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A new family of neotropical freshwater fishes from deep fossorial Amazonian habitat, with a reappraisal of morphological characiform phylogeny (Teleostei: Ostariophysi)

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We present the taxonomic description of Tarumaniidae, a new family of South American freshwater fishes including a new genus (*Tarumania*) and species (*Tarumania walkerae*) from the Central Amazon. The new taxon displays an extraordinary set of unique characteristics, which sets it apart from all other known bony fishes, either in South America or elsewhere. Tarumaniidae has reverse-imbricated scales on the head, 244 or more scales along the midlateral lateral series, an 11-chambered swimbladder extending along most of the body, an anteriorly deflectable pelvic fin and a platybasic skull, among other unusual traits. Although the general habitus of *Tarumania* gives little hint of its phylogenetic placement, examination of internal anatomy is largely elucidative concerning the main features of its relationships. For example, *Tarumania* has a complete Weberian apparatus, comprising a set of characteristics supporting its position in Otophysi and Ostariophysi. Additional comparative evidence corroborates its placement in the order Characiformes, including some trademark characiform synapomorphies such as the presence of a hypertrophied lagenar capsule. We conducted a phylogenetic analysis on the basis of previously published morphological evidence for Characiformes, with the inclusion of *Tarumania* and additional relevant taxa and characters. Results support the position of *Tarumania* as a part of the superfamily Erythrinoidea and sister group to the neotropical Erythrinidae. Our increased taxonomic representation of Erythrinidae in the matrices firmly corroborates *Tarumania* as sister group to the whole of Erythrinidae and not to a subgroup of that family. *Tarumania walkerae* is a predator, which inhabits vast leaf-litter deposits in the Rio Negro drainage, and is found deeply buried in isolated pools during the dry season. It is the first characiform with an anguilliform body shape and fossorial habits. The unprecedented combination of phenotypic traits, behaviour and habitat adds substantially to the larger picture of freshwater fish diversity. Although its microhabitat is difficult to sample, the geographical range of *T. walkerae* includes areas close to major urban centres and which have been ichthyologically surveyed for many years. The fact that a relatively large and highly distinctive fish such as *Tarumania* remained undiscovered until now is testimony to the still-incomplete state of knowledge of biodiversity in Amazonian waters.

ADDITIONAL KEYWORDS: Amazon – Characiformes – Erythrinoidea – new genus – new species – phylogeny – systematics – taxonomy.

INTRODUCTION

Knowledge on the biodiversity of bony fishes is still incomplete, with hundreds of new species discovered and described every year, mostly from tropical regions. Nearly all of these novelties can be easily placed into known higher groups and represent variations on well-defined patterns. The finding of an entirely new living fish, which does not clearly fit into any of the previously recognized orders and families, is a rare event worldwide. Only six families of recent fishes have been newly found in the past 50 years (Scoloplacidae Bailey

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& Baskin, 1976; Hexatrygonidae Heemstra & Smith, 1980; Sundasalangidae Roberts, 1981; Megachasmidae Taylor *et al*., 1983; Lacantuniidae Rodiles-Hernandez *et al*., 2005 and Protanguillidae Johnson *et al*., 2011).

We here report on the discovery of an extraordinary new species of fish from the Amazon which, when first found, could not be clearly allied to any of the recognized families or orders of bony fishes, either in South America or elsewhere. The fish has been known for over 15 years from a single juvenile and poorly preserved specimen collected during a limnological survey. Despite a considerable degree of publicity in the ichthyological community and even some coverage in the popular press, it took several more years until actual populations were located and additional specimens collected for study. The additional material confirmed early suspicions that the fish was absolutely unique in a number of traits, some of which were without parallel among bony fishes. Aspects of its biology, although as yet known only superficially, are as remarkable as its anatomy. In this paper, we present a formal taxonomic description of the fish as a new species, genus and family, along with a general overview of the most important features of its external and internal anatomy. Given the relevance and distinctiveness of the new taxon, it is important that its formal taxonomic description is presented ahead of more detailed phylogenetic studies. Our data, however, indicate that the new taxon is a member of Otophysi and belongs to the order Characiformes. It represents the first truly fossorial and anguilliform-shaped member of that order. An analysis based on phenotypic data further shows that the new taxon is part of the characiform subgroup called Erythrinoidea, a clade traditionally including neotropical families Ctenoluciidae, Erythrinidae and Lebiasinidae, plus the African Hepsetidae. Within that group, it is further hypothesized as sister group to Erythrinidae, while not phylogenetically internested in that family. The discovery of the new taxon is eloquent demonstration that major elements of the freshwater fish fauna may elude capture for a long time, even in easily accessible areas that have been repeatedly sampled.

MATERIAL AND METHODS

Morphology

All measurements were taken with a digital caliper to the nearest 0.1 mm. Definition of measurements and their abbreviations are as follows: total length (TL) – from tip of snout until posterior end of caudal fin; standard length (SL) – from tip of snout to posterior margin of hypural plate, matching externally the anterior border of the half-moon-shaped dark band at caudal-fin base; head length (HL) – from tip of snout to posterior end of opercle, without associated membrane; head depth (HD) – depth of head at end of opercle; head width (HW) – measured at middle of opercles; body depth (BD) – depth of body at dorsal-fin origin; body width (BW) – measured at dorsal-fin origin; pre-dorsal distance (PD) – from tip of snout to origin of dorsal fin; post-dorsal distance (PoD) – from last dorsal-fin ray to base of hypural plate; caudal-peduncle length (CaPeLen) – from last anal fin ray to base of hypural plate; caudal-peduncle depth (CPDep) – deepest part of caudal peduncle; interorbital distance (IO) – shortest distance between the eyes; orbital diameter (OD) – horizontal diameter of eye; internarial distance (ID) – distance between anterior and posterior nares; anterior internarial width (AIW) – shortest distance between the anterior nares; posterior internarial width (PIW) – shortest distance between the posterior nares; snout length (SnL) – from tip of snout to anterior border of orbit; dorsal-fin length – length of longest dorsal-fin ray; pectoral-fin length – length of longest pectoral-fin ray; pelvic-fin length – length of longest pelvic-fin ray; anal fin length – length of longest anal-fin ray; caudal-fin length – length of longest caudal-fin ray; notochord length – length of visible portion of notochord at upper caudal-fin lobe.

Fin-ray counts included unbranched (in Roman) and branched (in Arabic) separated by a plus sign rays; scales on lateral line were counted mainly on the third dorsal series above pectoral-fin insertion; caudal-peduncle scales was the number of series of scales on the left side of the caudal peduncle at its midlength (circumpeduncular count was inapplicable due to the extremely compressed morphology of the caudal peduncle); total vertebral number included four vertebrae in the Weberian apparatus and the compound terminal centrum was counted as one.

Specimens intended for direct osteological examination were cleared and stained for bone and cartilage according to a modification of the method of Song & Parenti (1995). Other specimens were radiographed with digital x-rays.

Phylogenetic analysis

The phylogenetic position of the new taxon was assessed exclusively on the basis of morphology because at this time material available no longer yields DNA sequences usable for phylogenetic analysis by usual extraction methods. Additional field expeditions are planned to collect new material suitable for molecular studies. Alignment with major teleost subdivisions was on the basis of direct character evidence that leave no doubt as to the position of the new fish in Ostariophysi, Otophysi and Characiformes (discussed below). Determining its position within characiforms required more detailed analysis. There is wide-ranging disagreement about higher-level characiform relationships. Analyses to date have diverged profoundly

as to the main groupings within the order, and the incongruence is severe even after making allowances for different taxonomic representation in the various studies. Incongruence pervades multiple levels of the hypotheses and is not concentrated on particular portions of the tree. Also, rampant disagreements hold both within morphological (cf. Lucena, 1993; Buckup, 1998; Moreira, 2007; Mirande, 2010) and molecular data (cf. Ortí, 1997; Calcagnotto, Schaefer & DeSalle, 2005; Javonillo *et al.*, 2010; Oliveira *et al.*, 2011). Although clades based on morphology seem somewhat more stable, some molecular analyses have even failed to recover a monophyletic Characiformes, with the aggravating factor that the topologies of non-monophyly do not match in different studies (see review in Nakatani *et al.*, 2011). Among morphological analyses, those by Lucena (1993) and Moreira (2007) are unpublished, while the more recent published database of Mirande (2010) focused on the family Characidae, with comparatively limited representation of other families and therefore little bearing on higher-level characiform relationships. Our attempts at resolution of the phylogenetic position of *Tarumania* thus relied mainly on Buckup (1998) and Vari (1995). Buckup (1998) was the first published attempt at a quantitative analysis to include most characiform families, an undertaking motivated by a need to formulate a hypothesis on the relationships of Characidiinae. Its results relied on a parsimony analysis of 80 morphological characters and 27 terminals. Terminal taxa were representatives of most characiform families, with some represented by a single terminal and others by two or more. Some subgroups were not included, but taxonomic density and representation were enough to provide a first hypothesis on the broad phylogenetic structure of the Characiformes. Vari (1995) focussed on the neotropical family Ctenoluciidae but included a phylogenetic analysis comprising also Erythrinidae, Hepsetidae and Lebiasinidae, on the basis of 88 characters and 16 terminal taxa. That study includes denser concentration of terminals and characters relevant for resolving the relationships of Erythrinoidea, where preliminary evidence indicated that the new taxon reported herein might belong. Matrices from Buckup (1998) and Vari (1995) were combined into a single larger data set (Appendix 1 and Table 2), after critical consideration of individual characters, including a number of corrections and refinements, and then complemented by additional characters from other sources. Terminals were basically a summation of those in the two analyses, plus our new taxon, with Ctenoluciidae represented by *Boulengerella cuvieri* and *Ctenolucius hujeta* only, rather than all seven species in the family as in Vari (1995). The representative chosen for the genus *Copella* was *Copella arnoldi*, recently hypothesized as the sister group to all other species in the genus (Marinho, 2014). *Lebiasina panamensis* of Buckup (1998: 144) is today included in *Piabucina* (Weitzman & Weitzman, 2003) and therefore was used as representative of that genus. *Lebiasina bimaculata*, in turn, was used as representative of *Lebiasina* (a species also used in Vari, 1995).

Table 1. Selected measurements and counts of holotype (HT) and 11 paratypes (PT) of *Tarumania walkerae*

	HT	PT		
		Range	Mean	±SD
Standard length	81.6	44.9–151.2		
Percent of standard length				
Head length	15.3	11.6–18.2	15.4	2
Head depth	8.9	6.4–10.8	8.7	1.2
Body depth	9	7.1–10.3	8.9	1
Caudal-peduncle length	14.2	12.0–14.8	13.7	0.9
Caudal-peduncle depth	9.9	8.9–10.7	9.8	0.6
Pre-dorsal length	71.3	61.9–75.4	69.8	4.2
Dorsal-fin length	11.1	7.2–11.5	10.5	3.1
Anal-fin length	7.4	6.7–13.0	9.1	1.8
Percent of head length				
Head depth	58	49.7–63.1	56.7	3.7
Interorbital distance	33.7	24.1–35.4	30.1	3.7
Orbital diameter	4.6	4.1–7.2	5.8	1.2
Counts			Mode	
Dorsal-fin rays	i + 6	i–ii + 4–6	i + 6	
Pectoral-fin rays	i + 10	i–ii + 7–10	ii + 8	
Pelvic-fin rays	i + 5	i + 5, 6	6	
Anal-fin rays	iii + 9	i–iii + 9–11	ii + 10	
Principal caudal-fin rays	8/10	8/10	8/10	
Lateral-line scales	267	244–267	262	
Caudal-peduncle scales	25	23–28	25	

Characters in Vari (1995) relevant exclusively for relationships within Ctenoluciidae were excluded (nos. 5–8, 10, 11, 13–16, 29–31, 34, 35, 37, 39, 40, 48–50, 52, 53, 59, 60, 62, 63, 67, 73, 77–80 and 88). The combined matrix includes 33 taxa and 128 characters, summarized in Appendix 1 and Table 2, which also include any explanations necessary in addition to those in original sources. Analyses of both Vari (1995) and Buckup (1998) included an all-zero outgroup, summarizing polarity assumptions in a comparative context broader than the ingroup. This device was maintained

Table 2. Character matrix for characiform representatives, including *Tarumania*

Character / Taxon	5, 10, 15, 20, 25, 30, 35, 40, 45, 50, 55, 60, 65, 70, 75, 80, 85, 90, 95, 100, 105, 110, 115, 120, 125
Outgroup	0???000?00?0?0000?000?00000?0?1??00?0000000??00100?00??0000000?000????0?0??00?000000000000000000000000000000000000000000000000
Acestrorhynchus	1010111000000000000000100001010010110000000111011000000000000010110010000000001000000000000000000000000000010111000000000000000000
Alestes	101000001000100000100100010001011011000000011100100000000000001001011100200?000000000000000000000000000000000000000000000000000
Boulengerella	1?1011001010001111010000000101101011001000010101101000000?1?0101002111001100010001111111111111011111011 1?01100111 1?100111100000
Brycon	100000100000100000000100000001011011000000011100100000000000001011001?00200000000100000000000000000000000000000000000000000000000
Bryconops	10000011000010000000010000000101101000000000111001000000000000010110010002000000010000000000000000000000000000000000000000000000000
Characidium	01100010110??000001000000000001101001000000000?1101000000100001101000111020000000100000000000000000000000000000000000000000000000
Charax	100000010000100000000110010000101111000000000111101000000001000010111010100000000010000000000000000000000000000000000000000000000
Chilodus	111000000010100000000010100000000010?00000110101101010000000100100000111 0?00?21010000000000000000000000000000000000000000000000000
Citharinus	0111000000000100000100100010011100000000000000000010000000000001010010010111001000000000000000000000000000000000000000000000000000
Copella	1010000010?1011111001101000000100011100000010111111111000000010100000100000000000000100000000100000000000000000000100000000000000
Crenuchus	0010001011110100000101010000002101011000000001111111000001100011010?000111120000000000000000000000000000000000010000000001000000000
Ctenolucius	1?1011001010001111010000000101 1?1011001000010101101000000 11?0101002111001100010001111111111 2111011111111 1001110111101 1001110 0000
Cynopotamus	1000000100001000000001100100001011110000000001111010100000100001011101010000000000100000000000000000000000000000000000000000000000
Distichodus	0111000000000100000100010000000111100100000000000100000000000010010000101110010000000000000000000000000000000000000000000000000000
Erythrinus	1010000110100010010110000010020010100000000000111101000110000010100000200000001001000100001111011000001010021101001000011200111 11
Hemiodus	0110001000001000001001000100010010010100000111?1100000000000000110000110120000000000000000000000000000000000000000000000000000000
Hepsetus	1?00?100101000111100010000110100101100000000011110100000011?0101000111000100000000100101000000010100000001000000000 100000000000000
Hoplerythrinus	1010000110100010010110100010020011100000000000111101000110001010100000200000001001000100001111011000001010121101001000011200111 11
Hoplias	1010000010100010010110000010020011110000000000111101000110000010100000100000001001000100001111011000001010021101001000011211111 10
Lebiasina	1010000010000011110010010000010 01?110000000101111110000000000010100000102000001000000100001000100000000000001000000010110000000 00
Nannostomus	?010000010?101111100100100000001000011000000010110111111000000010100010102000000000000000000000001000000000000000000000100?0000000 00
Oligosarcus	1000001100001000000001000100001010010000 0?00111101000000000000010110010002000000010000000000000000000000001000000000000000000000 0
Parodon	01100000100010100110010001000110000?0100000101??1010000000000010000010002001000000000000000000000000000000000000000000000000000 00
Phenacogaster	100000110000100000000110010000101101000000001?111100000000100001011101010200000001000000000000000000000000000000000000000000000 00
Piabucina	1010000010000011010010010000010 01?11000000010111111000000000001010000010200000100000010001100010000000000000100000001000010000000
Prochilodus	111000000000100000000100000011 1?0000000111111110101000000000001000001100?00?010100000000000000000000000000000000000000000000000 00
Pyrrhulina	1010000010?1011111001101000000 1?1?11100000001011111111100001001010000010000000000000001000000001000000000000000000000100000000000 0
Schizodon	1110000000000100000000010000000100000000000011011110101000000000000101000001000000000000000000000000000000000000000000000000000 00
Steindachnerina	0110000000000100000100100000011100 0?0000111110100101000000000000100000 1100?00?0101000000000000000000000000000000000000000000000 00
Tarumania	1010000010?00?1??1011100000001011?110000 0?0000111011111?011?1101000000100000000000?????0000?0?1??000000001001100000?0?001001111000
Tetragonopterus	100000110000100000000110010000101101000000000101101000000000000010111010102000000001000000000000000000000000000000000000000000000 00
Xenocharax	01??000000000100?00100000000000111100100000000000100000?000001001000010111001000000000000000000000000000000000000000000000000000 0

See text for taxonomic composition and character 1 evidence. For 2 descriptions and explanations of each character. see Appendix 1.

in the present analysis as a device to locate the position of the root in accordance with inferences about direction of character-state transformations in original studies and the present one. Results were verified with and without the outgroup.

Coding of character states proposed in previously published phylogenetic analyses was undertaken in tandem with direct examination of conditions in specimens of taxa showing the various states previously identified in the respective publication. This procedure assured full understanding of the limits and boundaries of relevant variation previously identified by other authors. Any changes or corrections in previous interpretations or codings are discussed in Appendix 1.

Data matrices for phylogenetic analyses were assembled with the program Mesquite ver. 3.10. Parsimony analysis was implemented with the program TNT ver. 1.5 (Tree analysis using New Technology, Goloboff & Catalano, 2016; freely available through the Willi Hennig Society). Calculations used traditional searches, 10 random seeds, 1000 replicates, TBR algorithm and 100 trees saved per replication. The best score was hit 769 times. Bootstrap values were absolute frequencies obtained with standard sampling with replacement on 10 000 replicates. Data were also subject to a Bayesian estimate of relationships. The use of Bayesian inference for morphological characters is still controversial, with several performance-comparison studies biased by the model chosen to generate simulated data, unrealistically large simulated data sets and levels of homoplasy (O'Reilly *et al.*, 2016). Still, the use of some statistical inference method has value as a means to compare results beyond a strictly parsimony framework. Bayesian analyses were made with the program MrBayes 3.2 (Ronquist, 2012) using the Mkv model (adapted from Lewis, 2001), which implements ascertainment bias correction to account for the systematic omission of invariant and autapomorphic characters typical of morphological data matrices, as in the present case. Sample and print frequencies were 500, and diagnostic frequency was 5000. Average SD of split sequences was 0.009367, and posterior scale reduction factor was close to 1.0 for all parameters, both after 1 million generations.

Comparative material examined

The comparative material listed herein was utilized for estimating the generality of taxonomically relevant conditions in the new taxon and for the coding of character states in the phylogenetic analysis. Representatives of all genera and of the majority of species utilized as terminals in Buckup (1998) and Vari (1995) were directly examined. Taxa used as terminals in the phylogenetic analysis are marked with an asterisk (*). Because the alignment of the new taxon with Characiformes is quite well corroborated by direct evidence, the majority of the comparative material examined belongs to that order. Number of specimens refers to number examined, not total number in respective lot. Skeletal preparations are indicated by BC (cleared and stained for bone and cartilage), B (cleared and

stained for bone only) or SK (dry skeletal preparation). **Clupeiformes**: *Denticeps clupeoides*, MZUSP 84776, 2 BC. **Gonorynchiformes**: Chanidae: *Chanos chanos*, USNM 347536, 1 BC. Gonorynchidae: *Gonorynchus* sp., MZUSP 63663, 1 BC. **Cypriniformes**: Cyprinidae: *Campostoma anomalum*, MZUSP 45955, 1 BC. **Characiformes**: Acestrorhynchidae: *Acestrorhynchus pantaneiro*, MZUSP 83435, 1 BC; Alestidae: *Alestes longipinnis*, MZUSP 60302, 1 BC; *Brycinus imberi*, MZUSP 62623, 1 BC; Anostomidae: *Leporinus striatus*, MZUSP 117104, 3 BC; (*)*Schizodon fasciatus*, MZUSP 3579, 1 B; Characidae: *Brycon* sp., MZUSP 112111, 1 SK; (*)*Bryconops affinis*, MZUSP 39909, 1 BC; (*)*Charax* cf. *leticiae*, MZUSP 59511, 4 BC; *Carnegiella strigata*, MZUSP 742492, 2 B; *Cheirodon interruptus*, MZUSP 18894, 2 BC; *Cynopotamus kincaidi*, MZUSP 19987, 1 BC; *Gasteropelecus sternicla*, MZUSP 38238, 3 BC. *Oligosarcus argenteus*, MZUSP 37257, 1 BC. (*)*Oligosarcus paranensis*, MZUSP 87582, 1 B. *Salminus franciscanus*, MZUSP 79859, 1 BC; *Phenacogaster* sp., MZUSP 88851, 1 BC; *Stygichthys typhlops*, MZUSP 87678, 1 BC; (*)*Tetragonopterus argenteus*, MZUSP 52120, 1 BC; Chilodontidae: *Caenotropus labyrinthicus*, MZUSP 52352, 1 BC; (*)*Chilodus punctatus*, MZUSP 2169, 1 B. Citharinidae: *Citharinus latus*, MZUSP 84480, 2 BC; Crenuchidae: (*)*Characidium lauroi*, MZUSP 64536, 1 BC; *Characidium* sp., MZUSP 42872, 1 BC; (*)*Crenuchus spilurus*, MZUSP 20310, 1 BC; Ctenoluciidae: (*)*Boulengerella cuvieri*, MZUSP 24162, 1 BC; *Boulengerella lateristriga*, MZUSP 32133, 2 B; *Boulengerella maculata*, MZUSP 8207, 1 B; (*)*Ctenolucius hujeta*, MZUSP 47708, 1 B. Curimatidae: *Curimatella alburna*, MZUSP 42565, 1 BC; *Steindachnerina insculpta*, MZUSP 28825, 2 B; Cynodontidae: *Hydrolycus scomberoides*, MZUSP 26177, 1 BC; *Rhaphiodon vulpinus*, MZUSP 24077, 1 B; Distichodontidae: *Distichodus cf. engycephalus*, MZUSP 60305, 1 RD; (*)*Distichodus cf. maculatus*, MZUSP 22225, 1 RD; (*)*Xenocharax spilurus*, MZUSP 50358, 1 BC; MZUSP 50358, 1 BC; Erythrinidae: (*)*Erythrinus erythrinus*, MZUSP 34350, 2 BC; (*)*Hoplerythrinus unitaeniatus*, MZUSP 47695, 1 BC; *Hoplias curupira*, MZUSP 32366, 1 B; *Hoplias intermedius*, MZUSP 47723, 1 B; *Hoplias lacerdae*, MZUSP 47715, 1 B; (*)*Hoplias malabaricus*, MZUSP 28163, 1 B; MZUSP 47726, 1 B. Gasteropelecidae: *Thoracocharax stellatus*, MZUSP 40453, 1 BC; Hemiodontidae: *Hemiodus gracilis*, MZUSP 7048, 1 BC. Hepsetidae: (*)*Hepsetus odoe*, MZUSP 84469, 1 BC. Lebiasinidae: (*)*Copella arnoldi*, MPEG 8305, 2 BC; *Copella compta*, INPA 9162, 3 BC; *Copella eigenmanni*, MZUSP 81443, 3 BC; *Lebiasina astrigata*, MEPN 4418, 2 BC; (*)*Lebiasina bimaculata*, MZUSP 80085, 3 BC; *Lebiasina festae*, MNRJ 14542, 1 BC; (*)*Nannostomus unifasciatus*, MZUSP 117086, 2 B; (*)*Piabucina panamensis*, MZUSP 47705, 1 BC; (*)*Pyrrhulina australis*, MZUSP 59567, 2 BC. Parodontidae: *Parodon nasus*, MZUSP 19345, 1 BC. Prochilodontidae: *Prochilodus brevis*, MZUSP 37584, 1 B. Serrasalmidae: *Serrasalmus brandti*, MZUSP 57550, 1 BC. **Siluriformes**: Diplomystidae: *Diplomystes mesembrinus*, MZUSP 62595, 1 BC. Nematogenyidae: *Nematogenys inermis*, MZUSP 88522, 2 BC; MZUSP 107493, 1 BC. **Gymnotiformes**: Gymnotidae: *Gymnotus carapo*, MZUSP 22246, 1 BC. Rhamphichthyidae: *Rhamphichthys hahni*, MZUSP 59297, 1 BC.

TAXONOMIC ACCOUNTS

TARUMANIIDAE FAM. NOV.

Type genus: Tarumania gen. nov. described below.

Species included: Tarumania walkerae sp. nov. (Figs 1–3) described below.

Diagnosis: Distinguished from all other families of Osteichthyes by the presence of a swimbladder composed of 11 longitudinally arranged interconnected compartments extending along most of the body, immediately ventral to the vertebral column (Fig. 4; vs. swimbladder with one or two compartments). Also unique among teleosts (except Platytroctidae) by the presence of reverse-imbricated scales (i.e. with free margins directed anteriorly) covering most of the head (Fig. 5; vs. scales with normal imbrication throughout body and head). Further distinguished from all other Ostariophysi by having two rows of teeth on the maxilla (Fig. 6; vs. single row). Uniquely diagnosed from all other Characiformes by each of the following characters: the numerous vertebrae (69–70; vs. 68 or fewer), pleural ribs (41–44; vs. 32 or fewer) and scales (244–267 along midlateral row and 25 rows on caudal peduncle; vs. 162 or fewer); the spatulate caudal peduncle (Fig. 1; vs. oblong or round in cross-section); the lanceolate caudal fin (Fig. 1; vs. bifurcated. emarginate or round); and the platybasic skull, with the parasphenoid expanded and conjoined with the remainder of the neurocranium, forming the floor of the braincase (Fig. 7; vs. skull tropibasic). Other characters not necessarily unique to the taxon but still rare or unusual across a wide taxonomic array include: pelvic fins long and in the living fish deflectable 180 degrees anteriorly (Fig. 3; arrow); a flexible 'neck' that can bend the head at a right angle relative to the trunk; the infraorbital bone series reduced to single plate-like element lacking a sensory canal; the interopercle with a large semicircular notch along the dorsal margin (Fig. 8); the presence of a single upper pharyngeal toothplate (corresponding to the posterior element in other characiforms) (Fig. 9); a large hypural-like bone located between haemal spines of

Figure 1. ***Tarumania walkerae*** **gen. et sp. nov.**, holotype, INPA 33737.

Figure 2. ***Tarumania walkerae*** **gen. et sp. nov.**, holotype, INPA 33737. Dorsal (a) and ventral (b) views of head

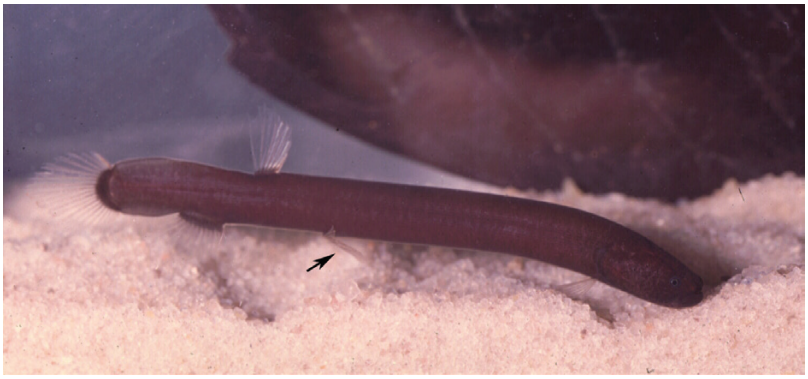

Figure 3. Live specimen, juvenile, of *Tarumania walkerae*, paratype, MZUSP 120543, shortly after collection. Arrow shows pelvic fins in anteriorly deflected position.

second and third ural centra (Fig. 10). Other characters variably shared with a number of other clades but still useful to diagnose the taxon include the laterosensory canal system mostly absent on the neurocranium and body but present in the nasal, dentary and preopercle; the teeth all unicuspidate, with two on each jaw hypertrophied and caniniform (Figs 5, 8); the eyes very small and located on the anterior portion of the head (Figs 1–3); the external notochord and larval pectoral fin persistent, the former in specimens up to 50-mm SL and the latter up to 30-mm SL; the cranial fontanels closed (Fig. 7); the central part of the frontals and parietals elevated and exposed on the surface of the head in large specimens, forming an ornamented platform (Fig. 7); the post-temporal fossae absent (Fig. 7); the intercalar absent (Fig. 7); the frontals expanded laterally, forming shelves along the anterior half of the skull (Fig. 7); the mesethmoid anteriorly expanded (Fig. 7); the quadrate-metapterygoid foramen absent or not differentiated (Fig. 8); the postcleithra and suprapreopercle absent; the supraoccipital spine deeply sunk in the anterior trunk musculature.

Remarks: As shown below, our investigation into the phylogenetic position of the new taxon concludes that it is the sister group to the family Erythrinidae. In purely nomenclatural terms, such positioning is compatible either with an expansion of the latter family or with the erection of a new family. Both choices result in exclusively monophyletic named taxa and therefore conform to the principles of phylogenetic classification. Given such flexibility, our choice for a new family rests on considerations additional to criteria of monophyly. First, the inclusion of *Tarumania* in Erythrinidae would result in profound modifications of the composition and range of morphological and biological variation seen in that family, which has been stable for more than a century. This would create information-retrieval problems with a vast amount of data in previous literature. Second, most of the traditionally recognized diagnostic characters in Erythrinidae are not present in *Tarumania*, rendering such familial allocation difficult to integrate with established taxonomic practice. Finally, the large phenotypic distance between *Tarumania* and species of Erythrinidae meets or exceeds that seen among characiform families in general, making a separate family for the genus a solution fitting the established classification of the order. Inclusion of *Tarumania* into an expanded Erythrinidae is clearly a less satisfactory solution and one that would incur more disturbance than necessary in the classification of characiforms. Recognition of a separate family more closely reflects the biological reality of the entities involved and better promotes nomenclatural stability.

TARUMANIA GEN. NOV.

Type species: Tarumania walkerae sp. nov.

Diagnosis: As for the family.

Etymology: From the river Tarumã-Mirim, tributary of the lower Rio Negro, first known locality of the new taxon. A noun in nominative singular. Gender feminine.

TARUMANIA WALKERAE SP. NOV.

[FIGS 1–3]

Holotype: INPA 33737, 81.6-mm SL, marginal pool of Igarapé Tarumã-Mirim (tributary to Rio Negro), Amazonas State, Manaus, Brazil (02.90965°S 60.22915°W), coll. L. Rapp Py-Daniel, J. Zuanon and M. de Pinna, 2 September 2006.

Paratypes (all from Brazil, State of Amazonas): INPA 16563, 1 ex, *c.* 23-mm SL, Igarapé do Camarão, Igarapé Tarumã-Mirim, col. Ilse Walker, 28 January 1999; INPA 25747, 3 specimens (1 c&s), 87.3- to 151.2-mm SL, Rio Negro at Parque Nacional das Anavilhanas, paraná do Lago do Prato, Novo Airão (~02.72°S 60.75°W), coll. J. Zuanon, 22 August 2001; INPA

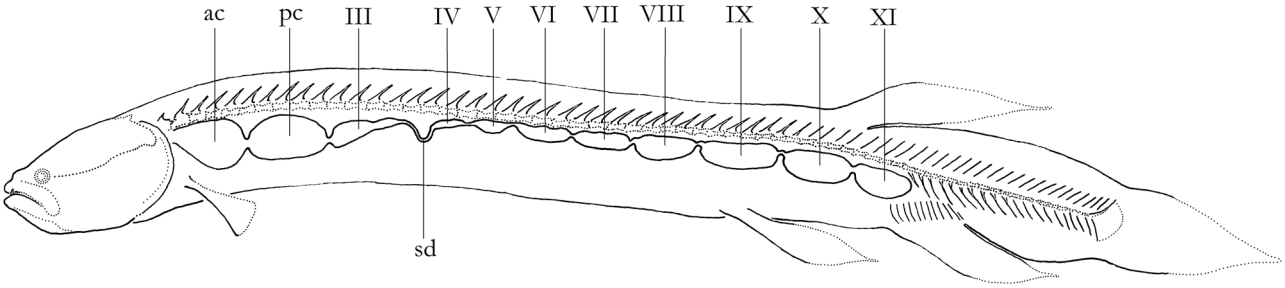

Figure 4. Schematic representation of swimbladder of *Tarumania walkerae*, based mostly on INPA 26241, 51.5-mm SL. ac, anterior swimbladder chamber; sd, sinusoid swimbladder duct. Roman numerals II–XI represent sequential swimbladder chambers.

Figure 5. *Tarumania walkerae*, paratype, INPA 21603, lateral view of head showing reverse-imbricated scales. Specimen cleaned of superficial mucus.

26241, 3 ex, 44.9- to 51.2-mm SL, same data as holotype, but at 2.90830°S 60.22873°W; INPA 26245, 11 ex, 38.4- to 61.5-mm SL (56.35–62.02 mm), collected with holotype; INPA 26246, 2 ex, 44.7- to 45.2-mm SL, collected with holotype; INPA 26248, 1 ex, 63.5-mm SL, same data as holotype, but 02.89637°S 60.22833°W; INPA 33733, 3 ex, 58.5- to 102.8-mm SL same locality as holotype, coll. J. Zuanon *et al*., 11 February 2002; 35585, 11 ex, 17.5- to 99.9-mm SL, Manaus, Igarapé Tarumã-Mirim, col. J. Zuanon, 3 February 2010; INPA 42299, 7 ex, 57.5- to 87.0-mm SL, Manaus, Igarapé Tarumã-Mirim, pool inside forest, col. J. Zuanon *et al*., 20 December 2011; INPA 42302, 6 ex, 26.7- to 37.6-mm SL, Manaus, Igarapé Tarumã-Mirim (02°54′35″S 60°13′45″W), col. J. Zuanon *et al*., 27 January 2010; INPA 52935, 1 ex, 22.9-mm SL, Parque Nacional das Anavilhanas, Igarapé Açu (tributary to Rio Negro), Novo Airão (−2.8220100000 −60.8708600000), coll. D. Bastos *et al*., 4 May 2016; INPA 53174, 1 ex, 73.0-mm SL, Manaus, pool near Rio Tarumã (−2.9016380000 −60.2292800000), col. D. Bastos *et al*., 12 October 2016; MZUSP 120543, 11 ex (1 c&s), 42.2- to 76.1-mm SL, collected with holotype; MZUSP 120544, 1 ex C&S, 98.4-mm SL, collected with holotype (preserved after 2 years in captivity); MZUSP 120545, 3 ex (1 c&s), 46.4- to 52.6-mm SL, same data as INPA 26241.

Etymology: The specific name honours eminent limnologist Ilse Walker [Instituto Nacional de Pesquisas da Amazônia, Manaus (INPA)], not only for her lifelong contribution to the knowledge of Amazonian ecology but also for having collected the first (and for some years, only) known specimen. The epithet is a noun in the genitive feminine case.

Diagnosis: As for the family.

Description: Body greatly elongate (BD ~9% of SL) and approximately oval in cross-section, ending in highly compressed, spatulate caudal peduncle deeper than rest of body. Proportional measurements provided in Table 1. Anal and urogenital openings located immediately anterior to origin of anal fin. Myotomes narrow and numerous. Head small (~15% of SL), its profile continuous with that of the body in live and recently preserved specimens (partly dehydrated specimens with well-defined groove dorsally between head and trunk). Dorsal trunk musculature produced anteriorly to cover posterior part of cranium. Snout blunt, ending anteriorly in large and slightly upturned mouth, with lower jaw longer than upper one. Posterior margin of upper jaw reaching to vertical through posterior margin of eye. Eye small, located on anterior fifth of head in lateral view. Anterior and posterior nares not juxtaposed, separated from each other by considerable distance, longer than eye diameter. Anterior naris positioned immediately dorsal to upper lip and produced on surface of the head as small mound. Branchiostegal membranes united to each other, free from isthmus, forming wide branchial opening. Maxilla with two rows of conical teeth, straight or slightly curved, for part of its dentate surface. Jaw dentition described in ‘Selected osteological features’. Infraorbital laterosensory canal absent. Skull roof without cranial fontanels. Part of frontal and parietal bones prominent and exposed on dorsal surface of the head in large specimens. Numerous neuromast lines over head and anterior part of the body. Body neuromasts mostly arranged as short vertical rows of five or six elements. Supraoccipital spine invisible externally. Dorsal fin

short-based and lanceolate, i or ii + 4–6, its origin at ~70% of SL. Pectoral fin short, i or ii + 7–10, its length approximately half of HL, attached on ventral fourth of thorax. First pectoral-fin ray approximately half as long as others, adpressed to second ray. Pelvic fin large, i + 5 or 6 (i.e. all rays branched), extending posteriorly to vertical through base of dorsal fin. Anal fin ii + 9 + i, its base more than twice as long as that of dorsal fin and its origin slightly anterior to vertical through tip of adducted dorsal fin. Caudal fin lanceolate or oblong and no differentiation between upper and lower lobes, with 8 + 10 principal rays plus four accessory rays in lower lobe. Caudal-fin attachment area more extensive ventrally than dorsally. Adipose fin absent. Squamation fine and extremely uniform in size, covering entire body in regular narrow rows, as well as most of the head (including entire perimeter of orbit), except lips and exposed top of skull. Scales on head similar in morphology to those on body, but with different imbrication, that is free margins not directed posteriorly. Imbrication pattern changes along limit between trunk musculature and head. Scales at interface with free margins directed laterally or ventrally. Such orientation maintained in scales over gill covers and posterior portion of cheeks. Free scale margins shifting to progressively more anterior orientation over anterior portion of cheeks, until completely reversed on dorsal part of head (Fig. 5). Scales in midlateral series of body 244–267, none perforated by lateral-line pores, 21 or 22 scale rows between origins of dorsal and pelvic fins. Modally 25 series of scales on caudal peduncle. Predorsal scales 168–193. Vertebrae 64 or 65 (43–45 precaudal and 21–22 caudal). Pleural ribs 41–44. Anterior branchial arch with 11 or 12 gill rakers, 3 or 4 upper and 8 lower (posterior lower one sometimes at limit).

Swimbladder subdivided into 11 compartments, positioned in longitudinal series immediately ventral to vertebral column (Fig. 4). Series arranged in anterior row of three and posterior row of eight, connected by sinuous duct. Individual compartments varying in shape and size. Size of compartments increasing towards anterior and posterior ends, with smallest ones approximately in middle of abdominal cavity. First compartment corresponding in position and shape to anterior chamber of swimbladder in other characiforms. All other compartments represent subdivisions of the posterior chamber. Anterior chamber largest of all in volume, with wide cordiform shape in ventral view. All subsequent chambers narrower than first one. Second chamber cylindrical, longer than first one. Third chamber conical, bottle shaped and markedly smaller in volume than its predecessors, with posterior atrium-like region tapering posteriorly into narrow sinusoid duct expanding slightly into fourth chamber, smallest of all. Constriction separates fourth from slightly larger fifth chamber. Sixth chamber larger still. All subsequent chambers similar in shape, although progressively larger posteriorly, except for last chamber, slightly smaller and more roundish than its predecessor, and abutting against posterior limit of abdominal cavity, dorsally to anterior anal-fin pterygiophores. All swimbladder chambers connected via short ducts, except third and fourth, connected via long sinusoid duct described above. Wall of anterior chamber noticeably thicker than that of subsequent chambers, otherwise uniformly thin and delicate. Ductus pneumaticus opening ventrally from second chamber, close to limit with first one. Swimbladder configuration described is constant in four specimens dissected.

Pigmentation: Overall ground colour dark brownish, slightly less dark ventrally. Subtle differences in the density of pigment forming irregular small blotches on the dorsum and flanks, partly merging into irregular vertical or slanted bars on anterior third of trunk, sometimes extending across dorsum. Barred pattern more intense on caudal peduncle, sometimes changing into irregular blotches. Areas of procurrent caudal-fin rays dorsally and ventrally on caudal peduncle darker than rest of peduncle in small specimens, but indistinguishable in larger individuals. Dorsal and ventral edges of caudal peduncle outlined as very dark thin line. Scales with dark exposed portions collectively forming pattern of fine longitudinal stripes covering entire body, visible under close examination. Dark slanted lines on lower half of flanks outlining limits of myomeres. Head as dark as body. Snout and area of opercle darker than rest of the head, with sides of cheeks slightly lighter. Dorsal and lateral sides of head with numerous short thin light lines corresponding to neuromast lines. Central portion of isthmus with same colour as abdomen, with adjacent portion of branchiostegal membrane distinctly darker than rest of ventral aspect of head. Caudal fin with very dark posteriorly convex semilunar mark across base, covering ~15% of length of longest (central) rays at its widest. Heavy dark pigment covering basal third of anal fin, more intense at its ventral limit, forming very dark stripe in some specimens. Rest of fin abruptly hyaline. Dorsal fin with dark field over its basal 10–20%, otherwise hyaline. Pectoral and pelvic fins with dark fields at bases, more pronounced on former, forming dark spot with elongate dark fields radiating alongside fin rays. Remainder of both fins hyaline. Colour of small individuals (up to 6.0-cm SL) very dark and uniform, nearly black. In life, colour pattern obviously mimics dead leaves in habitat, with hyaline portions of fins practically invisible.

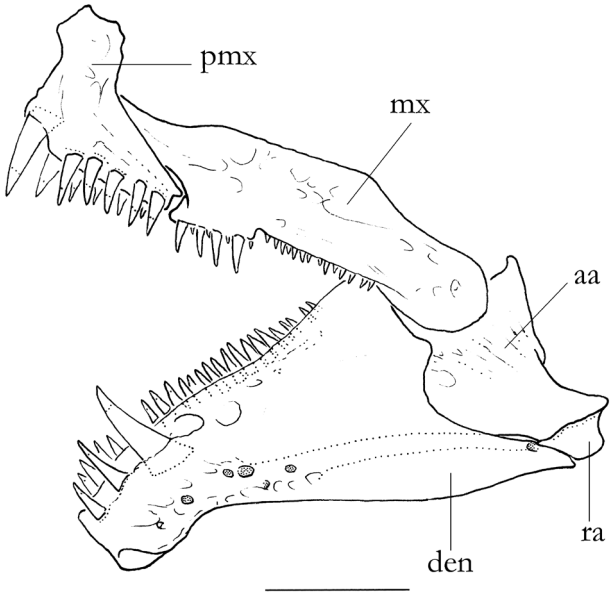

Figure 6. Jaws of *Tarumania walkerae*, paratype, INPA 25747, 151.2-mm SL, lateral view. aa, angulo-articular; den, dentary; mx, maxilla; pmx, premaxilla; ra, retroarticular.

Maximum size: 151.2-mm SL (a specimen from INPA 25747).

Geographical distribution: So far endemic to the Rio Negro basin, from the Rio Tarumã-Mirim, tributary to the Rio Negro near the city of Manaus, and from the Anavilhanas archipelago, on the main Rio Negro (Fig. 11). The two localities are ~60 km apart in straight line.

Selected osteological features

Jaws, dentition and orbital series (Figs 6, 8): The maxilla is curved anteriorly when abducted. Its proximal end is narrower than the rest of the bone, ending in a round blunt tip that articulates with the ventral surface of the ascending process of the premaxilla. The premaxilla has a broad flat ascending process, with a sparsely ornamented dorsal surface articulating with the dorsal surface of the mesethmoid. The lower jaw is deep and stout, with heavily ossified bones (Figs 6, 8). The dentary has an irregular tunnel along its ventrolateral margin for the passage of the corresponding portion of the latero-sensory canal. The lower jaw symphysis is formed by flattened interdigitations. The angulo-articular is large and lies mostly on the mesial surface of the dentary, although its posterior portion is also widely exposed laterally. There is a large hook-like process producing from the posterodorsal portion. The lower jaw has a double articulation, a dorsal one with the quadrate and a ventral one with the interopercle. The angulo-articular bears the socket for the dorsal articulation with the quadrate condyle. The ventral articulation is intermediated by the retroarticular.

The inner dentary tooth row extends along almost the entire free margin of the dentary, from the symphysis to nearly the top of the coronoid process. That row has 26 or 27 small conical teeth, evenly disposed, closely positioned and gradually increasing in size medially. The outer dentary row is short, with three or four widely spaced out teeth and restricted to the anterior portion of the bone. The two mesial teeth are as large as the largest teeth of the inner row. The third tooth is larger. The lateralmost (posterior) tooth is markedly hypertrophied and caniniform. There is a large pit on the surface of the bone posterior to the caniniform tooth, usually with a replacement tooth cap in it. The maxilla has two rows of teeth. The inner row has 18–21 small conical teeth evenly spaced and increasing in size only slightly anteriorly. That row extends along a well-defined bone crest. The outer row comprises four or five conical teeth located on a bone platform, at a distance from the inner row. The outer-row teeth are approximately twice as large as those of the inner row. The premaxilla also has two rows of teeth. The inner row is formed by nine or ten conical teeth that gradually increase in size medially until the large caniniform tooth, which is the medialmost element of the series. That caniniform tooth lies in a position aligned with the outer row, but is actually an element of the inner row, and forms an offset counterpart to the caniniform tooth of the lower jaw. The entire inner tooth row lies along a well-defined bony crest along the ventral surface of the premaxilla. The outer tooth row of the premaxilla is shorter than the inner one and is composed of four or five similar-sized teeth, larger and more widely spaced than those of the inner row. The rows of teeth of the maxilla and premaxilla are aligned, forming continuous biting surfaces. The dentition of the lower jaw is continuous across the symphysis, while the upper jaw has a well-defined toothless gap medially between the large caniniform teeth.

The orbital series is reduced to a roundish-triangular plate-like bone located ventral to the orbit. It lacks a sensory canal, is deeply sunk in the soft tissue of the anterior region of the cheeks and is not closely connected to any other skeletal element. It is not exposed on the surface of the integument and is not visible externally. Its position suggests a homology to the second infraorbital of other characiforms: ventrally to the orbit and adjacent to the fold of soft tissue that accommodates the distal portion of the maxilla when the mouth is closed. Also, it covers laterally most of the distal portion of the adducted maxilla but does not extend beyond its distal margin (as would be expected from the third infraorbital).

Neurocranium (Fig. 7): The entire skull is platybasic, with broad, flattened dorsal and ventral surfaces, broadly separating orbits. The mesethmoid is anteriorly expanded into a roughly ellipsoid cornual disc. Posteriorly, it expands markedly into a roughly losenge-shaped, dorsally ornamented platform, ending posteriorly into a pointed triangle between frontals. The frontals are broad and roughly rectangular (Fig. 7a), united at the midline via a wavy suture. The frontals extend laterally as wide shelves alongside most of the anterior portion of the neurocranium. The central portion of the frontal is ornamented over the exposed and elevated area of the skull roof (Fig. 7a). The parietals are large and heavily ossified, with central anterior portion elevated into a well-defined ornamented platform, posteriorly round, continuous with a corresponding part of the frontals anteriorly. The sphenotics are long and narrow in dorsal aspect, but deep in lateral view, and extend for most of the length of the parietals and the posterior portion of the frontals. Their lateral margin is flush with the rest of the neurocranium. A roughly triangular flange extends laterally from the posterior part of each sphenotic. The pterotic is irregularly shaped, with a small yet well-defined spine directed posterolaterally. The supraoccipital is large, although still smaller in area than each of the parietals. A median keel is present on the posterior portion of the supraoccipital, ending in a small pointed process that represents a reduced version of a supraoccipital spine. The epioccipitals are large roundish structures with elevated flanges directed posteriorly. The vomer is a short stout structure, anteriorly tripartite, with a long median blunt tip and two shorter claw-like lateral arms. The broadest part of the vomer bears large bilateral facets for the articulation with the palatines, and it ends posteriorly in a short median process wedged

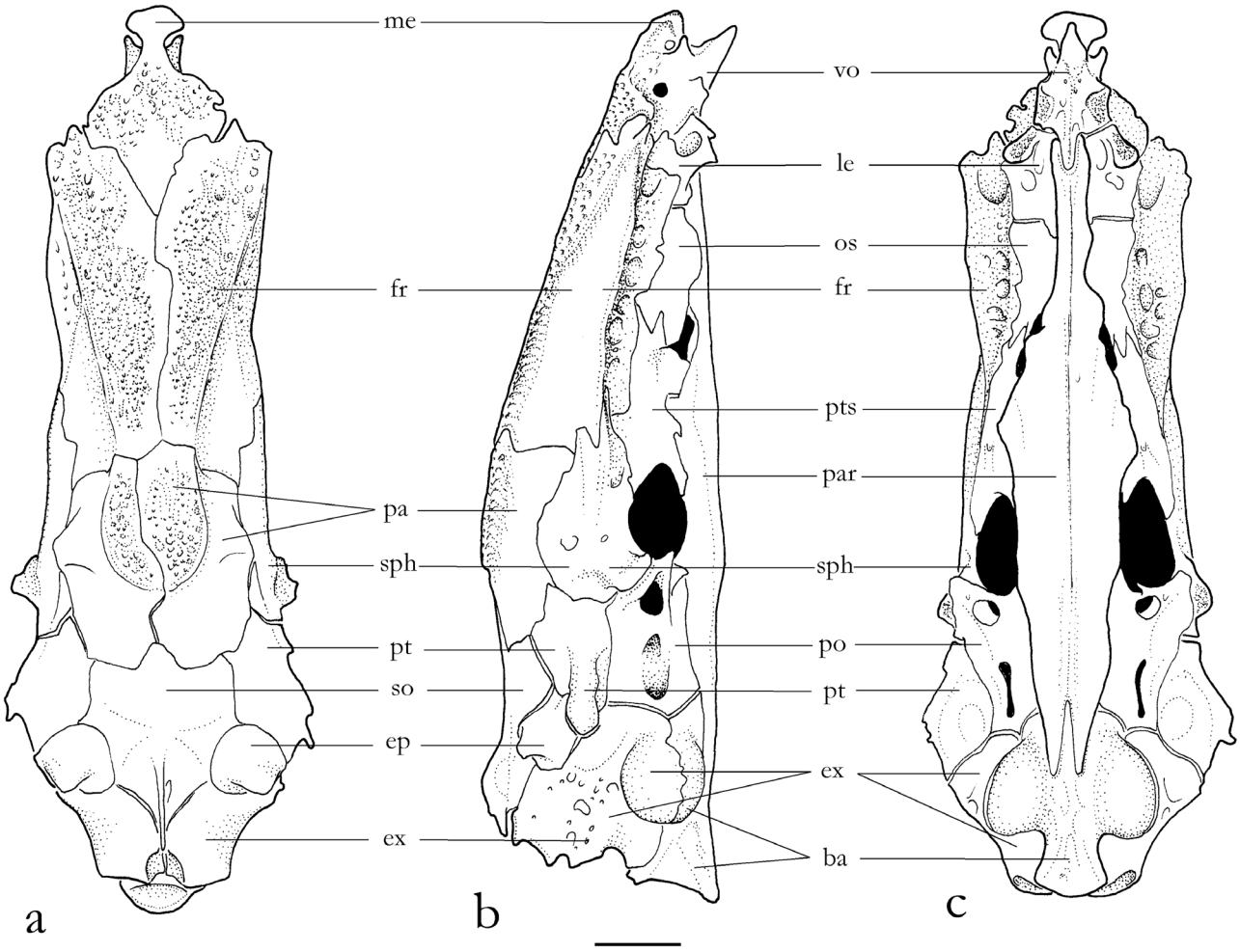

Figure 7. Cranium of *Tarumania walkerae*, paratype, INPA 25747, 151.2-mm SL. (a) Dorsal view; (b) ventral view; (c) lateral view. Scale bar = 1 mm. ba, basioccipital; ep, epioccipital; ex, exoccipital; fr, frontal; le, lateral ethmoid; me, mesethmoid; os, orbitosphenoid; pa, parietal; par, parasphenoid; po, prootic; pt, pterotic; pts, pterosphenoid; so, supraoccipital; sph, sphenotic; vo, vomer.

in the anterior portion of the parasphenoid. The lateral ethmoids are roughly rectangular, broadest slightly anterior to their midlength. A large facet occupies more than one third of the anterolateral margin of the lateral ethmoid, forming a single compound facet for the palatine with that anteriorly on the vomer. The orbitosphenoids contact synchondrally the lateral ethmoids anteriorly, and posteriorly form an interdigitating suture with the pterosphenoids (Fig. 7b). The ventral margins of the two bones near their area of contact have roundish recesses, which together form a large foramen at their border with the parasphenoid. The pterosphenoid is broadly concave posteriorly, forming the anterior margin of a large foramen. The posterior part of that foramen is formed by the prootic, which has a large anterolateral triangular flange trespassed by a round fenestra (Fig. 7b, c). Another foramen (the auditory foramen), narrow and elongate, extends longitudinally along the posterior part of the prootic. The basioccipital has tumescent bulla formed in part also by the ventral part of the exoccipital (Fig. 7b, c). The parasphenoid (Fig. 7b) is the longest single bone in the entire skeleton, tightly joined with the rest of the neurocranium and forming the floor of the braincase.

Suspensorium and opercular apparatus (Fig. 8): The opercle is a large roughly triangular plate, with mostly straight dorsal and anterior margins and a gently convex posteroventral margin. It articulates with the dorsal portion of the hyomandibula and has a short process extending dorsally, just lateral to that articulation. The very large interopercle has a broad bilobed posterior margin, which accommodates the ventral portion of the opercle. It extends anteriorly and articulates directly with the lower jaw, via the retroarticular. The interoperculo-mandibular ligament is therefore very short. The dorsal margin of the interopercle has a conspicuous and well-defined semicircular recess, hidden in lateral view by the overlapping preopercle, but clearly visible medially. The large subopercle extends to the posterior tip of the interopercle.

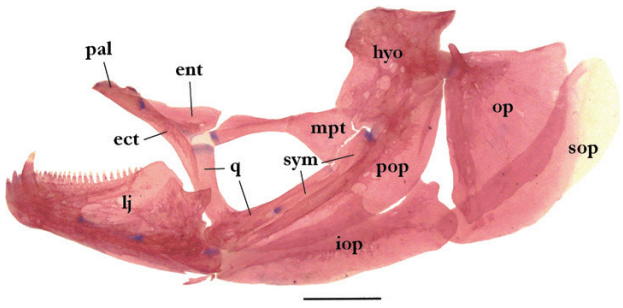

Figure 8. Suspensorium, opercular apparatus and lower jaw of *Tarumania walkerae*, paratype, MZUSP 120544, 98.4-mm SL, medial view. Scale bar = 2 mm. ect, ectopterygoid; ent, entopterygoid; hyo, hyomandibula; iop, interopercle; lj, lower jaw; mpt, metapterygoid; op, opercle; pal, palatine; pop, preopercle; q, quadrate; sop, subopercle; sym, symplectic.

The longest element in the suspensorium is the preopercle (Fig. 8), extending as a crescent-shaped lamina along most of the posteroventral surface of the complex, from the articulation of the opercle to nearly that of the lower jaw. The tips of the preopercle are narrow, and anteriorly, there is the ventral opening of the preopercular latero-sensory canal. The hyomandibula is an irregular-shaped bone. Its articular facet with the neurocranium is angulate and posterior so that the dorsal margin of the hyomandibula is prolonged as a short blunt process. The metapterygoid has a wide posterior portion, roughly triangular, extended anteriorly as a thin neck, slightly wider anteriorly, that articulates synchondrally simultaneously with the dorsal tip of the quadrate and the palatine cartilage (Fig. 8). There is no differentiated metapterygoid foramen. The quadrate is an L-shaped structure, with the horizontal arm slightly longer that the vertical one. The symplectic is a long rod-like bone, wider posteriorly, with its anterior half accommodated in a groove on the horizontal arm of the quadrate and not overlapping the hyomandibula posteriorly. A large fenestra is formed in the middle of the suspensorium, delimited by the metapterygoid dorsally and the quadrate anteroventrally. The palatine is a roughly rectangular bone tightly wedged between the pterygoids and articulating medially with the vomer and lateral ethmoid, via separate cartilage-lined facets.

Branchial and hyoid skeleton (Figs 9, 12): The first basibranchial is a small cap-like bone anteriorly articulating with the posterior end of the basihyal without intervening stained cartilage (Fig. 9a). The second basibranchial is more than twice as long as the first one, and it is flared at both extremities. The third basibranchial is slightly longer than the second one, and it is flared anteriorly only. The cartilage uniting the second and third basibranchials is continuous. The fourth and last basibranchial is entirely cartilaginous, roughly lozenge shaped (with a somewhat produced anterior end) and with a long posterior process formed as a prolongation of a ventral median keel. There are three ossified hypobranchials (Fig. 9a). The first and second ones are similar in shape, roughly pentagonal, with cartilages at their medial and posterior articular surfaces. The third hypobranchials are mostly cartilaginous and fused medially, forming a roughly v-shaped structure, their ossified portion is reduced to a cone-shaped cap anteriorly on each side. There is a medial tunnel in the cartilage, which accommodates the posterior tip of the third basibranchial ventrally and the anterior end of the fourth basibranchial dorsally.

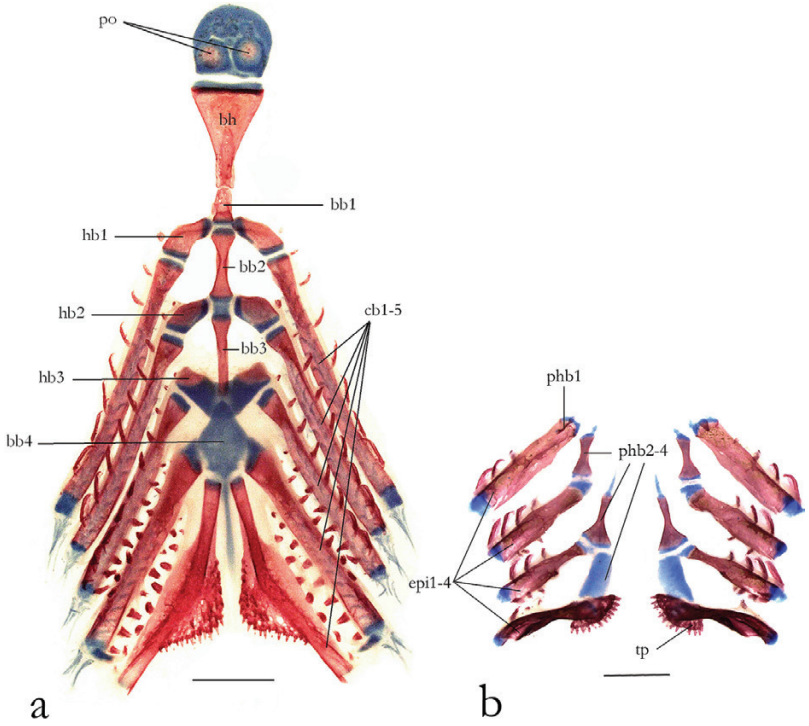

Figure 9. Branchial arches of *Tarumania walkerae*, paratypes, dorsal views; (a) MZUSP 120544, 98.4-mm SL; (b) INPA 25747, 151.2-mm SL. (a) Ventral arches; (b) dorsal arches (gill filaments removed). Scale bars = 1 mm. acb, accessory element of ceratobranchial 4; bb1–4, basibranchials 1–4; bh, basihyal; cb1–5, ceratobranchials 1–5; epi1–4, epibranchials 1–4; hb1–3, hypobranchials 1–3; phb1–4, pharyngobranchials 1–4; po, paired ossifications of basihyal cartilage; tp, upper pharyngeal toothplate.

There are five ceratobranchials (Fig. 9a). The middle portion of the fifth ceratobranchial is expanded and supports the lower pharyngeal toothplates. On the first branchial arch, there are three or four upper and eight lower ossified gill rakers (the last lower one is sometimes at the articulation between the ceratobranchial and the epibranchial), and 14 upper and 19 lower gill filaments (plus one or two at the articulation). The accessory element of ceratobranchial 4 (usually identified as the fifth epibranchial but actually not homologous with the epibranchial series; Carvalho, Bockmann & de Carvalho, 2013) is an elongated cartilage attached to the distal end of the fourth ceratobranchial. All four epibranchials are large and well ossified (Fig. 9b), with the anterior two elements roughly rectangular. The third epibranchial has a narrow neck-like median portion. The fourth epibranchial is vertically expanded, with a flange associated with an uncinate process. The first pharyngobranchial (Fig. 9b) is an extremely thin cylinder with slightly expanded extremities, oriented dorsoposteriorly and articulating proximally with the medial end of the first epibranchial. It is the smallest and most delicate element in the branchial skeleton and billaterally asymmetrical in some specimens (such as the one in Fig. 9b). The second pharyngobranchial is a trumpet-shaped bone spanning the distance between the medial ends of the first and second epibranchials. The third pharyngobranchial has a broader posterior end and a narrower anterior portion, prolonged anteriorly as a thin pointed cartilage. The third pharyngobranchial articulates posteriorly with both the third epibranchial and the roughly rectangular cartilaginous fourth pharyngobranchial. The single small lozenge-shaped upper pharyngeal toothplate (Fig. 9b) is supported entirely by the fourth epibranchial, although it overlaps slightly also with the posterior margin of the fourth pharyngobranchial. The longest axis of the toothplate is aligned with the fourth epibranchial and is almost perpendicular to the axis of the fourth pharyngobranchial. Such topological relationships with surrounding elements indicate that it corresponds to the posterior upper pharyngeal toothplate in other characiforms, itself homologous with the fifth toothplate in other teleosts (Nelson, 1969; Vari, 1979). The basihyal is a flat fan-like bone, markedly expanded anteriorly and with an anteriorly straight edge connected with a large cartilage plate (Fig. 9a). The morphology of this cartilage is variable. In two smaller specimens, it is a

single semicircular plate with no sign of subdivisions. In one of the larger specimens, it is clearly subdivided into two separate blocks basally, which irregularly fuse together distally. In that same specimen, round ossifications develop bilaterally on each of the basal blocks of the cartilage (Fig. 9a). In another large specimen (INPA 25747), the cartilage plate has a large medial fenestra, forming a median tunnel.

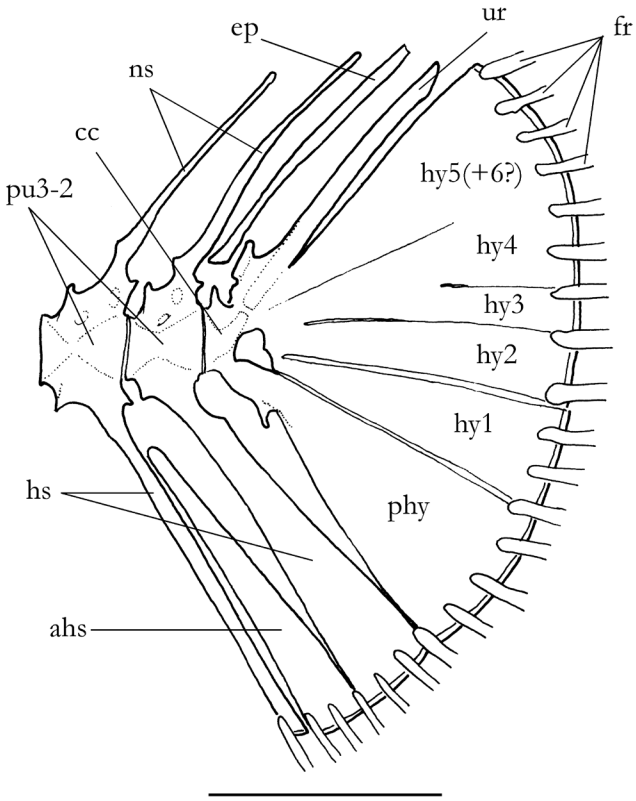

Figure 10. Caudal skeleton of *Tarumania walkerae*, paratype, MZUSP 120543, 61.6-mm SL, lateral view. Scale bar = 1 mm. ahs, accessory haemal spine; cc, compound caudal centrum; ep, epural; fr, fin rays; hs, haemal spine; $hy_{1-}n$, hypural 1–*n*; ns, neural spine; phy, parhypural; pu3–2, preural centra 3 and 2; ur, urostyle.

The anterior ceratohyal (Fig. 12) is roughly hourglass-shaped and articulates synchondrally (but also with a narrow bar of interdigitating suture on the lateral surface) with the conical posterior ceratohyal, which has a cartilage plug at its posterior tip. The interhyal is a simple cylindrical bone, slightly flared at its ventral end (Fig. 12). The hypohyals are tightly sutured, with the dorsal one in the shape of a short cone and the ventral one with anterior processes forming the articulation with the anterior portion of the urohyal. The urohyal is composed mostly of its vertical lamina, with a small bilobed anterior articular head. There are four branchiostegal rays, progressively longer posteriorly (Fig. 12).

Caudal skeleton (Fig. 10): Caudal skeleton very variable and poorly calcified in many specimens. Fusion among hypural elements may vary from complete to incipient. Description below applies to specimen illustrated in Figure 10, which is representative of the most common condition. The compound caudal centrum is a very short, continuous ventroposteriorly with the fused parhypural. The first hypural is strongly connected to the parhypural and, in some specimens, fused to it in part of their contact. It is truncated basally and does not contact the centrum. The second hypural is also basally attenuated by the diastema for the caudal artery, but the dorsal part of its base approaches the caudal centrum. The third hypural is the narrowest of the series and its fine base contacts the centrum. The dorsalmost hypural element is a single very large plate, which supports all the upper principal caudal-fin rays, probably formed by partial or total fusion of hypurals. Dorsally, the caudal skeleton includes a single long

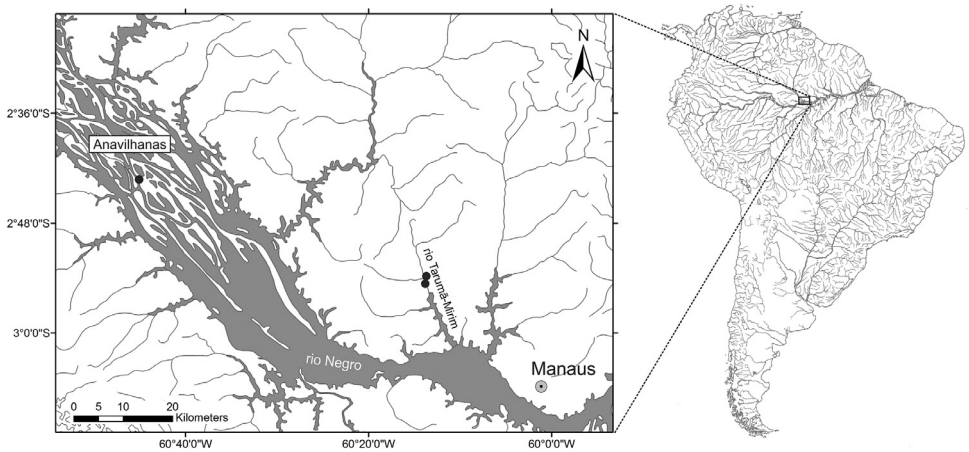

Figure 11. Geographical distribution of *Tarumania walkerae*.

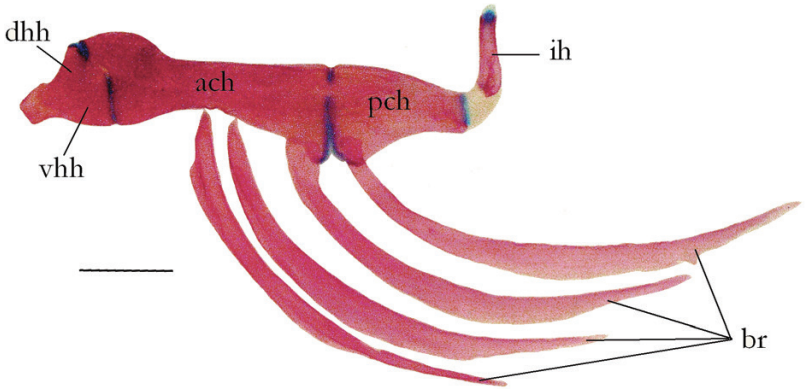

Figure 12. Hyoid arch of *Tarumania walkerae*, paratype, MZUSP 120544, 98.4-mm SL, left side, lateral view. Scale bar = 1 mm. ach, anterior ceratohyal; br, branchiostegal rays; dhh, dorsal hypohyal; ih, interhyal; pch, posterior ceratohyal; vhh, ventral hypohyal.

epural and a thin urostyle. Remnants of free uroneurals (not shown in Fig. 10) are represented by feeble irregular ossifications near the tip of the urostyle. A very large supranumerary non-sessile haemalspine-like element, or an accessory haemal spine, is present anteriorly to the parhypural. It is expanded distally in a hypural morphology and positioned close to the similar shaped haemal spine of the second preural centrum. This element does not contact any centrum and has a distal cartilage lining. It supports accessory caudal-fin rays in similar fashion to the hypural elements near it.

Weberian apparatus and supraneurals (Fig. 13): A complete Weberian apparatus is present. The first vertebral centrum is smaller than more posterior centra and has short, knob-like, transverse processes ventrolaterally. The second centrum has a large and stout transverse process extending laterally to the maximum width of the Weberian apparatus. The tripus is formed by a central body in the shape of an equilateral triangle, prolonged posteriorly as a long curved transformator process, extremely thin distally. The concha scaphium is large and fits into a recess on the posterior margin of the exoccipital. The spine of the scaphium is small but well differentiated, and its ventral articular process abuts against the dorsolateral surface of the first centrum. The intercalarium is a complex bone bearing a very long ascending process curved along the lateral surface of the neural arch of the third centrum. The ventral process, in turn, articulates with the dorsal surface of the base of the parapophysis of the second centrum. The claustrum is a thin arc resting on the dorsal margin of the scaphium, with its longest axis oriented almost horizontally in lateral view.

The os suspensorium extends ventrally from the parapophysis of the fourth centrum as a transverse strut in ventral view, approaching but not contacting its counterpart at the midline. Upon approaching the margin of centra, it bends abruptly anteriorly at a right angle, extending straight anteriorly along the ventral surface of the fourth and third centra. In large specimens, the anterior portion of the os suspensorium is firmly linked or ankylosed to the ventral surfaces of the third and fourth centra, but in smaller specimens, it is mostly free. The neural complex is shortened dorsoventrally, with its dorsal process deflected anteriorly to nearly the horizontal and slightly expanded anteriorly to contact the dorsal portion of the exoccipitals.

The large anterior supraneural (Fig. 13) has a robust anterodorsal arm abutting against the posterodorsal margin of the exoccipital. Its dorsal margin forms a straight line slanted towards the dorsal margin of the skull. There a series of post-Weberian supraneurals each positioned immediately anterior to the distal tip of neural spines and visible in preparations available in continuous sequence of 14 or 15 elements starting from the first rib-bearing centrum (fifth) until vertebra 19 or 20. In small specimens, the entire series is composed of small oblong cartilaginous bodies. Nine anterior elements are partly ossified in the largest specimen available (INPA 25747, 151.2-mm SL), while only the first is ossified in second largest c&s specimen (MZUSP 120544, 98.4-mm SL).

Pectoral girdle (Fig. 14): The post-temporal is a very long and thin bone, with a fine proximal tip nearly reaching its counterpart at the midline of the skull, near the centre of the dorsal surface of the supraoccipital. The posterior end of the post-temporal laterally overlaps and articulates with the dorsal portion of the similarly sized supracleithrum, which is a flat bone expanding markedly towards its ventral portion. The cleithrum is a long curved bone with a tridimentionally complex shape. The scapula and coracoid are

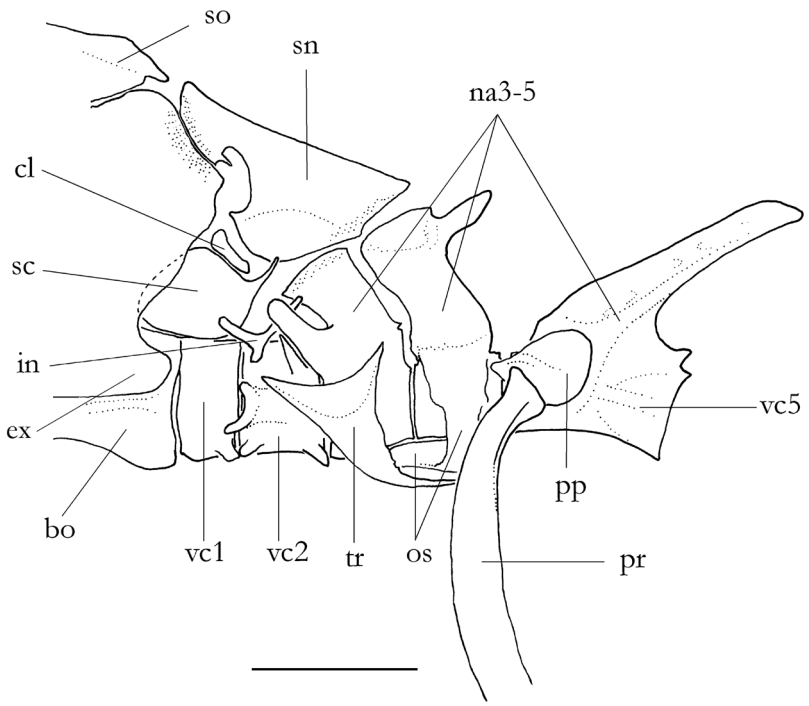

Figure 13. Weberian apparatus of *Tarumania walkerae*, paratype, MZUSP 26245. Scale bar = 1 mm. bo, basioccipital; cl, claustrum; ex, exoccipital; in, intercalarium; na3–5, neural arch; os, os suspensorium; pp, parapophysis; sc, scaphium; sn, supraneural; so, supraoccipital; tr, tripus; vc, vertebral centrum.

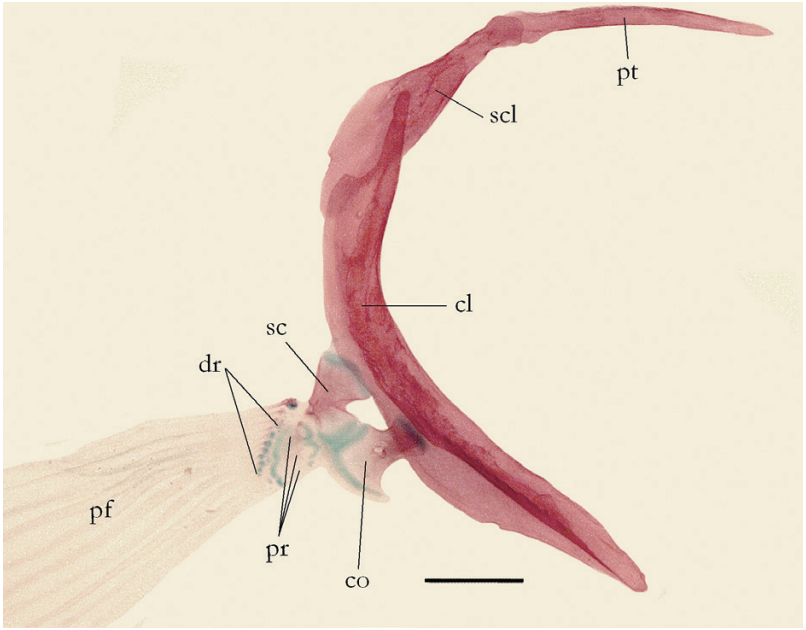

Figure 14. Pectoral girdle of *Tarumania walkerae*, paratype, MZUSP 120544, 98.4-mm SL, left side, anterolateral view. Scale bar = 1 mm. cl, cleithrum; co, coracoid; dr, distal radials; pf, pectoral fin; pr, proximal radials; pt, post-temporal; sc, scapula; scl, supracleithrum.

similarly shaped bones, attached directly onto the flat surface of the cleithrum, approximately at its middle portion. The dorsally located scapula is slightly smaller than the immediately ventral coracoid, which entirely lacks a ventral arm, and is extremely reduced compared to the condition in most other characiforms

(Fig. 14). There are three poorly ossified proximal pectoral radials (the first one is twice as broad as others and perhaps represents a fusion of two elements) and ten small round cartilaginous distal radials. The ventral portion of the pectoral girdle, formed exclusively by the cleithra, is united feebly at the midline, only by soft tissue. Extrascapulars, mesocoracoids and postcleithra are absent.

Pelvic-fin girdle: The basipterygia are flat elongate bones lying in parallel along the floor of the abdominal wall, along the vertical approximately through vertebrae 33–36. The two elements are closely linked at the midline and are positioned at a ventrally concave angle relative to each other, so that the cross-section of the conjoined structure is v-shaped. The ischiac process is entirely cartilaginous but only its small basal portion stains with alcian blue. Most of the ischiac process is actually composed of two long curved processes extending anteriorly within the thick body wall. Such an unusual morphology of the basipterygium is certainly related to the extreme movability of the pelvic fins, which can be deflected 180° anteriorly, independently of each other.

Ecological notes

All specimens known of *T. walkerae* were collected deeply buried into massive leaf-litter deposits in isolated pools in the riparian forest (Fig. 15). Some sites had no standing water, while other were up to 70-cm deep. The deeper levels of such deposits change into a dense mat of tangled roots. All such pools join the main river channel during the high-water season, which presumably allows specimens of *T. walkerae* to move and colonize suitable habitats. The species so far has only been found in temporary pools, during the low-water period. Its whereabouts during the flood season are yet unknown, in large measure due to difficulties in collecting during such time. The only other fish consistently co-occurring with *Tarumania* is an undescribed species of the catfish genus *Phreatobius*, although some other species, mostly represented as juveniles, have been sporadically caught in the same pools, such as *Microsternarchus bilineatus*, *Brachyhypopomus beebei*, *Apistogramma* sp., *Aequidens pallidus*, *Scoloplax dolicholophia*, *Microphilypnus amazonicus*, *Curimatopsis* sp., *Brycon* sp., *C. punctatus*, *Nannostomus eques* and *Copella* cf. *nattereri*. All such occurrences are probably just stray specimens that accidentally got trapped in the pools because of water-level changes in the hydric cycle. It is likely that *T. walkerae* follows the water–substrate interface along the hydric cycle, staying in more superficial layers when there is plenty of standing water and sinking into deep substrate as the water level recedes.

Tarumania is a carnivore, preying on invertebrates. Some captured specimens regurgitated whole small freshwater shrimps of the genus *Euryrhynchus*. Accessory aerial respiration was observed, in the form of air taken via the mouth and held temporarily in the branchial cavity, which, along with the gular region,

Figure 15. Habitat of *Tarumania walkerae*, isolated pools in floodplain area of the Rio Tarumã-Mirim, State of Amazonas, Brazil (02.90965°S 60.22915°W), photographed in 2006.

becomes noticeably inflated on such occasions. In the aquarium, aerial respiration is induced by low-water conditions. A freshly collected specimen maintained in captivity soon engaged in aerial respiration when confined in a shallow container. The fish gulped air at surface and kept it in the oral cavity for nearly 35 s before expelling an air bubble to take another gulp almost immediately; the same fish repeated such behaviour up to ten times in sequence.

A large live nematode (identified as *Goezia spinulosa*) was found in the branchial cavity of a specimen, which died after two years in an aquarium. Further dissection of that specimen further revealed the presence of acari both on the gills and in the intestines. Live specimens of *Tarumania* can move equally easily forwards and backwards, and its pelvic fins can move independently of each other and deflect 180 degrees anteriorly. The fish displays remarkable stability and manoeuvrability in the water column and can remain stationary in contorted positions in narrow spaces amidst irregular substrate, not contacting any surface. They also show 'neck' mobility, whereby the head moves independently of the trunk to a pronounced degree, a condition similar to that described for the Australian galaxioid *Lepidogalaxias salamandroides* (cf. Berra and Allen, 1989). *Tarumania* and *Lepidogalaxias* also share other convergent similarities, such as a spatulate caudal peduncle and similarly shaped and positioned fins, as well as fossorial habits for at least part of their life cycle.

Phylogenetic relationships of *Tarumania*

Due to its extreme morphological modifications, both in kind and degree, the phylogenetic relationships of *T. walkerae* are not immediately evident even in its broad aspects. The discussion below starts with its placement within major teleost subdivision. The first three inclusive clades, Otophysi, Characiphysi and Characiformes, are demonstrated by direct character evidence from comparative osteology. The corroboration for each of those components is listed in the respective section below, with numbering as in Fink & Fink (1981, 1996), reference to figures where the condition can be observed in *Tarumania* and comments when necessary. Beyond that, the position of *Tarumania* is not as easily resolved, in part because of uncertainties in the knowledge of relationships within Characiformes and therefore our proposals at that level rely on more detailed analysis.

Tarumania *as Otophysi*: The presence of a complete Weberian apparatus (Fig. 13) provides definite evidence for the inclusion of *Tarumania* in Otophysi, the major subgroup of Ostariophysi. Those and other otophysan characters identified by Fink & Fink (1981, 1996) can be directly confirmed in *Tarumania*: (30) Endochondral portion of the metapterygoid (Fig. 8) axe-shaped, double-headed (cypriniforms and characiforms) or single-headed (siluriforms). (59) Anterior one (Characiphysi) or two (Cypriniformes) supraneurals expanded ventrally to form a synchondral joint with the neural arches of the third and fourth vertebrae (Fig. 12; this character is a corrected version presented in Fink & Fink, 1996, of a previous version in Fink & Fink, 1981 that read 'second supraneural absent'). (66) First neural arch modified into scaphium (Fig. 13). (69) Second neural arch modified into intercalarium (Fig. 13). (78) Anterior vertebral centra foreshortened relative to more posterior centra (Fig. 13). As explained in Fink & Fink (1996), the situation of this character is rather more complex than originally described in Fink & Fink (1981), with various different patterns of reduction. In many cases, the foreshortening does not follow regularly the sequence of centra. Regardless of the details, the pattern seen in otophysans is not found in outgroup teleosts. *Tarumania* has obvious foreshortening typical of otophysans, with the first four centra greatly shortened relative to the fifth and more posterior centra. The first centrum is shortest, slightly over half the length of the second one, while the second through fourth are approximately the same length, equivalent in turn to approximately half the length of the fifth centrum. (81) Anteriormost two parapophyses fused to centra (Fig. 13). (85) Rib and parapophysis of third centrum modified into tripus (Fig. 13). (88) Rib and parapophysis of fourth centrum fused and with a median process (os suspensorium; Fig. 13). (102) Pelvic bone bifurcated anteriorly (in *Tarumania*, as in the majority of other characiforms, the bone is anteriorly single, probably representing a reversal typical of most members of the order). (110) Caudal skeleton with a compound terminal centrum formed by the first preural centrum, plus one or two ural centra, plus the anterior pair of uroneurals (Fig. 10). (114) Hypural 2 fused to compound caudal centrum (Fig. 10). The unusual caudal-skeleton morphology of *Tarumania* needs some interpretation with regard to this character. The parhypural is markedly expanded into a large plate, which seems to be the widest single element in the caudal skeleton. Hypural 1 is separated from the compound centrum by a hiatus typical of characiforms, but it is fused at the base with the ventral portion of hypural 2. The latter is fused to the compound centrum, but its ventral margin does not make a straight line to the centrum, but makes a dorsal curvature before joining the centrum. This seems to be a result of the dorsal expansion of the characiform hiatus mentioned above. The situation is further confused by the proximal fusion between hypural 2 and more dorsal elements. In any event, *Tarumania* shares the otophysan condition of a hypural 2 fused to the compound

centrum. (123) Olfactory tracts elongate, so that olfactory lobes are located near the nasal rosette and not adjacent to the telencephalon. This character was subsequently considered to be ambiguous evidence of otophysan monophyly by Fink & Fink (1996) because of more complex character-state conditions and distributions than previously reported. In any event, the olfactory tracts in *Tarumania* are short and adjacent to the telencephalon, a condition that bears little consequence as to the placement of the taxon at the level discussed. (126) Presence of sinus impar (posteromedian extension of the perilymph system of the ear). The presence of the sinus impar in *Tarumania* is inferred on the basis of the presence of the cavum sinus impar, a median opening ventral to the foramen magnum and which serves as passage to the sinus impar in all otophysans.

Tarumania *as Characiphysi*: Nearly all of the synapomorphies previously proposed for characiphysans (Fink & Fink, 1981, 1996) are present in *T. walkerae* as follows. (2) Vomer articulating anteriorly with the mesethmoid (Fig. 7b). (3) Mesethmoid with anterior processes articulating directly with the premaxillae. (39) Maxilla positioned posterolateral to the lateral process of the mesethmoid, not articulating directly with the mesethmoid. (61) Second supraneural absent (corrected according to Fink & Fink, 1996; Fig. 12). (62) Single expanded supraneural tilted anteriorly and articulating with the posterior margin of the cranium (Fig. 12). (68) Scaphium extending well anteriorly to border of first vertebral centrum (Fig. 13). (72) Anterior margin of third neural arch relatively close to posterior border of neurocranium (Fig. 13). (73) Dorsal part of third neural arch with distinct short anterior margin vertical in orientation. This character is not visible in *Tarumania*, as in most characiforms (Fink & Fink, 1981, 1996). (75) Spine of third neural arch extending anterodorsally from arch (not visible in *Tarumania*). (77) Fifth neural arch fused to its centrum (Fig. 13). (79) Pronounced foreshortening of the anterior three vertebrae, especially the first one (Fig. 13; cf. character 78 for Otophysi above). (82) Parapophysis absent on first centrum (Fig. 13). (86) Parapophysis portion of tripus attached to respective centrum by a thin, flexible bony lamella. (97) Baudelot's ligament attaching to skull at the region of the cranial condyle or lagenar capsule. The attachment in *Tarumania* is on the ventral surface of the basioccipital, near the occipital condyle. (112) Haemal spine of second preural centrum fused to its centrum, and parhypural and first hypural fused to the compound caudal centrum. This character has been originally stated differently in Fink & Fink (1981) but later corrected in Fink & Fink (1996). In *Tarumania*, as in other characiforms, hypural 1 is apomorphically separated from the centrum by a hiatus in adults (Fig. 10; see character 113 for Characiformes below), but the reported ontogenetic fusion (Fink & Fink, 1996) has not been observed in *T. walkerae* because growth series are yet unavailable.

Tarumania *as Characiformes*: As with preceeding clades, there is direct evidence of an affinity of *Tarumania* with the Characiformes. Most of the characters provided for the monophyly of the order by Fink & Fink (1981, 1996) are present in *T. walkerae*, once allowances are made for pronounced secondary modifications in certain cases. In some instances, the latter effect actually renders conditions unobservable in *Tarumania*, but in most cases, the apomorphic conditions are present beyond doubt: (9) Presence of a foramen on the ventral surface of the prootic through which the utricular otolith is visible (Fig. 7b). (12) Presence of a dorsomedial opening into the post-temporal fossa – this character cannot be observed in *T. walkerae* because the taxon lacks a post-temporal fossa. (15) Lagenar capsule large, globular, projecting well lateral to the cranial condyle (Fig. 7b, c). (43) Replacement teeth for outer-row dentary teeth and some premaxillary teeth forming in trenches or crypts in the bone. (44) Jaw teeth multicuspidate – jaw teeth in *T. walkerae* are all unicuspidate (Figs 6, 8), an exception within characiforms but one which is seen also in many other members of the order, most of them predatory. Occurrences of unicuspidate teeth in characiforms have been considered as reversals (Fink & Fink, 1981, 1996), an interpretation with which we concur. The condition in *Tarumania*, although out of the norm for characiforms in general, is actually in line with its presumed relationships with erythrinoids (see below), a group that includes many taxa with unicuspidate teeth. (71) Third neural arch with elongate anterodorsal process projecting laterally to the ascending process of the intercalarium (Fig. 13). (113) Hypural 1 separated from compound caudal centrum by a hiatus (Fig. 10).

Relationships of Tarumania *within Characiformes*

A hypothesis on the phylogenetic position of *Tarumania* required the compilation of a data matrix of morphological characters for Characiformes, as explained in the Material and Methods. A parsimony analysis of that data set (Appendix 1 and Table 2), including *Tarumania* and representatives of several characiform families (see Material and Methods), resulted in two trees (L = 312, CI = 0.474, RI = 0.743), which differ only in the relationships of the members of the basally positioned Distichodontidae and Citharinidae (the two families form a monophyletic group in one tree and not in the other, and in the latter, distichodontids form a trichotomy at the base, with citharinids as sister group

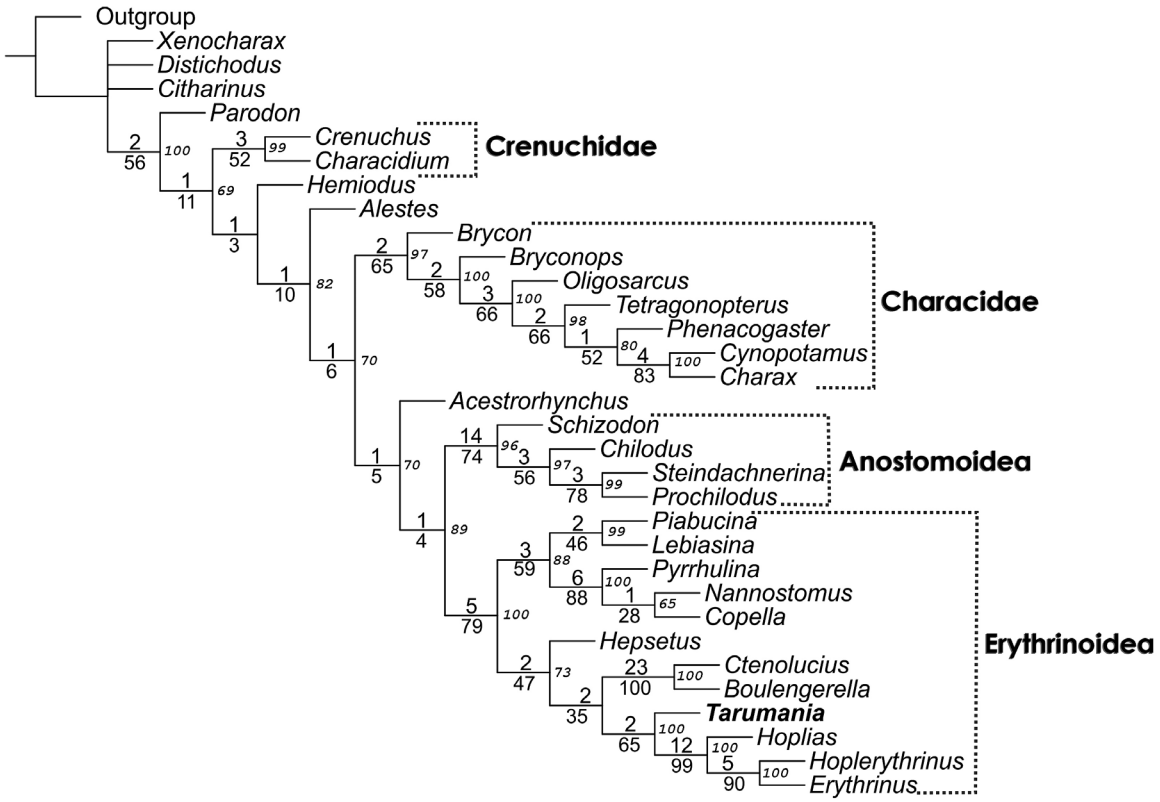

Figure 16. Phylogenetic position of *Tarumania* on a strict consensus tree of two most parsimonious trees ($L = 312$) calulated on a compiled data matrix for Characiformes (Appendix 1 and Table 2). Numbers above and below each nodes are absolute Bremer support and Bootstrap values, respectively. Posterior probabilities for clades identical to those in a Bayesian inference analysis are in smaller type italics at each split.

to all other characiforms). Apart from that, a strict consensus tree (Fig. 16) is almost totally resolved. Erythrinoids and all its constituent families are monophyletic, with Lebiasinidae, Hepsetidae, Ctenoluciidae, Tarumaniidae and Erythrinidae, in that order, forming a succession of sister groups. Clade support (Fig. 16) is extremely low in some portions of the tree, but strong for Erythrinoidea as a whole and for its individual families, as well as for Tarumaniidae plus Erythrinidae. In fact, bootstrap support for the latter clade is stronger than that for the family Lebiasinidae. Our analysis thus reveals a few well-supported facts about the phylogenetic position of *Tarumania* within characiforms: first, it is part of the superfamily Erythrinoidea. Second, it is the sister group to the family Erythrinidae. The complete matrices, with characters and taxa, as well as any needed explanations, are presented in Appendix 1 and Table 2. Results of a Bayesian analysis of the same data (parameters described in the Material and Methods) yielded results largely congruent with those of parsimony. Figure 16 provides posterior probability values for all clades that are identical in both analyses. The clade joining *Tarumania* plus Erythrinidae, as well as that for the latter family, both have maximum posterior probabilities.

Some of the evidence for our hypothesized position of *Tarumania* deserves especial mention. Its inclusion among the superfamily Erythrinoidea is supported by a few characters long recognized as diagnostic for the group, such as the continuous scale covering across the occiput and supraoccipital spine (Roberts, 1969; Vari, 1995). A clade containing *Tarumania* plus the Erythrinidae is supported by a set of particularly conspicuous features. In all erythrinids, the coracoids are markedly reduced in size, so that their anterior portion, or ventral limb, is much shorter than the adjacent cleithrum (Weitzman, 1964; Roberts, 1969). Such reduction is carried to an extreme unique degree in *Tarumania*, where the coracoid is nearly as small as the scapula and lacks any trace of the anterior limb.

A reduction of principal caudal-fin rays has been reported, surprisingly recently, as a distinguishing feature of erythrinids among characiforms (Netto-Ferreira, 2006). Part of such reduction is also seen in Tarumaniidae. In both taxa, there are nine fin rays in the upper lobe of the caudal fin. Apparently, this

is a unique condition in characiforms, with nearly all other members of the order having ten such rays. Incidentally, another reduction in the lower caudal-fin lobe, to eight rays, is a synapomorphy for erythrinids only. *Tarumania* has the plesiomorphic count of nine such rays in the lower lobe, a condition matching that in all other characiforms. The shape of the caudal fin itself provides still another easily observable qualitative evidence. Tarumaniidae and Erythrinidae are the only characiforms with a round caudal fin. In the former, the fin has its middle rays prolonged, resulting in a lanceolate shape. Still, this is obviously derived from a round condition or vice-versa, with no trace of lobation. All other characiforms have either bilobed or forked caudal fins, with upper and lower portions clearly discernible externally.

Other characteristics are less decisively conclusive than previous ones, but still provide circumstantial support for an erythrinid affinity of *Tarumania*. The lack of an adipose fin is one of those. Although that fin has been homoplastically lost in several unrelated groups of characiforms, elsewhere within erythrinoids it is missing only in some lebiasinids. The loss of the adipose fin is thus homologous in Erythrinidae and Tarumaniidae.

The morphology of the basihyal provides additional instances of conspicuous features previously thought to be unique to erythrinids yet also present, in modified form, in *Tarumania*. The unique double anterior cartilage of the basihyal previously reported as a synapomorphy for Erythrinidae (Vari, 1995) is indeed unique to that family. However, a less extreme version is partially present in Tarumaniidae. In the latter, the anterior basihyal cartilage has a tendency towards a bilateral subdivision in large specimens. The cartilage may be split basally, with the distal portion remaining continuous, so that the entire structure looks as if basally subdivided or trespassed by a tunnel. In one specimen of *T. walkerae*, there are two discoidal, bilaterally disposed, ossifications on the basihyal cartilage (Fig. 9). Although different from the fully subdivided condition of the basihyal cartilage in erythrinids, we consider the tendency towards bilateral subdivision of the basihyal cartilage in *Tarumania* as homologous to the situation in that family. All such modifications are present only in large specimens of *T. walkerae*, with smaller ones having a simple undivided basihyal cartilage as in the plesiomorphic condition. Our view of the variation in this character is reflected in the coding presented in Appendix 1 and Table 2, but since there are very few large specimens of *Tarumania* currently available, this interpretation needs corroboration by additional material.

While the list of tarumaniid-erythrinid synapomorphies is quite convincing, another set of traits are shared exclusively by the Erythrinidae, showing that the latter is monophyletic as currently constituted and that *Tarumania* is not internested in the family. Within erythrinids, the number of branchiostegal rays is consistently five (Weitzman, 1964; Roberts, 1969), while *Tarumania* and other characiforms normally have only four such rays. The increased branchiostegal ray count in erythrinids has been parsimoniously interpreted as a synapomorphy for the family (with a few homoplastic occurrences elsewhere in characiforms; Vari, 1995), a hypothesis here corroborated and one which is not shared with *Tarumania*. Likewise, the uniquely broadened and complex structure of the symplectic in erythrinids (Oyakawa, 1998) is not seen in Tarumaniidae, where the bone has the plesiomorphic morphology for the symplectic in characiforms, a relatively simple bent bony cylinder with cartilage caps at the extremities.

One of the peculiar features of the opercular apparatus of *Tarumania* is the large space left between the dorsal margin of the bone and the neurocranium. Normally, in characiforms, that entire area is covered by the opercle, which leaves no soft tissue exposed. A somewhat similar situation is also seen in Erythrinidae and Hepsetidae. But here situation is not obvious as in *Tarumania* because the space is shielded by the supraopercle, a peculiar ossification exclusive to those two taxa. Once the supraopercle is removed, a triangular area of soft tissue is quite evident along the straight anterior portion of the dorsal margin of the opercle, a situation similar to that in *Tarumania*. This characteristic, although enticing as preliminary evidence, was not included in our characiform matrix because it is necessary first to quantify it more precisely across the entire array of characiform variation.

We point out that our phylogenetic proposal is just a first effort. As pointed out above (see also Discussion below), characiform phylogenetics as inferred both by morphology and DNA sequences is in a state of uncertainty, despite several major efforts in recent years. While the synapomorphies uniting Tarumaniidae with Erythrinidae are qualitatively quite convincing, properly testing our proposed solution will require an extensive total-evidence reanalysis of the Characiformes.

DISCUSSION

Our hypothesis (Fig. 16) based on the combined characiform matrix (Appendix 1 and Table 2) is similar in general outlines to those of Vari (1995) and Buckup (1998). The monophyly of Erythrinoidea is strongly corroborated, and relationship of its constituent families is identical to those hypothesized by Vari (1995), with Erythrinidae (plus, in our case, Tarumaniidae) forming the sister group to Ctenoluciidae. Hepsetidae, in turn, forms the sister group to that clade.

A monophyletic Lebiasinidae is the sister group to all remaining erythrinoids. The sister group to Erythrinoidea is the Anostomoidea (a novel hypothesis), with *Acestrorhynchus* as sister to the two superfamilies. Parodontidae is the sister group to all other characiforms except distichodontids and citharinids. Crenuchidae, Hemiodontidae and Alestidae are successive sister groups to all other characiforms. Our hypothesis differs from that of Buckup in a number of relevant features. For example, in the latter, Erythrinoidea have Lebiasinidae, Erythrinidae and Hepsetidae + Ctenoluciidae in a trichotomy. Also, in Buckup's hypothesis, the sister group to erythrinoids is *Acestrorhynchus*. Molecular analyses of Characiformes have not corroborated a monophyletic Erythrinoidea as traditionally composed, although some subsections of it have been recovered. Ortí & Meyer (1997) had Erythrinidae plus Hepsetidae forming a clade, but Lebiasinidae and Ctenoluciidae were disjunct, with the former as sister group to Serrasalmidae and the latter forming a clade with the characid genus *Gnathocharax*. Erythrinoids in Calcagnotto *et al.* (2005), although not forming a monophyletic group, were more closely associated than in Ortí & Meyer (1997), with Hepsetidae as sister group to Ctenoluciidae plus Lebiasinidae (and Alestidae as their closest relative). The next node down their tree shows Erythrinidae plus Crenuchidae as the sister group to the other four families. So Erythinoidea in Calcagnotto *et al.* (2005) would be monophyletic with the addition of Alestidae and Crenuchidae. The most extensive molecular phylogeny for Characiformes (Oliveira *et al.*, 2011) concentrated on the family Characidae but had significant representation of other families in the order. However, resolution in the non-characid portion of the tree was poor. Erythrinoid families were mostly scattered in a large basal polytomy (Ctenoluciidae, Lebiasinidae, Erythrinidae), with Hepsetidae forming a clade with Alestidae (itself forming part of the same polytomy). Therefore, there is little resolution in the results of Oliveira *et al.* (2011) relevant for the elucidation of erythrinoid relationships. In any case, save for the Hepsetidae/Alestidae clade, the polytomies at the relevant part of the tree still allow for a possible monophyletic Erythrinoidea. On the other hand, Oliveira *et al*. is the first published molecular study to test, and corroborate, the monophyly of the Erythrinidae because it included representatives of all three genera in the family. This result is relevant as a baseline for future attempts at testing the position of *Tarumania* on the basis of molecular data.

Unquestionably, the most intriguing characteristics of *Tarumania* are its autapomorphies. Foremost among those is the multi-chambered swimbladder, with its 11 chambers and a duct between the third and fourth compartments. This trait is apparently unique among actinopterygians. The only vaguely similar condition seems to occur in the African schilbid catfishes belonging to the genus *Irvineia*, which have a long posterior caecum of the swimbladder extending posteriorly to the end of its long anal fin and subdivided by a regular series of constrictions (Trewavas, 1943, 1964). Beyond such similarities, the situation in the two taxa differs in a number of important aspects. In *Irvineia*, the swimbladder extends along the ventral part of the body, dextrally or sinistrally, alongside the base of the anal fin, while in *Tarumania*, it is positioned medially ventral to the vertebral column. Also, the intervening sinusoid duct in the series of chambers in *Tarumania* is lacking in *Irvineia*. Finally, the chambers in *Irvineia* are progressively smaller posteriorly, different from the situation in *Tarumania*, where the smallest chambers are more or less in the middle of the series. Long swimbladders are also seen in the gonorynchiforms *Phractolaemus*, *Kneria* and *Parakneria* (Thys van den Audenaerde, 1959, 1961; Fink & Fink, 1996), but here the organ is internally subdivided by trabeculations typical of air-breathing adaptations, rather than differentiated into well-defined chambers. Among the putatively close relatives of *Tarumania*, there are no instances of multi-chambered swimbladders, although the posterior swimbladder chamber is often markedly elongated and in some cases alveolate as an air-breathing especialization.

Preliminary evidence suggests that aerial breathing in *Tarumania* does not involve the swimbladder. Accessory air breathing exists in some members of putatively close relatives of *Tarumania*, such as *Hoplerythrinus* and *Erythrinus* in Erythrinidae and *Lebiasina* and *Piabucina* in Lebiasinidae (Graham, Kramer & Pineda, 1977, 1978; Kramer, 1978; Graham, 1997). In all such cases, there is swimbladder involvement, and in some of them (species of *Erythrinus* and some of *Lebiasina* and *Piabucina*), there is a specialized alveolate region that functions as a gas-exchange organ in the anterior portion of the posterior swimbladder chamber. No such modifications are present in any of the 11 swimbladder compartments of *Tarumania*, which are all non-alveolate. Additionally, observation of live individuals during air breathing suggests that most or all of the air gulped stays in the oral cavity. If any air goes into the swimbladder, it must be only a small amount. A mechanism of oesophageal pumping and exhalation as that described for *Hoplerythrinus* (Liem, 1989) is not apparent from our observations although, of course, it cannot be discarded without more detailed study. This suggests that the primary function of the peculiar swimbladder of *Tarumania* is hydrostatic. It is probably related to its quite impressive ability to remain neutrally buoyant and stationary in variably contorted positions (M. de Pinna, J. S. Zuanon, L. Rapp Py-Daniel, pers. observ. in aquarium

conditions). The functional significance of the extraordinary swimbladder modifications in *Tarumania* offers fascinating opportunities for future research.

In addition, most peculiar among tarumaniid autapomorphies is the presence of reverse-imbricated head scales, a condition not found in any other freshwater fish taxon and extremely rare otherwise. Elsewhere, the only other such case occurs in the marine meso- and bathypelagic alepocephaloid family Platytroctidae, where some species have fields of reverse-imbricated scales on the anterior part of the body and/or head (Matsui & Rosenblatt, 1984). At this time, we do not know of any clear functional role for reverse imbrication in the head scales of *Tarumania* or whether one should be expected.

Some unusual tarumaniid traits are shared in mosaic with a few other characiform taxa. The supranumerary autogenous haemal spine near the caudal skeleton has been seen also in *S. typhlops* (C. Moreira, pers. comm. and pers. observ.) and is reported to occur also in *Poptella* (M. Pastana, pers. comm.). *Stygichthys typhlops* also has a single infraorbital bone corresponding to the second element (Moreira *et al.*, 2010: 1819), as in *Tarumania* (but in contrast to the latter, *Stygichthys* retains a sensory canal). Interestingly, the second infraorbital is the earliest element of the infraorbital series to ossify in characiforms (Yamamoto *et al.*, 2003). Its isolated presence in some adult taxa suggests that it is also the last to disappear and that the presence of the unique second infraorbital is a result of developmental truncation. Finally, we note that the extreme reduction of the coracoids in *Tarumania* (Fig. 12) is also paralleled in *Stygichthys* (pers. observ. and Moreira, 2007, fig. 46), although the thin mesocoracoid in the latter is absent in the former. The existence of three quite unusual characteristics shared between *Tarumania* and *Stygichthys* raises obvious questions about a possible relationship between the two taxa. Their shared fossorial or subterranean habitats invite further suspicion. However, *Stygichthys* seems to be related to other characiform taxa, as per two phylogenetic analyses that included the taxon as a terminal and placed it deeply internested within the family Characidae (Moreira, 2007 for morphology and Oliveira *et al.*, 2011 for molecular data), at a vast phylogenetic distance from Erythrinoidea. If that is the case, similarities between *Stygichthys* and *Tarumania* are the result of convergence.

The large caniniform teeth in *Tarumania* have thin axial ridges at the base, more prominently on the lingual face of the dentary canines. A similar trait has been observed in a few other predatory teleosts including the osteoglossiform *Arapaima* (Meunier, Brito & Leal, 2013) and characiforms *Hoplias* (Meunier, De Mayrinck & Brito, 2015) and *Oligosarcus* (Thomasset, 1928). In all such cases, the ridges have been associated with the presence of plicidentine (Meunier, De Mayrinck & Brito, 2015), a trait considered rare among actinopterygians. If axial dental ridges are considered as a reliable anatomical proxy, then *Tarumania* will be one additional teleostean taxon with plicidentine. The phylogenetic significance of that needs more detailed study, but it is worth noting that axial ridges have also been seen in *Hoplerythrinus* but not in *Lebiasina* or *Piabucina* among the material examined.

On the other hand, there are some unusual characteristics that are intriguingly similar in *Tarumania* and lebiasinids. *Tarumania* has a long and persistent notochord terminus, until a size much larger than that observed for ostariophysans in general (a vestige is still seen in specimens as large as the holotype; Fig. 1). A similar condition has also been reported in some lebiasinids (Hoedeman, 1950; Nakatami *et al.*, 2001; Taguti *et al.*, 2009), where the wiggling tip of the notochord serves as an important means of propulsion in small young specimens (Hoedeman, 1950). Such peculiarities are not present in erythrinids (cf. Nakatami *et al.*, 2001). The lack of information on the distribution of this condition in most relevant taxa impedes its coding and inclusion in a data matrix at present. Still this shows that contradictory evidence exists, although the weight of evidence clearly favours an erythrinid affinity for Tarumaniidae.

Finally, we point out that despite relatively intense ichthyological exploration of the Rio Negro since the 19th century, by pioneers including none other than Alfred Russell Wallace (Toledo-Piza Ragazzo, 2002), a remarkably distinctive fish such as *Tarumania* remained entirely unknown until recently. Its discovery in proximity of a large urban centre, in localities, which have been repeatedly explored for fish diversity, further underscores the fact that major elements of tropical biodiversity remain unknown. We predict that *T. walkerae*, and perhaps related forms yet undiscovered, may be present throughout the Amazon basin and that further exploration of the fossorial habitat will yield other major discoveries.

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Appendix 1. List of characters and abbreviated descriptions used in combined matrix of characiform relationships, numbered sequentially. Characters 1–80 match the numbering in Buckup (1998). Numbers 81–123 are from Vari (1995), with original numbering in parentheses. Characters 124–128 are from other sources, as referenced. Characters from Vari (1995) relevant exclusively for relationships within Ctenoluciidae (nos. 5–8, 10, 11, 13–16, 29–31, 34, 35, 37, 39, 40, 48–50, 52, 53, 59, 60, 62, 63, 67, 73, 77–80 and 88) were not included. Additional omitted characters (due to redundancy or other reasons as explained) are listed at the end. All multistate characters are additive. Character 40 represents a set of 12 characters with identical state distributions and is accordingly assigned a weight of 12 (see explanation below).

1. Mesethmoid. 0, trifurcate anteriorly; 1, articular processes greatly reduced or absent.

2. Lateral ethmoid wing. 0, well developed; 1, greatly reduced.

3. Ventral diverging lamellae of mesethmoid. 0, well developed 1, reduced or absent.

4. Region of mesethmoid-vomer joint. 0, medial portion of joint flat or traversed by midsagittal osseous or cartilaginous crest; 1, connected by pair of osseous processes separated by deep medial fossa.

5. Mesethmoid-vomer joint. 0, simple synchondral joint across midline of oral cavity; 1, formed by osseous interdigitations along midline of oral cavity. Fusion between vomer and mesethmoid in *Hepsetus* (cf. Buckup, 1998: 128) renders the character unobservable in that taxon, which is therefore coded (?) herein.

6. Attachment of ectopterygoid to vomer and mesethmoid. 0, attached to ventrolateral border of vomer by sheat of connective tissue; 1, ectopterygoid inserted n ventral surface of area near vomer-mesethmoid articulation by ligment attached to socket or bony facet.

7. Rhinosphenoid bone. 0, absent; 1, present.

8. Frontal bone. 0, area lateral to anterior portion of supraorbital canal not conspicuously expanded; 1, expanded platform lateral to supraorbital canal, over lateral ethmoid. The states as described are difficult to delimit objectively, and this character was inactivated by scoring it as an invariant state to all terminals.

9. Frontal bone. 0, midsagittal fontanel present anterior to epiphyseal bar; 1, midsagittal fontanel present anterior to epiphyseal bar.

10. Paired frontal foramina. 0, frontal without lateral foramen associated with modified fibres of ophthalmic nerve; 1, frontal with lateral foramina posterodorsal to orbit, immediately medial to supraorbital canal and anterior to epiphyseal branch of that canal, associated with fibres of ophthalmic nerve that re-enter braincase after short path along posterior wall of orbit.

11. Anastomosis between supraorbital and pterotic sensory canals. 0, supraorbital canal continuous with pterotic canal; 1, two canals not connected to each other. Coded as '?' in *Tarumania* because relevant canals are absent.

12. Frontal-pterotic joint. 0, frontal and pterotic in direct contact dorsally; 1, pterotic excluded from contact with frontal by interposition of sphenotic. Coded as '0' in *Tarumania* despite the lack of contact between frontal and pterotic in that taxon because the condition is not homologous, being caused by interposition of the parietal, not the sphenotic.

13. Dorsolateral margin of skull. 0, mostly straight, with origin of *dilatator operculi* muscle located under lateral edge of frontal; 1, dorsolateral margin of skull vaulted by presence of dilator groove.

14. Pterotic bone. 0, with latero-sensory canal; 1, without latero-sensory canal. Coded as '?' in *Tarumania* because latero-sensory canals are absent from entire braincase (and also reduced in rest of body).

15. Parietal fontanel. 0, present in adults; 1, closed in adults.

16. Parietal branch of supraorbital canal. 0, branch from supraorbital canal extending from postorbital area of frontal into parietal; 1, parietal branch absent or not reaching parietal. Coded as '?' in *Tarumania* because latero-sensory canals are absent from entire braincase (and also reduced in rest of body).

17. Supratemporal latero-sensory canal. 0, extending from extrascapular to parietal; 1, entirely absent. Coded as '?' in *Tarumania* because latero-sensory canals are absent from entire braincase (and also reduced in rest of body).

18. Squamation on supraoccipital spine. 0, spine not covered with scales; 1, spine completely covered with scales.

19. Ventromedial opening of post-temporal fossa. 0, absent; 1, foramen leading into post-temporal fossa present near joint between exoccipital and epioccipital.

20. Antorbital bone. 0, present; 1, absent.

21. Supraorbital bone. 0, present; 1, absent.

22. Ectopterygoid teeth. 0, present; 1, absent.

23. Mesopterygoid teeth. 0, absent; 1, present.

24. Fenestra between quadrate and metapterygoid. 0, well developed, usually circular or oval in shape; 1, absent or greatly reduced.

25. Anterohyal bone. 0, hyoid artery entirely enclosed in dorsal through or tube in anterohyal; 1, hyoid artery emerging from anterohyal canal immediately anterior to posterodorsal corner of anterohyal.

26. Preopercular canal. 0, not crossing over anterodorsal corner of opercle; 1, extending over anterodorsal corner of opercle, traversing base of opercular spine.

27. Suprapreopercular bone. 0, absent or represented by simple tube surrounding preopercular canal; 1, plate like, very large. Mispelled 'supraopercular' in Buckup (1998: 128).

28. Cranial articulation of hyomandibula. 0, articular surface short, with posterior end of articulation aligned with posterior spine-like process of pterotic; 1, articular surface extensive, its posterior edge extending to posterolateral corner of correspondingly elongate pterotic.

29. Opercular bone. 0, no distinctive flange on lateral surface; 1, distinctive flange extending posteroventrally from anterior corner of opercle.

30. Number of branchiostegal rays. 0, three rays; 1, four rays; 2, five rays.

31. Premaxilla. 0, with conspicuous upper ramus; 1, undivided or weakly divided into upper and lower rami.

32. Premaxillary dentition. 0, single functional row of teeth; 1, two or more rows of functional teeth.

33. Reduction of maxilla. 0, maxilla very small, usually not extending beyond first infraorbital bone; 1, maxilla relatively large, reaching at least second infraorbital bone.

34. Enlargement of maxilla. 0, maxilla not reaching posteriorly to third infraorbital; 1, maxilla reaching to third infraorbital. Coded as '?' in *Tarumania* because third infraorbital is missing in that taxon.

35. Symphysis of lower jaw. 0, simple articular surface; 1, interdigitating hinge-like joint.

36. Inner dentary tooth row. 0, absent; 1, present.

37. Dentary. 0, ventral surface of dentary posterior to symphysis without conspicuous notch; 1, notch present along ventral border of dentary immediately posterior to symphysis.

38. Coronoid process. 0, formed in part by dorsoventrally elongate angulo-articular; 1, coronoid process restricted to dentary bone.

39. Ligamentum primordiale. 0, ligament or sheath of connective tissue connected to medial face of maxilla and permitting considerable movement to posterior end of maxilla; 1, short strong ligament extending from posterodorsal margin of maxilla to anterior face of angulo-articular ridge forming dorsolateral limit of articulation between angulo-articular and quadrate.

40. Branchial arches. This character summarizes an array of specializations in the branchial apparatus of Curimatidae and Prochilodontidae, in a total of 12 synapomorphies exclusive to that assemblage (Vari, 1989: 51–52; see Buckup, 1998: 130). Such subdivision was considered irrelevant for the analysis of Buckup, but here the character is assigned a weight of 12 to reflect the evidential support previously proposed in Vari (1989).

41. Fourth upper pharyngeal toothplate. 0, toothed; 1, toothless.

42. Fourth and fifth upper pharyngeal toothplate. 0, in direct contact; 1, lacking direct contact. Coded as '?' in *Tarumania* because relevant toothplates are missing.

43. Scaphium. 0, connected to sinum imparis through foramen magnum; 1, connected to sinum imparis through pair of foramina separated from foramen magnum by pair of osseous struts.

44. Ventral process of vertebra 2. 0, pair of ossified processes extending from ventral surface of centrum 2, forming part of connective sheath surrounding dorsal aorta; 1, corresponding to synapomorphies 10 and 11 in Vari (1989: 51–52) exclusive to Curimatidae and Prochilodontidae. The processes in *Tarumania* are very small but present.

45. Spine of third neural arch. 0, absent or restricted to lateral surface of neural arch; 1, extending anterodorsally and contacting lateral surface of large supraneural in Weberian apparatus. State (1) was reported as present in *Hoplias* by Buckup (1998), but in all specimens examined of the genus (and of other Erythrinidae), it was absent or very small, so it was corrected to (0).

46. Joint between neural arches of vertebrae 3 and 4. 0, well-developed synchondral joint; 1, reduced or absent.

47. Supraneural preceding neural spine of vertebra 4. 0, present; 1, absent. Coding for this character is inverted relative to that in Buckup (1998) in order to maintain State (0) as the putatively plesiomorphic one (also entered for the outgroup). *Chilodus* was coded as having the supraneural in Buckup (1998), but as the opposite condition here because in the material examined the first supraneural posterior to the supraneural complex is anterior to the neural spine of the fifth vertebra, and the one preceding the fourth spine is absent. *Xenocharax*, originally coded as (?) was changed to (0) because a small supraneural in the correct position is definitely present in the specimen examined. All species of *Nannostomus* have been reported as lacking the supraneural anterior to the fourth neural spine by Netto-Ferreira (2006) and the genus is therefore coded accordingly in this study, and not as (?) as in Buckup's matrix.

48. Contact between anterior supraneural and neural spine of vertebra 4. 0, lamellar portion of large supraneural adjacent to skull well developed, extending posteriorly towards neural spine of fourth vertebra; 1, supraneural extending only to neural arch of fourth vertebra.

49. Neural arch of vertebra 4. 0, autogenous; 1, fused with centrum.

50. Rib of vertebra 4 (modified as part of Weberian apparatus). 0, with conic or subcylindric lateral extremity, never closely connected with rib of fifth centrum; 1, rib of fourth centrum mostly lamellar, with posterior margin closely associated with ventral margin of rib of fifth centrum.

51. Rib of vertebra 5. 0, with medially directed process near base; 1, without process near base.

52. Extrascapular bone. 0, present; 1, absent.

53. Post-temporal bone. 0, with medial process connected by ligament to intercalar; 1, articulating directly with pterotic, without medial process.

54. Supracleithrum. 0, with latero-sensory canal branch; 1, without canal.

55. Coracoid. 0, large, extending to anterior end of cleithrum; 1, reduced, not reaching anterior end of cleithrum.

56. Pectoral girdle. 0, interosseous space present between cleithrum and coracoid; 1, interosseous space absent. Coded as '?' in *Tarumania* because the extreme reduction of coracoids makes the character unobservable.

57. Posterior margin of cleithrum. 0, convex near pectoral-fin base or slightly sinuous; 1, notched near base of pectoral fin, with ventral margin of notch forming distinct process.

58. Postcleithrum 2. 0, present (either autogenous or fused with postcleithrum 3); 1, absent. Coded as (?) in *Boulengerella* because *B. lateristriga* and *B. maculata* have state (1) while all other species in the genus have state (0) (Vari, 1995: 27). The single postcleithrum in *Hepsetus* is considered as postcleithrum 1, as per interpretations in Vari (1995: 26, 27; also expressed in matrix coding on p. 7) and Buckup (1998: 131) and contrary to Vari, (1983: 36).

59. Postcleithrum 3. 0, present (either autogenous or fused with postcleithrum 2); 1, absent.

60. Postcleithra 2 and 3. 0, separate, ossified as autogenous units; 1, fused.

61. Pectoral-fin rays. 0, single unbranched ray in leading edge of fin; 1, two or more unbranched rays in the leading edge of fin.

62. Pelvic bone. 0, anteriorly bifid; 1, not bifid.

63. Number of pelvic-fin rays. 0, 9 or fewer; 1, 10 or more.

64. Dorsal fin. 0, posterior two dorsal-fin rays articulating with same pterygiophore; 1, posterior dorsal-fin pterygiophore with a single ray.

65. Anal fin. 0, with 13 or fewer rays; 1, with 19 or more rays.

66. Anal fin. 0, 37 or fewer; 1, 38 or more.

67. Caudal bony stays. 0, absent; 1, small, delicately ossified; 2, large, laminar and thickly ossified. The presence of bony stays was considered as a synapomorphy for Ctenoluciidae in Vari (1995) and Buckup (1998), the latter author apparently restricting the definition of such structures to the extreme morphology seen in that family. Vari (1995: 32), however, reported that bony stays, albeit in less developed form, are also present in many members of Alestidae (first noticed in *Hydrolicus* by Roberts, 1969). Murray & Stewart (2002) later even proposed the presence of caudal bony stays as a synapomorphy for the Alestidae. Zanata & Vari (2005) mapped in detail the occurrence of caudal-fin bony stays in Alestidae, noting their presence in most members of the family except *Chalceus* and a clade including some of the smaller species in the family. It is clear that the pronounced condition in ctenoluciids is exclusive to that family, but also that there is no morphological reason to refute a hypothesis of primary homology with the less extreme situation in alestids. Therefore, the character is recoded herein in three states: (2) exclusive for ctenoluciids, (1) for *Alestes* and (0) for all remaining taxa. *Xenocharax* was assigned (?) in Buckup (1998) but is herein changed to (0), as also done in Zanata & Vari (2005: 141). Finally, we note also that there is a coding mistake in Vari (1995), with the state assignment in table 1 (p. 8) not matching the correct one in the Matrix (p. 7) and text (p. 32).

68. Number of epurals. 0, one; 1, two or more.

69. Number of epurals. 0, two or fewer; 1, three. This and the preceding characters could be meaningfully combined into a single ordered multistate character. The original coding was maintained for ease with communication with its original published source.

70. Number of uroneurals. State 0: two pairs, State 1: one pair, State 2: no free uroneurals. Originally coded in Buckup (1998) as two states only: 1 (one pair) and 2 (two pairs), with outgroup coded as '?'. State zero was not assigned to any terminal. This character was recoded with an additional state to account for taxa without free uroneurals, as an ordered multistate.

71. Hypurals 1 and 2. 0, not fused; 1, fused.

72. Tooth morphology. 0, all teeth conical; 1, bicuspid teeth present; 2, tricuspid or multicuspid teeth present.

73. Dentition. 0, teeth variously arranged, but never as in state 1; 1, teeth unicuspid, numerous, similarly sized, with crowns regularly curved posteriorly along main axis of mandible.

74. Nasal bone. 0, positioned directly anterior to frontal; 1, positioned directly anterior to, and contiguous with, supraorbital bone.

75. Olfactory bulbs. 0, positioned immediately anterior to telencephalon; 1, positioned anteriorly, in contact or nearly so with posterior surface of lateral ethmoids.

76. Buccopharyngeal apparatus. 0, absent; 1, present. This characters summarizes a set of 15 buccopharyngeal synapomorphies exclusive to Anostomidae and Chilodontidae in Vari, (1989: 50, characters 44–58).

Buckup (1998) considered such subdivision irrelevant for the resolution of the focus of his study (relationships of Characidiinae). Here a single character is maintained but assigned a weight of 15 to reflect original evidential support in Vari, (1989).

77. *Adductor mandibulae* muscle. 0, internal division (= stegalis of Datovo & Vari, 2013) of *adductor mandibulae* without a separate medial portion originating from the mesopterygoid and metapterygoid; 1, internal division of *adductor mandibulae* with a separate medial portion that arises from the lateral surface of the mesopterygoid and metapterygoid and attaches laterally to the tendinous band located along the medial surface of the remaining portion of the internal division of the *adductor mandibulae*.

78. *Dilatator operculi* muscle. 0, origin bounded anteriorly by the vertically oriented sphenotic spine; 1, origin in orbital roof on ventral surface of frontal, reaching opercle through tunnel or trough located between frontal and sphenotic spine (which is horizontally oriented). We agree with the considerations regarding the primary homology of the condition in Erythrinidae and Ctenoluciidae with those in *Acestrorhynchus* and Lebiasininae (of Lebiasinidae) made by Buckup (1998: 133). Regarding the Lebiasininae, there was apparently a coding error in the matrix of Vari (1995: 7). The text (Vari, 1995: 330) clearly states that the conditions are morphologically equivalent, but parsimony considerations reveal that they are convergent. Despite that, representatives of Lebianininae were coded as (0), thus implying non-homology *a priori*. Herein, representatives of Lebiasininae (*Lebiasina* and *Piabucina*), *Acestrorhynchus*, all Erythrinidae and Ctenoluciidae are coded as sharing state (1).

79. Hyohyoidei abductor muscle. 0, with discrete origin from anteroventral margin of urohyal and anteromedial surface of hyoid arch; 1, with broad origin across entire ventral surface and lateral margins of ventrolateral wings of urohyal.

80. Scales. 0, with circuli om posterior surface; 1, without circuli on posterior surface.

81(2). First infraorbital. 0, anterior portion not elaborated; 1, anterior portion with medial and anterior processes.

82(3). First infraorbital and supraorbital. 0, separate; 1, in contact.

83(4). Margins of first infraorbital and supraorbital. 0, not interdigitating; 1, interdigitating.

84(12). Fourth infraorbital. 0, well developed; 1, reduced or absent.

85(17). Nasal. 0, tubular, 1, with dorsal and ventral lamellae.

86(18). Nasal. 0, length less than width of orbit; 1, slightly longer than orbit; 2, distinctly longer than orbit (reduced to two-state because state subdivision is relevant for relationships within Ctenoluciidae only).

87(19). Nasal. 0, situated anterior to frontal; 1, situated at least partially anterior to supraorbital.

88(21). Lateral ethmoid. 0, with well-developed blade-like process laterally and no process or small process for articulation with palatine; 1, with relatively small blade-like process laterally and prominent transversely elongate process articulating with palatine.

89(22). Frontal. 0, not distinctly expanded anteriorly along margin of nasal; 1, distinctly expanded anteriorly along margin of nasal. This character was proposed as a synapomorphy for ctenoluciids in text (Vari, 1995: 13), but the matrix (p. 7) codes it as (1) in ctenoluciids, *Lebiasina*, *Piabucina* and all erythrinids. Material examined shows that the derived condition is present in ctenoluciids only, in agreement with the text and as coded in the present matrix, and that the original matrix is mistaken.

90(23). Sphenotic spine. 0, spine approximately vertical, with dorsal portion proximate to main portion of bone and continuous with ventral surface of frontal; 1, spine more horizontal, with dorsal portion proximate to main portion of bone and not continuous with ventral surface of frontal. This character is present in the Ctenoluciidae, Erythrinidae and the subfamily Lebiasininae (*Lebiasina* and *Piabucina*) of Lebiasinidae (but not the Pyrrhulininae), as proposed by Vari (1995) and confirmed here. Vari (1995: 14) considered the derived condition to be homoplastic in the clade Ctenoluciidae + Erythrinidae, on the one hand, and in the Lebiasininae on the other hand, under the overall most parsimonious scheme of relationships. Nevertheless, Vari's matrix codes the derived condition as exclusive to ctenoluciid taxa, in apparent contradiction with the actual distribution of states in relevant taxa and information in text. This is corrected in the present matrix, with the derived condition coded as present in ctenoluciids, erythrinids and lebiasinins. *Tarumania* is coded as (?) because it lacks a sphenotic spine entirely and cannot be coded as either of the states recognized.

91(24). Frontal. 0, without lateral process extending to contact lateral process of sphenotic; 1, with lateral process extending to contact lateral process of sphenotic.

92(25). Sphenotic spine. 0, extending anteriorly to transverse plane through joint between sphenotic and pterosphenoid; 1, extending anteriorly to transverse plane through joint between pterosphenoid and orbitosphenoid; 2, extending anteriorly distinctly anterior to transverse plane through joint between pterosphenoid and orbitosphenoid. *Tarumania* is coded as (?) because the sphenotic spine is entirely absent.

93(26). Epiphyseal bar. 0, epiphyseal bar either a distinct transverse bar within fronto-parietal fontanel or a ridge across ventral surface of frontal; 1, no indication of epiphyseal bar.

94(27). Parietal branch of latero-sensory canal in frontal and parietal. 0, present; 1, absent. Coded as (?) in *Tarumania* because of the generalized reduction of the latero-sensory canal system.

95(28). Posterior portion of supraorbital canal that contacts pterotic canal. 0, present; 1, absent. Coded as (?) in *Tarumania* because of the generalized reduction of the latero-sensory cana system.

96(32). Plate-like suprapreopercle. 0, absent; 1, present.

97(33). Premaxilla. 0, not distinctly elongate; 1, elongate.

98(36). Maxilla. 0, with distinct anterodorsal process and movably articulated with premaxilla; 1, lacking distinct anterodorsal process and immovably attached to rear of premaxilla.

99(38). Ligamentum primordiale. 0, relatively flat and attaching to anterodorsal portion of maxilla; 1, distinctly thickened and attaching to central portion of maxilla.

100(41). Dentary and Meckel's cartilage. 0, not distinctly elongate; 1, elongate.

101(42). Median mandibular fossa. 0, largely open medially; 1, largely enclosed by broad plate extending ventrally from dorsomedial margin of main portion of dentary.

102(43). Coronomeckelian bone. 0, situated dorsal of Meckel's cartilage; 1, located within Meckel's cartilage.

103(44). Area of attachment of ligamentum primordiale on lower jaw. 0, broad attachment onto fascia of adductor mandibulae muscle and rear of lower jaw; 1, restricted attachment onto distinct process and adjoining region of posteroventral portion of angulo-articular.

104(46). Teeth. 0, not as in 1; 1, large and compressed distally.

105(51). Attachment of anterior portion of suspensorium to neurocranium. 0, not as in 1; 1, via a thick ligament extending from palatine to mesethmoid.

106(54). Mesopterygoid teeth. 0, absent; 1, present [*Boulengerella* coded as (?) because state 1 is seen only in *Boulengerella maculata* and *Boulengerella lateristriga*; Vari, 1995].

107(56). Basihyal cartilage. 0, continuous, with no sign of bilateral subdivision; 1; with some degree of bilateral subdivision; 2, fully divided bilaterally. Character recoded from original two-state character to accommodate additional variation displayed by *Tarumania*.

108(57). Lateral surface of anterior and posterior ceratohyals. 0, without interdigitations; 1, with interdigitations.

109(58). Medial surface of anterior and posterior ceratohyals. 0, without interdigitations; 1, with interdigitations. Recoded as a two-state character. Originally coded with an additional state (2) (interdigitations highly developed), which could not be objectively delimited in the material examined. Interdigitations were reported as absent in *Acestrorhynchus* by Vari (1995: 25; citing Roberts, 1969: fig. 37) but are actually present in the material examined of the genus, which is thus coded as (1).

110(60). Number of branchistegal rays on posterior ceratohyal. 0, one; 1, two.

111(61). Branchiostegal rays. 0, three of four rays; 1, five rays.

112(66). Form of tripus. 0, distinctly triangular anteriorly; 1, elongate.

113(68). Fourth pleural rib. 0, ventral portions situated under fourth centrum; 1, angled posteriorly, with ventral portions extending distinctly under fifth centrum.

114(70). Transverse process of the third neural arch. 0, narrow; 1, wide. *Tarumania* is variable for this character and is therefore coded as (?).

115(71). Transverse process of the third neural arch. 0, extending anteriorly to laterally overlap the ascending process of intercalarium; 1, falling short of ascending process of intercalarium. Originally with 3 states, but recoded as a 2-state character because state 2 ('process greatly reduced') is relevant for relationships within ctenoluciids only.

116(72). Latero-sensory canal system on body. 0, complete; 1, limited to anterior of body. Coded as (?) in *Tarumania* because of the generalized reduction of the sensory canal system and in *Boulengerella* because *B. lateristriga* and *B. maculata* have state (1) while remaining species in the genus have state (0).

117(75). Scales at rear of parietal. 0, not inserting into groove along rear of parietal; 1, scales inserting into such a groove.

118(76). Anal-fin rays. 0, not sexually dimorphic; 1, sexualy dimorphic, with rays expanded.

119(81). Adipose fin. 0, present; 1, absent [species of *Nannostomus* are variable for this character and the genus is coded as (?)].

120(84). Central portion of dilatator operculi muscle. 0, neither constricted nor with central ligamentous band; 1, constricted, with central ligamentous band.

121(85). Anterior portion of dilatator operculi muscle. 0, not broadly expanded into orbit; 1, expanded and reaching at least one-half distance across orbit; 2, greatly expanded and reaching to lateral ethmoid. Although described by Vari (1995: 34) as sharing state 1, *Piabucina* is coded in his matrix (p. 7) as state (0). This is apparently a coding mistake and the genus is here assigned state (1).

122(86). Adductor mandibulae muscle. 0, not arising from sphenotic spine; 1, arising in part from sphenotic spine.

123(87). Levator arcus palatini muscle. 0, arising only from ventral portion of sphenotic spine; 1, arising from entire ventral margin of sphenotic spine.

124. Shape of caudal fin. State 0: forked or bilobed, with clear differentiation between upper and lower lobes. State 1: round or oblong, with no external differentiation between upper and lower lobes (Oyakawa, 1998: 91–92).

125. Number of principal caudal-fin rays in upper lobe. State 0: 10 rays, State 1: fewer than 10 rays (modified from Netto-Ferreira, 2006: 180).

126. Number of principal caudal-fin rays in lower lobe, State 0: 9 rays or more, State 1: 8 rays (modified from Netto-Ferreira, 2006: 181–182).

127. Morphology of symplectic. State 0: a simple cylinder of bone with little or no additional ossification. State 1: extensive laminar ossification dorsally on its contact with the mesial (but not lateral) surface of the rest of the suspensorium (Oyakawa, 1998: 53–54).

128. Condition of infraorbital 6. State 0: in a single element. State 1: horizontally split in two elements. This character has been observed from classical taxonomic treatments of the taxa corresponding to *Erythrinus* and *Hoplerythrinus* (Spix and Agassiz, 1829) and later used as evidence of relationships in Oyakawa (1998).

Deleted characters from Vari (1995, numbering original).

1. Antorbital. 0, present; 1, absent. Equivalent to Buckup no. 20.

9. Supraorbital. 0, present; 1, absent. Equivalent to Buckup no. 21.

20. Mesethmoid and vomer. 0, abutting each other ventrally or with vomer overlapping ventral surface of mesethmoid; 1, medial process of vomer inserting into matching depression on posteroventral surface of mesethmoid. Equivalent to Buckup no. 5.

47. Crown of teeth. 0, not recurved; 1, recurved. Equivalent to Buckup no. 73.

55. Metapterygoid-quadrate fenestra. 0, distinct rotund or ovate opening; 1, absent. Equivalent to Buckup no. 24.

64. Postcleithrum 3. 0, present; 1, absent. Equivalent to Buckup no. 59.

65. Postcleithrum 2. 0, present; 1, absent. Equivalent to Buckup no. 58.

69. Tripus and fourth pleural rib. 0, joined by loose connective tissue; 1, joined by variably developed ligament; 2, joined by discrete ligament; 3, joined by thick ligament. The ligament in question seems to be the radial ligament connecting the inner face of the transformator process of the tripus with a corresponding knob on the os suspensorium (fourth pleural rib of Vari). Such structures correspond, respectively, to the 'radial fibres of the tripodes' and 'radial nodule' in Bridge & Haddon (1893: figs 21 and 22). This character was not utilized because the four states recognized in Vari (1995) do not seem clearly distinct in specimens examined and could not be objectively coded for the present analysis.

74. Scales at rear of head. 0, not extending over supraoccipital spine to medial portions of parietal; 1, extending over supraoccipital spine to medial portions of parietal. Equivalent to Buckup no. 18.

82. Caudal-fin bony stays. 0, present; 1, absent. Equivalent to Buckup no. 67.

83. Dilatator operculi muscle. 0, origin limited to lateral surface of frontal and posterior surface of sphenotic spine, muscle fan shape; 1, origin not from lateral surface of frontal, but at least in part from within orbit, muscle pinnate. Equivalent to Buckup no. 78.