CONTRIBUTIONS FROM THE MUSEUM OF PALEONTOLOGY

THE UNIVERSITY OF MICHIGAN

VOL. 28, NO. 5, PP. 93-100 September 30, 1991

PHYLOGENETIC AND ECOLOGICAL SIGNIFICANCE OF CHANNIDAE (OSTEICHTHYES, TELEOSTEI) FROM THE EARLY EOCENE KULDANA FORMATION OF KOHAT, PAKISTAN

BY

LOIS J. ROE

MUSEUM OF PALEONTOLOGY
THE UNIVERSITY OF MICHIGAN
ANN ARBOR

CONTRIBUTIONS FROM THE MUSEUM OF PALEONTOLOGY

Philip D. Gingerich, Director

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

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

PHYLOGENETIC AND ECOLOGICAL SIGNIFICANCE OF CHANNIDAE (OSTEICHTHYES, TELEOSTEI) FROM THE EARLY EOCENE KULDANA FORMATION OF KOHAT, PAKISTAN

By

LOIS J. ROE[1]

Museum of Paleontology
and Department of Geological Sciences
The University of Michigan

Abstract.— A new genus and species of fish, *Eochanna chorlakkiensis*, belonging to the Family Channidae (Osteichthyes: Channiformes) is described from the early Eocene Kuldana Formation of Kohat District in Pakistan. The type specimen is an isolated anguloarticular. Two other channid fossils are referred to this new species. The anguloarticular is diagnosed as channid based on a combination of three characters, none of which by itself is unique to Channidae. These are: (1) presence of two distinct, laterally separated facets for articulation with the quadrate; (2) anguloarticular contributing to the coronoid process; and (3) unfused angular, articular, and retroarticular. The presence of two laterally separated articular facets is characteristic of all Recent and Neogene fossil channids examined, and two laterally separated facets are present in only one other group, Synbranchiformes (swamp eels). This lends support to the hypothesis of Lauder and Liem (1983) that Channiformes are most closely related to Synbranchiformes. The presence of channid fossils in Kuldana sediments is the earliest record of the family in freshwater deposits and indicates that Channiformes existed as a distinct phylogenetic entity in the early Eocene.

INTRODUCTION

The family Channidae constitutes one of the most widespread and abundant primary freshwater fish families on the Indian subcontinent. Channids, known also as snakeheads or murrels, are heavily-scaled fishes, with long, spineless dorsal and anal fins. They are voracious predators that commonly grow to over a meter in length, and are able to breathe air using an accessory breathing apparatus known as a labyrinthine organ (Liem, 1963). Fossilized skull bones of channids are often easily recognized by the impressions left by scales embedded in the exterior surface of the skull.

---

[1]Present address: National Oceanic and Atmospheric Administration, Office of Oceanic and Atmospheric Research, 1335 East-West Highway, Silver Spring, Maryland 20910; and Department of Paleobiology, National Museum of Natural History, MRC NHB-121, Smithsonian Institution, Washington, D.C. 20560

TABLE 1—Specimens of Recent fishes compared in this study

Perciformes
Anabantidae
Anabas testudineus, UMMZ 205293-S (Philippines)
Ctenopoma multispinnis, UMMZ 200062-S (Zambia)
Osphronemus gouramy, UMMZ 213912-S (locality unknown)
Osphronemus olfax, USNM 043929 (Mauritius)
Channiformes
Channidae
Channa gachua, UMMZ 171693 (Java)
Channa marulius, UMMZ 187867 (Bangladesh)
Channa micropeltes, UMMZ 209262 (Southeast Asia)
Channa ocellata, UMMZ 66528 (China)
Channa pleurophthalmus, UMMZ 171681 (Sumatra)
Channa striata, UMMZ 187842 (Thailand); USNM 272143, 272144, and 272147 (localities unknown)
Parachanna obscura, UMMZ 195013 (Ghana)
Synbranchiformes
Synbranchidae
Synbranchus marmoratus, UMMZ 207383-S (Paraguay)

Channidae is not a speciose group, with only about 15 species in three genera (Smith, 1945; Mirza, 1975; Jayaram, 1981; Teugels and Daget, 1984). As many as 75 species have been described, but many of these have been synonomized (J. H. Hutchison, pers. comm., 1988). Recognition of species is based almost entirely on external morphology and meristic characteristics. Channids are united by the following synapomorphies (Lauder and Liem, 1983):

1. Otic bullae for sacculith, utriculith, and lagenolith are contained in the prootic bone
2. Metapterygoid with prominent anterodorsally directed uncinate process
3. Two ventral aortae emerge separately from the bulbus arteriosus
4. Gas exchange with air in the suprabranchial and buccopharyngeal cavities, which remain in open communication throughout the breathing cycle

Day (1914) and Bhimachar (1932) described the osteology of *Channa striata* (= *Ophicephalus striatus*), but no comparative osteological study of all channid taxa has been published. Fossil and extant taxa are difficult to compare and the order as a whole is in need of revision. This problem is compounded by inaccuracies in reporting osteological features, as noted by Lauder and Liem (1983). Lauder and Liem themselves omitted the sphenotic in their figures of the skull of *Channa striata* (1983, p. 179, fig. 59A). Currently, all living Asian species are referred to *Channa*, while the three African species are referred to *Parachanna* (Teugels and Daget, 1984). *Parachannichthys* Gayet (1988) from the Miocene of India is the only extinct genus.

Berg (1940) proposed that Channidae be placed in their own order, Channiformes (= Ophicephaliformes). Liem (1963) noted several osteological characters that he considered support for Berg's (1940) proposal. Channiformes have often been allied with the Anabantoidei (gouramies) based on the fact that both possess a modified first epibranchial, which allows them to breathe air. Liem (1963, p. 70) argued that this relationship was not based on strong evidence, saying that the resemblance between the two groups is limited to this one feature that itself is "...specifically adaptive to a shared ecology, and therefore probably a convergent feature." Lauder and Liem (1983) hypothesized that Channiformes are the plesiomorphic sister-group of Synbranchiformes (swamp eels), based on the following four characters: (1) posterior coalescing of the left and right sides of the forebrain; (2) adductor mandibulae hypertrophied and specialized into A1 and A2 divisions; (3) fourth branchial arteries modified;

and (4) fins without spines– a character originally listed by Liem (1963, p. 71) as an osteological difference between Channiformes (= Ophicephaliformes) and Anabantoidei.

Extant channids are widely distributed throughout west central Africa (Berra, 1981) and south and southeast Asia (Smith, 1945; Berra, 1981; Jayaram, 1981). Their presence elsewhere is due to introduction by humans. Only a few fossil occurrences of Channidae are known. Channid fossils have been documented from the Eocene and Neogene of India (Khare, 1976; Lydekker, 1886; Sahni and Khare, 1977; Sahni et al., 1981; Sahni et al., 1984; Gayet, 1988), the Neogene of Pakistan (Pilbeam et al., 1979), and the Neogene of Nepal (Munthe et al., 1983). In Southeast Asia, channids are known from the Pleistocene of Java (Boeseman, 1949). Channids are unknown as fossils from Africa.

The three channid fossils described here all come from the early Eocene Kuldana Formation in the Panoba anticline north of Chorlakki village, in the Kohat District of Pakistan. These specimens will be deposited at the Geological Survey of Pakistan in Islamabad (GSP-UM). Recent specimens used for comparison in this study are listed in Table 1. These are housed in the University of Michigan Museum of Zoology (UMMZ) and the U.S. National Museum of Natural History (USNM).

SYSTEMATIC PALEONTOLOGY

Class OSTEICHTHYES
Order CHANNIFORMES
Family CHANNIDAE

Eochanna, new genus

Type and only species.—*Eochanna chorlakkiensis*, new species.

Diagnosis.—Differs from all other Channidae in having the two articular facets of the anguloarticular in different planes, with no pronounced cleft between them to receive the dorsal edge of the quadrate. Incomplete fusion of the angular and articular distinguishes this fossil from the extant *Channa micropeltes*.

Etymology.—Greek *eo-*, dawn, and *channē*, fish.

Eochanna chorlakkiensis, new species

Figs. 1A-C, 2A-C

Holotype.—GSP-UM 781, partial left anguloarticular.

Referred material.—GSP-UM 780, a partial left sphenotic, and GSP-785 a partial right epiotic.

Type locality.—Continental red beds of the Kuldana Formation at Chorlakki, about 4 km NNW of Chorlakki village, Kohat District, North West Frontier Province, Pakistan, 33°37'20" N latitude, 71°55'20" E longitude. See Gingerich et al. (1979a), Wells (1983), and Thewissen et al. (1987) for more detailed descriptions.

Age and distribution.—Late early Eocene (Gingerich and Russell, 1990, pp. 2-3). Known from the type locality only.

Diagnosis.—As for the genus, see above.

Etymology.—Named for type locality, Chorlakki.

Description.—GSP-UM 781 is an incomplete left anguloarticular (Fig. 1A-C), which consists of three bones: the angular (the anterior ossification), the articular, and the retroarticular (the posterior ossifications). The specimen is missing approximately the anterior third of the dorsal and ventral flanges of the articular that insert into the dentary. A small fragment of the lateral portion of the lateral articular facet is broken away, and the posteroventral edge of the element, including part of the articular and the retroarticular, is incomplete. The specimen is 3.5 cm in

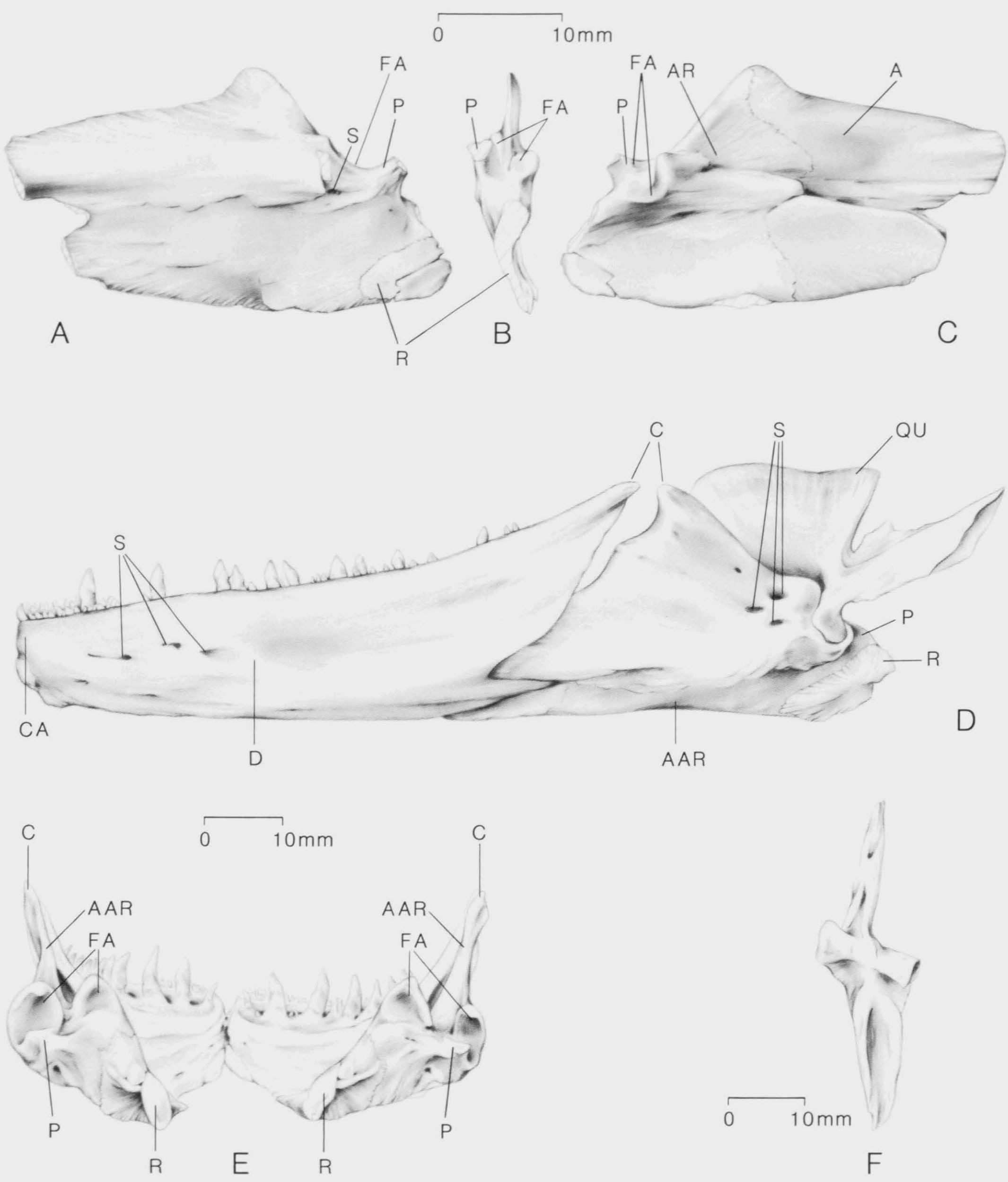

FIG. 1— *Eochanna chorlakkiensis*, n. gen., n. sp., from Chorlakki. A-C, left anguloarticular (Holotype, GSP-UM 781) in medial, lateral, and posterior views. D-E, lower jaw of *Channa micropeltes* (UMMZ 200062-S) in left lateral and posterior views showing shapes and positions of bones and articular facets. F, left quadrate of *Channa micropeltes* (UMMZ 200062-S) in anterior view showing ridge that slides into cleft between articular facets of anguloarticular. Element abbreviations are as follows: *A*, angular bone; *AAR*, anguloarticular bone; *AR*, articular bone; *CA*, cartilage; *CO*, coronoid; *D*, dentary bone; *FA*, articulation facet of articular bone; *P*, postarticular process of articular bone; *R*, retroarticular bone; *S*, openings for mandibular sensory-canal tubes and pores.

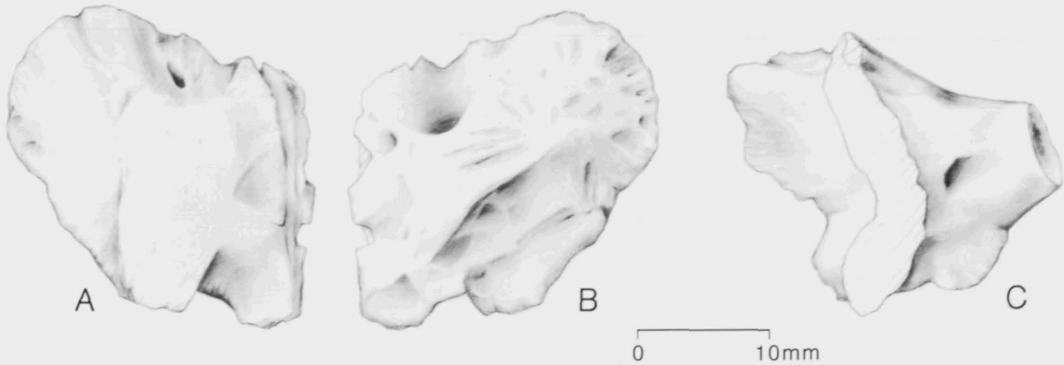

FIG. 2— *Eochanna chorlakkiensis*, n. gen., n. sp., from Chorlakki. A-B, left sphenotic (GSP-UM 780) in dorsal and ventral views. C, right epiotic (GSP-UM 781) in dorsal view.

length and 2.0 cm in greatest height, which is at the apex of the coronoid region. The lateral surface of this specimen (Fig. 1A) is somewhat striated, except where abrasion has removed the original surface. The medial surface of the element (Fig. 1C) is smoother than the lateral surface, as is generally the case with the skull bones of fish.

The sutures between the bones are fairly visible. The suture between the angular and the articular is best seen on the medial surface of the specimen (Fig. 1C). The suture begins just posterior to the apex of the coronoid process and is concave anterodorsally between the apex and the midline of the articular. It then appears to curve back posteriorly around the anterior part of the midline and straighten out at a point posterior to the dorsal part of the suture until it reaches the ventral edge of the element (Fig. 1C).

The angular is not clearly defined because only the dorsal part of its suture with the articular is visible on the specimen. As with all recent channids, the angular bifurcates anteriorly into dorsal and ventral flanges, which insert into the dentary. This bifurcation is clearly seen on GSP-UM 781, but the specimen is broken a few centimeters anterior to the cleft, so the anterior features of these flanges cannot be observed.

The articular bone has two articular facets of nearly equal dimensions (Fig. 1B). One of the facets is situated ventrolaterally to the coronoid process; the other ventromedially to the coronoid. The lateral facet, about 3 mm wide and 4 mm high, is concave dorsally. The medial facet is about 5 mm wide and 5 mm high, and it is concave dorsomedially and directed slightly more posteriorly. The lateral facet contains the postarticular process. The medial facet has a dorsal, posteriorly directed process overhanging the surface of that facet. As noted in the diagnosis, the two articular facets are in different planes, with an approximately 30° angle between them. The entire articular surface of both facets is nearly continuous, except that there is a narrow opening between them that appears to be natural rather than a break.

The retroarticular is a small bone located along the posteroventral edge of the specimen, below the articular facets (Figs. 1A, 1C). The specimen is slightly broken in this region, but the suture can be distinguished by the change in texture and color of the bone in the posteroventral region: the retroarticular is slightly smoother and lighter in color than the surrounding bone.

GSP-UM 780 (Figs. 2A-B) is diagnosed as a channid left epiotic based on its geometry, texture, the inward curvature of its posterior dorsal process, and the presence of a fossa for receiving an overlapping posterior process of the parietal. None of these features is known to be a synapomorphy of channid taxa.

GSP-UM 785 (Fig. 2C) is diagnosed as a channid left sphenotic by its geometry and the presence and placement of fossae anterior and posterior to the descending process for articulation with the prootic. None of these features is known at present to be a synapomorphy of channids.

Discussion.—Of the three specimens described above, only GSP-UM 781 demonstrates any apomorphies by which it can be diagnosed as a member of the Channidae, and recognized as distinct from all other channids examined. Recognition of GSP-UM 781 as a channid anguloarticular is based on a combination of three characters, none of which by itself, is unique to Channidae. The three characters are: (1) presence of two distinct, laterally separated facets for articulation with the quadrate; (2) contribution of the anguloarticular to coronoid process; and (3) presence of distinct ossifications of angular, articular, and retroarticular (see Nelson, 1973a, 1973b, for a synopsis of the anguloarticulars of other actinopterygians). Distinct ossifications are seen in all extant channids examined except *Channa micropeltes* (Fig. 1D-E), which has the angular and articular solidly fused.

Only one other actinopterygian, *Synbranchus*, has two distinct, laterally separated facets for articulation between the anguloarticular and quadrate, with a cleft for receipt of the dorsal part of the quadrate. The anguloarticular of *Synbranchus* does not contribute to the coronoid process. *Amia* has two articular surfaces on its anguloarticular, but only one of these is on the posterior edge and articulates with the quadrate. The other articular surface is a convexity on the posterodorsal surface of the articular and articulates with the preopercle. Some sparoids (perhaps all) have two facets, but in all specimens examined these are essentially one continuous facet, with a ridge running diagonally through dividing the facet unevenly into a large dorsal portion and a much smaller ventral one. The two facets are in different planes, but are oriented very differently than those of GSP-UM 781 and do not possess a cleft between them as do both channids and *Synbranchus*. The fact that *Synbranchus* possesses a double articular facet on the articular lends some support to the hypothesis of Lauder and Liem (1983) that Channiformes and Synbranchiformes are sister groups. Neither of the anabantoids examined (*Ctenopoma multispinnis*, *Osphronemus gouramy*) possesses a double articular either, so the case for a close relationship between Channiformes and Anabantoidei is not supported by characters of the anguloarticular.

In most of the extant channids examined, e.g., *Channa marulia* and *Channa striata*, the angular and the articular are separate ossifications, with a clearly visible suture between them. The retroarticular is also a separate ossification. *Channa micropeltes* is the one exception among the species examined: while the retroarticular remains a separate ossification, the angular and articular are completely fused. *Eochanna* more closely resembles channids other than *C. micropeltes* in the pattern of ossification of the angular and articular.

In some specimens, the posterior part of the dentary almost completely surrounds the angular, making the suture less obvious, but two ossifications are definitely present. Although the path of the suture in *Eochanna chorlakkiensis* (GSP-UM 781, Fig. 1C) is almost identical to the anterior and posterior contours of the anguloarticular and dentary, respectively, in *Channa micropeltes*, closer examination of the fossil reveals a cleft that separates the articular into dorsal and ventral processes that insert into the dentary. The two ossifications are in fact the angular and the articular.

DISCUSSION

Eocene channid material has been described from the Subathu Formation (Jammu and Kashmir, India) by Khare (1976). Gayet (1988) described a new genus, *Parachannichthys*, from the Neogene Siwaliks of India, as the earliest representative of Channidae. She was apparently unaware of Eocene specimens described by Khare (1976).

The Chorlakki locality and its fauna have been described in several papers (Gingerich et al., 1979a, 1979b; Wells, 1983; de Broin, 1987; Gayet, 1987; Rage, 1987; Thewissen et al., 1987; and Gingerich and Russell, 1990). There is some uncertainty about the age of the Kuldana Formation and uncertainty about its age relative to the Subathu Formation (see Russell and Zhai, 1987, and Gingerich and Russell, 1990, for discussion). If Eocene red beds south of the Himalaya increase in age from east to west (Gingerich and Russell, 1981; Russell and Zhai, 1987; Wells and Gingerich, 1987), then the Chorlakki locality in northwestern Pakistan is probably older than other Kuldana Formation localities farther east in Pakistan and older also than the Subathu Formation in Pakistan and Indian parts of Kashmir (Thewissen et al., 1987). The Chorlakki channids appear to predate those described by Khare (1976) as being middle Eocene in age, and these are probably the oldest known representatives of the family.

The importance of the Chorlakki channids lies in the morphology of the anguloarticular (GSP-UM 781), which clearly possesses two laterally separated articular facets, a character of Neogene fossil and extant channids and of *Synbranchus*. This character may be a synapomorphy of Channiformes and Synbranchiformes. The presence of the character in the Chorlakki specimen suggests that Channiformes had already emerged as a distinct phylogenetic entity by the late early Eocene.

The Kuldana channid specimens are important ecologically because they constitute the oldest record of Channidae in an unambiguously freshwater environment. Channidae are considered a primary freshwater fish group (restricted to freshwater), but channids described from the Subathu Formation (Khare, 1976) occur as members of a faunal assemblage that is interpreted as almost exclusively estuarine and marine. It is quite possible, of course, that the Subathu specimens were transported from a freshwater environment, but their early appearance in both freshwater (Kuldana Formation) and estuarine or marine environments (Subathu Formation) is worth noting.

ACKNOWLEDGEMENTS

I thank Drs. C. E. Badgley, P. D. Gingerich, G. R. Smith, and J. G. M. Thewissen for reading the manuscript and providing helpful discussion. I would also like to thank P. Buckup, B. Dyer, D. Johnson, R. Stearley, J. G. M. Thewissen, S. Vogel and J. Williams for their helpful insights. I thank Dr. Gingerich and the Geological Survey of Pakistan for making the fossils available for study. D. Nelson and J. Williams furnished comparative material from the University of Michigan Museum of Zoology (UMMZ) and U.S. National Museum (USNM) collections, respectively. The figures were drawn by Bonnie Miljour.

LITERATURE CITED

BERG, L. S. 1940. Classification of fishes both recent and fossil. Edwards Brothers, Ann Arbor, Michigan: 1-517.

BHIMACHAR, B. C. 1932. The cranial osteology of *Ophicephalus striatus* Bloch. Journal of Mysore University, 6: 72-86.

DAY, A. L. 1914. The osseous system of *Ophicephalus striatus* Bloch. Philippine Journal of Science, 9D: 19-55.

DE BROIN, F. 1987. Lower vertebrates from the early-middle Eocene Kuldana Formation of Kohat (Pakistan): Chelonia. Contributions from the Museum of Paleontology, University of Michigan, 27: 169-186.

GAYET, M. 1987. Lower Vertebrates from the Early-Middle Eocene Kuldana Formation of Kohat (Pakistan): Holostei and Teleostei. Contributions from the Museum of Paleontology, University of Michigan, 27: 151-168.

———. 1988. Découverte du plus ancien Channiforme (Pisces, Teleostei): *Parachannichthys ramnagarensis* n.g., n.sp., dans le Miocène moyen des Siwaliks (Ramnagar, Jammu et Cachemire, Inde). Implications paléobiogéographies. Comptes Rendus de l'Académie des Sciences de Paris, Série 2, 307: 1033-1036.

GINGERICH, P. D., and D. E. RUSSELL. 1990. Dentition of early Eocene *Pakicetus* (Mammalia, Cetacea). Contributions from the Museum of Paleontology, University of Michigan, 28: 1-20.

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

GINGERICH, P. D., 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.

KHARE, S. K. 1976. Eocene fishes and turtles from the Subathu Formation, Beragua Coal Mine, Jammu and Kashmir. Journal of the Palaeontological Society of India, 18: 36-43.

JAYARAM, K. C. 1981. The Freshwater Fishes of India, Pakistan, Bangladesh, Burma and Sri Lanka– a Handbook. Zoological Survey of India, Calcutta: 1-475, 13 pl.

LAUDER, G. V., and K. F. LIEM. 1983. The evolution and interrelationships of actinopterygian fishes. Bulletin of the Museum of Comparative Zoology, 150: 95-197.

LIEM, K. F. 1963. The comparative osteology and phylogeny of the Anabantoidei (Teleostei, Pisces). Illinois Biological Monographs, 30: 1-149.
LYDEKKER, R. 1886. Indian Tertiary and post-Tertiary Vertebrata. Memoirs of the Geological Society of India (Palaeontologica Indica), 10(3): 1-264 (Tertiary Fishes: 241-258).
MIRZA, M. R. 1975. Freshwater fishes and zoogeography of Pakistan. Bijdragen tot de Dierkunde, 45: 143-180.
MUNTHE, J., B. DONGOL, J. H. HUTCHISON, W. F. KEANS, K. MUNTHE, and R. M. WEST. 1983. New fossil discoveries from the Miocene of Nepal include a hominoid. Nature, 303: 331-333.
NELSON, G. J. 1973a. Notes on the structure and relationships of certain Cretaceous and Eocene teleostean fishes. American Museum Novitates, 2524: 1-31.
———. 1973b. Relationships of clupeomorphs, with remarks on the structure of the lower jaw in fishes. In P. H. Greenwood, R. S. Miles, and C. Patterson (eds.), Interrelationships of Fishes. Academic Press, London, pp. 333-349.
NELSON, J. S. 1984. Fishes of the World. Wiley-Interscience, New York: xiii + 1-532.
PILBEAM, D., A. K. BEHRENSMEYER, J. C. BARRY, and S. M. I. SHAH. 1979. Miocene sediments and faunas of Pakistan. Postilla, 179: 1-45.
RAGE, J. C. 1987. Lower vertebrates from the early-middle Eocene Kuldana Formation of Kohat (Pakistan): Squamata. Contributions from the Museum of Paleontology, University of Michigan, 27: 187-193.
SAHNI, A., S. V. SRIKANTIA, T. M. GANESAN, and C. WANGDUS. 1984. Tertiary fishes and mollusks from the Kuksho Formation of the Indus Group, near Nyoma, Ladakh. Journal of the Geological Society of India, 25: 744-747.
SAHNI, A., 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 the Indian subcontinent during the early Paleogene. Bulletin de la Société Géologique de France, 7: 689-695.
SAHNI, A., and S. K. KHARE. 1977. A middle Siwalik fish fauna from Ladhyani (Haritalyangar), Himachal Pradesh. Biological Memoirs Series 1, 2 (1 and 2): 187-221.
SMITH, H. M. 1945. The freshwater fishes of Siam or Thailand. Bulletin of the U.S. National Museum, 188: 1-622.
TEUGELS, G. G., and J. DAGET. 1984. *Parachanna* nom. nov. for the African snakeheads and rehabilitation of *Parachanna insignis* (Sauvage, 1884) (Pisces, Channidae). Cybium, 8(4): 1-7.
THEWISSEN, J. G. M., P. D. GINGERICH and D. E. RUSSELL. 1987. Artiodactyla and Perissodactyla (Mammalia) from the early-middle Eocene Kuldana Formation of Kohat (Pakistan). Contributions from the Museum of Paleontology, University of Michigan, 27: 247-274.
WELLS, N. A. 1983. Transient streams in sand-poor red beds: early-middle Eocene Kuldana Formation of northern Pakistan. Special Publications of the International Association of Sedimentologists, 6: 393-403.
WELLS, N. A., and P. D. GINGERICH. 1987. Paleoenvironmental interpretation of Paleogene strata near Kotli, Azad Kashmir, northeastern Pakistan. Kashmir Journal of Geology, 5: 23-41.