. Addison-Wesley Publishing Company, Reading, Massachusetts, 432 pp.

SHAH, S. M. I. 1977. Stratigraphy of Pakistan. Memoirs of the Geological Survey of Pakistan, 12:1-138.

SHUVALOV, V. F., and V. M. CHKHIKVADZE. 1979. The stratigraphic and systematic position of certain fresh-water turtles from new Cretaceous localities in Mongolia. *In*: R. Barsbold (ed.), Fauna mezozoya i kaynozoya Mongolii, Sovmestnaya Sovetsko-Mongol'skaya Paleontologicheskaya Ekspeditsiya, Trudy, Moscow, 8:58-74. [In Russian]

SMITH, A.G., and J. C. BRIDEN. 1977. Mesozoic and Cenozoic Paleocontinental Maps. Cambridge University Press, Cambridge, 63 pp.

STAMP, L. D. 1922. An outline of the Tertiary geology of Burma. Geological Magazine, 59:481-501.

SWINTON, W. E. 1939. A new fresh-water tortoise from Burma. Records of the Geological Survey of India. 74:548-551.

THOMAS, H., S. SEN, M. KHAN, B. BATTAIL, and G. LIGABUE. 1982. The lower Miocene of As Sarrar (Eastern Province, Saudi Arabia). Atlal, Journal of Saudi Arabian Archaeology, 5:109-136.

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

WILLIAMS, E. E. 1953. Fossils and the distribution of Chelyid turtles. 1. "*Hydraspis*" *leithii* (Carter) in the Eocene of India is a pelomedusid. Breviora, 13:1-8.

WOOD, R. C. 1970. A review of the fossil Pelomedusidae (Testudines, Pleurodira) of Asia. Breviora, 357:1-24.

YOUNG, C.C., and M. CHOW. 1962. Some reptilian fossiles from the "red beds" of Kwangtung and Chekiang. Vertebrata PalAsiatica, 6:130-137.

EXPLANATION OF PLATE 1

(Reduced slightly from natural size, scale in cm.)

Chorlakkichelys shahi gen. et sp. nov., holotype GSP-UM 500, from Chorlakki, Kohat District, Pakistan.

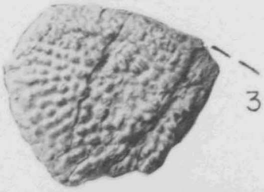
Fig. 1—Medial part of the right hypoplastron, ventral view.
Fig. 2—Same as Fig. 1, dorsal view.
Fig. 3—Part of the first right peripheral, dorsal view.
Fig. 4—Part of the second right peripheral, dorsal view.
Fig. 5—Part of the second left peripheral, dorsal view.
Fig. 6—Fifth right peripheral, external view.
Fig. 7—Same as Fig. 6, internal view.
Fig. 8—Part of the sixth right peripheral, external view.
Fig. 9—Pleural plate fragment, dorsal view.
Fig. 10—Part of the eighth right peripheral, dorsal view.
Fig. 11—Pleural plate fragment, dorsal view.
Fig. 12—Pleural plate fragment, dorsal view.

Chorlakkichelys shahi gen. et sp. nov., Chorlakki, referred specimens.

Fig. 13—GSP-UM 501, pygal.
Fig. 14—GSP-UM 502, sixth left peripheral.
Fig. 15—GSP-UM 503, suprapygal fragment.
Fig. 16—GSP-UM 504, neural fragment.


1

2

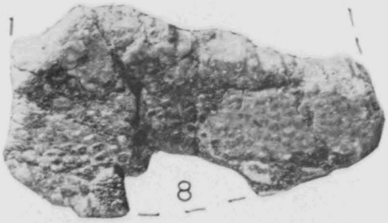

3


4

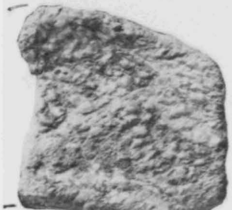

5

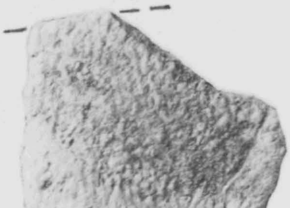

6


7

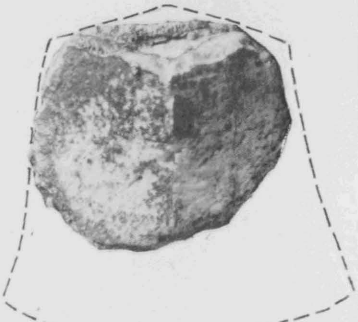

8

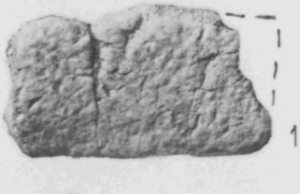

9


10


11


12


13


14


15

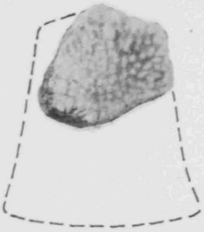

16

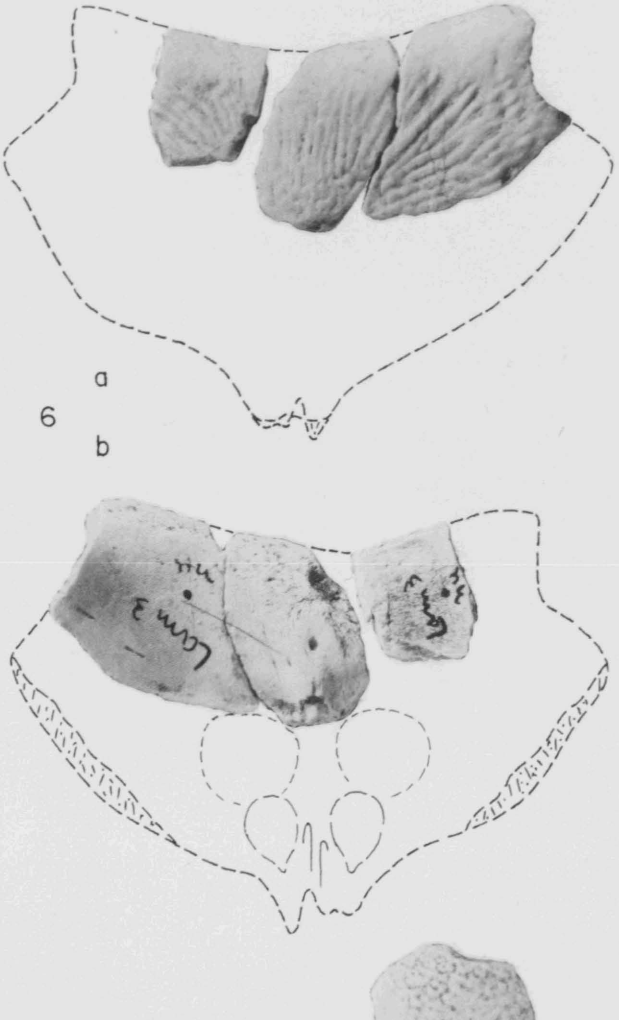
EXPLANATION OF PLATE 2

(Figs. 1-5 enlarged, left scale. Figs 6-8 reduced slightly, right scale. Scales in cm.)

Chorlakkichelys? sp. from Lammidhan, Kala Chitta Hills, Attock District, Pakistan.

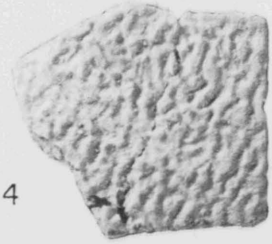
Fig. 1—GSP-UM 518, pygal fragment, dorsal view.
Fig. 2—GSP-UM 521, part of the second left peripheral plate, dorsal view.
Fig. 3—GSP-UM 519, seventh left peripheral, dorsal (*a*) and ventral (*b*) views.
Fig. 4—GSP-UM 516, pleural fragment, dorsal view.
Fig. 5—GSP-UM 524, left hypoplastron fragment, ventral (*a*) and dorsal (*b*) views.
Fig. 6—GSP-UM 523, nuchal plate fragment, dorsal (*a*) and ventral *b*) views, with reconstruction of the missing parts, showing (in *b*) the typical muscular impresses and vertebral structures of a Carettochelyid nuchal plate.
Fig. 7—GSP-UM 525, nuchal fragment, dorsal view.
Fig. 8—GSP-UM 526, posterior peripheral fragment, dorsal (*a*) and ventral (*b*) views.


1

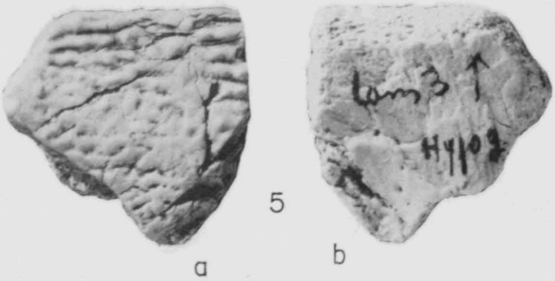

6

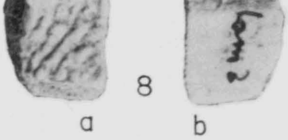

2


3


4


7


5


8

0 3 cm

0 3 cm

EXPLANATION OF PLATE 3

(Figs. 3-8 and 12-17 enlarged, left scale. Figs 1, 2, 9, 10-11 reduced slightly, right scale. Scales in cm.)

Chorlakkichelys? sp. from Jhalar and Chharat, Kala Chitta Hills, Attock District, Pakistan.

Jhalar
Fig. 1—GSP-UM 508, second left pleural, dorsal view.
Fig. 2—GSP-UM 509, fifth right pleural, external view.
Fig. 3—GSP-UM 511, left hypoplastron fragment, dorsal (*a*) and ventral (*b*) view.
Fig. 4—GSP-UM 510, left epiplastron fragment, ventral view.
Fig. 5—GSP-UM 515, peripheral plate fragments, dorsal view.
Fig. 6—GSP-UM 513, peripheral plate fragments, dorsal view.

Chharat
Fig. 7—GSP-UM 506, fourth right peripheral, internal (*a*) and external (*b*) views.
Fig. 8—GSP-UM 507, second right peripheral plate fragment, dorsal (*a*) and ventral (*b*) views.
Fig. 9—GSP-UM 539, pleural fragment, dorsal view.
Fig. 10—GSP-UM 541, neural fragment, dorsal view.

EXPLANATION OF PLATE 3 (continued)

Trionychinae indet.

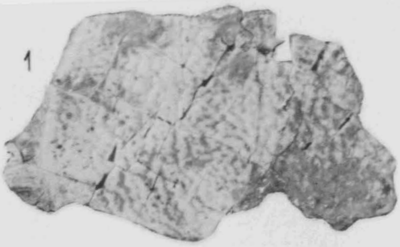
Chorlakki
Fig. 11—GSP-UM 535, left pleural fragment, dorsal (*a*) and ventral (*b*) views.
Fig. 12—GSP-UM 536, pleural fragment, dorsal view.
Fig. 13—GSP-UM 537, pleural fragment, dorsal view.

Lammidhan
Fig. 14—GSP-UM 543, pleural fragment.
Fig. 15—GSP-UM 546, pleural fragment.

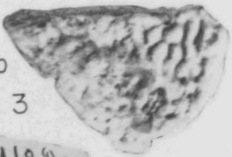
Jhalar
Fig. 16—GSP-UM 542, pleural fragment.

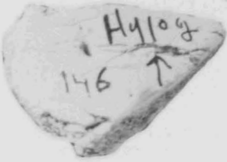
Indeterminate (Pelomedusid or Emydid ?) turtle.

Bawar Nala
Fig. 17—GSP-UM 550, neuropleural fragment.


1

2


b

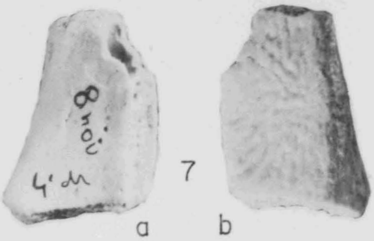


a 3


4


5


6


7
a b

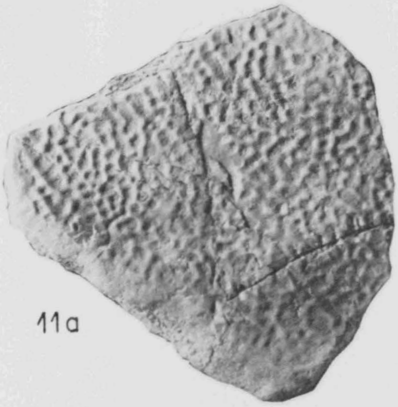

a b
8

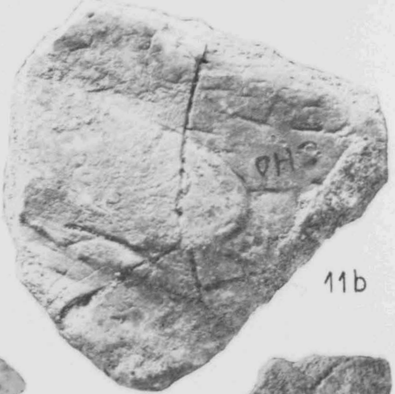

9

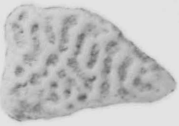

10


13


12

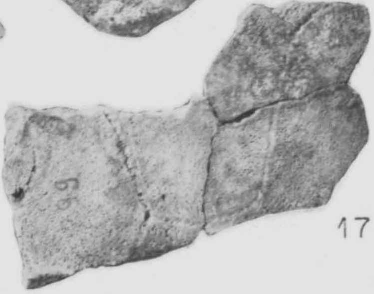

11a


11b


15


14


16


17

0 4 cm

0 4 cm

LOWER VERTEBRATES FROM THE EARLY-MIDDLE EOCENE KULDANA FORMATION OF KOHAT (PAKISTAN): SQUAMATA

by

J. C. Rage[1]

Abstract.—The early-middle Eocene locality of Chorlakki, in the Kohat District of Pakistan, has yielded a small herpetofauna including one lizard (*Tinosaurus* sp.) and two snakes (both boids, one an erycine and the other a boine). This is the first report of early Cenozoic squamates from Pakistan. The snakes from Chorlakki are the oldest terrestrial snakes known from Asia.

INTRODUCTION

The Cenozoic squamate record of Asia is very poorly known. The new specimens described here from Chorlakki, an early-middle Eocene locality in the Kohat District of the North West Frontier Province, Pakistan, provide the first evidence of early Cenozoic squamates from Pakistan. Unfortunately, very little squamate material is present in this fauna, and the condition of much of it is poor. Identifiable material represents one lizard and two snakes. The latter are the oldest terrestrial snakes known from Asia.

SYSTEMATIC PALEONTOLOGY

Order SQUAMATA
Suborder SAURIA
Family Agamidae
Genus *Tinosaurus* Marsh, 1872

Tinosaurus sp.
Fig. 1

Referred specimens.—GSP-UM 552 and 553, isolated teeth.

Description.—Two isolated teeth, with a fragment of supporting bone, are referred to the family Agamidae, commonly known as chisel-teeth lizards. The teeth are distinctive. Their implantation is acrodont, that is to say, their base is fused to the "occlusal" margin of the supporting bone (they do not root in pits). The teeth are strongly compressed laterally, but their base remains swollen. They display three antero-posteriorly aligned cusps. The median cusp is

---

[1] Laboratoire de Paléontologie des Vertébrés (U.A. 720), Université Paris VI, 4 Place Jussieu, 75252 Paris FRANCE

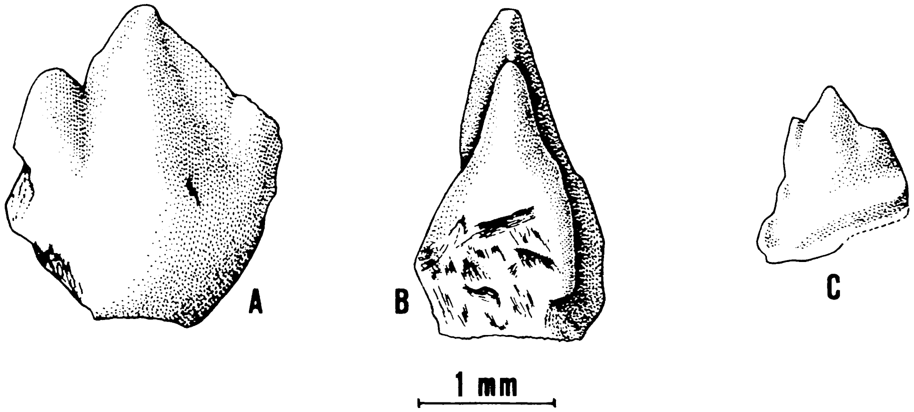


FIG. 1— *Tinosaurus* sp. from Chorlakki. A-B: GSP-UM 552, tooth in lateral (A), and anterior or posterior view (B). C: GSP-UM 553, tooth in lateral view.

the strongest and the highest one. Anterior and posterior cusps are lower and comparatively small.

On the larger tooth (GSP-UM 552; Fig 1A, B) one of the two small cusps is broken off, but these two cusps were probably at the same level on both sides of the main cusp. The latter is broad at the base, but much thinner near its two occlusal edges. The occlusal edges are, consequently, very sharp. The remaining small cusp does not exhibit such marked thinning, but the occlusal edges are also rather sharp.

The smaller tooth (GSP-UM 553; Fig. 1C) is shorter and relatively higher than the larger one. One of its small cusps lies at a lower level than the other, and it is comparatively blunt (perhaps worn). In this tooth, the occlusal edges of the cusps do not display the same marked thinning as seen on the median cusp of the larger tooth.

In spite of these differences, the two teeth may belong to the same species. In Agamidae, the dentition is heterodont. In agamids the anterior teeth are pleurodont instead of acrodont (Moody and Rocek, 1980). Moreover, the teeth of the acrodont series are not notably similar. The fossil agamid *Tinosaurus* is still poorly known. These teeth may be referable to *Tinosaurus* but the range and polarity of observed variations are still unknown. All that is known is that the size of the teeth increases posteriorly through the first and second thirds of the dental series and then they decrease (Hecht and Hoffstetter, 1962). Also, in distinction to the living Agamidae, there are no caniniform teeth in *Tinosaurus*.

Discussion.—At present, five species of *Tinosaurus* are recognized as being valid (Estes, 1983): *T. stenodon* Marsh 1872, from the early and middle Eocene of North America; *T. pristinus* (Leidy 1872), from the middle Eocene (Bridgerian) of North America (Hecht, 1959); *T. lushihensis* Dong, 1965 from the early late Eocene of Honan, China; *T. asiaticus* (Gilmore, 1943) from the Eocene (Ulan Shireh Formation; ? early late Eocene) of Inner Mongolia, China; and *T. doumuensis* Hou, 1974 from the middle or late Paleocene (Dou-mu Series) of Anhui, China. Other *Tinosaurus* specimens, not identified to species, have been reported from the earliest Eocene of Belgium (Hecht and Hoffstetter, 1962; Godinot et al., 1978), and from the early Eocene of France (Russell et al., 1982). At present *Tinosaurus* is known from the Paleocene (middle or late Paleocene) of Asia and the Eocene of Asia, Europe, and North America.

The teeth from Chorlakki are clearly different from the triconodont teeth of *T. doumuensis* because they are longer and lower, and their cusps seem to be more acute. In European

Tinosaurus the cusps of the teeth are more distinct, especially the median cusp which is very short and high. In conclusion, the Chorlakki specimens appear to compare well with the two Eocene species from North America, and with *T. lushihensis* from the early late Eocene of China, but detailed comparison is not possible due to the fragmentary nature of the fossils.

Suborder SAURIA indet.

A very fragmentary vertebra (GSP-UM 561) belongs to an indeterminate lizard.

Suborder SERPENTES
Family Boidae

Nine rather fragmentary vertebrae are identified as snakes; four of these are well preserved and identifiable to subfamily. All of the snake vertebrae from Chorlakki are referred to Boidae because they are clearly shorter than they are wide, they have no projecting prezygapophysial processes, and the centrum is broadest at its anterior end. The known vertebrae as a group represent two distinct taxa.

Subfamily Erycinae
Fig. 2A-E

Referred specimens.—GSP-UM 554, and 774 isolated vertebrae.

Description.—These vertebrae are small and rather poorly preserved. In dorsal view, they are slightly shorter than they are wide, and they are notably narrow between the prezygapophyses and postzygapophyses. The zygosphene has two lateral lobes, but its central part is damaged on both vertebrae. The prezygapophysial facets are wide. The base of the neural spine is long and reaches the posterior part of the zygosphene. A very obtuse and shallow median notch indents the posterior border of the neural arch.

In ventral view, the centrum is rather elongate and slightly widened anteriorly; subcentral ridges are well marked. The centrum bears a thin and acute haemal keel. On GSP-UM 774 the posterior half of the haemal keel is very salient (there is no trace of breakage, so that this prominent part does not represent the base of a damaged hypapophysis).

Examining the vertebrae in lateral view, the neural spine is partly broken off on both vertebrae; it is low and it comprises an anterior thin sloping part and a slightly thickened posterior part. The interzygapophysial ridges are very sharp and the subcentral ridges are straight. The paradiapophyses are badly worn but lateral foramina are present. The anterior face of the vertebra displays a zygosphene of moderate thickness, with a slight dorsal convexity. The prezygapophyses are slanting; there are no projecting prezygapophysial processes. Paracotylar foramina are absent. The paradiapophyses lie comparatively far from the centrum and their articular surfaces are oriented somewhat downward.

In posterior view, the neural arch is strongly depressed and the roof of the zygantrum is comparatively thin. There are no foramina on either side of the zygantrum.

The vertebra GSP-UM 554 is somewhat surprising because, as a rule, vertebrae whose haemal

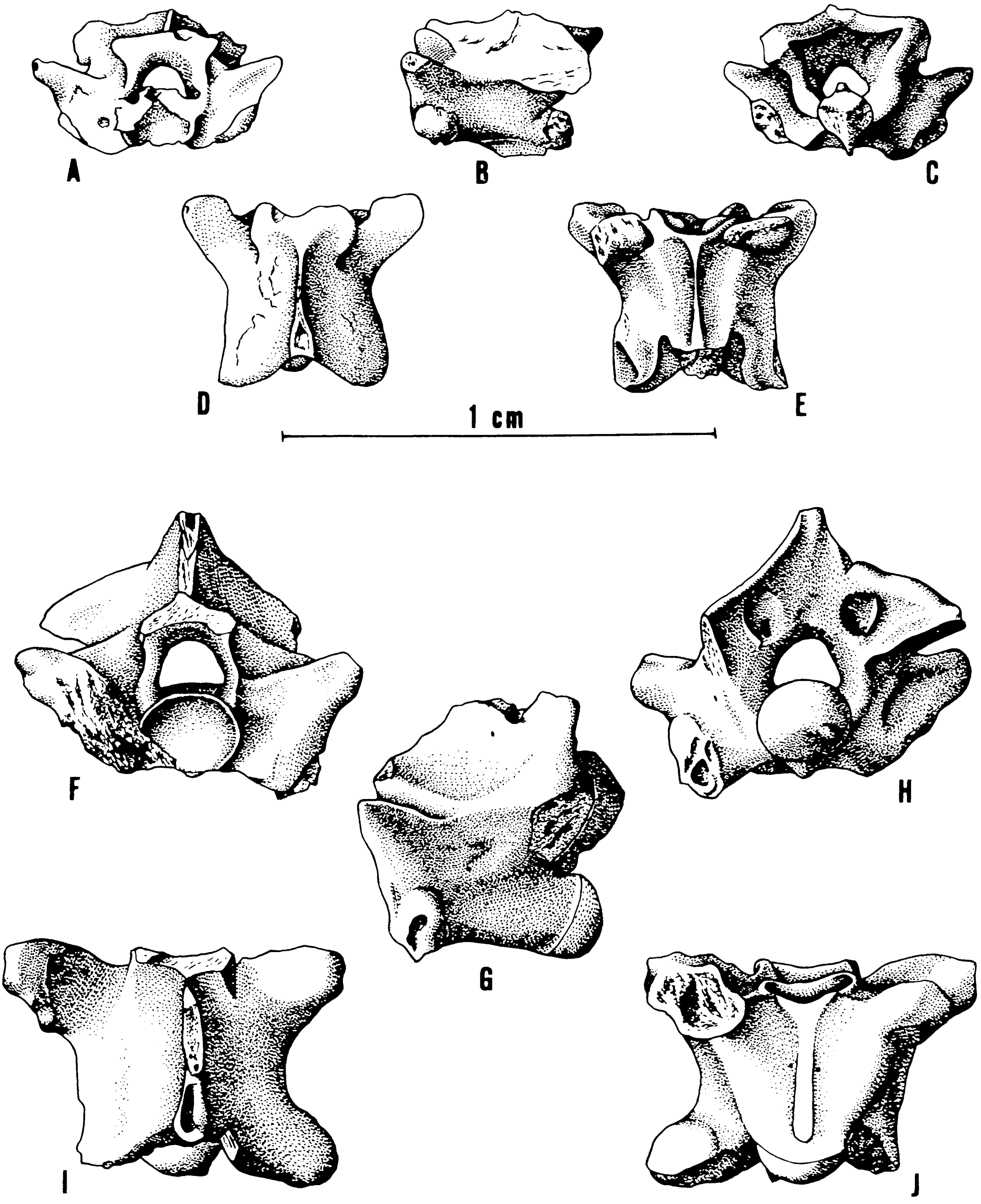


FIG. 2— Boidae from Chorlakki. A-E: GSP-UM 554, Erycinae, trunk vertebra, anterior face (A), left lateral face (B), posterior face (C), dorsal face (D), and ventral face (E). F-J: GSP-UM 555, Boinae, trunk vertebra, anterior face (F), left lateral face (G), posterior face (H), dorsal face (I), and ventral face (J).

keels have a prominent posterior half occur anteriorly in the vertebral column (excepting sometimes the posteriormost trunk vertebrae, in which the haemal keel may protrude ventrally—in such a case the salient part occupies only a very short posteriormost part of the centrum length; such posterior hypapophyses are called "cloacal hypapophyses"). On the other hand, the morphology of the paradiapophyses, which lie rather far from the centrum and whose articular facets face downward, is characteristic of posterior trunk vertebrae. Thus, the vertebra described here displays usual characteristics of both rather anterior and posterior trunk vertebrae. Apart from this peculiarity, the vertebra agrees well with those of Boidae.

The most striking character of these vertebrae is the strong flattening of the neural arch; this might be the result of postdepositional deformation. Nevertheless, the thinness of the roof of the zygantrum conveys the suggestion that the neural arch was depressed before fossilization. Assuming, then, that the neural arch was originally depressed, these vertebrae may be referred, within Boidae, to the subfamily Erycinae.

Discussion.—Erycinae, sand boas, are known since the early Paleocene (Puercan) from North America (*Helagras prisciformis*; Rage, 1984): they are represented today by 13 extant species, most of them living on sandy soils in arid regions. Erycinae constituted an important part of the snake fauna during the Cenozoic (Hoffstetter and Rage, 1972; Holman, 1979). As the vertebrae from Chorlakki probably represent a new species (or even genus), they do not yield any useful biostratigraphic information.

Subfamily Boinae

Fig. 2F-J

Referred specimens.—GSP-UM 555 and 556, isolated vertebrae.

Description.—Vertebra GSP-UM 555 is markedly larger than the preceding ones. In dorsal view, it is shorter than wide, and it is markedly narrow between the prezygapophyses and postzygapophyses. The zygosphene is partly broken so that its exact shape remains unknown. The prezygapophysial facets were apparently comparatively elongate. The median notch in the posterior border of the neural arch is rather shallow. The base of the neural spine is very long, and anteriorly it approaches the lip of the zygosphene.

In ventral view the centrum is well delimited by the subcentral ridges that diverge anteriorly. The ventral surface of the centrum is somewhat concave and the haemal keel is very blunt and rather inconspicuous; both these characteristics may be the result of postdepositional deformation.

In lateral view, the neural spine appears very long; its anterior edge arises abruptly from the roof of the zygosphene, and the posterior edge is slightly overhanging. The upper part of the neural spine is broken off, which prevents determination of its height. Sharp interzygapophysial ridges connect prezygapophyses and postzygapophyses. The subcentral ridges are almost straight. The diapophysial part of the paradiapophysis is notably narrower than the parapophysial part. Small lateral foramina are present.

In anterior view, the remaining part of the zygosphene is about as wide as the cotyle. The prezygapophyses are tilted upward; there were probably no projecting prezygapophysial processes. The cotyle is almost circular; paracotylar foramina are lacking. The paradiapophyses project markedly under the centrum. In posterior view the neural arch is moderately vaulted and the roof of the zygantrum is rather thick. On the posterior margin of the neural arch, there are no foramina on either side of the zygantrum.

The vertebra GSP-UM 556 is very fragmentary. The posterior part of the neural arch is somewhat displaced and slightly distorted; the thickness of its posterolateral parts indicates that it was not depressed. This vertebra is distinguished from GSP-UM 555 by its narrower general shape and by the presence of a well marked, wide and blunt haemal keel. Because of the vaulted morphology of the neural arch, this vertebra could belong to the same species as GSP-UM 555 but it represents a more posterior trunk vertebra than the latter.

This snake may be referred to the subfamily Boinae on the basis of its nondepressed neural arch, well developed neural spine, and absence of foramina on either side of the zygantrum. Among Boinae, this snake resembles only the rather closely related genera *Paleryx* and *Palaeopython* (Rage and Ford, 1980) that are known from the upper Eocene (and perhaps the middle Eocene) of Western Europe, but it is well distinguished from both genera by the length of its neural spine, which is unusual in this subfamily. This snake probably represents a new species and genus but the available material is not sufficient to permit erection of a new taxon.

SERPENTES indet.

Five vertebrae (GSP-UM 557-560, two of them articulated) are too fragmentary or badly crushed to permit description or identification.

CONCLUSIONS

Only *Tinosaurus*, among fossils described here, provides any biostratigraphical information. This is, however, vague. *Tinosaurus* is known from the Paleocene of central Asia and the Eocene of central Asia, Europe, and North America. The presence of *Tinosaurus* at Chorlakki is consistent with the early-middle Eocene age inferred on the basis of mammalian fossils (Gingerich et al., 1983).

From a paleogeographic point of view it should be noted that *Tinosaurus* is characteristically Laurasiatic. Boinae and Erycinae are reported from the Paleogene of Asia for the first time; both subfamilies were widely distributed in the Eocene of Europe and North America.

LITERATURE CITED

DONG, Z.-M. 1965. A new species of *Tinosaurus* from Lushih, Honan. Vertebrata PalAsiatica, 9:79-81.

ESTES, R. 1983. Sauria terrestria, Amphisbaenia. Handbuch der Paläoherpetologie, part 10A. Gustav Fischer Verlag, Stuttgart, pp. 1- 249.

GILMORE, C. W. 1943. Fossil lizards of Mongolia. Bulletin of the American Museum of Natural History, 81:361-384.

GINGERICH, P. D., 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.

GODINOT, M., F. de BROIN, E. BUFFETAUT, J. C. RAGE, and D. E. RUSSELL. 1978. Dormaal: une des plus anciennes faunes éocènes d'Europe. Comptes Rendus de l'Académie des Sciences, Paris, Série D, 287:1273- 1276.

HECHT, M. K. 1959. Amphibians and reptiles. *In* P. O. McGrew et al., The geology and paleontology of the Elk Mountain and Tabernacle Butte area, Wyoming. Bulletin of the American Museum of Natural History, 117:130-146.

HOFFSTETTER, R., and J. C. RAGE. 1972. Les Erycinae fossiles de France (Serpentes, Boidae). Compréhension et histoire de la sous-famille. Annales de Paléontologie, Vertébrés, 58:81-124.

HOLMAN, J. A. 1979. A review of North American Tertiary snakes. Publications of the Museum, Michigan State University, Paleontological Series, 1:203-260.

HOU, L.-H. 1974. Paleocene lizards from Anhui, China. Vertebrata PalAsiatica, 12:193-200.

LEIDY, J. 1872. Remarks on *Chameleo pristinus*. Proceedings of the Academy of Natural History, Philadelphia, 1872:277.

MARSH, O. C. 1872. Preliminary description of new Tertiary Reptiles (Parts I and II). American Journal of Science, Series 3, 4:298-309.

MOODY, S., and Z. ROCEK. 1980. *Chamaeleo caroliquarti* (Chamaeleonidae: Sauria): a new species from the lower Miocene of Central Europe. Vestnik Ústředního Ústavu Geologickeho, Prague, 55:85-92.

RAGE, J. C. 1984. Serpentes. Handbuch der Paläoherpetologie, part 11, Gustav Fischer Verlag, Stuttgart, pp. 1-80.

______and R. L. E. FORD. 1980. Amphibians and squamates from the upper Eocene of the Isle of Wight. Tertiary Research, 3:47-60.

RUSSELL D.E., N. BONDE, E. BONE, F. de BROIN, M. BRUNET, E. BUFFETAUT, J. M. CORDY, J.-Y. CROCHET, H. DINEUR, R. ESTES, L. GINSBURG, M. GODINOT, M. C. GROESSENS, P. GIGASE, C. J. O. HARRISON, J.-L. HARTENBERGER, E. HOCH, J. J. HOOKER, A. N. INSOLE, B. LANGE-BADRE, P. LOUIS, R. T. J. MOODY, J. C. RAGE, J. REMY, K. ROTHAUSEN, B. SIGE, D. SIGOGNEAU-RUSSELL, R. SPRINGHORN, J. SUDRE, H. TOBIEN, M. VIANEY-LIAUD, R. VINKEN, and C. A. WALKER. 1982. Tetrapods of the northwest European Tertiary basin (International Geological Correlation Project 124). Geologisches Jahrbuch, Reihe A, Hanover, 60:17-77.