A FOSSIL GOURAMI (TELEOSTEI, ANABANTOIDEI) FROM PROBABLE EOCENE DEPOSITS OF THE OMBILIN BASIN, SUMATRA, INDONESIA

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ABSTRACT—Fossil fishes were first collected from deposits of the Sangkarewang Formation of the Ombilin Basin in Sumatra, Indonesia, in the 1870s, but a comprehensive study of these fishes was not published until almost 50 years later. New material from these deposits was collected in 2009, which included a small anabantoid fish. This fish is not conspecific with any of the material described previously and is here named as a new genus and species. A phylogenetic analysis indicates that the new anabantoid is closely related to Osphronemus among the taxa studied, and we place it in the family Osphronemidae. However, the new fish does not appear to belong to any of the named modern subfamilies, so we leave it in the family. Additionally, the osphronemid subfamilies are not recovered as a monophyletic group. The anabantoid named here and another previously described from the same locality are the only fossil anabantoids known. However, the age of the Sangkarewang Formation is not confirmed and has been variously attributed to Cretaceous, Palaeocene, Eocene, and Miocene, with Eocene being the presently favored estimate. Based on the presence of an anabantoid in these deposits, an Eocene age is reasonable and is not contradicted by the known fish fauna.

http://zoobank.org/lsid:urn.lsid.zoobank.org:pub:53281C25-8E47-4C67-9952-A994B47F6656

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

INTRODUCTION

Well over a century ago, fossils were collected from Tertiary deposits of the Sangkarewang Formation of the Ombilin Basin, Sumatra, Indonesia, with elements of the flora described in 1874 by Heer. In the same publication, the Swiss zooarchaeologist Rütimeyer (1874) documented two different fishes but named neither of them. Two years later, von der Marck (1876), followed closely by Günther (1876), published brief notes on the fishes, but a more comprehensive study of the fossil fish fauna was not published until almost 50 years later (Sanders, 1934). Von der Marck (1876) reported four new species in three new genera. Sanders (1934) subsumed three of von der Marck’s (1876) species into previously named living genera, retaining a single species from Günther (1876), and reported an additional 11 species.

Among the fauna, Sanders (1934) indicated the presence of the giant gourami, Osphronemus goramy, based on three specimens: one a fragment of the body and two more complete specimens of 13.5 and 19.5 cm standard length. Although Sanders (1934) provided meristics and measurements for the specimens, she noted few osteological features and did not describe any features of the skull in detail. In placing the fossils in the living genus, Sanders (1934) commented that the difference between the fossils and the living giant gourami—number of caudal vertebrae 18–19 in the living and 21 in the fossil—was insufficient for naming a new species. A more detailed osteological study was not done. Roberts (1992), in his revision of the genus Osphronemus, noted that the description and meristics of the fossil (which he reported as Miocene) were consistent with including it in the living genus. This fossil material should be reexamined to determine if it truly is conspecific with the living giant gourami; however, we are unsure of the whereabouts of the material Sanders examined. Although some of the material she examined is in the Naturalis Museum, Leiden (M. Friedman and M. Brazeau, pers. comm., 2012; P. Lambers, pers. comm., 2013), the whereabouts of the three gourami specimens, along with the majority of the material Sanders examined from Musper’s collections, are unknown to us, and these specimens have been presumed lost by other researchers (e.g., Taverne, 1978; P. Lambers, pers. comm., 2013). To our knowledge, this is still the only previously reported fossil anabantoid.

In 2009, a collecting trip to the Sangkarewang Formation of the Ombilin Basin, Sumatra, allowed us to recover over 200 more fish fossils, which are now being prepared. One of these is a small anabantoid, described in this paper. The number of caudal centra (15) and anal-fin spines (six in the new specimen and 11 in Sanders’ [1934] material) indicate that our new specimen is not conspecific with Sanders’ (1934) specimens. We here name this anabantoid as a new genus and species. Although relationships of living families of anabantoids are in dispute, we here follow the most inclusive definition for the Osphronemidae and include the new species in that family as elaborated below.

Geology

The Ombilin Basin, including the Sangkarewang Formation, has been extensively studied due to the presence of coal and oil shale deposits that are harnessed for energy resources. Sanders (1934) summarized the geology of the area as understood prior to her publication. She noted that the fish fossils came from deposits with interbedded sandstones and marls among breccias.
Anatomical Abbreviations—aa, anguloarticular; afptp, anal pterygiophores; bpt, basipterygium; bsp, basiphosphoenid; cl, cleithrum; den, dentary; dsp, dermophostenid; epi, epicoipital; fr, frontal; hy1–5, hypurals 1–5; hyo, hyomandibula; io2–4, infraorbitals 2–4; iop, interopercle; l, left; lac, lacrimal; le, lateral ethmoid; mx, maxilla; na, nasal; np, neural spines; op, opercle; pa, parietal; pd, possible left palatine; pel 1–2, postcleithra 1 and 2; pd, predorsal bones; phy, parhypural; pmx, premaxilla; pop, preopercle; pto, pterotic; pts, pterosphenoid; ptt, posttemporal; pu2–3, preural centra 2–3; qu, quadrate; r, right; ra, retro-articular; s, scale; sel, supracleithrum; soc, supraoccipital crest; ssp, subopercle; sus, suborbital shield; un, unareolous; us, urostylid centrum.

MATERIALS AND METHODS

The fossil described here was collected by the authors during field work in July and August of 2009, from the locality designated as Datarmasi-Sanahsirah Main Quarry (SO0°34′43.1″, E100°46′6.7″) sampling freshwater deposits in the Sangkarewang Formation. This locality is in the Ombilin Basin, Barisan Mountain Range, Sumatera Barat (West Sumatra) Province, Sumatra, Indonesia. Preliminary examination of the sediments by Bettis et al. (unpubl. National Geographic Society [NGS] report) indicated that the fish comes from deep-water lacustrine deposits. Work is ongoing to better understand the geology of this area.

The fossil is permanently housed in the Paleontology Collections (PAL) of the Institut Teknologi Bandung (ITB), Indonesia, under catalog number PALITB/TWL-213-2009 (TLW refers to Talawi, the area from which the fossils were excavated). The fossil was preserved with a thin layer of sediment over the bone and was prepared by hand to remove the soft sediment from the bone surface. Photographs were taken using a Nikon DXM 1200C digital camera mounted on a Zeiss Discovery.V8 stereo microscope. Comparative material examined is listed in Appendix 1.

Phylogenetic Analysis—A phylogenetic analysis was run with a limited number of taxa to determine the higher relationships of the new fossil species. Many characters used in the analysis were noted by Liem (1963) to distinguish among groups of anabantoids. Liem’s (1963) study was precladistic and characters were not presented as synapomorphies; therefore, these characters are reformulated (Supplemental Data 1) in terms of differing character states for use in a cladistic analysis. Other characters included here were noted during examination of the specimens, and some were previously used in an analysis of channids (Murray, 2012). Because the goal of the analysis is to determine the higher relationships of the fossil, only osteological characters were used. The phylogenetic analysis was run in PAUP 4.0b10 (Swofford, 2002), with all characters unordered and unweighted. The data matrix (Supplemental Data 2) was run in a branch-and-bound analysis (furthest addition sequence and default options). Taxa included with the anabantoids in the ingroup ( = Anabantomorpha of some authors, e.g., Near et al., 2013) are representatives of the presumed sister group to the Anabantoidi, the Channidae (Channa striata and C. micropeltes). Outgroups, following Norris (1994), are Nandus nandus and Badis badis, which may be placed in different families (Nandidae and Badidae; e.g., Kullander and Britz, 2002) or in separate subfamilies within Nandidae (e.g., Nelson, 2006), as well as Pristolepis fasciata (Pristolepididae). These three species were also part of the clade containing the channids and anabantoids found by Springer and Orrell (2004), and P. fasciata has in the past been included in the Nandidae.
Confident that it belongs with the anabantoids and their relatives. The modified scales and jaws of the spikefishes. Therefore, we are the specialized dorsal suction disk of the remoras and also lacks as three or more preural centra). Additionally, the fossil lacks the length of hypural 3 is as long anterodorsally than it is high (the length of hypural 3 is as long as three or more preural centra). Additionally, the fossil lacks the specialized dorsal suction disk of the remoras and also lacks the modified scales and jaws of the spikefishes. Therefore, we are confident that it belongs with the anabantoids and their relatives.

Among the outgroups, Badis and Nandus have a unique distally divided hemal spine on the second preural centrum (Barlow et al., 1968; Kullander and Britz, 2002), and Badis additionally has no suborbital shelf, excluding the fossil from those families. Pristolepids have a reduced number of principal rays (14) in the caudal fin and only three anal-fin spines, unlike the fossil. Among the ingroups, the snakeheads (Channidae) have no spines in their fins, unlike the Sumatran fossil, thus excluding the fossil from this family. Other details of the osteology of the fossil fish such as the form of the skull bones, in particular the high supracapsular crest, expanded infraorbital bones, and serrations on some of the bones of the opercular series indicate a closer relationship to the anabantoid families, rather than to the channids, nandids, badids, or pristolepids.

The anabantoids, or labyrinth fishes, constitute a relatively small group of genera that have an accessory breathing apparatus allowing them to breathe atmospheric oxygen while inhabiting oxygen-poor water. The accessory breathing apparatus is a complex elaboration of the first epibranchial bone supporting highly vascularized tissue (e.g., Forsellius, 1957). The families within the order, and the relationships among them, have been the subject of several studies, with no consensus of results (e.g., Barlow et al., 1968; Norris, 1994). In this paper, we arbitrarily follow Nelson (2006) and Ruber et al. (2006) and recognize the families Anabantidae, Helostomatidae, and Osphronemidae, with this last family including Belontiinae and Luciocephalinae, rather than recognizing these two latter groups as families (e.g., as in Wiley and Johnson, 2010). The Osphronemidae also includes the subfamilies Macropodinae and Osphroneminae. The Anabantoidae itself has been recognized as a separate order, as a suborder along with the Channidae in the Anabantiformes, or as a suborder in Perciformes (see Liem, 1963; Nelson, 2006; Wiley and Johnson, 2010). Luciocephalus has also been given its own suborder (e.g., Berg, 1940).

In this paper, we follow Nelson (2006) and Ruber et al. (2006) and consider the Anabantidae to include Anabas (two species), Clanodon (16 species), Microcorynosoma (12 species), and Sander (two species). The Osphroneminae contains only the genus Osphronemus (four species), and Belontiinae contains only Belontia (two species). The Macropodinae (as noted by Nasaka and Bogutskaia [2004], the name has been changed from Macropodinae, which is preoccupied by the kangaroo taxon; International Committee on Zoological Nomenclature [2003]) includes Macropodus (12 species), Pseudosphromenus (two species), Malpultua (one species), Parosphromenus (19 species), Trichopsis (three species), and Betta (73 species). Luciocephalinae contains two species of Luciocephalus along with Ctenops nobilis, two species of Parasphaerichthys, four or five species of Sphaerichthys, four species of Trichogaster, and five of Trichopodus (the latter are sometimes included in Trichogaster, e.g., as in Ruber et al., 2006). Helostomatidae is monotypic (Helostoma temminckii). Species numbers are from Eschmeyer (2013).

The Anabantidae have deep serrations or spines along the posterior edge of the opercle (Liem, 1963; pers. observ., A. M. M.); these are not present in the fossil, indicating that it is not of that family. Additionally, the fossil has an elongate pelvic ray that is not found in anabantoids. The dentary and premaxilla of Helostoma being edentate (Liem, 1967b), unlike the toothed jaws of the fossil, and the lack of a suborbital shelf in Helostoma indicate that the fossil is not part of the Helostomatidae.

The Osphronemidae has serrations on the second and third infraorbitals, has no distinct suborbital shelf, and possesses only ctenoid scales (Liem, 1963; pers. observ., A. M. M.). All these characters exclude the Sumatran fossil from this subfamily. Belontiinae possesses an ascending process of the premaxilla that is longer than the alveolar process (Liem, 1963; pers. observ., A. M. M.) and so more elongate than that of the fossil, which appears to be shorter than the alveolar process. The Sumatran fossil is also excluded from Luciocephalus, because that genus has no spines in the dorsal and anal fins (Britz, 1994; Nelson, 2006; pers. observ., A. M. M.). The genera Trichogaster, Sphaerichthys, and Parasphaerichthys, which formed the Trichogasterinae of Liem (1963), have the suborbital shelf formed by only the second infraorbital bone, with no contribution from infraorbital 3–5, whereas the fossil also has contributions from infraorbitals 2 through 5.

The elongate pelvic-fin ray of the fossil fish is of the same specialized type (see below) as that found in many of the gouramies. We therefore place the Sumatran fossil in the family Osphronemidae but leave it incertae sedis within the family. This position is partly supported by the phylogenetic analysis (see below).

Subdivision TELEOSTEI Müller, 1845
Order ANABANTIFORMES Berg, 1940
Suborder ANABANTOIDEI Berg, 1940
Family OSPHRONEMIDAE Bleeker, 1859
OOMBILINICHTHYS, gen. nov.

Type and Only Known Species—Ombilinicthys yaminii, sp. nov.

Diagnosis—As for type and only known species.

Derivation of Name—Named for the Ombilin Basin where the fossil deposits are located, and the Greek ending −ichthys meaning fish. Gender is masculine.

OOMBILINICHTHYS YAMINI, sp. nov. (FIGS. 1–4)

Holotype—PALITB/TWL-213-2009, housed in the paleontology collections (PAL) of the Institut Teknologi Bandung (ITB), Indonesia.

Type Locality and Horizon—Sangkarewang Formation, Tanahsirah Main Quarry (S00 34’11.1”, E100’46’6.7”), Talawi, Sumatera Barat (West Sumatra) Province, Sumatra, Indonesia.

Etymology—Named for Mohammad Yamin (1903–1962), historian, poet, playwright, and politician, who was born in Talawi, and was named a ‘National Hero of Indonesia’ in part for his role during the Indonesian Revolution for Independence.

Diagnosis—Osphronemid fish with four anal-fin pterygiophores inserting in the first interhemal space, compared with five
or more anal-fin pterygiophores in the first interhemal space in *Tricopterus* (5), *Osphronemus* (6), *Belontia* (5), and *Helostoma* (12) (counts from Springer and Smith Vaniz, 2008). Infraorbitals expanded, covering cheek as in some species of *Ctenopoma*, not reduced as in osphronemid species (see Liem, 1963; Norris 1994). Lacking serrations on the second and third infraorbitals (unlike Osphroneminae; Jayaram, 2013); spines present in dorsal and anal fins (unlike *Luciocephalus*), with apparently six anal-fin spines (fewer than in any species of *Parosphromenus* [7–9 in *P. parvulus* and *P. ornaticauda* but 10 or more in all other species; Kottelat and Ng, 2005], *Osphronemus* [9–13 anal-fin spines; Froese and Pauly, 2011], *Pseudosphromenus* [16–20 anal-fin spines;...
Description

General Body Form—The specimen is small, with a standard length (SL) of 37 mm. The body is quite deep (Fig. 1), being just under half of SL (18 mm). The head depth and head length are 15 mm (40% of SL). The dorsal- and anal-fin bases are quite long, about 12 or 13 mm (32–35% SL). The dorsal fin has its origin placed slightly more anteriorly than the origin of the anal fin, and the posterior-most dorsal-fin ray is also positioned slightly more anterior than the posterior-most anal-fin ray (Fig. 2). The caudal fin is not fully preserved but was likely rounded or emarginate.

Skull—The scales covering the skull bones obscure the sutures, making it difficult to determine the limits of the individual bones. The skull is deep, with a tall supraoccipital crest that extends anteriorly from the posterior-most point of the skull to the level of the posterior edge of the orbit (Fig. 3). Anterior to this, the crest appears to continue, but we interpret this as the right frontal and nasal bones having been pushed up and over the left frontal and nasal bones. Based on this, and the relief of the bones in the posterior part of the skull, the cranium was broad in this fish. There is a strong lateral ridge on the skull, which corresponds in position with a ridge on the parietal of Osphronemus goramy and is likely on the parietal of the fossil. Posterior to the ridge is a flattened shelf, which we interpret as the facet of the epipodial for articulation of the posttemporal; this latter bone is only partly preserved, and displaced posteriorly. A small depression in this area is identified as the posttemporal foramen; it is apparently located between the parietal, epipodial, and pterotic, as in O. goramy. The dermosphenotic is an irregularly shaped bone that meets the pterotic and frontal bones, but it appears to be excluded from forming part of the orbit by the fifth infraorbital bone and frontal.

The nasal bones are flat and rectangular, with the posterior end slightly wider than the anterior end. The lateral ethmoid is visible ventral to the nasal bones, and bone preserved posterior to it is identified as the pterosphenoid and basisphenoid, although the separation between the two cannot be seen. Details of the parasphenoid cannot be determined.

Opercular Region—The bones of the opercular region are also obscured by scales. The opercle is flattened dorsally and gently curved ventrally, probably with a concave margin on the dorsal part of the posterior edge. No spines ornament the posterior or ventral edge. Below the scales on the opercle is an area mostly free of squamation; we interpret this as the subopercle, but it could in fact be part of the opercle, because we cannot see a clear edge under the scales. The preopercle is distinctly serrated along its posteroventral edge, with 19 visible (Fig. 3). The sensory canal of the preopercle has been crushed so it appears open, but it was likely enclosed or covered with a flange in life. Between the ventral corners of the preopercle and opercle, the interopercle is just visible; it bears no spines.

Jaws and Suspensorium—The symphysis of the left and right premaxillae is preserved, along with the long ascending processes. The premaxillae bear short conical teeth. The articular heads of the left and right maxillae are in place just behind the ascending processes of the premaxillae (Fig. 3). The left dentary and anguloarticular are somewhat crushed, concealing details, but the sensory canal pores of the dentary are large and round. The retroarticular reaches dorsally to the level of the angulararticular facet for the quadrate and probably formed part of the facet.

Most of the suspensorium is covered by the jaw elements and infraorbital bones and thus cannot be seen. A small portion of the anterior projection of the palatine is visible; it is quite robust and cylindrical. The ventral part of the quadrate is also visible, but its articular condyle is broken. A bony fragment between the preopercle and infraorbitals probably corresponds to part of the metapterygoid. Dorsal to this, the broad hyomandibular head is visible anterodorsal to the opercle (Fig. 3).

Infraorbitals—The limits of each infraorbital are difficult to discern because of the scale covering; therefore, the edges illustrated (Fig. 3) are tentative. There are six infraorbital bones, including the dermosphenotic; there is no antorbital. The first infraorbital (lacrimal) is irregular in shape; the second is roughly square and smaller than all the others except the sixth (dermosphenotic). The second and third infraorbitals form the ventral edge of the orbit. Infraorbitals 4 and 5 are large and expanded, forming the posterior rim of the orbit and covering most of the cheek, but apparently not reaching the preopercle. No spines are present on the infraorbitals.

FIGURE 2. Ombilinichthys yamini, gen. et sp. nov. Reconstruction of the fish based on the holotype, PALITB/TLW-213-2009. The dorsal- and anal-fin pterygiophores are not clear in the fossil and have been reconstructed to interdigitate with the neural and hemal spines based on comparison with modern osphronemids.
visible on infraorbitals 2 through 6, but two spines are preserved on the lacrimal. A deep suborbital shelf is formed by infraorbitals 2 through 5. Whether the dermosphenotic contributes to the suborbital shelf cannot be seen, but it appears to be excluded from forming the lateral rim of the orbit. Bone preserved in the orbital area between the suborbital shelf and the parasphenoid is believed to belong to the suborbital shelf from the other side of the fish.

**Paired Fins and Girdles**—The pectoral girdle is partly displaced, and our identification of the bones is tentative. A thick flat bone extending posteriorly from the opercle is identified as the dorsal postcleithrum (Fig. 3). Between this and the presumed edge of the opercle is the dorsal plate of the cleithrum. These identifications could be incorrect, with the part identified as the cleithrum actually being part of the opercle and the posteriorly directed bone being a spine on the opercle; however, we believe

FIGURE 3. *Ombilinichthys yamini*, gen. et sp. nov., holotype, PALITB/TLW-213-2009, head and pectoral region. Photograph of specimen immersed in alcohol under polarizing light (top) and interpretive drawing (bottom). Scale bar equals 5 mm.
the first interpretation is more likely because of the texture and flatness of the presumed dorsal postcleithrum. The ventral postcleithrum is long and thin. Dorsal to the anterodorsal tip of the opercle is a partial bone we identify as the dorsal tip of the supracleithrum. Posterodorsal to this, the posttemporal has 18 rays forming a rounded fin that surpasses the anal-fin origin, almost reaching the midpoint of the body (Figs. 1, 2).

The thoracic pelvic fin has a robust spine and five rays. Two preserved rays are elongate (Figs. 1, 2), being about three times as long as the rest; we interpret these as being one from each side. Forselius (1957) noted that in the anabantids and Helostoma, the pelvic-fin rays are normal, but in osphronemids there is a unique elongation of one ray (with corresponding reduction in the others), such that a single branch of the original ray becomes a very long filiform thread (unbranched but segmented). The pelvic ray in the fossil is similarly modified such that it is a long, unbranched but segmented ray. The other rays in the fin are of normal length and not reduced in number, resulting in a fin that is more modified than those of anabantids, but not as modified as in living osphronemids such as Trichopodus (one long and two very reduced rays; pers. observ., A. M. M.) and Trichogaster (only a single elongate ray; Forselius, 1957; pers. observ., A. M. M.). The triangular portion of the right pelvic girdle is also preserved.

**Dorsal and Anal Fins**—The dorsal- and anal-fin spines and rays are somewhat displaced (Fig. 1), making numbers tentative. We count approximately 10 spines and seven rays in the dorsal fin and apparently six spines and 21 rays in the anal fin. There are at least 14 dorsal-fin pterygiophores preserved and perhaps 18 or more anal-fin pterygiophores present, but both fins would presumably have had more pterygiophores than those preserved. The flank of the body between the anal fin and the vertebral column is covered with scales, obscuring most of the anal-fin pterygiophores. However, just under the posterior extent of the pectoral-fin rays are preserved parallel bones that we interpret to be proximal portions of the first four anal pterygiophores based on their position and orientation (Fig. 3). Therefore, we assume that there are four pterygiophores inserting into the first interhemal space.

**Axial Skeleton**—Three thin supraneurals are positioned about equidistant between the posterior edge of the supraoccipital and the first dorsal pterygiophore (Fig. 3). They are of equal size, are oriented almost vertically, and have a small space between each. The neural spines below the supraneurals are displaced and difficult to interpret, but it appears that the supraneurals are dorsal to the second vertebral centrum.

Based on preserved centra and neural spines, there are 29 vertebrae including the urostylar centrum, of which 14 are abdominal and the rest are caudal (based on their position posterior to the first anal-fin pterygiophore). The vertebrae are as long (anteroposteriorly) as they are tall (dorsoventrally) and have large lateral pits.

**Caudal Fin**—The caudal skeleton is covered by scales, but the impressions of the underlying bones can be seen (Fig. 4). The elements of the caudal skeleton are somewhat displaced. There are five hypurals, all of which reach the urostylar centrum, except possibly the fifth. Hypurals 1 through 4 are of similar size, and the fifth hypural is somewhat smaller. The parhypural is comparable in size to hypurals 1 through 4. It does not reach the centrum, possibly because it has been displaced, but more likely because it did not reach the centrum in life; this is the case in at least some species of Trichogaster, Anabas, and Channa (Fujita, 1990; pers. observ., A. M. M.). There are two long, narrow epurals filling the gap between the long uroneural and the long neural spine of the second preural centrum. The uroneural is long and robust, more similar to that of Anabas and Channa rather than the shorter uroneural of Ctenopoma. Both neural and hemal spines of the caudal centra are elongate, reaching almost to the dorsal and ventral body walls. Whether or not accessory cartilages were present is not determinable.
There appear to be 16 branched principal caudal-fin rays (formula I.8.8.I, indicating one unbranched and eight branched rays in the dorsal lobe and eight branched rays followed by one unbranched in the ventral lobe). This number is not expected because the majority of percomorphs have 15 branched principal rays (I.8.7.I) in the caudal fin (e.g., Johnson and Patterson, 1993). However, Fujita (1990:table 2) found 16 branched principal rays in Trichogaster (as Colisa), in two specimens, although Johnson and Patterson (1993) counted I.6.7.1 and our examined specimen has a caudal formula of I.7.8.1. Clearly, this genus at least is quite variable.

All the rays of the caudal fin in the fossil are long, but the end of the fin is not preserved, so the overall shape cannot be determined; however, if it was not rounded, it was likely emarginate or only very shallowly forked.

**Scales**—Scales cover the whole body and are large in comparison with the size of the fish. Each scale is just over 1 mm in height and length, but slightly taller than long. There would have been 29 or 30 scales along the lateral length of the body (posterior to the opercle). The scales superficially appear to be cycloid, but a number of them preserve tubercle-like ctenii, very similar to the form found in Osphronemus goramy. In O. goramy, these tubercles form ctenii at the posterior edge, and it is likely they also did in the fossil, but the ctenii are not preserved or too small to be seen. The tubercles cover the posterior half of the scales. The scale focus is slightly anterior to the center of the scale, and there are about 16 circuli and 9 or 10 radii visible in some scales.

The scales cover the trunk, nape, throat, and the bases of the dorsal and anal fins. On the anterior portions of the dorsal and anal fins, scales are present on the spines almost to the distal tip of the fins. Scales also cover the lateral skull bones, being present on the opercle, cheek, infraorbitals, and the forehead, as well as the skull roof.

**PHYLOGENETIC ANALYSIS**

An analysis of relationships was done to determine if the fossil anabantoid was appropriately placed in the Osphronemidae. The analysis included the fossil and 12 taxa, of which the nandid, badid, and pristolepid taxa were designated as outgroups. The rest of the taxa sampled species of anabantomorphs (anabantoids and channids). Forty-three characters were assessed for the taxa

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**FIGURE 5**. Cladogram of relationships resulting from the phylogenetic analysis. **A, B, C**, the three shortest trees (84 steps) from the initial branch-and-bound analysis; **D, E**, the two resulting shortest trees (78 steps) from a branch-and-bound analysis excluding Luciocephalus.
Osphronemus of the Anabantomorpha, followed by nids are embedded in the Osphronemidae (represented by Anabantidae fossil, with it being either sister to in two trees of 78 steps. These two differ in the placement of the sister groups. All three trees have Helostoma as the basal member of the Anabantomorpha, followed by Osphronemus and the new fossil taxon. Luciocephalus is recovered as (1) the sister to Tri-
chopodus + Trichogaster, (2) sister to the group formed by these two plus Anabantidae + Channidae, or (3) sister to all of these plus the fossil (Fig. 5A–C).

The second analysis, which excluded Luciocephalus, resulted in two trees of 78 steps. These two differ in the placement of the fossil, with it being either sister to Osphronemus, or sister to Anabantidae + Channidae + Trichogaster + Trichopodus (Fig. 5D, E). This result was the same regardless of how we coded Osphronemus for character 11 (teeth absent [0], based on one of the examined specimens; or teeth present on posterior portion of paraphenoid [1], following Liem, 1963:fig. 17, and other examined specimens; or polymorphic [0/1]). It must be noted, however, that there are no clear synapomorphies to unite the fossil with O. goramy. Additionally, the anabantids and channids are embedded in the Osphronemidae (represented by Tri-
chopodus trichopterus, Trichogaster lalius, Luciocephalus pulcher, and O. goramy). Therefore, although the fossil is recovered as the sister group to O. goramy or between O. goramy and other members of the family, indicating support for its placement in the Osphronemidae, the family itself was not recovered as monophyletic in our analysis. This is similar to the results found by Norris (1994) in which the Helostomatidae was embedded in the Osphronemidae (as we use the term). Ruber et al. (2006), who included many more taxa in their phylogenetic analysis using mtDNA, recovered a monophyletic Osphronemidae; how-
ever, they used representatives of Channidae as outgroups and did not include Badis, Nandus, or Pristolepis in their analysis.

DISCUSSION

Anabantoid fishes are rare compared with the other taxa, par-
cularly cyprinids, in the Sumatran deposits we sampled. Of the more than 200 fish fossils recovered during our field season, only one has been identified as an anabantoid fish, although some material remains to be prepared. Similarly, among the hundreds of specimens examined by Sanders (1934), only three re-
presented anabantoids. The lack of anabantoids in the sediments may relate to a habitat preference. These fishes are adapted to air-breathing, and so might be expected to prefer shallower waters, whereas it is likely we collected fossils from deep-water sediments (Bettis et al., unpubl. NGS report).

The age of the sediments is still not satisfactorily determined, and the fishes collected do not resolve the issue. Ruber et al. (2006) used Sanders’ (1934) report of Osphronemus goramy from the Tertiary beds of Sumatra as a calibration point for their divergence time analysis. They considered the fossil to date from the late Eocene or early Oligocene and used the dates of 28.5 Ma (the boundary between early and late Oligocene) and 37.0 Ma (the boundary between middle and late Eocene) as the upper and lower bounds, or alternately, by using the younger age as a lower bound constraint, indicating the uncertainty in whether the fossil represented a stem-group or crown-group form. Ruber et al. (2006) found no constancy of rates of evolution within the Anabantoidei and thus used non-clock-like methods to deter-
mine divergence times. Based on different analyses, they placed the anabantoid root between about 103 and 35 Ma, and the split between African and Asian lineages between about 87 and 31 Ma. Not surprisingly, younger ages were found when the fossil was used as a stem lineage, rather than a crown group, for Osphronemus. Our description of the new anabantoid, and the likelihood that Sanders’ (1934) material is not conspecific, and probably not congeneric, with O. goramy, indicates that the younger ages would be more probable because these result from using the fossils as stem groups.

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APPENDIX 1. Material examined.

Anabantidae: *Anabas testudineus* (Bloch, 1792), two dried skeletons, UAMZ unnumbered; *Ctenopoma nigropannosum* Reich- enow, 1875, two dried skeletons, UAMZ unnumbered.

Helostomidae: *Helostoma temminckii* Cuvier in Cuvier and Valenciennes, 1831, one cleared and stained, UAMZ unnumbered.

Nandidae: *Nandus nandus* (Hamilton, 1822), two cleared and stained, UMMZ 208668.

Badidae: *Badis badis* (Hamilton, 1822), two cleared and stained, CAS SU35663; two cleared and stained, UMMZ 208795.

Osphronemidae: Osphroneminae—*Osphronemus goramy* Lacepède, 1801, two dried skeletons, ROM R6671, ROM R6957; Luciocephalinae—*Trichopodus trichopterus* (Pallas, 1770), one cleared and stained, UAMZ unnumbered; *Trichogaster latius* (Hamilton, 1822), one cleared and stained, UAMZ unnumbered.

Pristolepidae: *Pristolepis fasciata* (Bleeker, 1852), two cleared and stained, UMMZ 228920; two cleared and stained, CAS 81529.

Channidae: *Channa striata* (Bloch, 1793), one dried skeleton, ROM R1773; three dried skeletons, UAMZ unnumbered; *C. micropeltes* (Cuvier in Cuvier and Valenciennes, 1831), two dried specimens, UAMZ unnumbered, ROM R5226.