A fossil gourami (Teleostei: Anabantoidei) from probable Eocene deposits of the Ombilin Basin,
Sumatra, Indonesia

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Supplementary data 1. Characters and character states used in the phylogenetic analysis.

Characters from Liem's (1963) pre-cladistic study are here reformulated in terms of differing character states for use in a cladistic analysis. Other characters are newly formulated based on direct examination of the specimens, and some were previously used in an analysis of African channids (Murray, 2012). Because the goal of this analysis was only to determine the higher relationships of the fossil, only osteological characters were used. Specimens were observed directly, with additional information taken from figures in Liem (1963, 1967a, b, 1970), Norris (1994), and Voeun (2006). Some character states are autapomorphies of single taxa in this analysis; however, as they are more widely distributed in other groups not included here, they are kept in the character list. Data for *Luciocephalus* are from figures in Norris (1994) and Liem (1967a). Observations on specimens of *Badis* and *Pristolepis* were supplemented with information from figures in Norris (1994) and Barlow et al. (1968).

Skull Roof

1. Nasal bones: separated in midline (0); left and right meet in midline (1). In *Anabas*, *Ctenopoma*, *Trichopodus* and *Trichogaster* the nasal bones meet in the midline (e.g., Liem, 1963: figs. 1, 2), whereas in the rest of the species the left and right nasals are separated, or have a fontanelle between them (e.g., Liem, 1963: figs. 4, 5). The nasals of the fossil are displaced so that they overlap. Although they likely did not meet, based on the shape, this has been coded as unknown.
2. Nasal bones: flat (0); elongate and tubular (1). The nasal bones are flat in channids (see Murray, 2012: fig. 5) and all other included taxa, except for *Nandus*. This is an autapomorphy of that species in this database, however, Liem (1963) reported tubular nasals are also found in *Malpulutta* (Macropodusinae).

3. Supraoccipital crest in relation to skull roof: low, not raised dorsally above the rest of the skull roof (0); high, clearly raised above the level of the frontals and parietals (1). The supraoccipital crest is low in channids (e.g., Murray, 2012: fig. 3), and anabantids (e.g., Liem, 1963: figs. 14, 15), but high in *Osphronemus* (e.g., Liem, 1963: fig. 17) and the fossil. In some taxa, the supraoccipital crest posterior to the skull roof is somewhat higher, but where the supraoccipital contributes to the skull roof, the crest is low (e.g., *Trichogaster lalius*; see Liem, 1963: fig. 25).
4. Supraoccipital anterior extent in relation to of the left and right frontal bones: anterior part of supraoccipital bone distinctly separates left and right frontals (0); frontals not deeply separated posteriorly by the supraoccipital bone (1). Even in taxa with a large contribution of the supraoccipital to the skull roof, the anterior extent of the bone differs. In *Osphronemus* and the fossil, the frontals are not separated by the supraoccipital, however in *Channa*, *Helostoma*, *Trichogaster* and *Trichopodus* they are (e.g., Liem, 1963: figs. 4, 5, 12).
5. Parietal shape: roughly rectangular (0); large, shaped like inverted V (1); small, somewhat round (2). Liem (1967) noted the V-shaped parietal as a feature for Osphronemidae; *Helostoma* also has a somewhat V-shaped parietal, although of different form than *Osphronemus* (see Liem, 1963: figs. 4, 5). The fossil also appears to have a V-shaped parietal, although this is not entirely certain and therefore is coded as unknown.
6. Epioccipital “wings”—bones extend posteriorly past posterior edge of the skull: absent (0); present and prominent (1). The epioccipital bones in *Channa* have distinct posterior extensions (pers. obs.), which are not found in the other taxa.

Ventral Skull

7. Ethmoid posterior process: absent (0); present, extending into orbit (1). The ethmoid of *Trichogaster* has a process that extends posteriorly into the orbit. This process is also found in *Betta splendens*, and *Macropodus cupanus* (Liem, 1967: figs. 20 and 22). Channids also have a similar median process (e.g., Murray, 2012: fig. 3).
8. Parasphenoid relationship with basioccipital: parasphenoid underlies greater part of basioccipital (0); parasphenoid restricted anteriorly, does not underlie basioccipital (1). In *Channa*, *Anabas* and *Ctenopoma*, the parasphenoid extends posteriorly, underneath the basioccipital, whereas in *Trichopodus*, *Trichogaster* and some other taxa, the posterior edge of the parasphenoid meets the anterior edge of the basioccipital in a vertical suture. This character is associated with the presence of a pharyngeal process on both the parasphenoid and basioccipital (character 12), in that in most taxa where the processes are present, the two bones join in a vertical suture, however, these processes are present in *Ctenopoma* but the parasphenoid underlies the basioccipital such that the two bones have a horizontal suture between them (see Liem, 1963: fig. 15).
9. Parasphenoid transverse process: absent (0); present (1). The transverse process is present in *Helostoma*, *Anabas* and *Ctenopoma* (see Liem, 1963: figs. 40, 41, 44) but lacking in the other taxa (e.g., Liem, 1963:fig. 43; Murray, 2012: fig. 3B).
10. Parasphenoid posterior raised patch: absent (0); present, large and distinct (1). This character refers to an area of bone that is thickened, and clearly above the level of the rest of the bone, as found in some channids (e.g., Murray, 2012: fig. 2).
11. Parasphenoid teeth: absent (0); present posteriorly (1); present on the anterior portion of the parasphenoid (2). The raised area on the parasphenoid (character 10) may or may not bear

teeth, and teeth may be present in the absence of the raised area, sometimes on a transverse process (e.g., Liem, 1963: figs. 40, 41, 43). Teeth in most taxa are confined to the posterior region of the parasphenoid, however, teeth are present anteriorly on the parasphenoid of *Pristolepis* (pers. obs.). One of our examined specimens of *Osphronemus goramy* (ROM R6671) has no teeth on the parasphenoid, and the posterior portion of the parasphenoid does not extend ventrally beyond the level of the basioccipital. However, the specimen figured by Liem (1963: fig. 17) and other specimens (UMMZ 213912; D. Nelson pers. comm.; ROM R6957) clearly bear several teeth on the ventrally directed posterior process of the parasphenoid. The parasphenoid of ROM 6671 does not appear to be broken but it seems to be an anomalous individual, however, we have coded this character as polymorphic (0/1) in *Osphronemus*, but see Phylogenetic Analysis for discussion on the lack of differences in results when *Osphronemus* is coded 0 or 1 instead of polymorphic.

Posterior Skull

12. Foramen magnum: small, roof and lateral walls formed by exoccipitals (0); relatively large, postero-inferior portion of the supraoccipital forms part of the roof (1). The foramen magnum is large and has the dorsal edge formed by the supraoccipital bone in *Osphronemus*, *Helostoma*, and *Trichogaster* but it is much smaller and encompassed within the exoccipitals in *Anabas*, *Ctenopoma* and the channids (e.g., Liem, 1963: figs. 52, 53, 55, 62; Murray, 2012: fig. 4).
13. Basioccipital with paired articular processes for articulation with upper pharyngeal jaws: absent (0); present (1). Wiley and Johnson (2010:159; citing e.g., Britz, 2003) give a synapomorphy for Anabantiformes (= Anabantoidei + Channidae) as “basioccipital with

paired articular processes forming diarthrosis with upper pharyngeal jaws”. Britz (2003:427) gives the character as “[b]asioccipital with paired articular processes that permit free movement with upper pharyngeal jaws.” Liem (1963) noted a ‘pharyngeal process of the basioccipital’ to be present in various anabantiforms. There are no basioccipital processes in *Badis*, *Nandis*, and *Pristolepis*. We are not convinced that the basioccipital processes in all the anabantiforms are homologous, however, for now we retain this character as presented by Wiley and Johnson (2010).

Jaws and Suspensorium

14. Premaxilla dorsal process: absent (0); present (1). A small dorsal process is present on the premaxilla of *Osphronemus*, *Pristolepis* and *Nandus*. The two channids included in the analysis do not have a dorsal process, but at least one species (*Parachanna obscura*) has a large dorsal process on the premaxilla (Murray, 2012: fig. 7).
15. Premaxilla length of ascending process: short, one fifth to one half length of horizontal arm of premaxilla (0); long, one to 2.5 times that of horizontal body of premaxilla (1). Channids and anabantids have a short premaxillary ascending process whereas the process is long in osphronemids.
16. Maxilla lamellar shelf (a thinning of the ventrolateral margin of the maxilla to give a more gracile form): absent (0); present (1). This lamellar shelf is present in the channids.
17. Dentary teeth posterior to expanded symphyseal area: teeth all of same size (0); inner row of enlarged caniniform teeth and outer labial row of very small teeth along length of bone (1). The channids have enlarged caniniform teeth as well as small teeth along the dentary; dentary teeth in the other taxa are uniform size and shape.
18. Anguloarticular cleft between facets: absent (0); present and deep (1). Channids have a deep

cleft dividing the facet for articulation with the quadrate into two distinct parts (see Roe, 1991).

19. Metapterygoid articulation with symplectic process of hyomandibula: present (0); absent (1). The metapterygoid does not reach the hyomandibula in *Helostoma*, *Trichogaster* and *Trichopodus* (e.g., Liem, 1963: figs. 68, 74).
20. Metapterygoid with enlarged uncinat process reaching or almost reaching ventral surface of frontal (see Liem, 1963): absent (0); present (1). The metapterygoid in channids has a large anterodorsal projection that reaches and may be attached by soft tissue to the ventral surface of the frontals (e.g., Murray, 2012: fig. 3C).
21. Ectopterygoid: present (0); reduced (1). The ectopterygoid is present in *Luciocephalus* (following Britz, 1994; contra Liem, 1967) and in most of the other included taxa (Liem, 1963); however, *Trichogaster* and *Trichopodus* have a much reduced ectopterygoid.
22. Branchiostegal ray number: five (0); six (1). The channids, *Trichopodus* and *Trichogaster* have five branchiostegal rays, but the rest of the taxa have six. Liem (1963) considered the five branchiostegal rays of *Colisa* (= *Trichogaster*) to be a reduction from the original six, but here the outgroups have only five rays, indicating it may be the primitive state.
23. Number of branchiostegal rays articulating with posterior ceratohyal: two (the fifth and sixth) (0); only the most posterior one, whether it is the sixth of six or the fifth of five (1). Channids and anabantids have two rays (the fifth and sixth) articulating on the posterior ceratohyal, whereas in the other taxa only a single ray is on the posterior ceratohyal.
24. Fifth branchiostegal ray: same as the rest (0); enlarged, about twice as broad as the preceding ones (1). *Trichopodus* and *Trichogaster* have an enlarged posterior branchiostegal ray; *Luciocephalus* also has the fifth ray larger than the others (see Liem, 1967: fig. 7).

Infraorbital Bones

25. Infraorbital bones four and five: expanded, covering most of the cheek (0); with distinct plate-like portion or flange as well as sensory canal, but not covering all of the cheek (1); tubelike (2). The infraorbitals of *Anabas* are expanded, covering most of the cheek, whereas those of *Osphronemus*, *Trichopodus*, *Helostoma*, *Badis*, *Nandus* and *Pristolepis* are reduced to tube-like structures. In the channids, at least some species of *Ctenopoma*, and the fossil, the infraorbitals retain a flange in addition to the sensory canal tube, but the flanges do not cover the entire cheek (e.g., Norris, 1994; pers. obs.).
26. Serrations on the second and third infraorbital bones: absent (0); present (1). The *Osphroneminae* has serrations on the second and third infraorbitals according to Liem (1963); serrations are also present in *Nandus* and the fossil.
27. Lacrimal bone serrations: absent (0); present (1). The lacrimals of most taxa bear small spines or serrations along the ventral edge; these are absent in the channids and *Ctenopoma*.
28. Suborbital shelf: present (0); absent (1). *Osphronemus*, *Helostoma*, *Badus*, and *Nandus* have no suborbital shelf. A shelf is present in the other taxa including the fossil. Liem (1963) united the genera *Trichogaster*, *Sphaerichthys*, *Parasphaerichthys*, and *Colisa*, into the *Trichogasterinae* based on the suborbital shelf being formed by only the second infraorbital bone, with no contribution from infraorbitals 3-5. In the rest of the examined taxa including the fossil the shelf is formed by infraorbital bones 2-5. We have not added another state or separate character for the different contribution of the infraorbital bones to the suborbital shelf, as *Trichogaster lalius* is the only one in our analysis that differs.

Opercular Bones

- 29. Opercle posterior border: not serrate (0); serrate (1). The Anabantidae have deep serrations or spines along the posterior edge of the opercle (Liem, 1967; pers. obs.); these are not present in the fossil nor in any other included taxa.
- 30. Interopercular posteroventral border: not serrate (0); serrate (1). Serrations are lacking in the channids, *Trichogaster*, *Badis* and the fossil.
- 31. Subopercle, posteroventral border: not serrate (0); serrate (1). Only the channids, *Trichogaster*, *Badis*, *Nandus* and the fossil have no serrations on the subopercle.

Axial Skeleton

- 32. Vertebral total number: 31 or fewer (0); 39 (1); 50 or more (2). The channids have more than 50 vertebrae. Excluding *Luciocephalus*, the other taxa vary in numbers from 24 to 31, but there were no clear divisions to use to delimit other character states. State 1 of this character is an autapomorphy of *Luciocephalus* (Liem, 1967a:fig. 9).
- 33. Epipleural bones in caudal region: present (0); absent (1). In disarticulated specimens we could not determine the presence or absence of epipleural bones, so these species are not coded in the matrix.

Paired Fins and Girdles

- 34. Elongated pelvic ray: absent (0); present (1). The fossil has an elongate pelvic ray as is also found in *Trichopodus*, *Trichogaster* and *Osphronemus*.
- 35. Pelvic girdle left and right sides: firmly united forming a bilaterally symmetrical unit (0); not meeting at the midline (1). The anabantids have left and right pelvic girdles separated in

the midline, whereas the two sides are united in *Osphronemus*, *Badis*, and *Nandus*. The fossil appears to have the left and right sides united also.

36. Pelvic girdles: conjoined anterior tips not attached to cleithra or united with cleithral symphysis by a ligament (0); connected directly without need for ligament (1). A ligament connects the pelvic girdle to the cleithra in *Anabas*, *Trichopodus*, and *Trichogaster*. The pelvic girdle is more remote from the pectoral girdle in channids, and thus not connected directly.

Median Fins

37. Dorsal and anal fin spines: present (0); absent (1). The channids and *Luciocephalus* have no spines in their median fins (Nelson, 2006; pers. obs.).
38. Number of anal fin spines: five or more (0); three (1). *Pristolepis*, *Nandus* and *Badis* have only three anal fin spines. In our examined material there are five in *Ctenopoma*, nine in *Anabas*, 10 in *Trichopodus* and *Osphronemus*, 14 in *Helostoma*, 18 in *Trichogaster*, and the fossil has at least six spines.
39. Second preural centrum haemal spine: single (0), divided (1). Liem (1963) noted that the nandids (*Badis* and *Nandus*) have a unique distally divided haemal spine on the second preural centrum.
40. Extracaudal ossicle: absent (0); present (1). The channids have a bone between the haemal spines of the second and third preural centra (e.g., Murray, 2012: fig.10).
41. Hypural number: five (0); four or fewer (1). There are five hypurals in the channids, anabantids, *Luciocephalus*, *Badis* and *Pristolepis*. This number is reduced (independantly in

our analysis) to four in *Helostoma* and *Nandus*, and three in *Trichopodus*. The fossil has five hypurals.

42. Number of epurals: two (0); one (1). The two species of *Channa* differ in the number of epurals, with *C. striata* having one and *C. micropeltes* having two. There are two in the anabantids, *Trichopodus*, *Trichogaster* and the fossil, but the rest of the taxa have a single epural.
43. Hypurapophysis on parhypural: absent (0); present (1). The hypurapophysis is present and well developed in the channids (e.g., Murray, 2012: figs. 10 C, D) but absent in the other taxa including the fossil.

LITERATURE CITED

- Barlow, G. W., K. F. Liem, and W. Wickler. 1968. Badidae, a new fish family—behavioural, osteological, and developmental evidence. *Journal of Zoology*, London 156:415–447.
- Britz, R. 1994. Ontogenetic features of *Luciocephalus* (Perciformes, Anabantoidei) with a revised hypothesis of anabantoid intrarelationships. *Zoological Journal of the Linnean Society* 112:491–508.
- Britz, R. 2003. Anabantoidei (labyrinth fishes); pp. 427–435 in M. Hutchins, D. A. Thoney, P. V. Loisel and N. Schlager (eds.), *Grzimek's Animal Life Encyclopedia*, Vol. 5, Fishes II. Gale Group, Farmington Hills, Michigan.
- Liem, K. L. 1963. The comparative osteology and phylogeny of the Anabantoidei (Teleostei, Pisces). *Illinois Biological Monograph* 30:1–149.
- Liem, K. L. 1967a. A morphological study of *Luciocephalus pulcher*, with notes on gular elements in other recent teleosts. *Journal of Morphology* 121:103–134.

- Liem, K. L. 1967b. Functional morphology of the head of the anabantoid teleost fish *Helostoma temminckii*. *Journal of Morphology* 121:135–157.
- Liem, K. L. 1970. Comparative functional anatomy of the Nandidae (Pisces: Teleostei). *Fieldiana: Zoology* 56:7–166.
- Murray, A. M. 2001. The fossil record and biogeography of the Cichlidae (Actinopterygii: Labroidei). *Biological Journal of the Linnean Society* 74:517–532.
- Nelson, J. S. 2006. *Fishes of the World*. Third Edition. John Wiley and Sons, Inc. Toronto, 601 pp.
- Norris, S. M. 1994. The osteology and phylogenetics of the Anabantidae (Osteichthys, Perciformes). Ph. D. thesis, Arizona State University, 481 pp.
- Roe, L. J. 1991. Phylogenetic and ecological significance of Channidae (Osteichthyes, Teleostei) from the early Eocene Kuldana Formation of Kohat, Pakistan. *Contributions from the Museum of Paleontology, University of Michigan* 28:93–100.
- Voeun, V. 2006. *Osteological Guide to Fishes from the Mekong System in Cambodia*. Fishbone Collection, Phnom Penh, Cambodia, 209 pp.
- Wiley, E. O., and G. D. Johnson. 2010. A teleost classification based on monophyletic groups; pp. 123–182 in J. S. Nelson, H. P. Schultze, and M. V. H. Wilson (eds.), *Origin and Phylogenetic Interrelationships of Teleosts*. Verlag Dr. Friedrich Pfeil, München, Germany.

Supplementary data 2. Data matrix for the cladistic analysis of the characters in Appendix 2.

	11111 11112 22222									
Character	12345	67890	12345	67890	12345					
Taxon										
<i>Channa striata</i>	00000	10001	10100	11101	00001					
<i>C. micropeltes</i>	00000	10001	10100	11101	00001					
<i>Anabas</i>	10010	00010	10100	00000	01000					
<i>Ctenopoma</i>	10010	00010	10100	00000	01001					
<i>Trichopodus</i>	10002	10100	01111	00010	10112					
<i>Trichogaster</i>	10002	01100	01101	00010	10112					
<i>Helostoma</i>	00101	01110	01111	0-010	01102					
<i>Badis</i>	00102	00100	11011	00000	01102					
<i>Nandis</i>	01002	00101	10011	00000	01102					
<i>Pristolepis</i>	00110	00100	20011	00000	01102					
<i>Osphronemus</i>	00111	00100	A1111	00000	01101					
<i>Luciocephalus</i>	00000	10100	00111	00000	0011?					
<i>Ombilinichthys</i> gen. nov.	0011?	00???	????1	?0000	????1					

	22223	33333	33444	444
Character	67890	12345	67890	123
Taxon				
<i>Channa striata</i>	00000	02?00	01-01	011
<i>C. micropeltes</i>	00000	02?00	01-01	001
<i>Anabas</i>	01011	10001	00000	000
<i>Ctenopoma</i>	00011	10001	00000	000
<i>Trichopodus</i>	01000	10011	00000	100
<i>Trichogaster</i>	01000	00011	00000	000
<i>Helostoma</i>	01101	10100	10000	110
<i>Badis</i>	00100	00100	10110	010
<i>Nandis</i>	11101	00100	10110	110
<i>Pristolepis</i>	01001	10100	10100	010
<i>Osphronemus</i>	11101	10?10	10000	010
<i>Luciocephalus</i>	???00	01110	11-00	010
<i>Ombilinichthys</i> gen. nov.	11000	00110	10000	000

A = polymorphic for character states 0 and 1