

This article was downloaded by: [University of Bath]

On: 13 February 2014, At: 18:03

Publisher: Taylor & Francis

Informa Ltd Registered in England and Wales Registered Number: 1072954 Registered office: Mortimer House, 37-41 Mortimer Street, London W1T 3JH, UK



Journal of Natural History

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/tnah20>

Mastacembelidae (Teleostei; Synbranchiformes) subfamily division and African generic division: an evaluation

E. J. Vreven^a

^a Africa Museum, Vertebrate Section, Ichthyology ,
Leuvensesteenweg 13, B-3080 Tervuren, Belgium E-mail:

Published online: 15 Aug 2006.

To cite this article: E. J. Vreven (2005) Mastacembelidae (Teleostei; Synbranchiformes) subfamily division and African generic division: an evaluation, *Journal of Natural History*, 39:4, 351-370, DOI: [10.1080/0022293042000195975](https://doi.org/10.1080/0022293042000195975)

To link to this article: <http://dx.doi.org/10.1080/0022293042000195975>

PLEASE SCROLL DOWN FOR ARTICLE

Taylor & Francis makes every effort to ensure the accuracy of all the information (the "Content") contained in the publications on our platform. However, Taylor & Francis, our agents, and our licensors make no representations or warranties whatsoever as to the accuracy, completeness, or suitability for any purpose of the Content. Any opinions and views expressed in this publication are the opinions and views of the authors, and are not the views of or endorsed by Taylor & Francis. The accuracy of the Content should not be relied upon and should be independently verified with primary sources of information. Taylor and Francis shall not be liable for any losses, actions, claims, proceedings, demands, costs, expenses, damages, and other liabilities whatsoever or howsoever caused arising directly or indirectly in connection with, in relation to or arising out of the use of the Content.

This article may be used for research, teaching, and private study purposes. Any substantial or systematic reproduction, redistribution, reselling, loan, sub-licensing, systematic supply, or distribution in any form to anyone is expressly forbidden. Terms & Conditions of access and use can be found at <http://www.tandfonline.com/page/terms-and-conditions>

Mastacembelidae (Teleostei; Synbranchiformes) subfamily division and African generic division: an evaluation

E. J. VREVEN

*Africa Museum, Vertebrate Section, Ichthyology, Leuvensesteenweg 13, B-3080 Tervuren, Belgium;
e-mail: vreven@africamuseum.be*

(Accepted 12 January 2004)

Abstract

The family Mastacembelidae is currently divided into two subfamilies, the Mastacembelinae and the Afromastacembelinae. Within the African Afromastacembelinae two genera, *Caecomastacembelus* and *Aethiomastacembelus*, are recognized. Both the subfamily and the African generic division were critically evaluated mainly through X-ray analyses and osteological research. There is no supporting evidence for a split into two subfamilies. In addition, the present diagnosis of the African genera proved to be unworkable, and no convincing phylogenetic evidence supporting this classification is available. Therefore, pending new detailed phylogenetic research, the use of a subfamily classification within the family Mastacembelidae is not recommended. Furthermore, *Caecomastacembelus* and *Aethiomastacembelus* are placed in synonymy with the genus *Mastacembelus*.

Keywords: *Mastacembelidae*, *Mastacembelinae*, *Afromastacembelinae*, *Caecomastacembelus*, *Aethiomastacembelus*, *Mastacembelus*

Introduction

Mastacembelidae are percomorph fishes present in major parts of tropical and subtropical Africa, the Middle East and South-East Asia, north to China. They are closely related to the families Chaudhuriidae and Synbranchidae with which they form the order Synbranchiformes (Travers 1984a, 1984b).

Mastacembelidae are anguilliform fishes. Some species can attain a maximum length of about 1 m. Very characteristic is the rostral appendage which bears the two tubulated anterior nostrils on each side of a central rostral tentacle. The gill opening is reduced due to a connection of the opercular membrane with the lateral wall of the body. Mastacembelidae have a long series of well-separated dorsal spines, hence their name, spiny eels. They also have a short series of anal spines. Pelvic fins and the pelvic girdle are absent. Most species are characterized by a huge number of small cycloid scales. Characteristic for all African members of the family are the confluent dorsal, caudal and anal fins.

Travers (1984b) subdivided the Mastacembelidae into two subfamilies: the Mastacembelinae Travers, 1984 from the Oriental region, and the Afromastacembelinae Travers, 1984 endemic to Africa. Four genera of Mastacembelidae are presently recognized

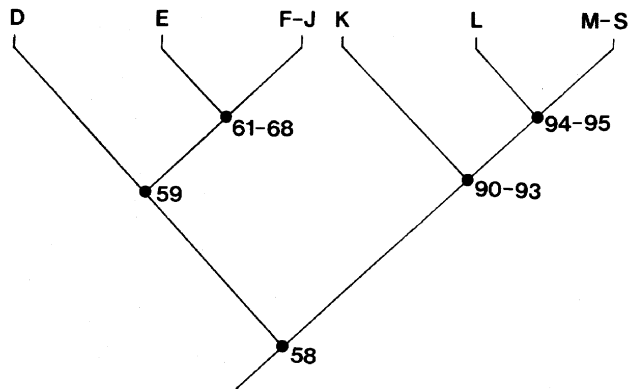


Figure 1. Phylogeny of the Mastacembelidae as proposed by Travers (1984b). Numbers are from Travers (1984b) and refer to principal synapomorphies. 58, Mastacembelidae; 59, Mastacembelinae; 61–68, *Macrognathus* (E, F–J); 90–93, Afromastacembelinae; 94–95, *Caecomastacembelus* (L, M–S); D, *Mastacembelus*; K, *Afromastacembelus*.

(Travers 1984b, 1988): two of them, *Mastacembelus* Scopoli, 1777 and *Macrognathus* Lacepède, 1800, within the Mastacembelinae, the other two, *Caecomastacembelus* Poll, 1958 and *Aethiomastacembelus* Travers, 1988, within the Afromastacembelinae (see Figure 1).

Kottelat (1991), Kottelat and Lim (1994) and Britz (1996) do not agree with some of the taxonomic changes introduced by Travers (1984b), including the present position of *Sinobdella* Kottelat and Lim, 1994 (= *Rhynchobdella* Bloch and Schneider, 1801 in Travers, 1984b) within the Chaudhuriidae, sister family of the Mastacembelidae. Instead, they propose placing *S. sinensis* (Bleeker, 1870) within the Mastacembelidae (Kottelat and Lim 1994; Britz 1996), in which it may form the sister group of all remaining mastacembelids (Britz 1996).

Also, Johnson and Patterson (1993) found some problems with Travers' (1984b) characterization of the Chaudhuriidae, as they found that some characters seem to be primitive, others may be primitive and others are possibly non-existent. Nevertheless, they regarded *Chaudhuri* Annandale, 1918 and *Rhynchobdella* (= *Sinobdella*) as primitive mastacembeloids.

The criticism was further developed by Britz (1996). He concluded that there are no significant similarities between *Sinobdella* and the Chaudhuriidae, except for the lost entopterygoid, that would support the inclusion of *S. sinensis* within the family Chaudhuriidae (for more details see Britz 1996). Britz (1996) mentioned two characters, the special articulation of the ectopterygoid with the lateral ethmoid via a cartilaginous meniscus, and the peculiar elongated shape and dorsally shifted position of the coronomeckelian bone, which are shared between *Sinobdella* and the mastacembelids but not found in the chaudhurids, synbranchids or any other teleost.

Material and methods

For a complete list of the examined specimens see below. Institutional abbreviations follow Leviton et al. (1985); c/s indicates cleared and stained.

X-rays were made with a Balteau 5–50 kV equipped with a Tubix cell, Type 6LA, Paris (France). Some cleared and stained specimens available at the AMNH, BMNH and

MRAC were examined, and additional specimens were cleared and stained using the method of Taylor and Van Dyke (1985).

One meristic needs some explanation. The caudal minus abdominal vertebrae number (CV – AV) is defined as the number of caudal vertebrae minus the number of abdominal vertebrae.

Results

Mastacembelinae

According to Travers (1984b) a single synapomorphy, four separate and autogenous hypurals, characterizes the Mastacembelinae as a monophyletic assemblage (see Travers 1984b and Figure 1, No. 59). The presence of four hypurals can indeed be regarded as an apomorphy when comparing this character state observed in Asian and Middle Eastern species (i.e. the Mastacembelinae) with the character state as usually observed in euteleosteans (six hypurals: see Rosen 1973).

However, even if the presence of four hypurals may be diagnostic within the suborder of the Mastacembeloidei (i.e. Chaudhuriidae and Mastacembelidae), it is also the plesiomorphic condition when comparing this character state with the one observed in *Sinobdella*, *Chaudhuria* and *Pillaiya* Yazdani, 1972, where only two hypural plates are found (Travers 1984a, 1984b).

Further, it is unlikely that the presence of four hypurals represents a synapomorphy of the Mastacembelinae when comparing this character state with the one observed in the African species (i.e. the Afromastacembelinae) where, according to Travers (1984b), only two hypural plates are generally found. Indeed, within this context the presence of four hypurals is rather considered a plesiomorphic condition. Therefore, there are difficulties in accepting the four separate hypural plates character as a synapomorphy of this subfamily.

But, more importantly, in addition the description of four separate hypurals is not correct. Indeed, several points of criticism can be formulated as to the use of the hypural plate character by Travers (1984b).

Mastacembelus mastacembelus (Banks and Solander, in Russell, 1794), type species of the genus *Mastacembelus*, does not have four separate and autogenous hypurals, the synapomorphic character reported by Travers (1984b). Indeed, within *M. mastacembelus* a considerable amount of intraspecific variation, from two up to four completely separate hypural elements, was observed (see Table I for more details). Further, it is evident from Travers' (1984a) own illustration of the caudal skeleton of this species that the hypural elements are partially fused with each other towards their distal edges (i.e. H1 with H2, and H3 with H4+H5). This important intraspecific variation clearly weakens the importance of this character for phylogenetic reconstruction. Additional evidence for important intraspecific variation (from two up to four separate hypurals) was also found in other Oriental Mastacembelidae species examined [i.e. *Macrogathus aculeatus* (Bloch, 1786), *Macrogathus aral* (Bloch and Schneider, 1801), *Macrogathus keithi* (Herre, 1940), *Macrogathus maculatus* (Cuvier in Cuvier and Valenciennes, 1832), *Macrogathus pancalus* Hamilton, 1822, *Mastacembelus armatus* (Lacepède, 1800), *Mastacembelus erythotaenia* Bleeker, 1850 and *Mastacembelus unicolor* Cuvier (ex Kuhl and Hasselt), in Cuvier and Valenciennes, 1832] (see Table I for more details).

A considerable amount of interspecific variation was also observed when various Oriental Mastacembelidae species were compared (see Table I).

Table I. Intraspecific variation in caudal skeleton formula and caudal fin formula in some Oriental Mastacembelidae species (all data collected from X-rays).

Species	Status	TL (<i>n</i>)	Caudal skeletal formula	Caudal soft fin ray number (<i>n</i>)	
<i>Masta.</i>	Syntype	371	1 Ph, 2 H	19 (1)	
	<i>mastacembelus</i>	Syntype	567	1 Ph, 3 H	18 (1)
	Syntype	306	1 Ph, 3(4) H	17 (1)	
	Specimens	215–356 (4)	1 Ph, 2 H	16 (1); 18 (1); 19 (1);	
	Specimens	189–582 (2)	1 Ph, 3 H	20 (4)	
	Specimen	307	1 Ph, 4 H		
<i>Macro. aculeatus</i>	Specimen	232	1 Ph, 2 H+2+1 H	15 (8); 16 (1)	
	Specimen	191	1 Ph, 1 H+2+1 H		
	Specimen	211	1 Ph, 1 H+1[3] H		
	Specimen	190	1 Ph, 1[2] H+1[3] H		
	Specimen	185	1 Ph, 1[2] H+1[2] H		
	Specimens	144–213 (2)	1 AHS+1 Ph+1[2] H+1[3] H		
	Specimen	178	1 AHS+1Ph+1 H+1[3] H		
	Specimen	194	1 (1 Ph+2 H)+1[3] H		
<i>Macro. aral</i>	Specimens	153–177 (2)	1 Ph+2 H*, 3 H*	14 (2); 15 (1); 16 (5)	
	Specimen	150	1 Ph, 2 H*, 1 H, 2 H*		
	Specimen	158	1Ph, 2 H, 1 H		
	Specimens	146–165 (4)	1 Ph+2 H*, 2 H*		
<i>Macro. keithi</i>	Paratypes	55–137 (8)	1 (1 Ph+2 H), 1[3] H	13 (1); 14 (3); 15 (2); 16 (1); 18 (1)	
	Specimens	185–226 (2)	1 (1 Ph+2 H), 1[3] H	15 (1); 16 (1)	
<i>Macro. maculatus</i>	Specimen	188	1 Ph, 1[2] H, 1[2] H	11 (1); 12 (4); 13 (2);	
	Specimens	191–233 (2)	1 Ph, 2 H, 1[2] H	14 (1); 15 (2)	
	Specimens	213–236 (3)	1 Ph, 2 H, 1[3] H		
	Specimen	157	1 (1 Ph+2 H), 1 H		
	Specimens	184	1 (1 Ph+2 H), 1[2] H		
	Specimen	212	1 (1 Ph+2 H), 1[3] H		
<i>Macro. pancalus</i>	Neotypes	103–126 (3)	1 (1 Ph+1 H), 1[2] H	12 (2); 13 (1)	
	Specimens	75–142 (16)	1 (1 Ph+1 H), 1[2] H	12 (4); 13 (5); 14 (6); 15 (1)	
<i>Macro. armatus</i>	Specimen	250	1 Ph, 1 H, 1 H	13 (4); 14 (3); 15 (3);	
	Specimen	248	1 Ph, 2 H, 2 H	18 (1)	
	Specimens	199–231 (4)	1 Ph, 2 H, 1 H		
	Specimen	195	1 Ph, 2 H, 1[3] H		
	Specimens	179–203 (2)	1 (1 Ph+1 H), 1[2] H		
	Specimens	192–194 (2)	1 (1 Ph+2 H), 1[2] H		
<i>Masta. erythrotaenia</i>	Type	290	1 Ph, 2 H, 1[2] H	14 (1)	
	Specimens	249–563 (8)	1 Ph, 2 H, 2 H	14 (2); 15 (8); 16 (3);	
	Specimens	309–640 (2)	1 (1Ph+2 H), 2 H	17 (2)	
	Specimen	505	1 Ph, 2 H, 1[2] H		
	Specimen	340	1 Ph, 2 H, 1[3] H		
	Specimen	515	1 Ph, 2 H, 1 H		
	Specimen	270	1 Ph, 1[2] H, 2 H		
	Specimen	584	1 Ph, 1 H, 2 H		
	<i>Masta. unicolor</i>	Specimen	179	1 Ph, 2 H, 2 H, 1 ADS	17 (1); 18 (7); 19 (4);
		Specimen	218	1 Ph, 2 H, 2 H	20 (2); 23 (1)
Specimen		257	1 (1 Ph+2 H), 2 H		
Specimens		160–217 (10)	1 (1 Ph+2 H), 1[2] H		
Specimen		285	1 Ph, 2 H, 1[2] H		
Specimen	182	1 Ph, 2 H, 1 H			

Footnote see next page.

According to Travers (1984b), within the Mastacembelinae which otherwise have four hypural plates, one species, *M. aculeatus*, has five hypural elements. This was interpreted by Travers (1984b) as a retention of the plesiomorphic condition. Contrary to Travers (1984b), I never observed five separate hypurals as the hypural elements are always more or less fused to each other (see Table I). *Macrognathus pancalus* is another exception mentioned by Travers (1984b) as it has only a single upper and a single lower hypural plate which was interpreted by Travers (1984b) as a highly derived condition convergent with that found in some African species.

As a result, there seems to be parallel occurrence within the suborder Mastacembeloidei of a reduction in the number of hypural plates by hypural fusion based on the following evidence: (1) there are only two, or only one [I observed one parhypural and only one large hypural in two cleared and stained specimens of *S. sinensis* (AMNH 11077 and AMNH 11078); these differences might illustrate some degree of intraspecific variation], hypural plate(s) in *Chaudhuria*, *Pillaia* and *S. sinensis*; (2) there are from five (*M. aculeatus*) to a single (*M. pancalus*) (the actual numbers are different: see above) hypural plate(s) in the species of the genus *Macrognathus* (Mastacembelinae); (3) there is an important intraspecific variation in the number of hypural plates; and (4) there are only two hypural plates (the actual number is different: see below) in the African Mastacembelidae species (Afromastacembelinae). Therefore, a reduced number of hypural plates due to, at least in part, hypural fusion seems to be an independent acquisition in several Mastacembeloidei lineages, i.e. Chaudhuriidae (*Chaudhuria caudata* Annandale, 1918 and *Pillaia indica* Yazdani, 1972), *Sinobdella sinensis*, *Macrognathus* (*M. pancalus*) and the Afromastacembelinae.

In conclusion, due to the high intra- and interspecific variability and the observed tendencies to hypural fusion in independent lineages, the usefulness of the hypural plate number character for phylogenetic reconstruction and classification within the Synbranchiformes is, at present, unfounded. This character, established by Travers (1984b) to define the Mastacembelinae as a monophyletic assemblage, most probably defines a paraphyletic assemblage.

There is another point that is crucial to the discussion of hypural plates, i.e. that without ontogenetic data, it is hard to determine how many and which hypurals fuse into hypural plates. For instance, it may be that two plates in one taxon represent fusion of 1+2 and 3+4 and that in another the two plates consist of hypural 1 and 2+3. Therefore, homology of elements fusing during ontogeny can only be evaluated through ontogeny (Britz, personal communication).

Travers (1984a), in his illustration of the caudal fin skeleton of *M. pancalus*, labelled the lower hypural plate as H1+2 and the upper plate as H3+4+5+6. A preliminary examination of an ontogenetic series of *M. pancalus* was undertaken. Early in ontogeny there are only four autogenous cartilaginous precursors for the hypurals. Then the two upper and the two lower hypurals, respectively, fuse together during ontogeny. Also, the lowest hypural fuses

TL, total length; *n*, number examined. The caudal skeletal formulae and caudal soft fin ray number on one single row are not necessarily observed on the same specimens. A plus (+) indicates that the elements are partially fused (most often towards their posterior end). Parentheses () refer to structures that are more tightly fused to each other than to other elements of the caudal skeleton. Numbers between square brackets [] indicate that a single structure is composed of several elements that are not completely fused. An asterisk (*) indicates that the elements are partially fused posteriorly only. Caudal skeleton formula: AHS (only reported when partially fused to other caudal elements), autogenous haemal spine; Ph, parhypural; H, hypural; ADS, autogenous dorsal spine.

partially with the parhypural. Homology of these four remaining hypural cartilaginous precursors cannot be determined.

Afromastacembelinae

First, the problems concerning the synapomorphies proposed by Travers (1984b) to define the monophyly of the African subfamily are discussed, and secondly the problems with the African generic division will be dealt with.

Travers (1984b) considered the subfamily *Afromastacembelinae* a monophyletic group based on four synapomorphies: (1) the lack of an ascending process on the urohyal, or direct articulation between this bone and basibranchial 1; (2) (a) hypural plates, generally two, (b) tendency for parhypural fusion to ventral edge of lower plate, (c) 8–10 principal fin rays and (d) confluent caudal fin; (3) the scapula foramen not completely bone-enclosed; and (4) a tendency to have noticeably more caudal than abdominal vertebrae (see Figure 1, Nos 90–93).

As formulated by Travers (1984b) a ‘tendency’ means that not all species included within such an assemblage display this character state. This raises the problem of delimiting monophyletic assemblages. Furthermore, a ‘tendency’ is not a character.

Criticism can be formulated concerning each of the four synapomorphies presented by Travers (1984b) to support the monophyly of the *Afromastacembelinae*.

(1) The lack of an ascending process on the urohyal or a direct articulation between this bone and basibranchial 1 is not unique to the *Afromastacembelinae*; it is also observed in the Asian genus *Chaudhuria* (Travers 1984b).

Furthermore, Travers (1984a) stated that in a number of Asian mastacembeloids (i.e. some *Macrogathus* species) also, the urohyal lacks an ascending process although these taxa are distinguished by a direct articulation between the anterodorsal surface of the urohyal and the keel on basibranchial 1.

In addition, the urohyal in *Mastacembelus oatesii* Boulenger, 1893 [see Figure 2 versus Figure 3 (*Mastacembelinae*: *M. mastacembelus*)] also lacks an ascending process [see Figure 4 (*Afromastacembelinae*: *M. nigromarginatus*)]. Therefore, following Travers’ hypothesis of the phylogeny of the *Mastacembelidae*, the loss of the ascending process on the urohyal would have occurred independently at least twice: i.e. once within the genus *Mastacembelus* and once within the *Afromastacembelinae*. As a result, this character does not provide strong evidence to support the monophyly of the *Afromastacembelinae*.

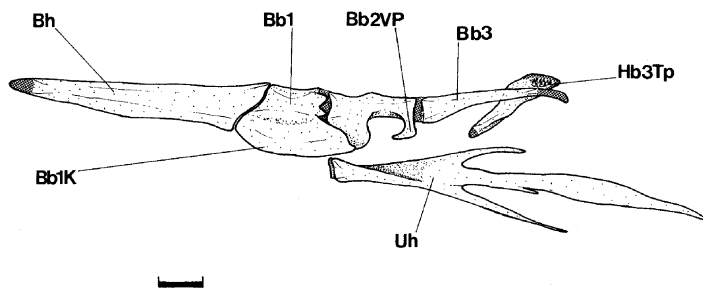


Figure 2. Basibranchial/urohyal arrangement of *Mastacembelus oatesii*, lateral view, left side (after Travers 1984a). Bb1–3, basibranchial 1 to 3; Bb1K, basibranchial 1 keel; Bb2VP, basibranchial 2 ventral process; Bh, basihyal; Hb3Tp, hypobranchial 3 toothplate; Uh, urohyal. Scale bar: 1 mm.

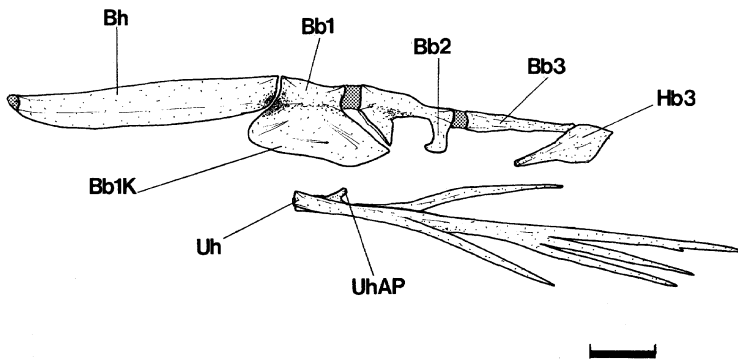


Figure 3. Basihyal and branchial bones of *Mastacembelus mastacembelus*, lateral view, left inverted view of right side (after Travers 1984a). Bb1–3, basibranchial 1 to 3; Bb1K, basibranchial 1 keel; Bh, basihyal; Hb3, hypobranchial 3; Uh, urohyal; UhAP, urohyal ascending process. Scale bar: 1 mm.

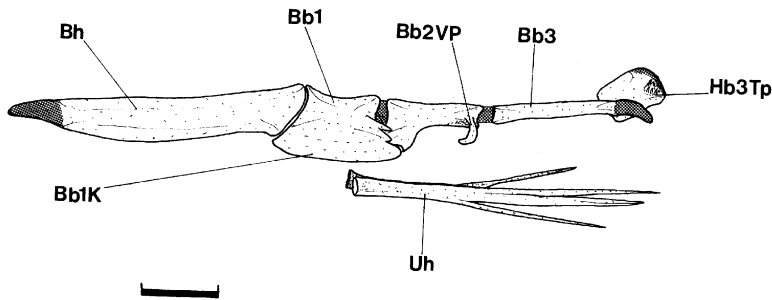


Figure 4. Basibranchial/urohyal arrangement of *Mastacembelus nigromarginatus*, lateral view, left side (after Travers 1984a). Abbreviations as in Figure 3. Scale bar: 1 mm.

(2a) Hypural plates, generally two, but three in *M. moorii* and even four in a single specimen of *M. vanderwaali* (Travers 1984a). There are more exceptions to the general presence of two hypural plates in Travers' (1984a, 1984b) publications. In his illustration of the caudal region of *M. vanderwaali* (Travers 1984a) one can indeed observe two separate hypurals (H2 and H3+4+5+6). However, he labels a third one as fused with the parhypural (Ph+H1). Therefore, there are three instead of two hypural plates. From Travers' (1984b) comments it can be concluded that in *Mastacembelus moorii*, *M. ophidium* and *M. paucispinis*, and in an undescribed species (subsequently described as *A. sexdecimspinus* Roberts and Travers, 1986) there should be a total of three hypurals (two upper elements and one lower element). As no supporting illustration was given this could not be verified. However, in the description of *A. sexdecimspinus* Roberts and Travers (1986) reported that the caudal skeleton is composed of two hypural plates and the parhypural is fused to the hypural one. From the drawings presented by Travers (1984a) it is obvious that two hypurals (or three as the two upper elements are imperfectly fused) were found in *M. congicus* Boulenger, 1899 and a single hypural was found in *M. ellipsifer* Boulenger, 1899 and *M. aviceps* Roberts and Stewart, 1976.

A high amount of interspecific, and also intraspecific, variation of the hypural plate number is also described for several Oriental species. As discussed above, this seems to suggest that there are strong tendencies within various groups of the Mastacembeloidei

towards fusion of the hypural plates. As such, the four separate hypural plates character provided by Travers (1984b) does not provide strong evidence for his dichotomy between Mastacembelinae and Afromastacembelinae. As a result this character, as defined by Travers (1984b), does not provide strong evidence to support the monophyly of the Afromastacembelinae.

(2b) Tendency for parhypural fusion to the ventral edge of the lower hypural plate (Travers 1984a). Indeed, fusion can be observed in several species illustrated by Travers (1984a): *M. frenatus*, *M. shiranus* and *M. vanderwaali* (largely fused) and *M. aviceps* (partially fused at base). On the contrary, there is no fusion in *M. congicus* and *M. ellipsifer*. Since Travers (1984b: 136) considers the fusion as a 'tendency' one could expect the actual fusion to be the most derived condition. This is not the case as *M. ellipsifer*, which shows the derived character state of having only one hypural, has a completely independent parhypural. As a result also this character is weak evidence to support the monophyly of the Afromastacembelinae.

(2c) Presence, or tendency to have 8–10 caudal fin rays (Travers 1984b). Indeed, all the African taxa illustrated by Travers (1984a, 1984b) have fewer than 10 caudal fin rays, except for *M. congicus* which has 11 caudal fin rays. But also other species are exceptional; *M. paucispinis* Boulenger, 1899 has 10–12, *M. sexdecimspinus* has 10–11 (Roberts and Travers 1986), *M. robertsi* (Vreven and Teugels, 1996) has 9–13 and *M. traversi* (Vreven and Teugels, 1997) has 11–12 caudal fin rays.

According to Travers (1984a), the Asian taxa have usually 16–20 caudal fin rays. Indeed, all Asian taxa illustrated by him have a higher number of caudal soft fin rays than the African taxa but certainly not all between 16 and 20 (*Macrogathus pancalus*, 12; *M. aculeatus*, 15 and *Mastacembelus erythrotaenia*, 15; see Travers 1984a: 112–113, Figure 75a–c). In addition, Roberts (1986, 1989) also reported several Asian species with a lower number of caudal fin rays than the 16–20 reported to be usual for the Asian taxa (*Mastacembelus erythrotaenia*, 14–15; *M. favus* (Hora, 1924), 12–15(17); *Macrogathus guentheri* (Day, 1865), 12–14; *M. maculatus*, 12–14; *M. semiocellatus* Roberts, 1986, 10–13).

Because of these additional data this 'tendency' proposed by Travers (1984b) as additional evidence for the monophyly of the Afromastacembelinae has become much too weak.

(2d) All Afromastacembelinae have a completely confluent dorsal, caudal and anal fin (Travers 1984b). Nevertheless, as reported by Travers (1984b) in several Asian Mastacembelinae species (e.g. *Mastacembelus armatus*, *M. caudiocellatus* Boulenger, 1893, *M. circumcinctus* Hora, 1924, *M. erythrotaenia* and *Macrogathus maculatus*), even if a distinct caudal fin is present, the fin is confluent basally with the dorsal and anal. According to Travers (1984a), in these Asian species a distinct caudal is still discernible as the caudal rays are longer than, and extend beyond the tips of, the last dorsal and anal fin rays.

However, in Roberts' (1986) identification key to the Mastacembelidae of Burma and Thailand *Mastacembelus armatus*, *M. erythrotaenia* and *M. favus* are diagnosed by dorsal and anal fins which are broadly joined to the caudal fin, and a caudal fin in which the outline is merged with that of dorsal and anal fins. In at least one *M. erythrotaenia* specimen examined (ROM 53683: 394 mm TL), and also in Sufi's (1956) illustrations of the species, a distinct caudal is not discernible and the caudal rays are not longer than the last dorsal and anal fin rays, resulting in a caudal fin very similar to that found in African species.

In some of the small *M. paucispinis* (e.g. MCZ 50562) and *M. congicus* (e.g. MRAC 63215-226 and MRAC 79-001-P-6343-6360) specimens examined the caudal fin rays are also somewhat longer than, and extend beyond the tips of, the last dorsal and anal fin rays, and so a distinct caudal remains somewhat discernible.

These data and observations bridge the supposed gap between the Mastacembelinae species and the Afromastacembelinae even further and again illustrate that this character employed by Travers (1984b) does not provide strong evidence for a dichotomy between Mastacembelinae and Afromastacembelinae.

According to Travers (1984a), among Asian mastacembeloids the caudal fin in *Sinobdella*, *Chaudhuria* and *Pillaia* is exceptional since it is confluent with the dorsal and anal fins, and has only eight or nine rays. This arrangement is similar to that in the African taxa, all of which have a confluent caudal composed, in the majority of species, of 8–10 principal rays (Travers 1984a). The confluence of dorsal, caudal and anal fins seems to reflect homoplasy: i.e. the independent acquisition of a comparable character state in several lineages as a result of convergent evolution, within the Mastacembeloidei. As such, the confluence of the unpaired fins, as defined by Travers (1984b), is not necessarily synapomorphic for the Afromastacembelinae.

According to Travers (1984a) the caudal fin in *Chaudhuria caudata* is ‘distinct from the dorsal and anal fins...’. Indeed, the distinct caudal had already been pointed out in the original description of *Chaudhuria caudata* by Annandale [(1918: 40) ‘The caudal fin is united to the dorsal and anal by a low membrane; its rays are completely segregated’]. According to Kottelat and Lim (1994) and Britz (personal communication), who looked at numerous *Chaudhuria caudata*, all of them have a separate caudal. Travers (1984a) contradicted his own description (Travers 1984a). A new species, *Chaudhuria fusipinnis* Kottelat and Britz (in Kottelat 2000) has recently been described with the caudal fin confluent with the dorsal and anal fins (Britz, personal communication).

In addition to the apomorphic characters mentioned above, Travers (1984b) also reported a few associated apomorphic caudal features. One of them is the tendency to a fused, short, spatulate and non-ray-supporting haemal spine on the second preural vertebra. However, Travers (1984a) himself reported that in *M. congicus* the haemal spine is ray-supporting, and extends from an autogenous haemal arch in a manner similar to that of most Asian taxa.

(3) According to Travers (1984b) in all African mastacembeloid taxa the scapula foramen lies across the anterior border of the scapula and is bordered by cartilage at its anterior edge (Figure 5), whereas in all Oriental species including *Sinobdella sinensis*, *Chaudhuria* and *Pillaia*, the foramen is completely bone-enclosed (Figure 6).

All figures of the pectoral girdle provided by Travers (1984a) agree with this statement. Nevertheless, in his text Travers (1984a) has a conflicting statement reporting that the character is present only in the majority of the African species. Based on this latter statement it might be possible to find African representatives where the scapula foramen is completely bone-enclosed. Indeed, in one of two cleared and stained specimens of *M. marcheii* and also in specimens of *M. ellipsifer* (BMNH unregistered) and *M. paucispinis* (MRAC 178099), the scapula foramen was found to be completely bone-enclosed on both left and right scapula (personal observation). In the other *M. marcheii* specimen the scapula foramen was completely bone-enclosed on one side but not on the other. As a result, in the majority, but not in all African species, the anterolateral part of the scapular foramen is enclosed by cartilage and this character does not support the monophyly of the African Mastacembelidae.

Problems with this character are not limited to African species but were encountered also in Oriental species. In *Sinobdella sinensis* the scapular foramen has two, well-separated holes, a small one situated within the borders of the scapula and completely enclosed by bone and another one situated towards the anterolateral margin of the scapula and clearly

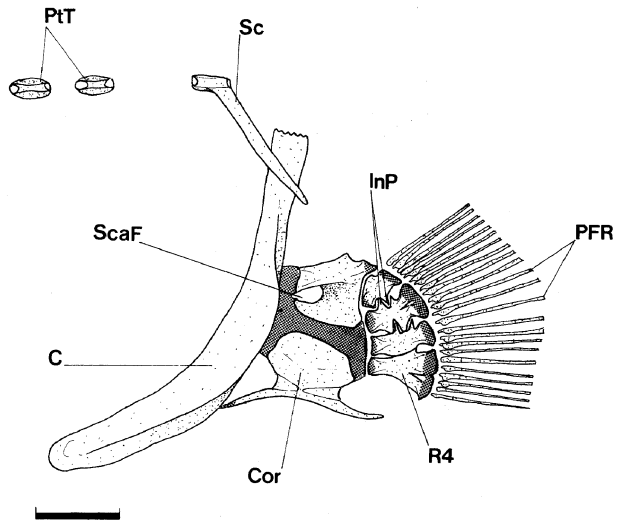


Figure 5. Pectoral girdle of *Mastacembelus nigromarginatus*, lateral view, left side (after Travers 1984a). C, cleithrum; Cor, coracoid; InP, interdigitating process; PFR, pectoral fin rays; PtT, post-temporale tubule; R4, radial (actonost) 4; Sc, supracleithrum; ScaF, scapular foramen. Scale bar: 1 mm.

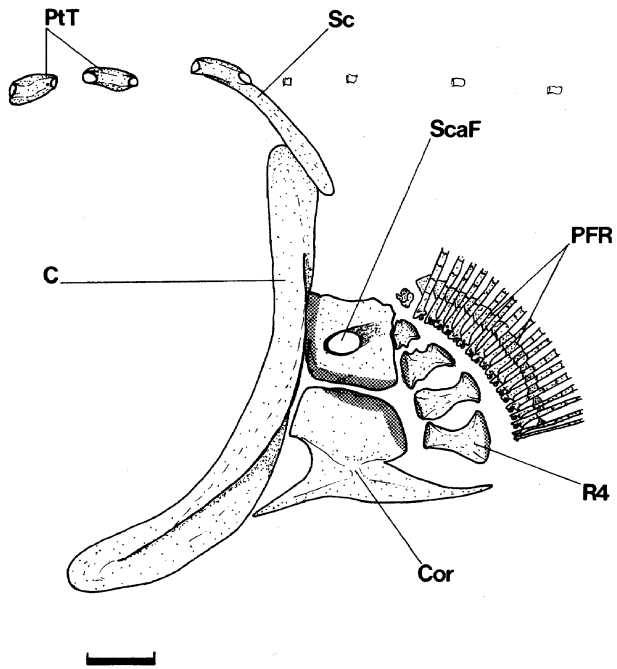


Figure 6. Pectoral girdle of *Mastacembelus mastacembelus*, lateral view, left side (after Travers 1984a). C, cleithrum; Cor, coracoid; PFR, pectoral fin rays; PtT, post-temporale tubule; R4, radial (actonost) 4; Sc, supracleithrum; ScaF, scapular foramen. Scale bar: 1 mm.

not completely bone-enclosed. At present it is not clear which one is homologous with the foramen found in the other Mastacembelidae, or if both are (Britz, personal communication). Therefore, its use to support the monophyly of any lineage within Synbranchiformes seems rather unconvincing. Based on these observations it is clear that further ontogenetic studies are necessary.

(4) Tendency to have noticeably more caudal than abdominal vertebrae. In his discussion of the vertebral column Travers (1984b) added that in all mastacembeloids, other than those with low vertebral counts, the caudal vertebrae number is generally greater due to an increase in total vertebrae number, which does not occur equally among caudal and abdominal vertebrae. Indeed, based on Travers' (1984b) data (see Table II) and as stated by himself (Travers 1984b), I confirm that some Afromastacembelinae species have a higher total vertebrae number, which is mainly due to a higher caudal vertebrae number when compared to some Mastacembelinae representatives. As a result, indeed, there is generally a greater difference between the caudal and abdominal vertebrae numbers in the former than in the latter species.

However, for the Mastacembelinae species listed by Travers (1984a), the caudal minus abdominal vertebrae number (CV – AV) varies from five up to 17 vertebrae in *Macrognathus* and from seven up to 12 vertebrae in *Mastacembelus* (see Table II), while in about half of the African species (17/37 species, i.e. $\pm 46\%$) the caudal minus abdominal vertebrae is also ≤ 17 vertebrae and in about one-third of the species (12/37 species, i.e. $\pm 32\%$) (see Table II) it is ≤ 12 vertebrae. Therefore, the phylogenetic value of this character, as defined by Travers (1984b), is questionable. Indeed, some African Mastacembelidae species do not seem to have higher caudal minus abdominal vertebral numbers than all or some of the *Macrognathus* and *Mastacembelus* species which clearly illustrates the problem of delimiting the groups defined by Travers (1984b). Indeed, Travers (1984a, 1984b) reported that low total and caudal vertebral counts were also observed in a number of African species, for instance *Mastacembelus albomaculatus*, *M. micropectus*, *M. plagiostomus*, *M. platysoma*, *M. tanganyicae* and *M. zebratus* from Lake Tanganyika, and *M. brachyrhinus*, *M. brichardi*, *M. crassus* and *M. aviceps* from the Lower Zairean rapids (see Table II). These low vertebral numbers are associated with other trends to reduction seen in fishes and the crevice-living Tanganyika species of the Lower Zaire rapids (Travers 1984b). The endemic Lower Zaire River mastacembeloid fauna shows a reversal of the general trend towards a greater number of caudal vertebrae seen in the African mastacembeloids (Travers 1984a).

Finally, the tendency of having noticeably more caudal than abdominal vertebrae could easily have developed several times, independently, within a single lineage or several lineages. As a result, this character is questioned as evidence supporting the monophyly of African Mastacembelidae (Afromastacembelinae).

Until 1958 all African mastacembelid species were described within the genus *Mastacembelus*. In 1958 a new, monotypic, spiny-eel genus, *Caecomastacembelus*, was described by Poll with *C. brichardi* as its type species, collected at Pool Malebo (formerly Stanley-Pool) downstream of the Kinsuka rapids in the Congo River basin. The most important generic characters were the apparent absence of the eyes and a more or less pronounced depigmentation of the skin. This blindness justified the introduction of a new genus (Poll 1958) in spite of the close relationship with the normally eyed species *Mastacembelus brachyrhinus* Boulenger, 1899, also collected from the lower Congo River basin.

Table II. Numbers of abdominal (AV), caudal (CV) and total (TV) vertebrae and caudal minus abdominal vertebrae (CV – AV) for all nominal species as provided by Travers (1984a) (modified after Travers 1984a).

	AV	CV	TV	CV – AV
Oriental mastacembeloid taxa				
<i>Chaudhuria caudata</i>	25	46	71	21
<i>Pillaia indica</i>	28	37	65	9
<i>Macrognathus aculeatus</i>	32	38	70	6
<i>Macrognathus aral</i>	32	39	71	7
<i>Macrognathus siamensis</i>	35	40	75	5
<i>Macrognathus caudiocellatus</i>	37	44	81	7
<i>Macrognathus circumcinctus</i>	30	47	77	17
<i>Macrognathus guentheri</i>	38	51	89	13
<i>Macrognathus keithi</i>	31	42	73	11
<i>Macrognathus maculatus</i>	32	44	76	12
<i>Macrognathus pancalus</i>	28	36	64	8
<i>Macrognathus zebrinus</i>	32	42	74	10
<i>Mastacembelus alboguttatus</i>	38	47	85	9
<i>Mastacembelus armatus</i>	38	50	88	12
<i>Mastacembelus erythrotaenia</i>	38	45	83	7
<i>Mastacembelus mastacembelus</i>	38	47	85	9
<i>Mastacembelus unicolor</i>	38	48	86	10
African mastacembeloid taxa				
<i>Mastacembelus albomaculatus</i>	38	44	82	6
<i>Mastacembelus ansorgii</i>	37	63	100	26
<i>Mastacembelus aviceps</i>	25	38	63	13
<i>Mastacembelus batesii</i>	42	54	96	12
<i>Mastacembelus brachyrhinus</i>	33	45	78	12
<i>Mastacembelus brevicauda</i>	40	58	98	18
<i>Mastacembelus brichardi</i>	32	42	74	10
<i>Mastacembelus congicus</i>	34	53	87	19
<i>Mastacembelus crassus</i>	22	44	66	22
<i>Mastacembelus cryptacanthus</i>	38	65	103	27
<i>Mastacembelus cunningtoni</i>	33	56	89	23
<i>Mastacembelus ellipsifer</i>	36	52	88	16
<i>Mastacembelus flavidus</i>	38	58	96	20
<i>Mastacembelus flavomarginatus</i>	39	50	89	11
<i>Mastacembelus frenatus</i>	40	55	95	15
<i>Mastacembelus goro</i>	40	49	89	9
<i>Mastacembelus greshoffi</i>	39	56	95	17
<i>Mastacembelus liberiensis</i>	33	70	103	37
<i>Mastacembelus loembergii</i>	38	63	101	25
<i>Mastacembelus longicauda</i>	38	66	104	28
<i>Mastacembelus marmoratus</i>	39	50	89	11
<i>Mastacembelus micropectus</i>	32	50	82	18
<i>Mastacembelus moorii</i>	33	63	96	30
<i>Mastacembelus niger</i>	40	51	91	11
<i>Mastacembelus nigromarginatus</i>	37	56	93	19
<i>Mastacembelus ophidium</i>	29	66	95	37
<i>Mastacembelus paucispinis</i>	28	53	81	25
<i>Mastacembelus plagiostomus</i>	40	48	88	8
<i>Mastacembelus platysoma</i>	29	42	71	13
<i>Mastacembelus reticulatus</i>	40	56	96	16
<i>Mastacembelus sclateri</i>	32	52	84	20
<i>Mastacembelus shiranus</i>	34	49	83	15
<i>Mastacembelus signatus</i>	32	54	86	22
<i>Mastacembelus stappersi</i>	38	58	96	20

Table II. (Continued).

	AV	CV	TV	CV – AV
<i>Mastacembelus tanganicæ</i>	39	48	87	9
<i>Mastacembelus vanderwaali</i>	32	50	82	18
<i>Mastacembelus zebratus</i>	28	44	72	16
<i>Mastacembelus sexdecimspinus</i>	32	56	88	24

The genus *Caecomastacembelus* was rejected by Roberts and Stewart (1976). They stated that the loss of the eyes and the usually associated depigmentation are reduction characters which, especially in genera such as *Rhamdia* and *Mastacembelus* in which the eyes are normally small and of secondary importance, can occur independently and without other notable changes. They justified their position by showing the impossibility to determine whether different species, which may be attributed to such a genus, did evolve independently. Furthermore, they pointed out that contrary to the objectives of a phyletic classification this would inevitably lead to the recognition of polyphyletic taxa. Therefore, they did not recognize any other genus distinguished solely by the absence of the eyes and a superficial depigmentation.

Contrary to Roberts and Stewart (1976), Travers (1984b) did recognize the genus *Caecomastacembelus* but changed completely the concept of the genus by including several other species. In fact, Travers (1984b) recognized two genera within the *Afromastacembelinae*: *Caecomastacembelus* and *Afromastacembelus* Travers, 1984 with its type species *Mastacembelus tanganicæ* Günther, 1893.

The genus *Caecomastacembelus* was redefined by Travers (1984b: 144) as ‘...fishes of small to moderately large size. With no pharyngobranchial 2 toothplate and less than five preopercular sensory canal pores. Species with atrophied eye tissues and one (i.e. type for genus) is anoptic. General morphological simplification (by secondary reduction and loss) occurs in microphthalmic and cryptophthalmic species’. Twenty-two species were tentatively assigned to the genus. Travers (1984b) mentioned that probably five additional species had to be included in the genus but that no material was available for study.

Two synapomorphies were listed by Travers (1984b) to support the monophyly of this assemblage, the absence of a toothplate on pharyngobranchial 2 and fewer than five preopercular sensory canal pores (see Travers 1984b: Figure 1, Nos 94, 95).

The genus *Afromastacembelus* was defined by Travers (1984b: 145) as ‘...fishes of moderate to large size; occur predomin[an]tly from eastern half of the continent and include species endemic to Lake Tanganyika. All *afromastacembeline* species, other than those assigned to *Caecomastacembelus*, provisionally lumped in this “catch-all” assemblage (which may not be monophyletic) pending closer examination of the groups interspecific relationships’. Sixteen species were tentatively placed in this genus. Travers (1984b) added that probably three more had to be included but that material was unavailable for study.

No synapomorphies were listed by Travers (1984b) to support the monophyly of this assemblage.

Travers (1988) revealed *M. tanganicæ* to be a member of the genus *Caecomastacembelus*. Since this species was the type species of the genus *Afromastacembelus*, according to the International Code of Zoological Nomenclature (ICZN, 1999: 64, Article 61.3.1.), the genus *Afromastacembelus* was placed in synonymy with *Caecomastacembelus*. For the other species previously allocated to the genus *Afromastacembelus* and not transferred to the genus *Caecomastacembelus* a new genus name, *Aethiomastacembelus*, was introduced (Travers

Table III. Character statement in the diagnosis of the *Afromastacembelinae* genera following Travers (1988, 1992a, 1992b).

<i>Aethiomastacembelus</i> Travers, 1988	<i>Caecomastacembelus</i> Poll, 1958
Type species: <i>Mastacembelus marcheii</i> Sauvage, 1879	Type species: <i>Caecomastacembelus brichardi</i> Poll, 1958
1. Fewer than 95 anal fin rays and tendency to have more dorsal than anal fin rays	1. Usually more than 100 anal fin rays and 100 dorsal fin rays and tendency to have more anal than dorsal fin rays
2. Ten to 20 principal caudal fin rays	2. Eight to 10 principal caudal fin rays
3. Tendency to have a pointed snout	3. Tendency to have a blunt snout
4. Jaw cleft extending beyond posterior nasal	4. Jaw cleft below or anterior to posterior nasal
5. Origin of first dorsal spine dorsal or just posterior to pectoral fin when flat against lateral wall of body	5. Origin of first dorsal spine posterior to pectoral fin when flat against lateral wall of body
6. Four to seven predorsal vertebrae	6. Eight to 12 predorsal vertebrae
7. Body depth greatest midway along length	7. Body height even for most of length
8. Median fins of even height	8. Median fins low and fleshy, increase in height caudally

1988). *Mastacembelus marcheii* Sauvage, 1879 was designated as the type species of this new genus. Important to mention is that previously Travers (1984b) had placed *M. marcheii* in the genus *Caecomastacembelus* because of the presence of a toothplate on the pharyngobranchial 2. As a consequence, the monophyly of the genus *Caecomastacembelus* was no longer supported by this supposedly synapomorphic character. The transfer of *M. tangerinae* from the genus *Afromastacembelus* to the genus *Caecomastacembelus* and the reverse transfer of *M. marcheii* were never properly justified by Travers (1988). Nevertheless, Travers (1992a, 1992b) presented new diagnoses of the genera (Table III). Travers (personal communication) mentioned that a suite of characters defines them and if used separately they could prove unreliable.

As a result of all these nomenclatorial changes, the generic position of some African spiny-eel species is largely confusing and it is especially unclear in which genus the different species should be placed (see also Seegers 1996).

Two main reasons can be given for the present confusion: (1) the many changes from one genus to the other and vice versa introduced by Travers himself without any clear justification (Table IV) and (2) the diagnosis of a genus (Table III) which in many cases is in contradiction with the character states observed. Seegers (1996) illustrated this problem based on the anal and dorsal soft fin ray numbers reported by Travers (1992b) for *Aethiomastacembelus*, *Caecomastacembelus* and the *frenatus* group. These problems were discussed in detail by Vreven and Teugels (1996). Study of the type material of both genera by Vreven and Teugels (1996) revealed several inaccuracies and contradictions in the diagnosis of both genera (Table V). For instance, the type specimens of *C. brichardi* have only four predorsal vertebrae whereas according to the diagnosis 8–12 predorsal vertebrae characterize species of the genus *Caecomastacembelus*. As a result, for this character *C. brichardi* agrees with the diagnosis of *Aethiomastacembelus* (four to seven predorsal vertebrae) rather than with that of *Caecomastacembelus*.

Similarly, there are also problems with the monophyletic characters of the Asian *Mastacembelinae* (see above) and, as a consequence, the validity of genera as separate

Table IV. Changes in generic placement of the African Mastacembelidae species since Travers (1984b).

Nominal species and subspecies	Tr., 1984b	Tr., 1986	Ro., 1986	Tr., 1988	Tr., 1992a	Tr., 1992b	Co., 1991	Vr., 1996, 1997
<i>M. albomaculatus</i> Poll, 1953	<i>Afro</i>			<i>Aethio</i> *			<i>Caeco</i>	
<i>M. ansorgii</i> Boulenger, 1905	<i>'Caeco'</i>							
<i>M. aviceps</i> Roberts and Stewart, 1976	<i>Caeco</i>							
<i>M. batesii</i> Boulenger, 1911	<i>Caeco</i>							
<i>M. brachyrhinus</i> Boulenger, 1899	<i>Caeco</i>							
<i>M. brevicauda</i> Boulenger, 1911	<i>Caeco</i>							
<i>C. brichardi</i> Poll, 1958	<i>Caeco</i> †							
<i>M. catchpolei</i> Fowler, 1936		<i>'Caeco'</i>						
<i>M. congicus</i> Boulenger, 1896	<i>Afro</i>			<i>Aethio</i> *		<i>Aethio</i>		
<i>M. crassus</i> Roberts and Stewart, 1976	<i>Caeco</i>							
<i>M. christyi</i> Worthington and Ricardo, 1936	–	–	–	–	–	–	–	–
<i>M. cryptacanthus</i> Günther, 1867	<i>'Caeco'</i>							
<i>M. cunningtoni</i> Boulenger, 1906	<i>Afro</i>			<i>Aethio</i> *			<i>Aethio</i>	
<i>M. decorsei</i> Pellegrin, 1919		<i>'Caeco'</i>						
<i>M. ellipsifer</i> Boulenger, 1899	<i>Afro</i>			<i>Aethio</i> *			<i>Aethio</i>	
<i>M. flavidus</i> Matthes, 1962	<i>Afro</i>			<i>Aethio</i> *			<i>Aethio</i>	
<i>M. flavomarginatus</i> Boulenger, 1898	<i>Caeco</i>							
<i>M. frenatus</i> Boulenger, 1901	<i>Afro</i>			<i>Aethio</i> *		<i>Caeco</i>	<i>Caeco</i>	
<i>M. goro</i> Boulenger, 1902	<i>Caeco</i>							
<i>M. greshoffi</i> Boulenger, 1901	<i>Caeco</i>							
<i>M. latens</i> Roberts and Stewart, 1976	<i>Caeco</i>							
<i>M. laticauda</i> Ahl, 1937	<i>'Caeco'</i>	–	–	–	–	–	–	–
<i>M. liberiensis</i> Boulenger, 1898	<i>Caeco</i>				<i>Aethio</i>			
<i>M. loenbergi</i> Boulenger, 1898	<i>Caeco</i>							
<i>M. longicauda</i> Boulenger, 1907	<i>Caeco</i>							
<i>M. marchei</i> Sauvage, 1879	<i>Caeco</i>			<i>Aethio</i> †				
<i>M. marmoratus</i> Perugia, 1891	<i>Caeco</i>							
<i>M. mellandi</i> Boulenger, 1914	–	–	–	–	–	–	–	–
<i>M. micropectus</i> Matthes, 1962	<i>Afro</i>			<i>Aethio</i> *			<i>Caeco</i>	
<i>M. moerui</i> Boulenger, 1914	<i>'Afro'</i>			<i>Aethio</i> *				
<i>M. moorii</i> Boulenger, 1898	<i>Afro</i>			<i>Aethio</i> *			<i>Caeco</i>	
<i>M. moorii nigrofasciatus</i> David and Poll, 1937	–	–	–	–	–	–	–	–
<i>M. mutombo</i> Pellegrin, 1936	–	–	–	–	–	–	–	–
<i>M. niger</i> Sauvage, 1879	<i>Caeco</i>							
<i>M. nigromarginatus</i> Boulenger, 1898	<i>Caeco</i>		<i>Afro</i>	<i>Aethio</i> *	<i>Aethio</i>			
<i>M. ophidium</i> Günther, 1893	<i>Afro</i>			<i>Aethio</i> *			<i>Caeco</i>	
<i>M. paucispinis</i> Boulenger, 1899	<i>Caeco</i>		<i>Afro</i>	<i>Aethio</i> *				

Downloaded by [University of Bath] at 18:03 13 February 2014

Table IV. (Continued).

Nominal species and subspecies	Tr., 1984b	Tr., 1986	Ro., 1986	Tr., 1988	Tr., 1992a	Tr., 1992b	Co., 1991	Vr., 1996, 1997
<i>M. plagiostomus</i> Matthes, 1962	<i>Afro</i>			<i>Aethio</i> *	<i>Aethio</i>		<i>Caeco</i>	
<i>M. platysoma</i> Poll and Matthes, 1962	<i>Afro</i>			<i>Aethio</i> *			<i>Aethio</i>	
<i>A. praensis</i> Travers, 1992					<i>Aethio</i>			
<i>M. reticulatus</i> Boulenger, 1911	<i>Caeco</i>							
<i>A. robertsi</i> Vreven and Teugels, 1996								<i>Aethio</i>
<i>M. sanagali</i> Thys van den Audenaerde, 1972	' <i>Caeco</i> '		<i>Afro</i>	<i>Aethio</i> *	<i>Aethio</i>			
<i>M. sclateri</i> Boulenger, 1903	<i>Caeco</i>							
<i>M. seiteri</i> Thys van den Audenaerde, 1972	' <i>Caeco</i> '							
<i>C. sp.</i> = <i>A. sexdecimspinus</i> Roberts and Travers, 1986	<i>Caeco</i>		<i>Afro</i>	<i>Aethio</i> *	<i>Aethio</i>			
<i>M. shiramus</i> Günther, 1896	<i>Afro</i>			<i>Aethio</i> *				
<i>M. signatus</i> Boulenger, 1905	' <i>Afro</i> '			<i>Aethio</i> *				
<i>M. stappersi</i> Boulenger, 1914	<i>Afro</i>			<i>Aethio</i> *				
<i>M. taeniatus</i> Boulenger, 1901	–	–	–	–	–	–	–	–
<i>C. taiaensis</i> Travers, 1992					<i>Caeco</i>			
<i>M. tanganycae</i> Günther, 1893	<i>Afro</i> [†]			<i>Caeco</i>			<i>Caeco</i>	
<i>M. thompsoni</i> Boulenger, 1917	–	–	–	–	–	–	–	–
<i>A. traversi</i> Vreven and Teugels, 1997								<i>Aethio</i>
<i>M. trispinosus</i> Steindachner, 1911	' <i>Afro</i> '			<i>Aethio</i> *				
<i>M. ubangensis</i> Boulenger, 1911	<i>Caeco</i>							
<i>M. vanderwaali</i> Skelton, 1976	<i>Afro</i>			<i>Aethio</i> *				
<i>M. victoriae</i> Boulenger, 1903	–	–	–	–	–	–	–	–
<i>M. zebratus</i> Matthes, 1962	<i>Afro</i>			<i>Aethio</i> *			<i>Caeco</i>	

References used: Tr., Travers; except for Tr., 1986, Travers et al., 1986; Ro., Roberts and Travers; Co., Coulter; Vr., Vreven and Teugels. Abbreviations: *Afro*, *Afromastacembelus*; *Caeco*, *Caecomastacembelus*; ' ', refer to species tentatively allocated to a genus; *Aethio**, species transferred from the genus *Afromastacembelus* to *Aethiomastacembelus* due to the nomenclatorial changes of Travers (1988); –, species already recognized as junior synonyms before Travers (1984b). [†]Type species.

monophyletic lineages needs confirmation as well. The monophyly of the genus *Macrognathus* was supported by eight synapomorphies (Travers 1984b) (see Figure 1, Nos 61–68). In contrast, the monophyly of the genus *Mastacembelus* was not supported by any synapomorphy (see Figure 1, lineage D).

Table V. Diagnostic characters of the type species of *Caecomastacembelus* and *Aethiomastacembelus* which are not in accordance with the generic definition as given by Travers (1988, 1992a, 1992b).

<i>Aethiomastacembelus</i> Travers, 1988	<i>Caecomastacembelus</i> Poll, 1958
Type species: <i>Mastacembelus marcheii</i> Sauvage, 1879	Type species: <i>Caecomastacembelus brichardi</i> Poll, 1958
2. Eleven to 13 principal caudal fin rays	1. Fifty-three to 57 dorsal fin rays and 56–61 anal fin rays
4. Jaw cleft anterior to posterior nasal	5. Anterior origin of first dorsal spine anterior to posterior end of pectoral fin when flat against lateral wall of body
8. Dorsal median fin higher than anal one	6. Four predorsal vertebrae

Conclusions

On the subfamily level

At present, a sister-group relationship between Mastacembelinae (Oriental region) and Afromastacembelinae (Ethiopic region) in the family Mastacembelidae, as proposed and defined by Travers (1984b), could not be confirmed; the use of the subfamilies is rejected to avoid further destabilization of Mastacembelidae nomenclature. The characters proposed to support their monophyly are unconvincing. Evidence is proposed suggesting that the Mastacembelinae at least is a paraphyletic assemblage.

Additional research on the phylogeny of the Mastacembelidae and at a higher taxonomic level of the suborder Mastacembeloidei and of the order Synbranchiformes is certainly necessary.

On the generic level

The nomenclature of the African genera has been highly confusing since the taxonomic changes introduced by Travers (1984b). At present, there is no phylogenetic evidence supporting their validity (monophyly) and there are no straightforward diagnostic character(s) available for their diagnosis.

The present situation is harmful to the stability of the generic nomenclature of the African Mastacembelidae. Therefore, I suggest that the present use of the genera *Caecomastacembelus* and *Aethiomastacembelus* should be abandoned and that both genera are here placed in synonymy with *Mastacembelus*.

Examined specimens

Oriental Mastacembelidae

Macrogathus aculeatus (Bloch, 1786)—ANSP 62787 (6 of 10, 178–194 mm TL); BMNH unregistered (1 c/s); BMNH 1889.2.1:3622–3625 (1 of 4 c/s); CAS 49490 (3 of 4, 185–232 mm TL). *Macrogathus aral* (Bloch and Schneider, 1801)—CAS 42592 (8 of 28, 146–177 mm TL); USNM 344664 (1 of 4, 184 mm TL). *Macrogathus siamensis* (Günther, 1861)—BMNH unregistered (1 c/s), specimen previously identified as *Macrogathus aculeatus* from Thailand but according to Roberts (1980) *M. aculeatus* is not known from

there. *Macrognaathus keithi* (Herre, 1940)—BMNH 1938.12.1:267 (1 paratype, 137 mm TL); CAS-SU 33017 (7 paratypes, 55–102 mm TL); CAS-SU 33740 (2, 185–226 mm TL). *Macrognaathus maculatus* (Cuvier in Cuvier and Valenciennes, 1832)—CAS-SU 39412 (8+1 of 32, 188–236 mm TL); USNM 326034 (3 of 50+, 157–212 mm TL). *Macrognaathus pancalus* Hamilton, 1822—BMNH 1858.8.15.80 (3 syntypes, 103–126 mm TL), stated to be the types by Günther; no type status (Hora 1929 *vide* Sufi, 1956); labelled as neotypes. CAS 50329 (6, 75–115 mm TL); CAS-SU 35644 (10, 106–142 mm TL). *Mastacembelus mastacembelus* (Banks and Solander, in Russell, 1794)—BMNH 1955.6.25:4–6 (3 syntypes, 306–567 mm TL); BMNH 1891.6.19.3 (c/s); BMNH 1974.2.22:1799–1806 (1 of 8 c/s); SMF 28589 (582 mm TL); SMF 28590 (189 mm TL); SMF 28591 (4, 63–306 mm TL); SMF 28592 (215 mm TL), SMF 28593 (2, 331–356 mm TL); SMF 28594 (307 mm TL). *Mastacembelus armatus* (Lacepède, 1800)—BMNH 1860.3.19:918 (433 mm TL) (type of *M. caudatus*); AMNH 10274 (2 c/s); ANSP 59570 (8 of 20, 81–131 mm TL); CAS 92579 (8 of 15, 179–248 mm TL); MCZ 47230 (1 c/s). specimen previously identified as *M. unicolor* a species which does not occur in Thailand (Roberts 1986, 1989). USNM 246766 (1 of 7, 194 mm TL); USNM 319465 (2 of 7, 231–250 mm TL). *Mastacembelus erythrotaenia* Bleeker, 1850—RMNH 6437 [6 specimens listed as syntypes, 290–640 mm TL], smallest of these specimens is probably holotype (Van Oijen, personal communication). AMNH 43433 (c/s); BMNH unregistered (c/s); BMNH unregistered (c/s); CAS-SU 33717 (2, 288–340 mm TL); ROM 30223 (3, 257–309 mm TL); ROM 52488 (284 TL) misidentified=*M. unicolor*; ROM 53683 (6, 249–544 mm TL); ROM 53684 (407 mm TL). *Mastacembelus unicolor* Cuvier (ex Kuhl and van Hasselt), in Cuvier and Valenciennes, 1832)—BMNH 1978.3.20:306–307 (1 of 2 c/s), specimen previously identified as *M. armatus* which however does not occur in Borneo (Roberts 1989); BMNH 1978.3.20:317 (c/s); and ROM 54191 (15, 160–285 mm TL). *Mastacembelus zebrinus* Blyth, 1858—MCZ 902 (c/s). *Mastacembelus* sp.—MRAC A1-023-P-0002–0003 (2, c/s). *Sinobdella sinensis* (Bleeker, 1870)—BMNH 1888.3.23:60–62 (3 specimens listed as syntypes: 119–169 mm TL); BMNH 1895.5.31:13–14 (1 syntype?, 202 mm TL); AMNH 11077 (159 mm TL); AMNH 11077SW (c/s); AMNH 11078 (3, 120–139 mm TL); AMNH 11078SW (c/s); ANSP 86782 (1 of 2, 179 mm TL); CAS-SU 23683 (2, 179–228 mm TL).

Note: species identifications as on the collection labels unless otherwise stated. Identifications have been verified through comparison with available literature and type material. The generic-level classification used above follows Travers (1984b). Using this classification it was possible to attribute all species to a genus contrary to Roberts' (1989) classification for which only a restricted number of species were listed. Based on the present knowledge, I was unable to decide which of these classifications deserved preference.

African Mastacembelidae

Mastacembelus albomaculatus Poll, 1953—BMNH unregistered (c/s); MCZ 49212 (c/s). *Mastacembelus aviceps* Roberts and Stewart, 1976—MCZ 50565 (6 paratypes, c/s). *Caecomastacembelus brichardi* Poll, 1959—AMNH 31999 (c/s); and MCZ 50255 (6, c/s). *Mastacembelus congicus* Boulenger, 1896—BMNH 1975.6.20:696–697 (2, c/s), MRAC 60926 (c/s), previously identified as *M. sclateri*; MRAC 164290 (c/s) (= *M.* sp.). *Mastacembelus crassus* Roberts and Stewart, 1976—MCZ 50258 (9 paratypes, c/s). *Mastacembelus* sp. (possibly *M. cryptacanthus* Günther, 1867)—BMNH unregistered (c/s). *Mastacembelus ellipsifer* Boulenger, 1899—BMNH unregistered (c/s). *Mastacembelus*

frenatus Boulenger, 1901—AMNH 215940 (c/s), MRAC 31437 (c/s), previously identified as *M. taeniatus*; MRAC 79-01-P-6339 (c/s), previously identified as *M. mellandi*. *Mastacembelus greshoffi* Boulenger, 1901—MRAC A1-023-P-0001 (c/s). *Mastacembelus liberiensis* Boulenger, 1898—AMNH 35421 (c/s). *Mastacembelus micropectus* Matthes, 1962—MCZ 49210 (2, c/s); MRAC 130812 (c/s). *Mastacembelus moorii* Boulenger, 1898—MRAC 63742 (c/s). *Mastacembelus niger* Sauvage, 1879—MRAC 137365 (c/s); MRAC 118719 (c/s), previously identified as *M. marmoratus*. *Mastacembelus paucispinis* Boulenger, 1899—MRAC 178099 (c/s). *Mastacembelus platysoma* Poll and Matthes, 1962—MRAC 78-25-P-38 (c/s). *Mastacembelus shiranus* Günther, 1896—BMNH unregistered (c/s). *Caecomastacembelus taiaensis* Travers, 1992—MRAC 73-10-P-7372 (paratype, c/s). *Mastacembelus tanganicæ* Günther, 1893—MCZ 49209 (2, c/s). *Mastacembelus vanderwaali* Skelton, 1976—AMG/P 3450 (5 paratypes, c/s). *Mastacembelus zebratus* Matthes, 1962—MCZ 49211 (c/s).

Acknowledgements

I thank Dr R. Britz (Eberhard-Karls Universität Tübingen, Germany), Dr J. Snoeks (MRAC), Prof. Dr G. G. Teugels (MRAC) and an anonymous referee for critically reading and commenting upon earlier drafts of this article, and G. Frateur (UFSIA) for correcting the English. Dr R. Britz kindly allowed me to study his personal ontogenetic series of *M. pancalus*. Dr M. L. J. Stiassny (AMNH), Dr W. G. Saul and Dr S. A. Schaefer (ANSP), O. Crimmen and J. Maclaine (BMNH), Dr D. Catania and Dr W. Eschmeyer (CAS and CAS-SU), Dr K. E. Hartel (MCZ), Dr E. Holm, Dr Winterbottom and M. Mouse (ROM), Dr F. Krupp (SMF), and Dr R. P. Vari, S. W. Jewett and L. Palmer (USNM) are acknowledged for the loan of specimens under their care.

References

- Annandale N. 1918. Fish and fisheries of the Inlé Lake. Records of the Indian Museum (Calcutta) 14:33–64.
- Britz R. 1996. Ontogeny of ethmoidal region and hyopalatine arch in *Macrogathus pancalus* (Percomorpha, Mastacembeloidei), with critical remarks on mastacembeloid inter- and intrarelationships. American Museum Novitates, American Museum of Natural History, New York 3181(2): 1–18.
- Coulter GW. 1991. Lake Tanganyika and its life. Natural History Museum Publications. Oxford and New York: Oxford University Press. 354 p.
- ICZN. 1999. International Code of Zoological Nomenclature, Adopted by the International Union of Biological Sciences. 4th edn, London: The International Trust for Zoological Nomenclature 1999 c/o The Natural History Museum. 306 p.
- Johnson GD, Patterson C. 1993. Percormorph phylogeny: a survey of Acanthomorphs and a new proposal. Bulletin of Marine Science 52(1): 554–626.
- Kottelat M. 1991. Notes on the taxonomy and distribution of some Western Indonesian freshwater fishes, with diagnoses of a new genus and six new species (Pisces: Cyprinidae, Belontiidae, and Chaudhuriidae). Ichthyological Exploration of Freshwaters 2(3): 273–287.
- Kottelat M. 2000. Diagnoses of a new genus and 64 new species of fishes from Laos (Teleostei: Cyprinidae, Balitoridae, Bagridae, Syngnathidae, Chaudhuriidae and Tetraodontidae). Journal of South Asian Natural History 5(1): 37–82.
- Kottelat M, Lim KP. 1994. Diagnosis of two new genera and three new species of earthworm eels from the Malay Peninsula Borneo (Teleostei: Chaudhuriidae). Ichthyological Explorations of Freshwaters 5(2): 181–190.
- Leviton AE, Gibbs RH Jr, Heal E, Dawson CE. 1985. Standards in herpetology and ichthyology: Part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. Copeia 3:802–832.
- Poll M. 1958. Description d'un poisson aveugle nouveau du Congo Belge appartenant à la famille des Mastacembelidae. Revue de Zoologie et de Botanique africaines, Bruxelles, Belgique 57(3/4): 388–392.
- Roberts TR. 1980. A revision of the Asian Mastacembelid fish genus *Macrogathus*. Copeia 3:385–391.

- Roberts TR. 1986. Systematic review of the Mastacembelidae or spiny eels of Burma and Thailand, with description of two new species of *Macrogathus*. Japanese Journal of Ichthyology 33(2): 95–109.
- Roberts TR. 1989. The freshwater fishes of Western Borneo (Kalimantan Barat, Indonesia). Memoires of the Californian Academy of Sciences 14:1–210.
- Roberts TR, Stewart DJ. 1976. An ecological and systematic survey of fishes in the rapids of the lower Zaïre or Congo River. Bulletin of the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA 147(6): 239–317.
- Roberts TR, Travers RA. 1986. *Afromastacembelus sexdecimspinus*, a new species of mastacembelid spiny-eel from rapids in the Cross River Basin, Cameroon. Cybium 10(2): 105–114.
- Rosen DE. 1973. Interrelationships of higher euteleostean fishes. In: Greenwood PH, Miles RS, Patterson C, editors. Interrelationships of Fishes. London: Academic Press. p 397–513.
- Seegers L. 1996. The fishes of the Lake Rukwa Drainage. Koninklijk Museum voor Midden-Afrika, Tervuren, België, Annalen, Zoologische Wetenschappen, Musée Royal de l'Afrique Centrale, Belgique, Tervuren, Annales, Sciences Zoologiques 278:1–407.
- Sufi SMK. 1956. Revision of the Oriental fishes of the Family Mastacembelidae. Bulletin of the Raffles Museum, Singapore 27:93–146.
- Taylor WR, Van Dyke GC. 1985. Revised procedures for staining and clearing small fishes and other vertebrates for bone and cartilage study. Cybium 9(2): 107–119.
- Travers RA. 1984a. A review of the Mastacembeloidei, a suborder of synbranchiform teleost fishes, Part I: anatomical descriptions. Bulletin of the British Museum (Natural History) Zoological Series 46(1): 1–133.
- Travers RA. 1984b. A review of the Mastacembeloidei, a suborder of synbranchiform teleost fishes, Part II: phylogenetic analysis. Bulletin of the British Museum (Natural History) Zoological Series 47(2): 83–150.
- Travers RA. 1988. Diagnosis of a new African Mastacembelid spiny-eel genus *Aethiomastacembelus* gen. nov. (Mastacembeloidei: Synbranchiformes). Cybium 12(3): 255–257.
- Travers RA. 1992a. *Caecomastacembelus tafiaensis* and *Aethiomastacembelus praensis*, two new species of Mastacembelid spiny-eels from West Africa. Ichthyological Exploration of Freshwaters 2(4): 311–340.
- Travers RA. 1992b. Mastacembelidae. In: Lévêque C, Paugy D, Teugels GG, editors. Faune des Poissons d'eaux douces et saumâtres de l'Afrique de l'Ouest (Tome 2 Collection faune tropicale, XXVIII). Paris: Office de la Recherche Scientifique et Technique d'Outre-Mer (ORSTOM); Tervuren, Belgium: Musée Royal de l'Afrique Centrale (MRAC). p 848–857.
- Travers RA, Eynikel G, Thys van den Audenaerde DFE. 1986. Mastacembelidae. In: Daget J, Gosse J-P, Thys van den Audenaerde DFE, editors. Check-list of the Freshwater Fishes of Africa, CLOFFA. Vol. II, Brussels: ISNB; Tervuren, Belgium: MRAC; Paris: ORSTOM. p 415–427.
- Vreven EJ, Teugels GG. 1996. Description of a new Mastacembelid species (Synbranchiformes; Mastacembelidae) from the Zaïre River Basin in Africa. Copeia 1:130–139.
- Vreven EJ, Teugels GG. 1997. *Aethiomastacembelus traversi*, a new spiny-eel from the Zaïre River basin, Africa (Synbranchiformes: Mastacembelidae). Ichthyological Exploration of Freshwaters 8(1): 81–87.