



On the paraphyly of *Homaloptera* (Teleostei: Balitoridae) and description of a new genus of hillstream loaches from the Western Ghats of India

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Abstract

Homaloptera van Hasselt 1823 as treated historically exhibits substantial morphological diversity and is paraphyletic based on both morphological and molecular data. The morphological diversity and phylogenetic relationships of *Homaloptera*, *Homalopteroides* Fowler 1905, *Homalopterula* Fowler 1940, and *Balitoropsis* Smith 1945, are elucidated. *Pseudohomaloptera* Silas 1953 is removed from the synonymy of *Homaloptera*. Homalopteroidini is created for the monophyly of *Homalopteroides* and *Homalopterula*; it is the sister group to balitorini Swainson 1839. *Ghatsa* n. gen. is created for species previously assigned to *Homaloptera* from the Western Ghats of India, and a redescription of *Ghatsa montana* (Herre 1945) is provided.

Key words: *Ghatsa*, *Balitoropsis*, *Homalopterula*, *Pseudohomaloptera*, *Homalopteroides*, *Helgia*, *Chopraia*, Loaches, Southeast Asia

Introduction

The limited information on phylogenetic relationships of hillstream loaches has led to inconsistent and often transient recognition of genera. Relationships among species historically assigned to *Homaloptera* van Hasselt 1823 have been particularly problematic, as noted by Fang (1930), Hora (1932), Kottelat (1998), Tan & Ng (2005), Tan (2009), and Randall & Page (2012). Several names historically synonymized with *Homaloptera* (*Helgia* Vinciguerra 1890, *Homalopteroides* Fowler 1905, *Chopraia* Prashad & Mukerji 1929, *Homalopterula* Fowler 1940, *Balitoropsis* Smith 1945, and *Pseudohomaloptera* Silas 1953) have been recognized as genera or junior synonyms in recent years (Randall 2012; Kottelat 2012; Kottelat 2013). Some of these recent classifications are without supporting data or diagnoses, which only adds to the confusion of balitorid classification. The objectives of this study were to test the most recent classifications (Randall 2012; Kottelat 2012; Kottelat 2013) by analyzing genetic and morphological data (including type species when available) to identify clades and to diagnose well-supported clades as genera using morphological criteria.

Material and methods

Morphological. Measurements follow Hubbs & Lagler (2004) or Kottelat (1984) (see Randall & Page 2012 for measurements from each source), and counts follow Randall & Page (2014). The definition of a rostral cap follows Roberts (1982). A central furrow refers to an indentation on the ventral surface of the head at the branchiostegal membrane just anterior to the isthmus. The terms origin and insertion refer, respectively, to the anterior and posterior ends of fin bases for paired and unpaired fins. Total lateral-line scale count includes scales on the caudal fin. Counts are given as ranges where taxa are distinguished by the mode of that range (M). Lengths were measured to the nearest 0.1 mm using digital calipers and taken on the left side when possible. All measurements are given in millimeters (mm). Head length and measurements of the body are given as proportions of standard length (SL). Measurements of the head are presented as proportions of head length (HL).

Key to genera diagnosed in this study

- 1a. Origin of dorsal fin anterior to or above origin of pelvic fin; lateral- and medial-rostral barbels in close proximity to one another; large rostral cap; fleshy pad between lateral portions of lower lip; 8½ (M) branched dorsal-fin rays 2
- 1b. Origin of dorsal fin posterior to origin of pelvic fin; rostral barbels widely separated; small rostral cap; fleshy pad between lateral portions of lower lip absent; 7½ (M) branched dorsal-fin rays 4
- 2a. Reddish tints on fins in life; predorsal scales ≥ 20; medium-sized keeled scales (Fig. 4D); 7 (M) branched pelvic-fin rays *Homaloptera*
- 2b. Absence of reddish tints on fins in life; predorsal scales < 20; large keeled scales (Fig. 4A & B); 8 (M) branched pelvic-fin rays 3
- 3a. Anus closer to pelvic-fin base than to anal fin *Balitoropsis*
- 3b. Anus closer to anal fin than to pelvic-fin base *Pseudohomaloptera*
- 4a. Scales large (Fig. 4C); predorsal scales ≤ 25; total lateral-line scales ≤ 52; caudal fin forked; adipose keel absent *Homalopteroides*
- 4b. Scales small (Fig. 4E & F); predorsal scales > 26; total lateral-line scales > 53; caudal fin truncated or slightly emarginated; adipose keel present 5
- 5a. Thick barbels and lips; fleshy lobes between lateral portions of lower lip; endemic to Sumatra *Homalopterula*
- 5b. Thin barbels and lips; no fleshy lobes between lateral portions of lower lip; endemic to Western Ghats of India *Ghatsa*

Comparative material. *Balitora brucei*: India: RMNH 11924 (neotype). *Balitora* sp.: Thailand: NIFI 02927 (3). *Bhavana australis*: India: MNHN 50-79 (1); CAS 62052 (2). *Cryptотора thamicola*: Thailand: NIFI 3046 (1). *Hemimyzon yaotanensis*: China: KU 21445 (1). *Neohomaloptera johorensis*: Peninsular Malaysia: CAS-SU 39840 (holotype), 39841 (paratype). *Sewellia elongate*: Laos: UF 185476 (3), 185488 (3). *Travancoria jonesi*: India: MNHN 1950-0080 (1).

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References

- Alfred, E.R. (1969) The Malayan cyprinoid fishes of the family Homalopteridae. *Zoologische Mededelingen (Leiden)*, 43, 213–237.
- Arunachalam, M., Johnson, J.A. & Rema, Devi, K. (2002) *Homaloptera santhamparaiensis*, a new species of balitorid fish (Teleostei: Balitoridae) from a Western Ghats stream of Kerala, India. *Acta Zoologica Taiwanica*, 13, 31–37.
- Böhlke, J.E. (1953) A catalogue of the type specimens of Recent fishes in the Natural History Museum of Stanford University. *Stanford Ichthyological Bulletin*, 5, 1–168.
- Dahanukar, N., Philip, S., Krishnakumar, K., Ali, A. & Raghavan, R. (2013) The phylogenetic position of *Lepidopygopsis typus* (Teleostei: Cyprinidae), a monotypic freshwater fish endemic to the Western Ghats of India. *Zootaxa*, 3700 (1), 113–139. <http://dx.doi.org/10.11646/zootaxa.3700.1.4>
- Darriba, D., Taboada, G.L., Doallo, R. & Posada, D. (2012) jModelTest 2: more models, new heuristics and parallel computing. *Nature Methods*, 9, 1–772. <http://dx.doi.org/10.1038/nmeth.2109>
- Fang, P.-W. (1930) New and inadequately known homalopterid loaches of China, with a rearrangement and revision of the generic characters of *Gastromyzon*, *Sinogastromyzon* and their related genera. *Contributions from the Biological Laboratory of the Science Society of China*, 6, 25–43.
- Fowler, H.W. (1940) Zoological results of the George Vanderbilt Sumatran Expedition, 1936–1939. Part II.—The fishes.

Proceedings of the Academy of Natural Sciences of Philadelphia, 91, 369–398.

- Herre, A.W.C.T. (1945) Notes on fishes in the Zoological Museum of Stanford University:XX, New fishes from China and India, a new genus, and a new Indian record. *Journal of the Washington Academy of Sciences*, 35, 399–404.
- Hora, S.L. (1932) Classification, bionomics and evolution of homalopterid fishes. *Memoirs of the Indian Museum*, 12, 263–330.
- Hora, S.L. (1949) Satpura hypothesis of the distribution of the Malayan fauna and flora to Peninsular India. *Proceedings of the National Institutes of Science of India*, 15, 345–351.
- Hubbs, C.L. & Lagler, K.F. (2004) *Fishes of the Great Lakes region, revised edition*. University of Michigan Press, Ann Arbor, Michigan, 276 pp.
- Indra, T.J. & Rema, Devi, K. (1981) A new species of the genus *Homaloptera* from Silent Valley, Kerala, s. India. *Bulletin of the Zoological Survey of India*, 4, 67–70.
- Jordan, D.S. (1920) The genera of fishes, part IV, from 1881 to 1920, thirty-nine years, with the accepted type of each. A contribution to the stability of scientific nomenclature. *Leland Stanford Jr. University Publications*, 43, 411–576.
- Karanth, K.P. (2003) Evolution of disjunct distributions among wet-zone species of the Indian subcontinent: testing various hypotheses using a phylogenetic approach. *Current Science*, 85, 1276–1283.
- Kearse, M., Moir, R., Wilson, A., Stones-Havas, S., Cheung, M., Sturrock, S., Buxton, S., Cooper, A., Markowitz, S., Duran, C., Thierer, T., Ashton, B., Meintjes, P. & Drummond, A. (2012) Geneious Basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics*, 28, 1647–1649.
<http://dx.doi.org/10.1093/bioinformatics/bts199>
- Kottelat, M. (1984) Revision of the Indonesian and Malaysian loaches of the subfamily Noemacheilinae. *Japanese Journal of Ichthyology*, 31, 225–260.
- Kottelat, M. (1987) Nomenclatural status of the fish names created by J. C. van Hasselt (1823) and of some cobitoid genera. *Japanese Journal of Ichthyology*, 33, 368–375.
- Kottelat, M. (1998) *Homaloptera yuwonoi*, a new species of hillstream loach from Borneo, with a new generic name for *H. thamicola* (Teleostei: Balitoridae). *Ichthyological Exploration of Freshwaters*, 9, 267–272.
- Kottelat, M. (2012) Conspectus cobitidum: an inventory of the loaches of the world (Teleostei: Cypriniformes: Cobitoidei). *The Raffles Bulletin of Zoology*, Supplement 26, 1–199.
- Kottelat, M. (2013) The fishes of the inland waters of southeast Asia: a catalogue and core biography of the fishes known to occur in freshwaters, mangroves and estuaries. *The Raffles Bulletin of Zoology Supplement*, 27, 1–663.
- Kottelat, M. & Chu, X.-L. (1988) The genus *Homaloptera* (Osteichthyes, Cypriniformes, Homalopteridae) in Yunnan, China. *Cybium*, 12, 103–106.
- Kottelat, M., Whitten, A.J., Kartikasari, S.N. & Wirjoatmodjo, S. (1993) *Freshwater Fishes of Western Indonesia and Sulawesi*. Periplus Editions, Hong Kong, 259 pp.
- Liu, S., Mayden, R.L., Zhang, J., Yu, D., Tang, Q., Deng, X. & Liu, H. (2012) Phylogenetic relationships of the Cobitoidea (Teleostei: Cypriniformes) inferred from mitochondrial and nuclear genes with analyses of gene evolution. *Gene*, 508, 60–72.
<http://dx.doi.org/10.1016/j.gene.2012.07.040>
- Madhusoodana Kurup, B. & Radhakrishnan, K.V. (2011) Fishes of the genus *Homaloptera* van Hasselt, 1823 in Kerala, with description of a new species *Homaloptera silasi*. *Journal of the Bombay Natural History Society*, 107, 224–226.
- Mayden, R.L., Tang, K.L., Conway, K.W., Freyhof, J., Chamberlain, S., Haskins, M., Schneider, L., Sudkamp, M., Wood, R.M., Agnew, M., Bufalino, A., Sulaiman, Z., Miya, M., Saitoh, K. & He, S. (2007) Phylogenetic relationships of *Danio* within the order Cypriniformes: a framework for comparative and evolutionary studies of a model species. *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution*, 308 (B), 642–654.
<http://dx.doi.org/10.1002/jez.b.21175>
- Mayden, R.L., Tang, K.L., Wood, R.M., Chen, W.-J., Agnew, M.K., Conway, K.W., Yang, L., Li, J., Wang, X., Saitoh, K., Miya, M., He, S., Liu, H., Chen, Y. & Nishida, M. (2008) Inferring the tree of life of the order Cypriniformes, the earth's most diverse clade of freshwater fishes: implications of varied taxon and character sampling. *Journal of Systematic Evolution*, 46, 424–438.
- Menon, A.G.K. (1987) The fauna of India and the adjacent countries. Pisces. Vol. IV. Teleostei – Cobitoidea. Part 1. Homalopteridae. *Zoological Survey of India*, i–x, 1–259.
- Miller, M.A., Pfeiffer, W. & Schwartz, T. (2010) "Creating the CIPRES Science Gateway for inference of large phylogenetic trees" in *Proceedings of the Gateway Computing Environments Workshop (GCE)*, 14 Nov. 2010, New Orleans, LA, 8 pp.
- Ng, H.H., Tan, H.H. & Lim, K.K.P. (1999) The inland fishes of Pulau Tioman, Peninsular Malaysia. *Raffles Bulletin of Zoology*, Supplement 6, 169–187.
- Tan, H.H. & Ng, P.K.L. (2005) *Homaloptera parclitella*, a new species of torrent loach from the Malay Peninsula, with redescription of *H. orthogoniata* (Teleostei: Balitoridae). *Ichthyological Exploration of Freshwaters*, 16, 1–12.
- Ott, G. (2009) Redescription of *Homaloptera riplei* (Fowler, 1940) from Sumatra, Indonesia (Teleostei: Balitoridae). *Bulletin of Fish Biology*, 11, 73–86.
- Parenti, L.R., Hadiaty, R.K., Lumbantobing, D.L. & Herder, F. (2013) Two new ricefishes of the genus *Oryzias* (Atherinomorpha: Beloniformes: Adriachthyidae) augment the endemic freshwater fish fauna of southeastern Sulawesi, Indonesia. *Copeia*, 2013, 403–414.

<http://dx.doi.org/10.1643/CI-12-114>

- Pethiyagoda, R. & Kottelat, M. (1994) Three new species of fishes of the genera *Osteochilichthys* (Cyprinidae), *Travancoria* (Balitoridae) and *Horabagrus* (Bagridae) from the Chalakudy River, Kerala, India. *Journal of South Asian Natural History*, 1, 97–116.
- Prashad, B. & Mukerji, D.D. (1929) The fish of the Indawgyi Lake and the streams of the Myitkyina District (Upper Burma). *Records of the Indian Museum*, 31, 161–223.
- Quenouille, B., Bermingham, E. & Planes, S. (2004) Molecular systematics of the damselfishes (Teleostei: Pomacentridae): Bayesian phylogenetic analyses of mitochondrial and nuclear DNA sequences. *Mol. Phylogenet. Evol.*, 31, 66–88.
[http://dx.doi.org/10.1016/S1055-7903\(03\)00278-1](http://dx.doi.org/10.1016/S1055-7903(03)00278-1)
- Randall, Z.S. & Page, L.M. (2012) Resurrection of the genus *Homalopteroides* (Teleostei: Balitoridae) with a redescription of *H. modestus* (Vinciguerra 1890). *Zootaxa*, 3586, 329–346.
- Randall, Z.S. & Page, L.M. (2014) A New Species of *Homalopteroides* (Teleostei: Balitoridae) from Sarawak, Malaysian Borneo. *Copeia*, 1, 160–167.
<http://dx.doi.org/10.1643/CI-13-055>
- Roberts, T.R. (1982) The Bornean gastromyzontine fish genera *Gastromyzon* and *Glaniopsis* (Cypriniformes, Homalopteridae), with descriptions of new species. *Proceedings of the California Academy of Sciences*, 42, 497–524.
- Roberts, T.R. (1989) The freshwater fishes of western Borneo (Kalimantan Barat, Indonesia). *Memoirs of the California Academy of Sciences*, 14, 1–210.
- Roberts, T.R. (1993) The freshwater fishes of Java, as observed by Kuhl and van Hasselt in 1820–23. *Zoologische Verhandelingen*, 285, 1–94.
- Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D.L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M.A. & Huelsenbeck, J.P. (2012) MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology*, 61, 539–542.
<http://dx.doi.org/10.1093/sysbio/sys029>
- Sabaj Pérez, M.H. (2012) Standard symbolic codes for institutional resource collections in herpetology and ichthyology: an Online Reference. Version 3.0. American Society of Ichthyologists and Herpetologists, Washington, DC. Electronically available from: <http://www.asih.org/> (Accessed 28 Feb. 2015)
- Silas, E.G. (1953) Classification, zoogeography and evolution of the fishes of the cyprinoid families Homalopteridae and Gastromyzonidae. *Records of the Indian Museum*, 50, 173–263.
- Šlechtová, V., Bohlen, J. & Tan, H.H. (2007) Families of Cobitoidea (Teleostei: Cypriniformes) as revealed from nuclear genetic data and the position of the mysterious genera *Barbucca*, *Psilorhynchus*, *Serpenticobitis* and *Vaillantella*. *Molecular Phylogenetics and Evolution*, 44, 1358–1365.
<http://dx.doi.org/10.1016/j.ympev.2007.02.019>
- Smith, H.M. (1945) The fresh-water fishes of Siam, or Thailand. *Bulletin of the United States National Museum*, 188, 1–622.
- Stamatakis, A., Hoover, P. & Rougemont, J. (2008) A rapid bootstrap algorithm for the RAxML Web servers. *Systematic Biology*, 57, 758–771.
<http://dx.doi.org/10.1080/10635150802429642>
- Stamatakis, A. (2014) RAxML Version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics*, 30 (9), 1312–1313.
- Swainson, W. (1839) On the natural history and classification of fishes, amphibians, & reptiles, or monocardian animals. *Spottiswoode & Co.*, 2, 1–448. [London]
- Swofford, D.L. (2003) PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4. Sinauer Associates, Sunderland, Massachusetts.
- Tan, H.H. (2009) A new species of hill stream loach (Teleostei: Balitoridae) from central Kalimantan, with redescription of *Homaloptera tateregani* Popta and *Homaloptera stephensoni* Hora. *Zootaxa*, 2171, 48–64.
- Tan, H.H. & Ng, P.K.L. (2005) *Homaloptera parclitella*, a new species of torrent loach from the Malay Peninsula, with redescription of *H. orthogoniata* (Teleostei: Balitoridae). *Ichthyological Exploration of Freshwaters*, 16, 1–12.
- Tang, Q., Liu, S., Yu, D., Liu, H. & Danley, P. (2012) Mitochondrial capture and incomplete lineage sorting in the diversification of balitorine loaches (Cypriniformes, Balitoridae) revealed by mitochondrial and nuclear genes. *Zoologica Scripta*, 41, 233–247.
<http://dx.doi.org/10.1111/j.1463-6409.2011.00530.x>
- van Hasselt, J.C. (1823) Uittreksel uit een' brief van den Heer J. C. van Hasselt, aan den Heer C. J. Temminck, geschreven uit Tjecande, Residentie Bantam, den 29sten December 1822. *Algemeene Konst- en Letter-Bode voor het Jaar 1823*, 2, 130–133.