

MIOCENE FISHES FROM LAKE PHETCHABUN IN NORTH-CENTRAL THAILAND, WITH DESCRIPTIONS OF NEW TAXA OF CYPRINIDAE, PANGASIIDAE, AND CHANDIDAE

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ABSTRACT

Fossiliferous beds at a depth of 2–4 m from Ban Nong Pla in Phetchabun province, north-central Thailand, have yielded 11 species of teleosts or bony fishes. The fossils, of Miocene age, occur in fluvio-lacustrine deposits in an ancient lake-bed in the Phetchabun intermontane basin. There are six cyprinoids or carps, three siluroids or catfishes, and two percoids. Five of the carps and one of the catfishes are similar to, and perhaps identical with, living species. One carp represents an extinct new genus and species, *Prolociosoma pasakensis*, superficially similar to the living genus *Luciosoma*. Another carp is an extinct species of the living genus *Hypsibarbus*. One catfish represents an extinct new genus and species of the family Pangasiidae, *Cetopangasius chaetobranchus*, specialized for feeding on plankton. The other two cannot be distinguished from the living bagrid catfish genera *Leiocassis* and *Hemibagrus*. The *Leiocassis* appears to be identical with the living species *L. siamensis*, while the *Hemibagrus* represents a previously undescribed extinct species, *H. major*. The two percoids, members of the family Chandidae or glassperches, are previously undescribed extinct species in the living genus *Parambassis*, *P. goliath* and *P. paleosiamensis*. *Parambassis goliath* attained nearly 27 cm standard length and may have been larger than any living chandid species. The most frequently encountered species in the assemblage are *Parambassis paleosiamensis* and *Prolociosoma pasakensis*, both with maximum standard lengths of about 10 cm. The pangasiid catfish *C. chaetobranchus*, attaining 50 cm, is relatively common, but the *Leiocassis* is represented by a single 12-cm specimen, and the *Hemibagrus* by a single incomplete specimen with an estimated standard length of nearly 1 m. The living carp genera are represented by only a few incomplete or fragmentary specimens of the subfamilies Barbinae (including *Mystacoleucus* sp) and Labeoninae (a single complete and one fragmentary specimen of *Bangana* sp).

The Ban Nong Pla fishes apparently lived in the open and near shore waters of Lake Phetchabun, and perhaps also in the delta and mouth of a large river flowing into it. The same fluvial sediments that led to their fossilization may have been responsible for killing the fish, when seasonal floods dumped huge amounts of sediment into the relatively clear waters of the lake. Lake Phetchabun probably was a self-contained or endorheic lake confined to the Phetchabun intermontane basin. Its endemic fishes presumably died out when the Miocene lacustrine ecosystem was replaced by the Pliocene and Recent fluvial ecosystem similar to today's Menam Pa Sak.

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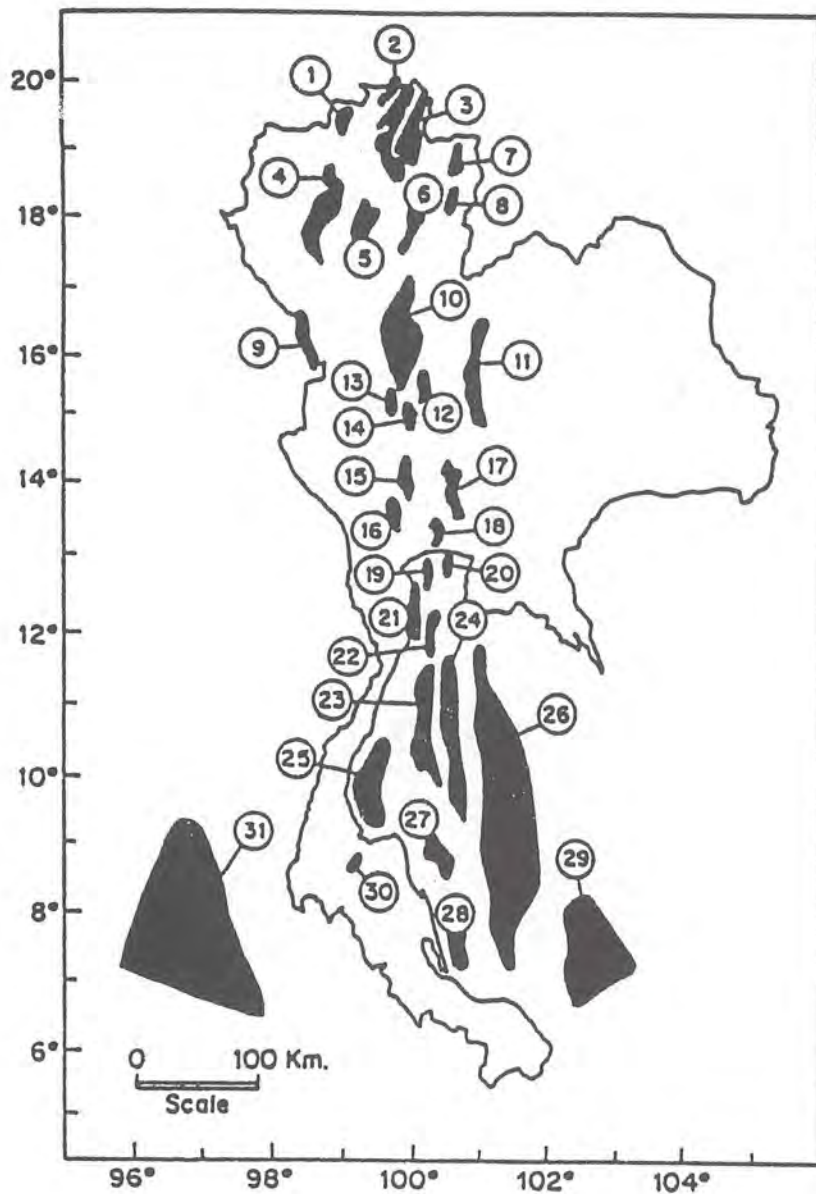


Figure 1. Miocene intermontane lacustrine basins of Thailand. The Petchabun intermontane basin is number 11. Fossil fish also have been found and reported from number 9 (Mae Sot) by Uyeno (1969) and found but not reported upon from number 5 (Lampang or Mae Moh) (personal observations). For further information on the basins see Polachan et al. 1991; Remus et al. 1993; and Lawwongngam and Philp 1993 (map from Lawwongngam and Philp 1993: 434).

INTRODUCTION

During the dry season in the first half of 1997, villagers of Ban Nong Pla excavated a rectangular irrigation reservoir with an area of 40x120 m to a uniform depth of 4 m. Thousands of fossils, fishes and leaves of higher plants, were sold to passers-by, and word of the find reached the press. Personnel from the Department of Mineral Resources and the National Center for Science Education visited the site on several occasions in May-June 1997 and obtained samples including the fish fossils reported on in this paper. The higher plants have yet to be studied, but there are several broad-leaved species of Magnoliaceae and other families. There are also turtles (none in DMR or NCSE collections) and leaves and stems of aquatic plants. Other tetrapod vertebrate groups and macroinvertebrates (including Mollusca and Crustacea) were not been found or at least not reported. The reservoir filled in the rainy season of late 1997, and no further fossils have been recovered.

Ecological conditions.—Ecological conditions in Southeast Asia generally, and in Thailand in particular, were very different during the Miocene and at other times in the Tertiary from what they are today. During prolonged periods of greatly lower sea level world-wide, the Gulf of Thailand was lowland broadly connecting mainland Southeast Asia and Indonesia. Most of the area now forming the gulf was drained by the Greater Sundaland River, with headwaters arising in the Malay peninsula, northern Sumatra, and western Borneo. During some periods the Mekong may have flowed into this system, but the Mekong then may not have been so large as it is now. Even so, the Greater Sundaland drainage was an enormous tropical river system rivaling the modern Amazon and Congo basins. During the Oligocene and Miocene it drained 30 or more intermontane basins in Thailand and the Gulf of Thailand. All or most of these intermontane basins were occupied for long periods by more or less large lakes, as indicated by extensive lacustrine (or fluvio-lacustrine) deposits. (Fig. 1) This system, nearly coextensive with the lowland parts of the Chao Phraya graben, occupied virtually all of the area that is now Thailand and the Gulf of Thailand except for the Northeast or Issan (REMUS, *ET AL.*, 1993). The so-called "Wichien Buri lake", in a sub-basin of the Phetchabun intermontane basin (*op cit.*: 427) was probably only the southern part of a greater Lake Phetchabun, which itself might have been at times only an arm of a much larger lake. These ancient graben-defined lakes ceased to exist by the end of the Miocene when they were replaced by a fluvial or riverine, erosional regime similar to that of the present time. The fossils reported upon here come from a fluvio-lacustrine deposit near the northwest shore of the old Phetchabun Lake. The deposit is presumably similar in all respects to the six lacustrine deposits reported from the southern half of the lake and the Wichien Buri sub-basin by REMUS, *ET AL.*, 1993: 430, fig. 8. The Miocene river that transported the sediments forming these deposits presumably was the fore-runner of the present Huai Ban Nong Pla (=Huai Kham Khat?), the river that filled the villager's irrigation reservoir in the latter half of 1997. This river is intermittent, drying up almost completely every year. At the time the Ban Nong Pla fossil deposits were formed, it was probably perennial (i.e. flowing year-round) and much larger. There are several reasons for thinking so. First, the Phetchabun Lake probably increased the amount of rain and the duration of the rainy season. Second, the forest of the time, as represented by the fossil leaves (including many broad-leaved species) probably was moister than the

present forest. Finally, the ancient Huai Ban Nong Pla and other rivers carried enormous amounts of sediment into the lake, presumably more than rivers of the present size could have done. When the lake conditions suddenly ended, the Phetchabun intermontane basin may suddenly have become much drier, with Huai Ban Nong Pla and other lesser streams drying up completely or becoming intermittent, and this is why the Ban Nong Pla fossil-bearing deposits only 2-4 m deep have not been eroded away.

Condition of Ban Nong Pla fish fossils.—The Ban Nong Pla fossil fishes are preserved in a finely grained claystone or mudstone. A piece of the stone associated with a fossilized head of a *Cetopangasius chaetobranchus* was analysed by Jate Jirajesda of the DMR and found to have the following components: quartz, kaolinite, illite, and montmorillonite. The resulting matrix is relatively soft and readily eroded by water. The matrix varies in color from pale grey or nearly white to orange, and the fossilized parts of fish are usually brown or reddish brown. The orange color is usually due to a very thin layer, probably of limonite. The fossil fish material is also soft and easily damaged, and in most of the specimens the bones in the head are more or less pulverized (particularly in the material of Pangasiidae), making detailed study of crania difficult. An exception to this general statement of the condition of the fossils and their matrix is our single very large specimen of *Hemibagrus major*, which is extremely hard, due to laterization or limonitization. Scales are not preserved in most of these fossils, with a few significant exceptions. Thus fragments of the scales themselves and impressions of the scales, including several scales of the lateral line series, are preserved on a fragment of a fossil cyprinid including the dorsal fin, thus permitting its identification with the large-scaled barb genus *Hypsibarbus*. The scales are also exceptionally well-preserved in a fragment of the labeoin cyprinid *Bangana*. The scales either are not preserved, or are very poorly preserved, in other cyprinid fossils from Ban Nong Pla. Fortunately the tubules of the lateral line scale series of the laterally-compressed cyprinid *Proluciosoma pasakensis* are beautifully preserved in several specimens, permitting an accurate count of the lateral line scale row as well as a fair idea of the overall squamation in this extinct taxon.

Location of Ban Nong Pla fossil fish deposit (Fig. 2).—Ban Nong Pla is located in Tambon Nam Hia, Amphoe Lom Sak, about 6–7 km NNW of Muang Lom Sak of Phetchabun province in north-central Thailand (Fig. 1). The coordinates of the actual fossil site are approximately 16°49'N by 101°11'26"E.

Age of Ban Nong Pla fossil fishes.—Lacustrine conditions prevailed in the Phetchabun intermontane basin intermittently, but for long periods of time, beginning in the Oligocene and extending to the end of the Middle Miocene (POLACHAN, *ET AL.*, 1991) or to the end of the Miocene (REMUS, *ET AL.*, 1993). We think that the fossil deposits at Ban Nong Pla, only 2–4 m below the surface, represent the last stage of lacustrine conditions and that their age is thus Middle or Late Miocene. but certainly more work is needed on the age of the site.

Meristic characters.—Counts of repetitious body structures such as vertebrae, fin rays and gill rakers are important in systematic studies of all teleost groups, including cyprinoids, siluroids and percoids. This is especially so in fossils, in which many of the characters useful for studying living species cannot be observed. Meristic characters of particular

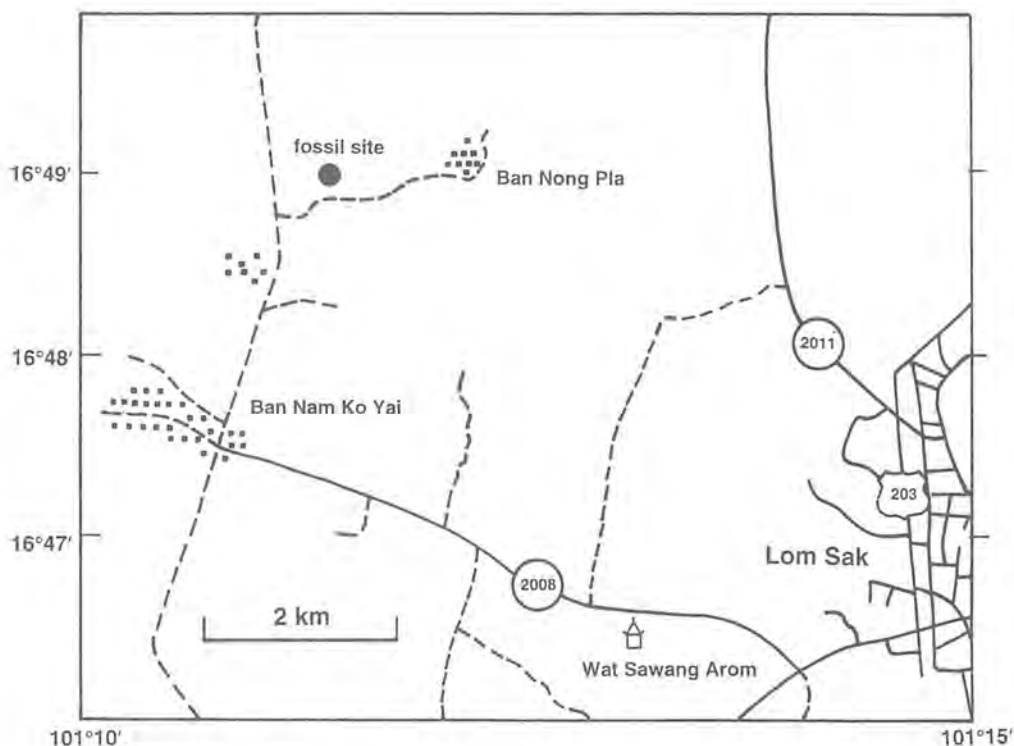


Figure 2. Location of Ban Nong Pla and its fossil fish site in north-central Thailand.

importance in the groups reported here include vertebrae and fin rays, particularly anal fin rays. Vertebral counts are much more informative if they are broken down into abdominal and postabdominal. Used in conjunction with subtle differences in coloration, the meristic characters of gill raker, anal fin, and vertebral counts are extremely helpful in distinguishing species of catfishes, including Pangasiidae. Fortunately, considerable data on meristic characters of all of the living pangasiid species is reported in ROBERTS & VIDTHAYANON (1991) and in VIDTHAYANON (1993). Abdominal and postabdominal vertebrae may be distinguished on the basis of their position in relation to anteriormost anal fin pterygiophore. The first abdominal vertebrae has its hemal spine lying posterior to the proximal end of the anteriormost anal fin pterygiophore. Such a definition, while only one of several that have been proposed, works consistently well for a wide variety of teleosts, and can be applied more readily and with more consistent results to radiographed specimens and fossils than other definitions. The anteriormost vertebrae associated with the Weberian apparatus are included in vertebral counts of ostariophysan fishes. As these vertebrae may be greatly modified and variously fused together, actually counting them is usually impossible or impractical. In most ostariophysans, including carps and catfishes, the first free vertebrae and the first rib-bearing vertebra posterior to the Weberian apparatus is the fifth vertebra.

Thus in practice, vertebral counts of these fishes begin with the fifth or first rib-bearing vertebra. There has been considerable discussion and disagreement as to the number of vertebrae incorporated in the Weberian complex centrum of catfishes. It seems that the number may differ considerably among catfishes families, and sometimes within genera or even within species, and that for any given fossil or even preserved specimens of living species it may be difficult or even impossible to determine the number of vertebrae incorporated into the complex centrum without detailed anatomical study. At present there seems to be no ready way to resolve this difficulty. For counts published in ROBERTS & VIDTHAYANON the first rib-bearing vertebra was considered to be the fifth, while in VIDTHAYANON (1993) it was considered to be the sixth. This is why vertebral counts in ROBERTS & VIDTHAYANON (1991: table 2) are one less than vertebral counts from the same data set in VIDTHAYANON (1993: tables 4 and 5). In this paper, we consider the first rib-bearing vertebra in Cyprinidae, Bagridae and Pangasiidae is counted as the fifth vertebra, in order to facilitate comparisons and for consistency with previously published data. When the number of vertebrae incorporated into the complex centrum for various taxa becomes established and can be readily verified in specimens, these data can be adjusted correspondingly.

A note is also necessary concerning fin-ray counts of dorsal and anal fins. Most of the taxa reported on in this paper have the last ray in the dorsal and anal fins "divided to the base." Anatomically, there may be two rays, but they articulate with a single pterygiophore or radial. Some authors include the last "half-ray" as one in counts, other report the "last ray" as $\frac{1}{2}$, and some omit it. Throughout this paper the last two rays, or last one and a half rays, is counted as one ray.

Standard length and proportional measurements.—Whenever possible, we present lengths of fossil fish specimens as standard length, the measurement used by ichthyologists working with specimens of living fishes. This is defined as the length of the fish from the tip of the upper jaw or the snout (whichever is more anterior) to the base of the caudal fin (or more accurately to the end of the middle of the hypural plate). With fossils in which the head or tail is missing or the body is distorted, accurate determination of standard length cannot be made. In many instances, however, fish are fossilized very nearly straight and it is possible to make accurate measurements of the standard length, which can then be used for reporting the proportional measurements of other body parts. The proportional measurements may be reported either as "times in standard length" or as "percentage of standard length".

SYSTEMATICS

The fossil fishes found at Ban Nong Pla may be classified as follows:

TELEOSTEI

OSTARIOPHYSI

CYPRINOIDEI

Cyprinidae

Barbinae

*Hypsibarbus**Hypsibarbus antiquus* new species*Mystacoleucus**Mystacoleucus* sp

Genus undetermined 1

Genus and species undetermined 1

Genus undetermined 2

Genus and species undetermined 2

Labeoninae

*Bangana**Bangana* sp

Cultrinae or Leuciscinae?

Proluciosoma new genus*Proluciosoma pasakensis* new species

SILUROIDEI

Bagridae

*Hemibagrus**Hemibagrus major* new species*Leiocassis**Leiocassis siamensis*

Pangasiidae

Cetopangasius new genus*Cetopangasius chaetobranchus* new species

PERCOMORPHI

PERCOIDEI

Chandidae

*Parambassis**Parambassis goliath* new species*Parambassis paleosiamensis* new species**Cyprinidae**

Six of the 11 species identified in the Ban Nong Pla fossil fish assemblage are carps, i.e., members of the Cyprinidae. This family (which includes the carps, barbs, and their kin) probably dominated Miocene freshwater fish faunas throughout Asia during the Miocene, as it does today. The six species represent six genera, at least four still living, and one genus that is extinct. Of the species belonging to extant genera, four are barbs or members of the subfamily Barbinae, and one belongs to the subfamily Labeoninae. The subfamily of the extinct genus is unclear; it might be Cultrinae, Leuciscinae, or even Bariliinae. This depends in part on whether it had barbels, which cannot be determined in the fossils. The Ban Nong Pla fossil Barbinae and Labeoninae are documented first, then the extinct new genus.

Hypsibarbus Rainboth 1996

Hypsibarbus Rainboth, 1996a: 20 (type species by original designation *Acrossocheilus malcolmi* Smith 1945 by original designation).

Dorsal fin with a large spine bearing 10–28 strong serrae; dorsal fin branched rays 8; anal fin branched rays 5; scales in lateral line scale row (to end of hypural fan) 23–32; lateral line complete; individual tubules on scales of lateral line scale row often with branches or secondary tubules; circumferential scale rows 20–24; circumpeduncular scale rows 14–16; total vertebrae 36–37 (post-Weberian vertebrae 31–32 according to RAINBOTH, 1996a: 22). When accessory tubules of the lateral line canal are only one or two, they usually are directed ventroposteriorly. When there are more than two, some may be directed dorsoposteriorly. Most of the 13 living species inhabit the mainstreams of large rivers and are highly migratory. The Mekong has more species than any other river system.

Hypsibarbus antiquus new species
Figs. 3–5

Holotype.—DMR: TF 5004.1, fragment comprising complete dorsal fin and up to 4 linear and 8 transverse rows of large scales on flank below dorsal-fin base; TF 5004.2, isolated nearly complete scale impression with extensive scale fragments 13.2x13.8 mm (in middle of fragmentary specimen of *Parambassis paleosiamensis*). In addition, DMR has a photograph of a large complete specimen in fine condition, three nearly complete but poorly preserved specimens (TF 5004.3–4, estimated standard lengths 73 and 96 mm) and numerous fragments mostly in poor condition, which may belong to this genus.

Our large scale-bearing fragment (DMR TF 5004.1) has dorsal fin with a strongly serrated last simple ray and 7 branched rays. The scales include a nearly complete transverse scale row (missing one or perhaps two uppermost and perhaps one lower most scale); transverse scale rows probably 5–6/1/2 or 3 (i.e. either 5 or 6 scale rows between dorsal fin origin and lateral line scale row/the lateral line scale row/and 2 or 3 rows of scales between lateral line scale row and pelvic fin origin). There are four scales in the lateral line series. The tubules are simple, without accessory branches or pores. The serrated dorsal-fin ray, dorsal-fin branched-ray count, number of transverse scale rows, and scale morphology are similar to those in living *Hypsibarbus*.

Mystacoleucus Günther 1868

Mystacoleucus Günther, 1868: 206 (type species *Systemus (Capoeta) padangensis* Bleeker 1852, by original designation).

Mystacoleucus comprises a half-dozen or so living species in Southeast Asia characterized by a procumbent predorsal pterygiophore. That is, the spinous base of the first dorsal fin pterygiophore is capable of being erected into an exposed position so that it projects anteriorly from the dorsal fin origin. The genus is further distinguished by 6 branched anal-fin rays (last ray divided to base). Our fossils from Ban Nong Pla include



Figure 3. *Hysibarbus antiquus*. Holotype. Private collection, Khun Chertchai Tortrakul.



Figure 4. *Hysibarbus antiquus*. DMR TF5004.1.



Figure 5. *Hysibarbus antiquus*. Two scales from lateral line scale row. DMR TF 5004.1.



Figure 6. *Mystacoleucus* sp., 79 mm (private collection).



Figure 7. *Bangana* sp., 161mm. DMR TF.



Figure 8. *Bangana* sp., estimated standard length 92 mm. DMR TF 5022.



Figure 9. *Bangana* sp., estimated standard length 92 mm. Scales. DMR TF 5022.



Figure 10. *Proluciosoma pasakensis* 76.5 mm (holotype). Branched anal-fin rays 6, vertebrae 21 or 22+18=39 or 40. DMR TF 5008.



Figure 11. *Proluciosoma pasakensis* (holotype). Head. DMR TF 5008.

several specimens that we identify with this genus. They are close to some of the living species, and might be conspecific with one of them. So far as we are aware, fossil *Mystacoleucus* have not been reported previously.

Mystacoleucus sp

Fig. 6

Study material.—DMR: TF 5005.1, 67 mm length of body without head in fine condition; TF 5005.2, estimated standard length 79 mm (tip of snout and lowermost part of head and body missing). NCSE: 78 mm estimated standard length (head missing); 79 mm standard length; 81.5 mm standard length (complete but in poor condition); 90 mm estimated standard length (head missing); 148 mm estimated standard length (head and pectoral fins missing).

Dorsal-fin branched rays 8; anal-fin rays usually 8 (9 in one specimen). Vertebrae 18?+16=34? Several specimens provide postabdominal vertebral counts of 16. Since most of our specimens are missing some of the anterior vertebrae or have damaged vertebral columns, we have only two doubtful counts of 18 for abdominal vertebrae. The meristic characters, body and fin shapes and fin positions are closely similar to the living genus *Mystacoleucus*, represented by about 6 species in Southeast Asia.

Genus and species undetermined 1

Study material.—DMR: TF 5006, 67-mm fragment with anal fin and part of caudal fin.

This unique fragment (including entire anal fin in good condition, distal third of pelvic fin, part of caudal fin including nearly entire lower lobe, and about five posteriormost vertebrae including hypural fan in very poor condition) represents an unidentified and possibly extinct large-scaled barb. Anal fin markedly falcate, with stout, non-serrate last simple ray and 6 branched rays. A few large scales on lower part of caudal peduncle. Caudal fin deeply forked. Shape of anal fin similar to that in living species of the barbin genera *Puntioplites* and *Barbodes*, but so far as we know species in these two genera have only 5 branched anal-fin rays. Scales on caudal peduncle of fossil larger than those on caudal peduncle of living *Barbodes*.

Genus and species undetermined 2

Study material.—DMR: TF 5007, estimated standard length 140 mm, fragment with dorsal, anal and caudal fins and posteriormost 18–19 vertebrae.

A deep-bodied barbin. Last simple ray of dorsal fin with serrated posterior margin. Dorsal-fin branched rays probably 7 (badly damaged); anal fin with last simple ray slender and non-serrate; anal-fin branched rays 5; anal-fin margin slightly concave; postabdominal vertebrae 14 or 15. Scales unknown.

Bangana Hamilton 1822

Bangana Hamilton, 1822: 277. 285 (type species *Cyprinus dero* Hamilton 1822, by subsequent designation of Jordan, 1917: 155).

Bangana is closely related to the more speciose labeonin genus *Cirrhinus*. It differs from *Cirrhinus* most notably in the development of a large rostral concavity, which however, only appears in larger individuals.

Bangana sp
Figs. 7–9

Study material.—DMR: TF 5022, completely scaled fragment with nearly complete dorsal fin, part of the pectoral fin, both pelvic fins, and anterior part of anal fin in excellent condition (estimated standard length 92 mm); NCSE, 161 mm standard length, complete specimen in fair condition.

Proportional measurements of 161-mm specimen (expressed as times in standard length).—Head 3.8; snout 12.7?; eye 14.8; body depth (at dorsal fin origin) 3.5; pectoral fin length 7.1?; pelvic fin length 5.7; predorsal length 2.0; prepelvic length 1.75; preanal length 1.2; caudal peduncle length 4.9; caudal peduncle depth 7.4? Dorsal-fin rays iii or ivl0? Vertebrae 24?+12?=36? Pelvic-fin origin on vertical line through base of anterior third of dorsal-fin base; anal-fin origin nearer to base of caudal fin than to pelvic-fin origin.

The DMR fragment is identified with the NCSE specimen because it has 10 branched dorsal-fin rays. The scales, about 12–13 in transverse series and with strong parallel radii, are morphologically like the scales of living *Bangana*. There are about 20 longitudinal scale rows in the fragment; thus we estimate the scales in the lateral line series at about 35. The section of vertebrae in this fragment is only partially exposed and therefore it is difficult to obtain an exact count of the vertebrae, but there seem to be about 20. In *Bangana* the numbers of longitudinal scale rows and of vertebrae correspond fairly closely, therefore the number of vertebrae in *Bangana* sp may be about 35–37. Pelvic-fin origin on a vertical through middle of dorsal-fin base.

The body and head shapes and the fin shapes and positions, as well as the meristic characters, of our fossils correspond very well to the living genus *Bangana*, of which there are a half-dozen or so nominal living species in Southeast Asia including the Mekong basin. The species are too poorly known to try to distinguish these fossils from most of them, although they evidently differ from *B. behri* Fowler 1937, which has 12–13 dorsal-fin soft rays.

Proluciosoma new genus

Type species.—*Proluciosoma pasakensis* new species.

Diagnosis.—A slender, elongate, and compressed cyprinid; mouth superior, with gape entirely anterior to eye; pharyngeal teeth in three rows (2,3,5?); dorsal fin with two simple rays, last simple ray unserrated, and 7 branched rays; anal fin invariably with 6 branched rays; lateral line complete, decurved to lower fourth of body; lateral line scale row probably with 32–34 scales; vertebrae 20–24+18–20=40–44. Maximum size probably about 10 cm.

Discussion.—*Proluciosoma* is similar in body shape and vertebral counts to some living species of the genus *Luciosoma* Bleeker 1855 (type species *Barbus setigerus* Valenciennes in Cuvier and Valenciennes 1842) and also shares with them the unusual character of 6 branched anal-fin rays. This count is invariable in the living species of

Luciosoma, as it is in our fossil material of *Proluciosoma*. *Luciosoma* is represented by five living species, all found in Southeast Asia. They differ consistently from *Proluciosoma* in having a much longer mouth (with gaping extending posteriorly well beyond front margin of eye); larger pairs fins, pectoral fins extending posteriorly to beyond pelvic-fin origin and pelvic fins to beyond anal-fin origin; and anal-fin origin on a transverse line through middle of dorsal-fin base. In *Proluciosoma* the paired fins are much more widely separated and the anal-fin origin is posterior to a transverse line through the base of the last dorsal-fin ray. The path of the lateral line and of the lateral line scale row is similar in the two genera, but *Luciosoma* has 37–44 scales in the lateral line series and *Proluciosoma* only 32–34. Most species of *Luciosoma* have barbels, but *L. setigerus* has no barbels. It is unknown whether *Proluciosoma* has barbels. Most members of Bariliinae, the subfamily including *Luciosoma*, have barbels, while Leuciscinae and Cultrinae lack them.

Proluciosoma pasakensis new species

Figs. 10–13

Holotype.—DMR: TF 5008, 76.5 mm standard length, complete specimen in fine condition.

Paratypes (all complete or nearly complete specimens, standard lengths).—DMR: TF 5009.1, 46.5 mm standard length; TF 5009.2, estimated 80 mm standard length nearly complete (snout missing); TF 5009.3, 46 mm standard length; TF 5009.4, estimated standard length 46 mm (complete except most of caudal fin and hypural fan missing); NCSE: 24.5 mm, 58+ mm (bent), 65 mm, 69.5 mm, 81 mm, 86.5 mm, 92 mm, and 96 mm standard length. In addition to the holotype and paratypes, DMR and NCSE have numerous specimens in poor condition or fragmentary (DMR 5010.1–27+).

Proportional measurements of holotype (expressed as times in standard length).—Head 4.1; snout 12.7; eye 19; body depth (at dorsal fin origin) 4.9; pectoral fin length 6.0; pelvic fin length 7.3; predorsal length 1.78; prepelvic length 1.96; preanal length 1.44; caudal peduncle length 4.25; caudal peduncle depth 9.6.

Pharyngeal teeth (Fig. 12).—The great majority of cyprinid genera and species have three rows of teeth on each of the paired pharyngeal bones in the throat. The tooth count usually is 2,3,5 or 2,3,4. The teeth of both pharyngeal bones are relatively well-displayed in the 76.5-mm holotype of *P. pasakensis*. There are three rows and the tooth count probably is 2,3,5. The count is difficult to confirm because each of the pharyngeal bones has a full set of fully-formed replacement teeth as well as a full set of functional teeth. In theory, both sets of teeth could be extracted and counted, which would probably give a total count of 18 or 22, depending on whether the pharyngeal tooth count is 2,3,4 or 2,3,5. In practice, however, this would destroy the tooth arrangement and might otherwise damage the holotype without providing a satisfying count, because several of the teeth are broken (and more likely to be broken in the process of extraction), and some teeth might already be missing—especially some of the replacement teeth, which are very loosely attached. The total count, moreover, appears to be about 20, indicating a functional tooth count of 2,3,5 is more likely than one of 2,3,4. In either case the count provides little or no information about phylogenetic relationships. It should be noted that the 20 or so teeth are all intimately

related to one pharyngeal bone. The other pharyngeal bone is displaced anteroventrally by a distance about equal to the length of a pharyngeal bone and is not visible in Fig. 13. The teeth are simple cones, the largest with slightly recurved crowns.

Scales.—The scalation, or to use the more correct term, squamation, of *Proluciosoma pasakensis* is known directly only by the beautifully-preserved tubules of the lateral line canal, readily observable in the holotype and several other specimens (Fig. 13). From the tubules it is possible to obtain a nearly exact count of 32–34 scales in the lateral line series, and thus a fair idea of the dimension of the scales. From the strongly curved pathway of the lateral line, it seems likely that the transverse scale rows were about 4–5/1/2–3 (i.e., four or five scale rows between the dorsal-fin origin and the lateral line scale row, the lateral line scale row itself, and two or three scale rows between the lateral line scale row and the pelvic-fin origin). There is no indication of whether smaller scales occurred on the base of the anal and caudal fins. It is possible that *Proluciosoma* was entirely scaleless except for the row of lateral line tubules.

Anal-fin rays.—The count of anal-fin branched rays is 6 in the holotype and in all or nearly all of the paratypes. In some of the non-type specimens the count may be 7 but in these specimens the anal fin is distorted or damaged and the count is doubtful.

Bagridae

Hemibagrus Bleeker 1862

Hemibagrus Bleeker, 1862: 9 (type species *Bagrus nemurus* Valenciennes in Cuvier and Valenciennes 1840 by original designation).

Hemibagrus major new species

Fig. 14

Holotype.—DMR: TF 5011, 960 mm estimated standard length, partial specimen with incomplete head, pectoral girdle and most of vertebral column but missing snout, upper and lower jaws; dorsal, pelvic, anal and caudal fins; and vertebrae posterior to anal fin (unique specimen). A tooth 3.0 mm long probably from the palatal tooth band has been kept separately.

Our unique Ban Nong Pla fossil specimen consists of five large and several very small pieces which fit together and give a combined length of 760 mm to the end of the last (40th or 41st) vertebra present. The largest piece comprises about three-fourths of the cranium and perhaps the entire pectoral girdle. The dorsolateral cranial outline, laterally-projecting portion of the exoccipital bone, and leading edge of the anterior half of a pectoral-fin spine can be observed, but not much else. The upper and lower jaws and the palate are missing. At least 65 mm of the anterior part of the cranium and snout are missing. The next three pieces consist mainly of the vertebral column with neural and hemal spines embedded in matrix; sections of vertebrae and spines are visible at the anterior and posterior broken surfaces of each piece. In the fifth and smallest of the five main pieces a large portion of the anal-fin pterygiophores and associated hemal spines are exposed but the entire anal fin is missing.

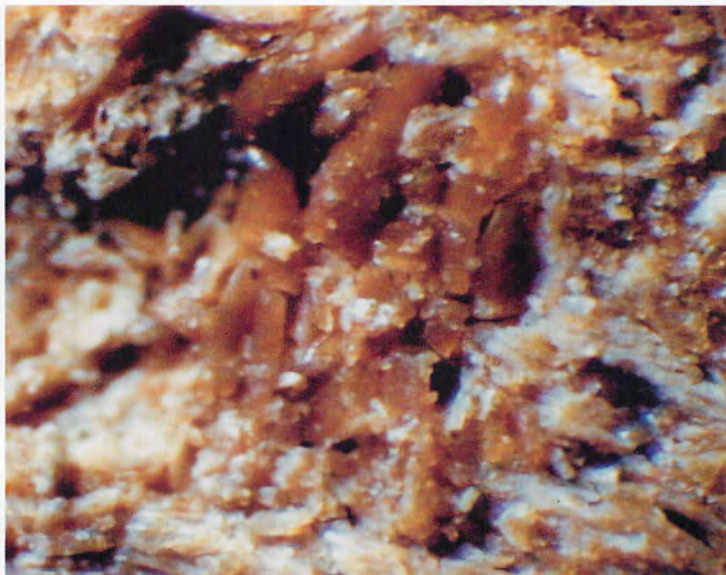


Figure 12. *Proluciosoma pasakensis* (holotype). Pharyngeal teeth. DMR TF 5008.

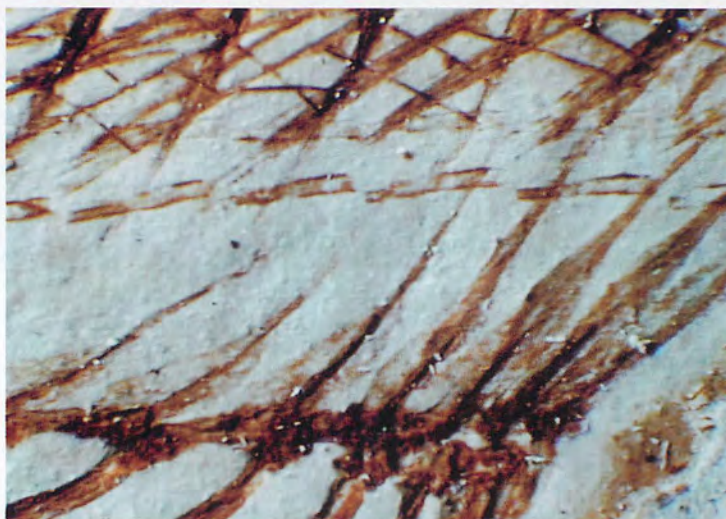


Figure 13. *Proluciosoma pasakensis* (holotype) Lateral line bony tubules; also ribs, intermuscular bones, and anal-fin pterygiophores. DMR TF 5008.



Figure 14. *Hemibagrus major*. Tooth from upper jaw. Length 3.0 mm; part of its base is missing. DMR TF 5011.



Figure 15. *Leiocassis siamensis*, 120 mm estimated standard length. Vertebrae 17+19=36. DMR TF 5012.

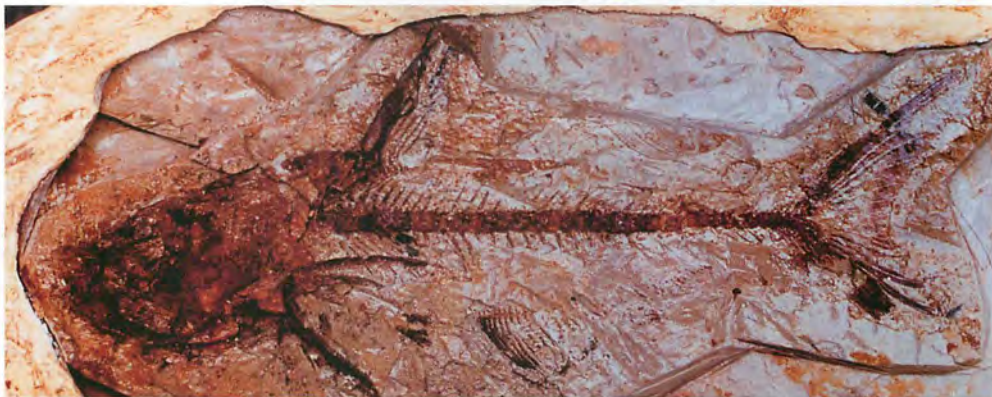


Figure 16. *Cetopangasius chaetobranchus*, 335 mm (holotype). Vertebrae 14+26=40. DMR TF 5013.



Figure 17. *Cetopangasius chaetobranchus*, dorsal aspect of head, pectoral fins, and anterior part of vertebral column (dorsal fin absent). DMR TF 5014.5.



Figure 18. *Cetopengasius chaetobranchus*, estimated standard length 35–40 cm. Gill rakers. DMR TF 5014.10.

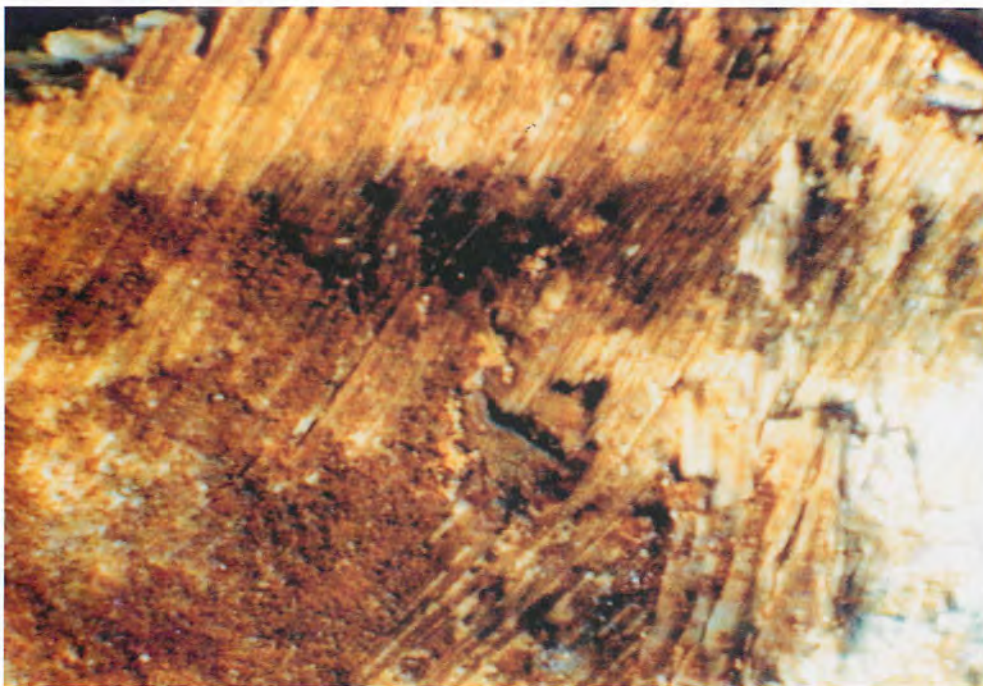


Figure 19. *Cetopangasius chaetobranchus*, estimated standard length 35–40 cm. Gill rakers. DMR TF 5014.10.



Figure 20. *Cetopangasius chaetobranchus*, estimated standard length 35–40 cm. Portion of pectoral-fin spine, DMR TF 5014.10.



Figure 21. *Cetopangasius chaetobranchus*, estimated standard length 50 cm. Pelvic girdles and fins. Pelvic fin rays probably 6/6. NCSE.

Tooth morphology.—A single tooth, 3.0 mm long, was extracted from the anterior tip of the large piece including the cranium (Fig. 14). Since the upper and lower jaw, and all or most of the vomer are missing, the tooth probably came from the posterior part of the palatal tooth band. The tooth consists of two discrete parts, a white conical tip which presumably represent a true tooth covered with enamel, and a much larger brownish base or pedicel, presumably osseous. Morphologically similar jaw teeth are present in living species of *Hemibagrus* (in Bagridae generally, including *Hemibagrus*, teeth of the upper and lower jaws and palatal tooth bands are morphologically similar). In teeth of preserved specimens of living fish the difference in coloration between the conical tip and the pedicellate base is less obvious, but the demarcation between them is evident.

Anal fin.—The anal fin itself is entirely missing, but all or nearly all of the anal-fin proximal pterygiophores except perhaps the last one or two are present, and most of them are exposed. The anteriormost pterygiophores, however, lie within piece 4 and perhaps in piece 3 are not exposed, and our radiographs are not clear enough to count them with confidence. Assuming that the posteriormost proximal pterygiophore on piece 5 actually is the posteriormost pterygiophores, then the anal fin has 11 pterygiophores. This probably corresponds to an anal-fin ray count of 3 unbranched and 9 branched rays, as in the living species *H. microphthalmus* and *H. wyckii*.

Vertebral count.—Examination of the exposed edges and of radiographs of the five pieces of our fossil *Hemibagrus* reveals 40 vertebrae between the cranium and just before the end of the anal fin. The vertebrae are distributed in the five pieces (numbered from anterior to posterior) as follows: piece 1, 3; piece 2, 21; piece 3, 7; piece 4, 9; and piece 5, 0. It seems likely that the three vertebra observed in piece 1 are the first three vertebrae. Although components of the Weberian apparatus associated with the first 4 vertebra cannot be made out in the radiographs, the anteriormost vertebra lies directly above the insertion of the pectoral fin spine, as in living *Hemibagrus*, and directly posterior to a structure tentatively identified as the basioccipital half-centrum. It is difficult to observe the anteriormost anal-fin pterygiophores in the radiographs of the fossil, so we have been unable to obtain a count of abdominal vertebrae. The 40th vertebra is not at the very end of the anal fin, but slightly anterior to it. The vertebral count to this point (either at the beginning of the caudal peduncle or one vertebra before it) in *H. microphthalmus* is only 33–35, and the number of vertebrae in the caudal peduncle is 14. If we suppose that its caudal peduncle has the same number of vertebrae, then the Ban Nong Pla fossil *Hemibagrus* would have a total of 54–56 vertebrae. This is 3–5 vertebrae more than recorded in *H. microphthalmus* or any other living species of Asian bagrid catfish. The high number of vertebrae is related to the large size of this species.

Estimation of standard length.—Direct measurement of standard length of the fossil is not possible because the anteriormost part of the head as well as the entire caudal peduncle is missing. The parts that are present have a total length of 760 mm, to which at least 60 mm have to be added for the missing snout and about 140 mm for the missing caudal peduncle, giving an estimated standard length of 960 mm.

Comparison with living species.—The largest living species of *Hemibagrus*, which may be most closely related to our extinct species *H. major*, is *H. microphthalmus* (Day

1878) new combination. This distinctive species is characterized by a very short, slender and non-serrate dorsal-fin spine; low gill-raker counts; high vertebral counts; and distinctive but variable coloration. Head broad and depressed. Barbels very long, maxillary barbel extending posteriorly to or beyond anal fin. Branchiostegal rays 11–12. Gill rakers on first gill arch 12–14. Total vertebrae 49–51 (see comments on catfish vertebral counts in Introduction). *Hemibagrus microphthalmus* is the largest living species of bagrid catfish in Southeast Asia, reportedly attaining 70 or 80 kg and over 2 m in length. A specimen of 45 kg and 130 cm has been examined by Ian Baird (in litt., 7 Aug. 1998). Feeding on fish, prawns and fruits, it may undergo spawning migrations or occur in substantial numbers following and preying on schooling cyprinids but it is probably solitary most of the time. It inhabits the main streams and large tributaries of the Irrawaddy, Salween, Tapi (peninsular Thailand), Meklong, Chao Phraya and Mekong basins. *Hemibagrus major* differs from *H. microphthalmus* in having an estimated 54–56 total vertebrae instead of only 49–51. There are 40 or 41 vertebrae to the end of the anal fin (and beginning of caudal peduncle), versus only 34–35 vertebrae to the same place in the living species. We suspect that our unique fossil specimen, with its estimated standard length of 96 cm, is only a large juvenile of a species that probably attained standard lengths of 2 m or more. Finally, the extinct species is known only from Lake Phetchabun, and may have been endemic to the lake. The only other living Asian bagrid species with recorded vertebral counts of 50–51, *Hemibagrus wyckii* (Bleeker 1858), attains only 40–50 cm standard length. *Hemibagrus microphthalmus* and *H. wyckii* appear to be closely related to each other and probably are the closest living relatives of *H. major*. While the two living species are morphologically fairly similar, *H. wyckii* differs strikingly in its overall black coloration with white marginal stripes on the caudal fin lobes.

Identification of *H. microphthalmus*.—There has been disagreement recently about the identification of this species. The first author reported that the Mekong bagrid usually identified as *Mystus wyckioides* Chau and Fang 1949 (type locality Mekong) is a junior synonym of *Mystus* (here *Hemibagrus*) *microphthalmus*, but did not elaborate (ROBERTS, 1993: 42). This identification was questioned by RAINBOTH, 1996b: 144, who pointed out that specimens from the Mekong did not agree with Day's original description of *M. microphthalmus* from the Irrawaddy. Our reasons for identifying *M. wyckioides* as *M. microphthalmus* are now provided, together with comments on the original description and the holotype of *M. microphthalmus*. In his fieldwork in Thailand the first author initially focused on the Mekong basin. Many specimens were collected and identified as *M. wyckioides*, at the time regarded as endemic to the Mekong basin. Subsequently, however, specimens of the same species were collected or observed in the Chao Phraya, Meklong, Tapi, and Salween basins in Thailand, and in the Irrawaddy basin in Burma.

Mekong specimens, especially juveniles, tend to be very distinctively colored, with a light blue head and body and red pelvic, anal, and caudal fins. Large adults often have similar coloration except the blue is not so bright. Specimens from the Chao Phraya, Meklong and Tapi have the same coloration. Coloration of specimens from the Salween is unknown. The only two fresh specimens observed from the Irrawaddy had the head body and fins uniformly greyish. Later, however, identical greyish overall coloration was observed in 20% of fish freshly caught in the Mekong below Khone Falls in southern Laos. We also have been informed that a live fish from the Meklong that was pale bluish with a red tail

when caught turned entirely black after being kept for sale in a cage placed in clear dark water inshore (Prajit Wongrat, pers. comm., August 1998). Live fish have also been observed in which the caudal fin was reddish-orange, orangish-red, or yellowish-orange. This is significant, because it indicates that the bright fin coloration, when present, is probably due to carotenoids rather than to blood circulating in the fins, and thus may depend on availability of food with high carotenoid content such as crustaceans. Two specimens of *M. microphthalmus* collected in the Irrawaddy in 1885 (identified by VINCIGUERRA, 1890) and two specimens recently collected in the Mekong were compared directly by the first author before publication of ROBERTS (1993). The Irrawaddy specimens had been in preservative for a long time but otherwise were similar in all external characters with the Mekong specimens. One specimen from the Mekong and one from the Irrawaddy had 12 gill rakers on the first gill arch, while the other Irrawaddy and Mekong specimens had 14. The four specimens were radiographed for vertebral counts. The Irrawaddy specimens had 49 and 50 vertebrae, the Mekong specimens 49 and 51. The specimens agreed extremely well in all respects except eye size with Day's original figure of *M. microphthalmus*, and in most respects with his original description, which may be reproduced here in full.

Macrones microphthalmus
pl. 100, fig. 4

Nga-ike Burmese.

B. [branchiostegal rays] x; D. 1/7110; P 119; V. 6; A. 12 (319); C. 17.

Length of head 4, of caudal $5\frac{1}{3}$, height of body $6\frac{3}{4}$ in total length (excluding the filamentous prolongation of the caudal fin). Eyes—diameter 6 in the length of head, 2 diameters from the end of snout, and $2\frac{1}{2}$ apart. The greatest width of the head equals its length excluding the snout. Upper jaw the longer, snout spatulate. Median longitudinal groove on the head reaches to the base of the occipital process, which latter is pointed, scarcely longer than wide at its base, and with a long interspace between it and the basal bone of the dorsal fin. Upper surface of the head nearly smooth, the few ridges not being tuberculated. Barbels—nasal ones reach the hind third of the eye, maxillary ones the base of the caudal, mandibular ones the first third of the pectoral, whilst the inner ones are shorter. Teeth—in an uninterrupted semilunar band across the palate. Fins—dorsal as high as the body, its spine very slender, only osseous at its base and articulated in the upper two-thirds: length of base of adipose dorsal equals that of the rayed fin, whilst the interspace between the two fins is of the same length. Pectoral as long as the post-orbital portion of the head, denticulated internally. Ventral nearly $\frac{1}{2}$ as long as head and just extends to the anal. Upper caudal lobes with a filamentous prolongation. Free portion of tail $\frac{1}{2}$ longer than high. Colours—of a light brown, shot with purple; fins darkest externally.

This fish is closely allied to *M. corsula*, but differs in the character of its dorsal spine, the length of its maxillary barbels, the smooth edges on its head, occipital process, &c.

Habitat.—Burma, along the valley of the Irrawaddi.

Thanks to the kindness of Chavalit Vidthayanon, the first author has compared two specimens recently collected from the Mekong with this description. As pointed out by Rainboth, there are a number of differences, viz. 1) All proportional measurements relative to eye diameter indicate a much larger eye; 2) Body height is 8–9 instead of 6; and 3). The coloration does not agree with coloration observed in these or in any other specimens tentatively identified by us as *H. wyckioides* or *H. microphthalmus*. The differences related to eye size are attributable to the small size of the specimen studied by Day. There remains of course, the difference in coloration. In situations like this, the identification is usually

resolved by examination of the type material. Day did not indicate any type material for *M. microphthalmus* or even the size of the specimen(s) he examined, and there has been no subsequent mention of a holotype or other type material for the species. From the description and figure, it seems likely that he had only a single small specimen, which should therefore be the holotype. The card file for the fish collection in the Zoological Survey of India (Calcutta) includes only a single entry for *M. microphthalmus*. This lot, 2592, consists of a single specimen, 141 mm standard length, accompanied by a handwritten label "Irrawaddi R., Day collection". It is certainly the specimen illustrated by Day and we identify it with confidence as the holotype. The statement by VISHWANATH & SINGH (1986:197) that this specimen (not regarded by them as the holotype) "is in a poor state and not suitable for comparative studies" must be disregarded. Although slightly dried, the specimen is in rather good condition and has not changed much since it was figured some 120 years ago. The dorsal fin spine is very thin and short, non-serrate; first gill arch with $3+0+9=12$ gill rakers; and vertebrae 27 or $28+22=49$ or 50 (first rib-bearing vertebra counted as fifth), thus agreeing in these characters with other specimens now identified as *H. microphthalmus* from the Irrawaddy and the Mekong (data on gill rakers and vertebrae not available for specimens from Salween, Tapi, Meklong and Chao Phraya basins).

Leiocassis Bleeker 1858

Leiocassis Bleeker, 1858:139 (type species *Bagrus poecilopterus* Valenciennes in Cuvier and Valenciennes 1840 by subsequent designation of Bleeker, 1862).

Leiocassis siamensis Regan 1913

Fig. 15

Leiocassis siamensis Regan, 1913: 550 (type locality Bangpakong River, Siam).

Study material.—DMR: TF 5012, 120 mm estimated standard length (complete except for anterior third of head and posterior third of caudal fin) (unique specimen).

Proportional measurements (expressed as times in estimated standard length).—Dorsal-fin spine length 6.3; dorsal-fin length 4.1; pectoral-fin spine length 5.2?; pelvic-fin length 9.2? (pelvic-fin rays broken distally); anal-fin base 8.6; prepelvic length 1.9; preanal length 1.6; caudal peduncle length 4.4; caudal peduncle depth 8.0?

Meristic characters.—Dorsal fin soft rays 7; dorsal fin spine short and slender, only half as long as soft rayed portion of dorsal fin, its posterior margin weakly and irregularly serrate; pectoral fin spine longer and stouter than dorsal fin spine, with about 10 large serrae; pelvic-fin rays 8?; anal-fin rays $iv10?$; principal caudal-fin rays 8/9; vertebrae $17+19=36$. Vertebral counts have not been recorded previously for *Leiocassis siamensis*. Two preserved Bangkok aquarium specimens (collection locality unknown) examined by us have $17+20=37$ vertebrae.

Leiocassis siamensis occurs in nearly all of the larger rivers in Thailand, including the Mekong, Chao Phraya, Bangpakong, Meklong, and Tapi. It is a nocturnal, secretive, non-migratory species, occurring usually as isolated individuals or in small numbers, so it is not surprising that our Ban Nong Pla fossil specimen is unique. This is apparently the first report of a fossil *Leiocassis*.

Pangasiidae

Pangasiidae are moderately to very large catfishes inhabiting big rivers in Southeast Asia. There are some 21–24 living species (ROBERTS, 1991; VIDTHAYANON, 1993; RAINBOTH, 1996b), 12 of them in the Mekong basin. The smallest, *Pangasius macronema*, attains only 25 cm, while the largest, *P. sanitwongsei* and *P. gigas*, attain 3 m and weights of 300 and 350 kg, respectively. Some relevant characteristics of Pangasiidae are summarized in Table 1. The Ban Nong Pla fossil fish assemblage includes numerous specimens of a previously unknown extinct genus and species. Fossil Pangasiidae have been reported before from Lower Tertiary deposits in the Padang highlands of Sumatra (SANDERS, 1934). The single species described, *Pangasius indicus* (van den Marck 1876) differs from all living species and from our new fossil species in having the combination of few anal-in rays (29?), few vertebrae (41), broad head, and very stout supraoccipital process (length of supraoccipital process 41% of cranial length without supraoccipital process) (from SANDERS, 1934: 22–29, pl. 4). It is not known whether the anal fin ray count of 29 includes the small anteriormost rays.

Cetopangasius new genus

Type species.—*Cetopangasius chaetobranchus* new species

Diagnosis.—*Cetopangasius* differs from all other Pangasiidae except *Pangasianodon gigas* in its very large head, and from *P. gigas* and all other known species in having extremely numerous gill rakers. It further differs from all or most other known species of Pangasiidae in the following respects: dorsal-and pectoral-fin spines very stout, dorsal-fin spine larger than pectoral-fin spine, both armed for nearly their entire length with large, stout serrae. Serrae on dorsal-fin spine flush with posterior edge of spine rather than lying in a convex depression. Dorsal-fin soft rays 7; pectoral-fin soft rays 13; pelvic-fin rays 5 or 6; anal-fin rays 38–42; vertebrae 14–15+26–28=40–41 or 42?

Cetopangasius chaetobranchus new species

Figs. 16–21

Holotype.—DMR TF 5013, 335 mm standard length complete specimen in fair condition (with *Parambassis paleosiamensis* posterior to caudal fin).

Paratypes.—DMR: TF 5014, 345 mm standard length complete specimen in fair condition (pelvic fins and part of anal fin missing); TF 5014.2, estimated standard length 108 mm, nearly complete specimen missing anterior one-third of head; TF 5014.3, 140 mm standard length, nearly complete specimen (missing most of caudal fin); TF 5014.4, 265 mm head, dorsal and pectoral fin, and anterior two-thirds of vertebral column; TF 5014.5, 185 mm, head and anterior 114 of vertebral column; TF 5014.6, 108 mm head (badly crushed); TF 5014.7, 151 mm postabdominal vertebral column with complete anal fin in good condition (anal-fin rays 42); TF 5014.8 estimated standard length 255 mm (head missing); TF 5014.9, caudal fin, complete except for anteriormost upper and lower procurrent fin rays (fine condition); TF 5014.10, estimated standard length 35 cm (head and anteriormost 24 vertebrae). NCSE: 266 mm from snout-tip to anal fin origin (estimated

Table 1. Some characteristics of living and extinct† species of Pangasiidae (sl=maximum standard length (cm); anal=anal fin rays; a/p vert=number of abdominal divided by number of postabdominal vertebrae; sup=length of supraoccipital process divided by length of cranium excluding supraoccipital process.

Taxon	Food habits	sl	anal	a/p vert	sup
<i>C. chaetobranchus</i> †	filter feeder	50	38–42	.05–.54	.32
<i>H. typus</i>	molluscivore	40?	30–31	.73	–
<i>H. waandersi</i>	molluscivore	80	38–42	.58–.62	.64
<i>P. gigas</i>	microphage, algivore?	300	30–35	.71–.75	.29
<i>P. hypophthalmus</i>	herbivore, omnivore, scavenger	120	30–35	.59–.68	.45
<i>P. bocourti</i>	omnivore	80	31–35	.74–.88	.49
<i>P. conchophilus</i>	omnivore, molluscivore, scavenger	100	25–30	.66–.73	.62
<i>P. djambal</i>	unknown	100	28–32	.67–.76	–
<i>P. humeralis</i>	herbivore?	40?	30–31	.71–.75	–
<i>P. indicus</i> †	unknown	–	29?	–	.41
<i>P. kinabatanganensis</i>	unknown	60?	27–30	.72–.75	–
<i>P. krempfi</i>	unknown	100	30–31	.77–.88	.61
<i>P. larnaudii</i>	piscivore, omnivore	130	27–30	.66–.84	.57
<i>P. lithostoma</i>	herbivore	–	40–41	.71	–
<i>P. macronema</i>	insectivore, herbivore, scavenger	25	32–35	.55–.59	.45
<i>P. micronema</i>	herbivore, insectivore	60?	29–38	.61–.80	.41
<i>P. myanmar</i>	unknown	–	32	.67–.71	–
<i>P. nasutus</i>	piscivore, carnivore	100	27–30	.69–.84	–
<i>P. nieuwenhuisi</i>	unknown	40?	30–31	.71	–
<i>P. pangasius</i>	molluscivore, omnivore	100	31–34	.66–.80	–
<i>P. pleurotaenia</i>	herbivore, insectivore	30	39–43	.55–.69	.51
<i>P. polyuranodon</i>	carnivore, molluscivore, herbivore	80	32–44	.54–.74	.41
<i>P. sanitwongsei</i>	piscivore, carnivore, scavenger	300	27–31	.76–.83	.42

standard length 48–52 cm); 195 mm, head, dorsal and pectoral fins, and anterior two-thirds of vertebral column; 183 mm, head, pectoral fins and anterior one-fourth of vertebral column (dorsal aspect); large incomplete specimen (badly fractured); caudal fin.

In addition to the type specimens, NCSE and DMR have numerous fragments referable to this taxon.

Proportional measurements of holotype (expressed as times in standard length).—Head 3.2; body depth (at dorsal fin origin) 4.5; dorsal-fin spine length 4.9?; pectoral-fin spine length 4.4; anal-fin base 3.1; pelvic-fin length 19.7?; predorsal length 2.4; prepelvic length 2.2; preanal length 1.8; caudal peduncle length 6.1.

This new genus and species is immediately distinguished from all other Pangasiidae by its extremely elongate and numerous gill rakers (Figs. 18–19). The head is also longer than any other species except *Pangasianodon gigas*, from which it differs in many respects. The combination of relatively low counts of vertebrae (especially of abdominal vertebrae) and high counts of anal-fin rays is unique within the family Pangasiidae (Table 2).

Oral dentition.—All Pangasiidae except large *Pangasianodon gigas* have bands of very numerous small conical teeth on the upper and lower jaws and on the vomer or palate in the roof of the mouth. The shape of the tooth bands on the jaws, and the size, shape, and number of palatal tooth bands, differ considerably in living Pangasiidae and are useful in distinguishing them (ROBERTS & VIDTHAYANON, 1991, fig. 2; VIDTHAYANON 1993, fig. 25). We have not been able to find teeth in any of our fossils specimens of *Cetopangasius chaetobranchus* preserved in lateral view. However, in the NCSE 183-mm specimen with exposed dorsal aspect, numerous small tooth-sockets are clearly visible on the maxillary (upper jaw) and mandibular (lower jaw) bones. The teeth themselves have fallen out. Thus it is likely that *C. chaetobranchus* normally had well-toothed upper and lower jaws. While we have not observed palatal teeth or tooth sockets in any of the fossils, it is likely that *C. chaetobranchus* also had palatal teeth, since these are present in all living members of the family except large *Pangasianodon gigas*.

Gill rakers.—Several of our specimens have more or less extensive portions of the branchial arches exposed, with fine bony structures extremely well preserved, considering the over-all crushed or pulverized condition of the head. The gill rakers are long, slender, and numerous, some of the largest (broken off from their bases) with a partial length of 10 mm. A section of lower gill arch 17 mm long from an incomplete specimen probably 30–40 cm standard length has over 100 gill rakers. The total length of the raker-bearing portion of lower limb must be at least 30 mm, so that the number of gill rakers on the lower limb of each gill arch may be 200 or more, and the total number of rakers on the upper and lower limbs of one arch perhaps 250–300. The total number of gill rakers on the first gill arch of living pangasiids ranges from 0 in *Pangasianodon gigas* over 50 cm standard length to 48 in *Pangasius bocourti* (VIDTHAYANON, 1993: 78–79, tables 2–3).

Branchiostegal rays.—Branchiostegal rays are seldom well-displayed in fossil catfishes, and usually impossible to count accurately. This is especially true in Pangasiidae, in which the rays are very slender and delicate. The branchiostegal rays are exceptionally well-displayed in the 265 mm DMR specimen. In places the rays of both sides are exposed, and in places the rays of only one side. There are at least 10 branchiostegal rays on each side.

Table 2. Vertebral counts in living and extinct† species of Pangasiidae.

	Abdominal vertebrae										Postabdominal vertebrae										Total vertebrae												
	14	15	16	17	18	19	20	21	22	23	23	24	25	26	27	28	29	30	31	32	39	40	41	42	43	44	45	46	47	48	49	50	51
<i>Cetopangasius chaetobranchus</i> †	2	1	-	-	-	-	-	-	-	-	-	-	2	1	1	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	
<i>Helicophagus typus</i>	-	-	-	-	1	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	
<i>Helicophagus waandersi</i>	-	-	-	1	1	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	
<i>Pangasianodon gigas</i>	-	-	-	-	-	2	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	
<i>Pangasianodon hypophthalmus</i>	-	1	7	-	-	-	-	-	-	-	3	4	1	-	-	-	-	-	-	-	-	1	2	4	1	-	-	-	-	-	-	-	
<i>Pangasius bocourti</i>	-	-	-	-	1	3	3	1	-	-	1	2	5	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	3	2	1	-	
<i>Pangasius conchophilus</i>	-	1	3	9	11	-	-	-	-	1	8	14	1	-	-	-	-	1	4	2	8	8	1	-	-	-	3	8	-	-	-	-	
<i>Pangasius djambal</i>	-	-	-	-	2	9	-	-	-	-	-	2	8	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Pangasius humeralis</i>	-	-	-	-	1	1	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	
<i>Pangasius indicus</i> †	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	
<i>Pangasius kinabatanganensis</i>	-	-	-	-	-	4	-	-	-	-	-	-	-	3	1	-	-	-	-	-	-	-	-	-	-	-	-	-	3	1	-	-	
<i>Pangasius krempfi</i>	-	-	-	-	1	1	2	-	-	-	-	1	1	-	1	1	-	-	-	-	-	-	-	-	-	-	-	1	2	-	-	1	
<i>Pangasius larnaudii</i>	-	-	-	3	1	1	1	-	-	-	1	3	2	-	-	-	-	-	-	-	-	-	-	2	2	1	-	-	-	-	-	-	
<i>Pangasius lithostoma</i>	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	
<i>Pangasius macronema</i>	17	9	1	-	-	-	-	-	-	-	-	-	-	4	12	7	3	-	-	-	2	10	6	6	1	-	-	-	-	-	-		
<i>Pangasius micronema</i>	-	-	1	4	14	12	1	-	-	-	-	6	17	2	1	4	2	-	-	-	-	-	-	3	10	12	4	3	-	-	-	-	
<i>Pangasius myanmar</i>	-	-	-	-	1	1	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	
<i>Pangasius nasutus</i>	-	-	-	1	4	5	1	-	-	-	-	1	8	2	-	-	-	-	-	-	-	-	-	1	8	2	-	-	-	-	-	-	
<i>Pangasius nieuwenhuisi</i>	-	-	-	-	1	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	
<i>Pangasius pangasius</i>	-	-	-	16	20	4	-	-	-	-	17	19	4	-	-	-	-	-	-	-	-	5	20	11	4	-	-	-	-	-	-	-	
<i>Pangasius pleurotaenia</i>	-	-	3	18	1	-	-	-	-	-	-	-	-	4	13	3	1	-	-	-	-	-	-	5	12	5	-	-	-	-	-	-	
<i>Pangasius polyuranodon</i>	-	-	2	4	4	1	-	-	-	-	-	-	-	3	1	6	1	1	-	-	-	-	-	-	-	1	3	3	2	1	1	-	
<i>Pangasius sanitwongsei</i>	-	-	-	-	-	-	1	8	1	-	-	-	-	2	6	2	-	-	-	-	-	-	-	-	-	-	-	-	2	6	2		

The true count probably is 10 or 11, but there might be as many as 13–15 on each side. Branchiostegal ray counts of living Pangasiidae (recorded for less than half of the species) range from 7 to 11 (ROBERTS & VIDTHAYANON, 1991; VIDTHAYANON, 1993). *Pangasius macronema* and *P. pleurotaenia* have 7–8; *H. waandersii*; *P. sanitwongsei* 9; and *Pangasianodon gigas*, *P. hypophthalmus* and *Pangasius pangasius* 10–11.

Ray counts of paired fins.—Pectoral- and pelvic-fin rays are difficult to count in fossil catfishes. In many specimens the fins are incomplete. Pelvic fins and their girdles are often missing entirely, even in otherwise complete specimens. The pectoral fins, on the other hand, with their usually heavy spines and heavy girdles anchored to the cranium, are well-represented in fossils, but there are other problems in obtaining accurate counts of their fin-rays. Pectoral and pelvic fins of opposite sides often overlap each other making it difficult to determine which rays belong to which side. In pectoral and in pelvic fins there is a tendency for the ray-halves of individual rays to separate. This may involve from only one or two rays to all of them. Finally, in catfishes generally, including Pangasiidae, the lowermost pectoral-fin rays are sometimes very small. If very small, they are difficult to detect even in whole preserved specimens or in radiographs of living species.

Our material of *Cetopangasius chaetobranchus* includes four specimens with pelvic fins. In two specimens (including 335-mm holotype) the fins are very small and seem to have only 5 rays. In the 198-mm paratype all of the pelvic-fin rays are badly splayed, so that there appear to be as many as 9–10 rays in each fin. Only the NCSE 266-mm incomplete specimen has the pelvic fins in very good condition, and they each seem to have 6 rays. Since 6 is the invariable pelvic-fin ray count in all living Pangasiidae except the two species of *Pangasianodon* which have 8–9, it is probably the normal count in *Cetopangasius*.

Several of our specimens of *C. chaetobranchus* have pectoral fins with 9–11 discernible rays, but this count is perhaps too low. The specimen in which the fin is best displayed, NCSE 183 mm (dorsal aspect), has 13 soft rays. Recorded counts of pectoral-fin rays in Pangasiidae range from 8 to 13.

Counts of anal-fin rays include the anteriormost simple or unbranched rays, of which there are usually 4–6. The first two or three of these rays are sometimes very small and may be tightly pressed against each other, so they are easily overlooked.

Maximum size.—The largest specimen in our material of *C. chaetobranchus* is represented by the incomplete NCSE specimen 266 mm long from snout-tip to anal fin. This comprises a large head with pectoral girdle attached, the pelvic girdle, and about 1/2 of the anal fin. The head, pelvic girdle, and anal-fin origin seem to be in their normal position. The distance from tip of lower jaw to pectoral-fin origin is 155 mm. Assuming that this measurement is proportional to that in the holotype, it indicates a standard length of about 52 cm, while the snout-tip to anal-fin origin length of 266 mm indicates a slightly shorter standard length of about 48 cm. Our DMR and NCSE fragmentary material includes caudal fins of many specimens of about 30–40 cm in standard length, leading us to suppose that this is the usual size of adults. Thus we think that the extinct species may not have attained much more than 50 cm, even though several living pangasiid species get much larger. This relatively small size for a pangasiid may be correlated with the relatively low number of only 40 or so total vertebrae.

Chandidae

The family Chandidae (formerly Ambassidae), known as glassperches because many of them are translucent or even transparent, is one of the few Recent percoid families represented in tropical Asia by numerous species living their entire lives in fresh water. The freshwater representatives appear to be morphologically and biologically more diverse than the equally or more numerous marine and estuarine species of the same family (ROBERTS, 1994). The Ban Nong Pla fossil fish assemblage includes two extinct species, both referred to the genus *Parambassis*. One species is the most common member of the Ban Nong Pla fossil fish assemblage. The other, less numerous but also well represented in our material, may be the largest known chandid. Osteological characters that may possibly indicate monophyly of the family Chandidae include a) first dorsal fin with 7 spines; b) dorsal-, anal- and pelvic-fin spines with a cancellous or compartmentalized internal structure; c) two large, hook-shaped predorsal bones; d) two epurals; e) first epural enlarged, not aligned with second epural, with a proximal posteriorly-directed hook, and extending from hypural centrum to base of procurrent caudal-fin rays; f) both epurals with distal processes extending onto and tightly bound with bases of procurrent caudal-fin rays. All of these possible synapomorphies have been observed by us in the two extinct species of *Parambassis* described here, as well as in most of the freshwater chandids from Asia. We have not checked for their presence in marine Chandidae, or in other percoid families that may or may not be closely related to Chandidae.

Parambassis Bleeker 1874

Parambassis Bleeker, 1874: 86 (type species by original designation *Ambassis apogonoides* Bleeker 1851).

Parambassis are medium to large-sized freshwater chandids; vertebrae 10+14-15=24-25; first dorsal fin with 7 spines; second dorsal fin with a spine and 9-17 soft rays; anal fin with 3 spines and 9-17 soft rays; scales medium- to small-sized for Chandidae, 40-80 or more in lateral line series; lacrimal or preorbital, supraorbital, and preopercular bones with serrate margins.

Comments.—*Parambassis* as currently recognized is a very diverse group, which may eventually be split into several genera. Involved are the nominal genera *Acanthoperca* Castelnau 1878, *Pseudambassis* Bleeker 1874, and *Pseudoambassis* Castelnau 1878. These and additional genera may be recognized eventually, but at present the species are too poorly known to assign them to different genera. If the living *Parambassis* are divided into several genera, generic status of the two extinct species described here will have to be reconsidered. The two Ban Nong Pla species evidently are related to a small living group of fine-scaled freshwater *Parambassis* and allied forms with 14-17 dorsal- and anal-fin soft rays found in mainland tropical Asia including India, Burma, Thailand, Indo-China and the Malay peninsula (ROBERTS, 1994), but even so they are perhaps more closely related to each other than they are to any of the living species. No fossil *Parambassis* have been described previously.



Figure 22. *Parambassis goliath*, 112 mm (holotype). DMR TF 5016.

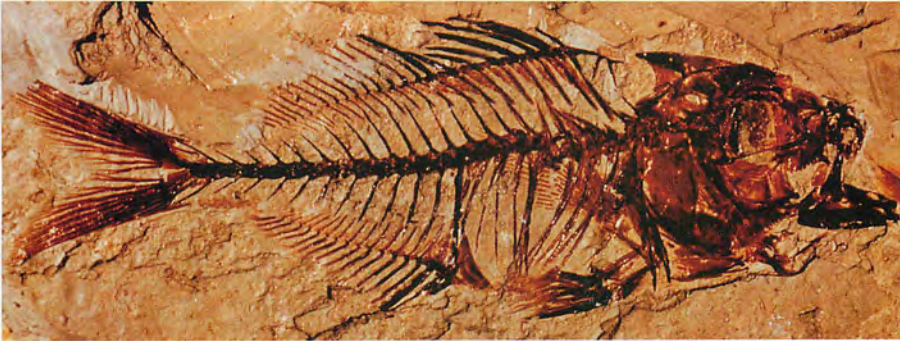


Figure 23. *Parambassis paleosiamensis*, 59.5 mm (holotype). DMR TF 5019.



Figure 24. *Parambassis paleosiamensis*, 59.5 mm (holotype). Predorsal bones. DMR TF 5019.

Figure 25. *Parambassi paleosiamensis*, estimated standard length 75 mm. Scale impressions on posterior part of body. DMR TF 5020.4.



Figure 26. *Parambassis paleosiamensis*, 59.5 mm. (holotype). Cancellous internal structure of anal-fin spines. DMR TF 5019.

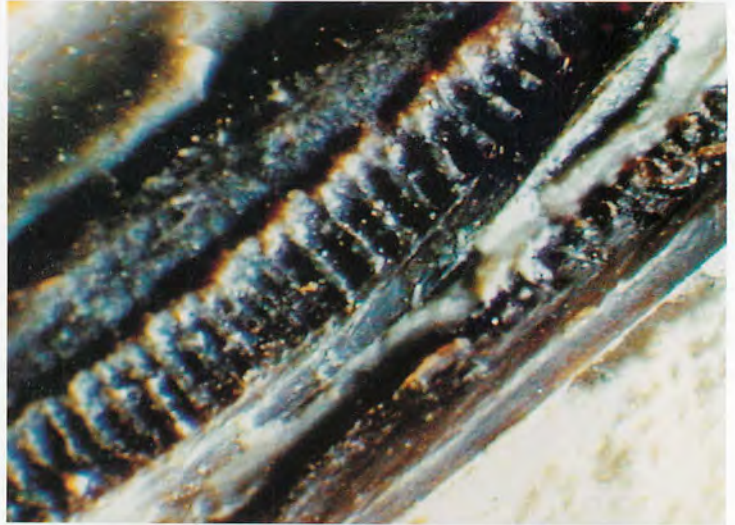
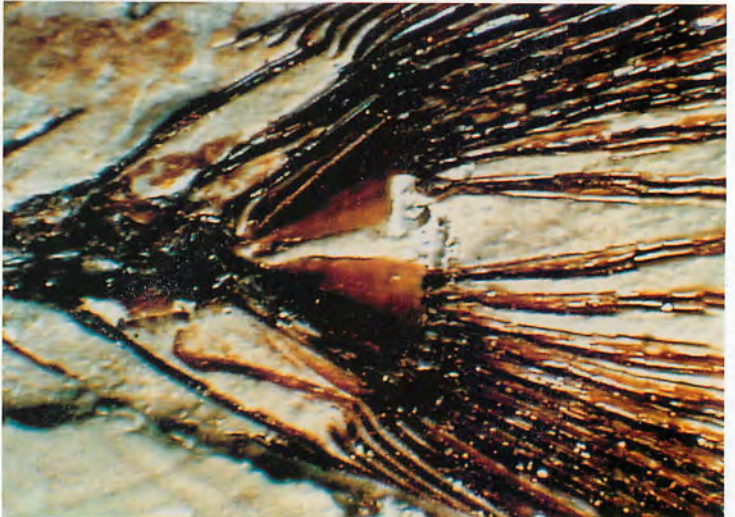


Figure 27. *Parambassis paleosiamensis*, 59.5 mm. (holotype). Caudal fin skeleton. Note specialized epural I. DMR TF 5019.



Parambassis goliath new species

Fig. 22

Holotype.—DMR: TF 5016, 112 mm, complete except for distal part of first two anal-fin spines and tips of caudal fin lobes.

Paratypes (complete or nearly complete specimens).—DMR: TF 5017.1, 38.5 mm standard length; TF 5017.2, 62.5 mm standard length; TF 5017.3, 76.5 mm standard length; TF 5017.4, 84 mm standard length; TF 5017.5, 98 mm standard length.

The following incomplete specimens, of particular interest because of their large size, are also identified as *P. goliath*.—DMR: TF 5018.1, nearly complete head 65 mm long (poor condition, with supraoccipital bone partially broken and pushed upward from rest of cranium); NCSE: 127 mm length to end of hypural fan (head missing, otherwise in fine condition; 105 mm NCSE fragment, including pectoral- and pelvic-fin girdles, anal-fin origin, and anteriormost ribs and vertebral column (fine condition; estimated standard length 270 mm).

Diagnosis.—*Parambassis goliath* has dorsal and anal fin ray counts similar to *P. paleosiamensis*, its presumed closest relative, but differs in having a larger head and deeper body, and in attaining a much larger size (27 cm versus only about 10 cm in standard length).

Proportional measurements of holotype (expressed as times in standard length).—Head 2.4; snout 7.7; eye 9.5; body depth (at dorsal fin origin) 2.7; pectoral fin length 5.0?; pelvic fin-spine length 8.0; predorsal length 2.1; second dorsal-fin spine 6.05; prepelvic length 2.2; preanal length 1.5; anal-fin base 3.9; caudal peduncle length 5.9; caudal peduncle depth 9.0?.

Meristic characters.—First dorsal fin invariably with 7 spines; second dorsal fin with spine and 14–16 soft rays; anal fin with 3 spines and 14–17 soft rays. Enlarged second and third anal fin spines of same length and width. Vertebrae 10+14–15=24–25.

Maximum size.—The 105-mm NCSE fragment clearly represents our largest fossil individual of *Parambassis*. Assuming that the morphometric relationships of the distances between the pectoral and pelvic girdles, the vertebral column, and the anal-fin origin are proportional in the complete specimens of smaller size we calculate its standard length as 270 mm. This is possibly larger than the largest recorded living chandid. The freshwater species *Parambassis gulliveri* from rivers in southern New Guinea and northern Australia, attains at least 220 mm standard length (ROBERTS, 1978: 54). It is unclear whether the length of 280 mm recorded for this species by WEBER & de BEAUFORT (1929: 404) refers to standard or total length. If it means standard length, then this species is as large as our *P. goliath*. But if it means total length, then the largest known of the living species is smaller than the extinct *P. goliath*. The second largest known living species, *Parambassis wolffii* (BLEEKER 1850) from rivers in mainland Southeast Asia and Indonesia, attains only 200 mm. All of the marine species are much smaller.

Comparisons of *P. goliath* with *P. paleosiamensis* and with living species.—See below.

Parambassis paleosiamensis new species

Figs. 23–27

Holotype.—DMR TF 5019, 59.5 mm SL, complete specimen in fine condition (with caudal fin of another specimen projecting into its mouth)

Paratypes (most complete or nearly complete specimens).—DMR: TF 5020.1a-b, 43.5 mm; TF 5020.2, 59 mm (between caudal fin lobes of holotype of *Cetopangasius chaetobranchus*); TF 5020.3, 72.5 mm; TF 5020.4 estimated standard length 72 mm (head missing; scale impressions on upper part of caudal peduncle); TF 5020.5, 62.5 mm standard length; TR 5020.6, 24 mm standard length; TF 5020.7, 62 mm standard length; NCSE: all complete or nearly complete, standard lengths 34.5 mm; 43.5 mm; 56 mm; 71.5 mm; 71.5 mm; 81 mm; 84 mm; 86 mm.

Additional specimens.—DMR and NCSE both have many partial specimens referable to this species, making it by far the most abundant species in our material of the Ban Nong Pla fossil fish assemblage (DMR TF 5021). Possibly some of the smaller and more fragmentary specimens included in this non-type material belong to *P. goliath*.

Proportional measurements of holotype (expressed as times in standard length).—Head 3.0; body depth (at dorsal-fin origin) 2.8; predorsal length 2.2; prepelvic length 2.2; preanal length 1.6; anal-fin base 3.7; caudal peduncle length 5.5.

Meristic characters.—First dorsal fin invariably with 7 spines; second dorsal fin with 1 spine and 14–16 soft rays; anal fin with 3 spines and 14–17 soft rays. Enlarged second and third anal fins of same length and width. Maximum size about 9–10 cm standard length. Vertebrae 10+14–15=24–25.

Scales.—The scales themselves are not preserved (or at least have not been observed by us) in any of our fossil *Parambassis*. Scale impressions, however, are discernible on the posterior part of the body in an incomplete DMR specimen of *P. paleosiamensis* (Fig. 12). There are 3–4 longitudinal scale rows between the neural spines of vertebrae 22–23, indicating a total lateral line scale row count of about 75–100. Such fine scales are characteristic of the living species of this exclusively freshwater genus (ROBERTS, 1994). Marine chandids all have much larger scales, only about 25–35 in the lateral line series.

Comparison with *P. paleosiamensis* and with living species—*Parambassis paleosiamensis* and *P. goliath* are both much larger than their closest living relatives. In *Parambassis ranga* (HAMILTON 1822), the largest of the living species with 14–17 branched anal-fin rays, the largest known specimen is only 71 mm standard length (ROBERTS, 1994: 280). This very abundant species occurs throughout much of India and Burma and in Thailand in the Salween basin. *Parambassis siamensis* (FOWLER 1937), a closely related species occurring throughout Thailand including the Menam Pa Sak, is even smaller, the largest known specimen only 50 mm standard length (op cit.: 282). These two species, which may be the closest living relatives of the Ban Nong Pla *Parambassis*, agree with each other but differ from the extinct forms in having a steeper and more concave predorsal profile, so that depth of head is much less than body depth. In *P. paleosiamensis* and *P. goliath* the predorsal profile is straighter and not concave, so that maximum head depth

is about equal to body depth. In this respect the extinct species superficially resemble some Serranidae more than they do other Chandidae. *Parambassis goliath* and *P. paleosiamensis* are very close morphologically. They differ most obviously in that *P. goliath* has a larger head and a deeper body, and attains a much larger size. The difference in head size and body depth is marked in all specimens except those smaller than 38.5 mm standard length. Our fossil *Parambassis* specimens below this size may consist entirely of *P. paleosiamensis* or may be a mixture of the two species.

CONCLUSION

When the Indian craton collided with Asia it derailed previously prevailing continental geomorphological processes and inaugurated a new regime of rapid and chaotic changes dominated by plate tectonics. Geological consequences include the extremely complex folding and up-thrust of the Himalayan and other central Asiatic mountain ranges; uplift of the Tibetan plateau; and formation of the Hengduang mountain ranges. These in turn led to the extraordinary divergent pathways of the Indus and Brahmaputra; the parallel gorges of the Mekong, Irrawaddy, Mekong and Yangtze rivers between ranges of the Hengduang mountains; formation of the Red River valley; and formation of a complex system of spectacular cross-faulted grabens in Thailand. Large lakes in these grabens dominated the Oligocene and Miocene landscape of Thailand. These and other changes wrought by the impact have profound implications for the climatology, ecology, and biotic composition of Asia. Full appreciation of the manifold changes by geologists, climatologists, ecologists, paleontologists and neontologists depends on a far more detailed knowledge of geological, climatological, faunistic and floristic and other conditions in India and Asia before as well as after the impact than is available at present.

The large but transitory Oligocene and Miocene lakes of Thailand were faunated by the Greater Sundaland drainage mentioned in the Introduction. There is only a little direct evidence from fossils concerning composition of the Greater Sundaland drainage fish fauna (SANDERS, 1934). This fauna may have populated numerous Oligocene and Miocene lakes comparable in size (and in some respects, geological history) to Lake Phetchabun. If the lakes were isolated from each other, in time or in space, each of them may have evolved endemic lacustrine fish species. So far the only direct evidence that this may have occurred is the Lake Phetchabun fossil fish assemblage. The immediate questions for further research is whether endemic fishes actually did evolve in many of these lakes, and, if so, did all of them die out when lacustrine conditions ended, or did some of them contribute to the modern riverine ichthyofaunas?

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