



# Eocene handfishes from Monte Bolca, with description of a new genus and species, and a phylogeny of the family Brachionichthyidae (Teleostei: Lophiiformes)

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The family Brachionichthyidae, commonly known as the handfishes, is a small group of lophiiform fishes, the living species of which are restricted in distribution mostly to shallow temperate and subtropical waters of Tasmania and southern and eastern Australia. Despite their narrow present-day distribution, and the extreme rarity of lophiiforms in the fossil record, handfishes are well represented in the Eocene of Monte Bolca, Italy. A revision of the known fossil material shows the presence of two fossil species in two monotypic genera, †*Histionotophorus* and †*Orrichthys* **gen. nov.** Diagnoses of the family Brachionichthyidae, the two fossil genera, as well as two recognized extant genera *Brachionichthys* and *Sympterichthys* are provided. An osteological analysis of †*Histionotophorus bassani* revealed many new features as well as reinterpretations of some previously described skeletal parts. A phylogenetic analysis of brachionichthyid genera and representatives of the antennarioid families Antennariidae, Tetrabrachiidae, and Lophichthyidae, using 36 morphological characters, strongly supported monophyly of brachionichthyids and antennarioids, the former taxon representing the sister group of the other families of the latter. Within the Brachionichthyidae, the two extant genera *Brachionichthys* and *Sympterichthys* form a species pair, as do the extinct genera †*Histionotophorus* and †*Orrichthys* **gen. nov.** Biogeographical considerations suggest that the present geographical range of handfishes can be considered a residual distribution of a temporally and spatially dynamic range shift.

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## INTRODUCTION

Fishes of the family Brachionichthyidae constitute one of the most distinctive lineages within the teleost order Lophiiformes. These fishes exhibit an unusual morphology consisting of an elongate, slightly compressed body, a prominent sail-like spinous dorsal fin, and arm-like pectoral fins, which, together with the pelvic fins, are used to walk or trot along the sub-

strate in a more or less typical tetrapod-like fashion. The extremities of the pectoral fins are reminiscent of human hands thus accounting for the English common name of ‘handfishes’ (see Whitley, 1949). Extant handfishes are sedentary bottom-dwellers that primarily inhabit the continental shelf of temperate and subtropical parts of Tasmania and southern and eastern Australia, where they feed primarily on small crustaceans (Last *et al.*, 1983; Gomon *et al.*, 1994). The biology of handfishes is poorly known and their typically small population sizes and restricted

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distributions make them highly vulnerable to disturbance. At least some species are considered to be critically endangered (Last & Bruce, 1996; Bruce *et al.*, 1998, 1999).

Handfishes were first discovered by the French explorer-naturalist François Péron (1775–1810), who collected several individuals during Nicolas Thomas Baudin's (1750–1803) voyage of discovery to New Holland aboard the *Géographe* (1800–1804). These specimens were later examined and described by Lacepède (1804) under the names *Lophius hirsutus* and *Lophius laevis*. Perhaps realizing that the latter was preoccupied by *Lophius laevis* Latreille, 1804, a junior synonym of *Histrio histrio* (Linnaeus, 1758), and recognizing as well the uniqueness of the taxon relative to *Lophius*, Cuvier (1817) reallocated the species to the genus *Chironectes* (= *Antennarius*) calling it *Chironectes unipennis*. However, for some unknown reason, he rejected the name *Lophius hirsutus* Lacepède, 1804, as well, describing it, along with a remarkably accurate drawing of the skeleton, under the name *Chironectes punctatus*. Somewhat later, Richardson (1844) described a third handfish species, *Chironectes politus*, based on a single specimen collected at Port Arthur, Tasmania, during the voyage of the H.M.S. *Erebus* and *Terror* (1839–1843).

Bleeker (1855) was the first to appreciate the morphological differences between handfishes and other members of the Antennarioidei, placing them in a new genus, *Brachionichthys*. In a review of the classification of the lophiiform fishes (= Pediculati), Gill (1863) placed the handfishes in a separate antennariid subfamily, the Brachionichthyinae, and later (Gill, 1878, 1883) provided a preliminary diagnosis of the subfamily, while also erecting a new genus *Sympterychthys*, based primarily on external characters of the spinous dorsal fin. In the first comprehensive systematic study of the Lophiiformes, Regan (1912) recognized the handfishes as a distinct antennarioid family, including only *Brachionichthys*, with no mention of *Sympterychthys*. The latter genus was redefined by McCulloch & Waite (1918), and another new species described, *Sympterychthys verrucosus*, based on new material from South Australia (see also McCulloch, 1929). Nearly 90 years later, Last *et al.* (2007), described yet another new species of the family, *Brachionichthys australis*, bringing the number of valid extant species to five (and pointing out as well the existence of additional undescribed species of the family; see also Last *et al.*, 1983; Gomon *et al.*, 1994).

Despite the scarcity of studies devoted to these fishes, their phylogenetic position and role in the evolution of lophiiform fishes have been discussed by several authors. In his celebrated monograph on fish skulls, Gregory (1933) considered *Brachionichthys* (as

a genus of the Antennariidae) to be the most primitive member of the Lophiiformes. In comparing it to other antennarioid genera, he concluded that it is 'much less specialized and in fact seems to give clues to the origin of the entire order' (p. 387); 'the skeleton is relatively very primitive in appearance save that the stout pectoral pterygials are reduced to two and the pectoral fin is truly pediculate' (p. 388; see also Gregory & Conrad, 1936; Gregory, 1951). However, this hypothesis of relationship has not been confirmed by subsequent studies (Eaton *et al.*, 1954; Monod, 1960). Based on a detailed osteological study, Pietsch (1981) redefined the lophiiforms in a cladistic context recognizing the basal position of the Lophioidei relative to all other members of the order, and that of the Brachionichthyidae amongst antennarioids (thus forming the sister group of the Lophichthyidae, Tetrabrachiidae, and Antennariidae; see also Pietsch, 1984a; Pietsch & Grobecker, 1987).

Considering the low extant diversity, restricted geographical distribution, and very meagre fossil record of antennarioids in general (Carnevale & Pietsch, 2006, 2009b), the existence of fossil representatives of the family Brachionichthyidae is quite surprising. The first description of Eocene handfishes from Monte Bolca was provided by Baron Achille De Zigno (1887). De Zigno presented a single, nearly complete specimen under the name †*Histiocephalus bassani*, dedicating the species to the Italian palaeontologist Francesco Bassani. A few years later, Eastman (1904) published a redescription based on specimens in the collection of the Museum of Comparative Zoology, Harvard University, noting that the generic name †*Histiocephalus* was preoccupied and therefore proposing the erection of a replacement name, †*Histionotophorus*.

The familial assignment of †*Histionotophorus* has been the subject of a long and intense debate. Although De Zigno (1887) provided no familial attribution, Sir Arthur Smith Woodward (1901), in his monumental *Catalogue of fossil fishes*, suggested a possible relationship to scorpaenid fishes. Eastman (1904), however, rejecting Woodward's hypothesis, assigned it to the family Lophiidae based on the presence of two pectoral-fin radials. This in turn, however, was rejected by Gill (1904: 846) who, on the basis of Eastman's figures, considered †*Histionotophorus* to be an antennariid, close to or even to be included within '*Pterophryne*' (= *Histrio*). Soon after, Eastman (1905) reiterated the arguments regarding the number of pectoral-fin radials and their systematic relevance for the assignment of †*Histionotophorus* to the Lophiidae. However, the latter hypothesis was again rejected by Regan (1912), who assigned †*Histionotophorus* to the Antennariidae, leaving an unpublished note with the material examined (NHM

19060) comparing it with the extant handfish genus *Brachionichthys*, which, like the fossil, has only two pectoral-fin radials and a membranous connection between the second and third dorsal-fin spines (see Rosen & Patterson, 1969). Le Danois (1964) considered †*Histionotophorus* to be an antennariid, closely related to the extant genera *Rhycherus* and *Tathicarpus*, and Blot (1980) did the same without further explanation. Finally, Pietsch (1981) demonstrated conclusively the brachionichthyid affinities of †*Histionotophorus* and observed also that it does not appear to differ substantially from *Brachionichthys*.

The work described here is another in a series of papers that focuses on the fossil record of lophiiform fishes (Carnevale & Pietsch, 2006, 2009a, b; Carnevale *et al.*, 2008). The initial purpose of this paper was a morphological and taxonomic definition of †*Histionotophorus bassani*. However, soon after the study began we realized that material referred to this taxon included a new and previously unrecognized taxon. When the osteological descriptions of the fossils were completed, the paper thus expanded into a cladistic analysis of the brachionichthyid fishes and their antennarioid relatives. Thus the present paper has two goals, a description of the anatomy of fossil handfishes from Monte Bolca and a cladistic interpretation of the phylogeny of handfishes and antennarioids. The biogeography of the family Brachionichthyidae is also discussed.

## GEOLOGICAL SETTING

The celebrated locality of Monte Bolca lies in the eastern part of Monti Lessini in the valley of the Fiume Alpone, approximately 2 km north-east of the village of Bolca, near Verona, northern Italy. This locality includes several productive sites characterized by different fossil content (see Tang, 2001). The best known of these sites is that of the Pesciara cave, which has been extensively exploited since the mid-sixteenth century for its superbly preserved fishes (e.g. see Blot, 1969; Gaudant, 1997), now disseminated in museums and private collections around the world. Moreover, finely preserved invertebrates (polychaete worms, jellyfish, cephalopods, crustaceans, and insects) and plants are also rather common in the fossiliferous strata of the Pesciara cave site.

The geology of the fish-bearing limestone strata has been investigated by several authors (e.g. Fabiani, 1914, 1915; Sorbini, 1968; Barbieri & Medizza, 1969; Massari & Sorbini, 1975) and more recently a new stratigraphical study has been realized by Papazzoni & Trevisani (2006). The deposits of the Pesciara cave site belong to the so-called 'Calcari Nummulitici', an informal unit of Eocene age widespread in the surroundings of Monte Bolca. The sedimentary succes-

sion outcropping at the Pesciara cave site consists of a calcareous block surrounded by volcanic deposits. The whole outcrop is less than 20 m thick and covers an area of a few hundred square metres. According to Papazzoni & Trevisani (2006), the Pesciara cave stratigraphical section is primarily characterized by a rhythmic alternation of finely laminated micritic limestone with fishes and plants and biocalcarenite/biocalcirudite-bearing benthic fossils. Fishes occur in varved limestone characterized by a micritic matrix, with sparse pyrite and bitumen. These fossils are usually fully articulated with complete squamation and, in certain cases, preserved pigmentation patterns (e.g. Blot, 1984; Bellwood & Sorbini, 1995; Tyler & Sorbini, 1999; Bannikov, 2004). The excellent preservation of the fossils, nearly complete absence of bioturbation, laminated style of the deposit, limited number of benthic taxa, and presence of bitumen and pyrite are indicative of poorly oxygenated bottoms during the deposition of the micritic limestone. The palaeoecological structure and palaeoenvironmental setting of the limestone deposits of the Pesciara cave site have been discussed by many authors, thereby resulting in a confusing scenario of palaeogeographical interpretations and reconstructions. Based on both sedimentological and palaeontological evidence, Sorbini (1968) and Massari & Sorbini (1975) suggested that these deposits originated in a tropical coastal lagoon in close proximity to coral reefs occasionally isolated from the open ocean. Subsequently, Landini & Sorbini (1996) realized a detailed comprehensive palaeoecological study primarily based on the ichthyofauna. They concluded that sedimentation occurred at a short distance from the coast, many dozens of metres in depth, in a silled depression with restricted circulation on the seafloor. The structure and composition of the fish assemblage clearly indicate that coral reefs and seagrass beds were present in close proximity to the depositional environment, as well as well-developed fluvial systems. More recently, Papazzoni & Trevisani (2006), on the basis of facies analysis and foraminiferal palaeoecology, hypothesized that the ichthyoliferous layers were deposited in a subtropical lagoon close to an emerged area, characterized by seasonal changes of water circulation, which affected the oxygen content on the seabottom. In summary, despite the lack of consensus about the physiography of the depositional environment and possible presence of coral reefs in its vicinity, all the authors concluded that the micritic sedimentation took place in a depressed basin characterized by permanent bottom anoxia and low hydrodynamic energy, close to the coast in a tropical or subtropical context.

The stratigraphical and palaeoenvironmental settings of the laminated micritic limestone, and the

taphonomic features and ecological spectrum of the fossil assemblage seem to indicate that the Pesciara cave limestone represents an obrutionary stagnation deposit (Seilacher *et al.*, 1985).

As indicated above, the Pesciara cave site lies within the lower-middle Eocene outcrop, commonly known as Calcari Nummulitici, which originated after the pelagic deposition of the Cretaceous-Eocene Scaglia Rossa Formation in a period characterized by intense volcanic activity (e.g. Barbieri *et al.*, 1982, 1991). Based on calcareous nannofossil content, Medizza (1975) referred the fossiliferous limestone of the Pesciara cave site to the *Discoaster subloidoensis* Zone, whereas Hottinger (1960), and more recently Papazzoni & Trevisani (2006), on the basis of the macroforaminiferans, assigned these deposits to the *Alveolina dainellii* Zone. Therefore, according to the biostratigraphical scheme proposed by Serra-Kiel *et al.* (1998), the Pesciara cave limestone could be referred to the SBZ 11 biozone, corresponding to the Middle Cuisian (late Ypresian; about 50 Mya).

The fish fauna of Monte Bolca is certainly one of the most important ichthyofaunistic fossil assemblages known. As a result of their excellent preservation, these fishes have been investigated by numerous palaeontologists and zoologists, the results of which have contributed greatly to modern systematic and phylogenetic studies. The fish assemblage consists of more than 250 species, including sharks, batoids, remnants of Mesozoic neopterygians (pseudodontiforms), and teleosts, representing as well the earliest record of an acanthomorph dominated fish assemblage, bearing the first representatives of almost all fish groups found on coral reefs today (Patterson, 1993; Bellwood, 1996; Landini & Sorbini, 1996). The morphology of the fishes recovered from Monte Bolca is almost indistinguishable from that of living representatives. Therefore, this extraordinary fossil assemblage marks the starting point in the known evolution of most reef fish groups (Bellwood & Wainwright, 2002), providing strong evidence of the stability of the taxonomic and morphological characteristics of tropical and subtropical marine ichthyofaunas throughout the Tertiary era.

Fishes of the order Lophiiformes are relatively rare in the fossiliferous limestone of the Pesciara cave site. Except for the brachionichthyid taxa described herein, the Monte Bolca fish assemblage includes at least one lophiid species and one recently described member of the family Antennariidae (Carnevale & Pietsch, 2009b). In a preliminary catalogue of the fish assemblage, Blot (1980) listed an undescribed ogcocephalid; however, a cursory overview of the material referred to this family clearly revealed that it cannot be assigned to the Ogcocephalidae, rather it is a member of the family Lophiidae.

## MATERIAL AND METHODS

Standard length (SL) is used throughout. Methods for taking counts and measurements follow Pietsch & Grobecker (1987), whereas osteological terminology, unless noted otherwise, follows Pietsch (1981). Material was cleared and double-stained with alizarin red S and alcian blue following the trypsin digestion technique of Potthoff (1984). Anatomical information extracted from the literature was confirmed by examining specimens whenever possible. The term 'handfish' is used here as a synonym of 'brachionichthyid'. All extinct taxa are marked with daggers (†) preceding their names. The procedures employed in the phylogenetic analysis are described below under 'Phylogenetic relationships'.

Material examined is archived in the following institutions: Carnegie Museum, Pittsburgh (CM); Commonwealth Scientific and Industrial Research Organization, Hobart, Tasmania (CSIRO); Museo Civico di Storia Naturale, Verona (MCSNV); Museum of Comparative Zoology, Harvard University, Cambridge (MCZ); Museo di Geologia e Paleontologia, Università di Padova, Padova (MGPD); Muséum National d'Histoire Naturelle, Paris (MNHN); Natural History Museum, London (NHM); National Museum of Victoria, Melbourne (NMV); Queensland Museum, Brisbane (QM); South Australian Museum, Adelaide (SAMA); Burke Museum of Natural History and Culture, University of Washington, Seattle (UW). The new genus and species of handfish reported here is known from two well-preserved specimens in part and counterpart. †*Hisionotophorus bassani* is known from at least a dozen specimens, nine of which were examined in this study. Comparative lophiiform material examined is listed below, all cleared and double-stained unless indicated otherwise:

Lophiidae: *Lophius americanus*, UW 22288, about 600 mm SL (dried skeleton); *Sladenia* sp., CSIRO H.2559-02, 133 mm SL; NMV A.24757, about 500 mm SL (dried skeleton).

Antennariidae: *Antennarius striatus*, UW 20768, 2, 65–67 mm SL.

Tetrabrachiidae: *Tetrabrachium ocellatum*, QM I.27988, 1 of 2, 49 mm SL; QM I.30596, 1 of 8, 56 mm SL.

Lophichthyidae: *Lophichthys boschmai*, UW 20773, 2, 44–47 mm SL.

Brachionichthyidae: *Brachionichthys australis*, UW 116842, 38.7 mm SL; UW 116843, 1 of 2, 55.0 mm SL; *Brachionichthys hirsutus*, NMV A.19954, 80 mm SL; UW 20769, 42 mm SL; *Sympterichthys unipennis*, UW 116844, 31.6 mm SL; UW116845, 34 mm SL; *Sympterichthys verrucosus*, UW 47153, 43.6 mm SL; *Sympterichthys* sp., UW 116842, 37 mm SL.

Chaunacidae: *Chaunax pictus*, UW 20770, 90 mm SL.

## SYSTEMATICS

SUBDIVISION TELEOSTEI *SENSU* PATTERSON & ROSEN, 1977

ORDER LOPHIIFORMES GARMAN, 1899

SUBORDER ANTENNARIOIDEI *SENSU* PIETSCH, 1984a

FAMILY BRACHIONICHTHYIDAE GILL, 1878

Brachionichthyinae Gill, 1878: 221, 222 (subfamily erected to include *Brachionichthys* and *Sympterichthys*).

*Type genus*: *Brachionichthys* Bleeker, 1855: 12, 21.

*Diagnosis*: A lophiiform family unique and derived in having two elongate pectoral radials (not reduced in number through ontogeny); ceratobranchials I–IV curved; five branchiostegal rays; a well-developed membrane between the second and third dorsal-fin spine; and lacking vomerine and palatine teeth. The family is further distinguished from all other antennarioid families in having the following combination of character states: mouth horizontal to slightly oblique; ventral surface of vomer flat; articular head of quadrate broad; two pharyngobranchials present; vertebral column slightly curved, not sigmoid; epurals absent; three cephalic dorsal-fin spines; third dorsal-fin spine membranously attached to posterior margin of head.

*Remarks*: Gill (1863, 1878) described the Brachionichthyidae as unique amongst lophiiform families in having an elongate body, reduced mouth, toothless palate, second and third dorsal-fin spines connected by a membrane, and reduced pelvic bones. To this definition, Regan (1912) added a few meristic features, the number of pectoral-fin radials (two) and vertebral and dorsal-fin ray counts. Le Danois (1964) introduced some problematic features into the diagnosis, mostly concerning external morphology (i.e. the position and presence or absence of various cutaneous papillae, tubercles, lateral-line pores, etc.) and morphometrics; however, most of these features show a wide intrafamilial variability and are of no systematic significance except at perhaps the species level. As a result of his cladistic analysis of antennarioid fishes, Pietsch (1981) presented a new diagnosis based primarily on skeletal features. Many of these supposed brachionichthyid apomorphies, however, are shown here to be limited to *Brachionichthys* and do not extend to the fossil genera and for this reason are excluded from the diagnosis presented here. Moreover, one of the features presented by Pietsch (1981), parietals meeting on the midline, dorsal to the supraoccipital, was not confirmed in this study. A

further possible brachionichthyid apomorphy, presence of three subdivisions of the inclinator muscle of the second spine, was reported by Winterbottom (1974); however, the observations about this feature are limited to *Brachionichthys* and do not extend to *Sympterichthys* and the fossils and for this reason are excluded from the present diagnosis.

GENUS †*HISTIONOTOPHORUS* EASTMAN, 1904

†*Histiocephalus* De Zigno, 1887: 31 (type species *Histiocephalus bassani* De Zigno, 1887: 31, by monotypy).

†*Histionotophorus* Eastman, 1904: 32 (replacement name for *Histiocephalus* De Zigno, 1887: 31, preoccupied by *Histiocephalus* Diesing, 1851: 80, 230, for a genus of nematodes, therefore taking the same type species, *Histiocephalus bassani* De Zigno, 1887: 31).

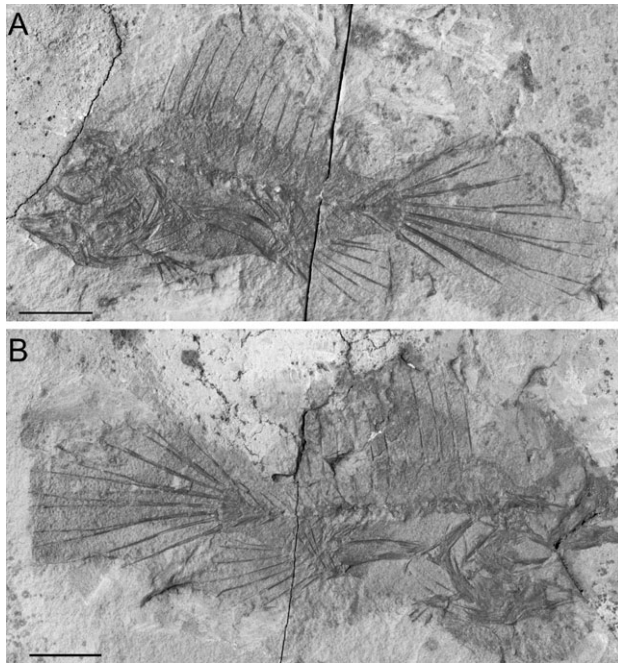
*Diagnosis*: A brachionichthyid genus unique and derived in having an elongate pointed caudal fin; foramina of the first dorsal-fin pterygiophore (which provide articulation for the illicium and second dorsal-fin spine) closely spaced; pterygiophores of the soft dorsal fin greatly enlarged; length of anal-fin base less than 20% SL; length of caudal peduncle greater than 15% SL. The genus is further distinguished from all other brachionichthyid genera in having the following combination of character states: jaw teeth small and appearing granular; vertebrae 19 (rarely 20); neural spines of abdominal vertebrae simple, not spatulate; haemal spines of abdominal vertebrae posteroventrally directed; first dorsal-fin pterygiophore greatly enlarged, hypertrophied; dorsal-fin rays 12–13; dorsal-fin rays extremely elongate; anal-fin rays eight to nine; pectoral-fin radials extremely elongate, length nearly 35% SL; body depth at origin of soft-dorsal fin nearly 42% SL; body depth at origin of anal fin approximately 31% SL; pectoral-fin rays seven; pelvic fin one spine and five rays; caudal-fin rays nine, the ventral-most ray greatly reduced; skin naked, without dermal spinules.

*Included species*: Monotypic.

†*HISTIONOTOPHORUS BASSANI* (DE ZIGNO, 1887)  
(FIGS 1–4)

†*Histiocephalus bassani* De Zigno, 1887: 23–24, pl. 1, fig. 9; Woodward, 1901: 579–580.

†*Histionotophorus bassani* Eastman, 1904: 32–33, pl. 1, figs 1–3; Eastman, 1905: 30; Gill, 1905: 845–846; Regan, 1912: 283; Le Danois, 1964: 141–144, figs 75–76; Rosen & Patterson, 1969: 442, fig. 60, pl. 76, fig. 2; Pietsch, 1981: 416–417; Frickhinger, 1991: 695.



**Figure 1.** †*Histionotophorus bassani* (De Zigno, 1887). A, B, holotype, MGPD 68487. Scale bars = 10 mm.

*Holotype:* MGPD 68487, nearly complete skeleton in part and counterpart, 55.1 mm SL; late early Eocene, Ypresian; Monte Bolca, Pesciara cave site.

*Additional material:* NHM 19060, complete skeleton, 16.4 mm SL, from the type locality; CM 5237, incomplete skeleton lacking the anterior part of the head skeleton and distal portions of dorsal-fin spines and rays, caudal-fin rays preserved as impression only; from the type locality. MCSNV I.G.23163, complete skeleton, 50.5 mm SL, from the type locality; MCSNV S.30, incomplete skeleton lacking the head and anterior part of the axial skeleton, from the type locality; MCSNV T.162/163, incomplete and poorly preserved specimen, from the type locality; MCSNV T.358, incomplete specimen lacking the caudal portion of the skeleton, 38.5 mm estimated SL, from the type locality. MCZ 5176a/5176b, nearly complete skeleton in part and counterpart, 34.5 mm SL, from the type locality; MCZ 5177a/5177b, nearly complete skeleton in part and counterpart, 38.4 mm SL, from the type locality.

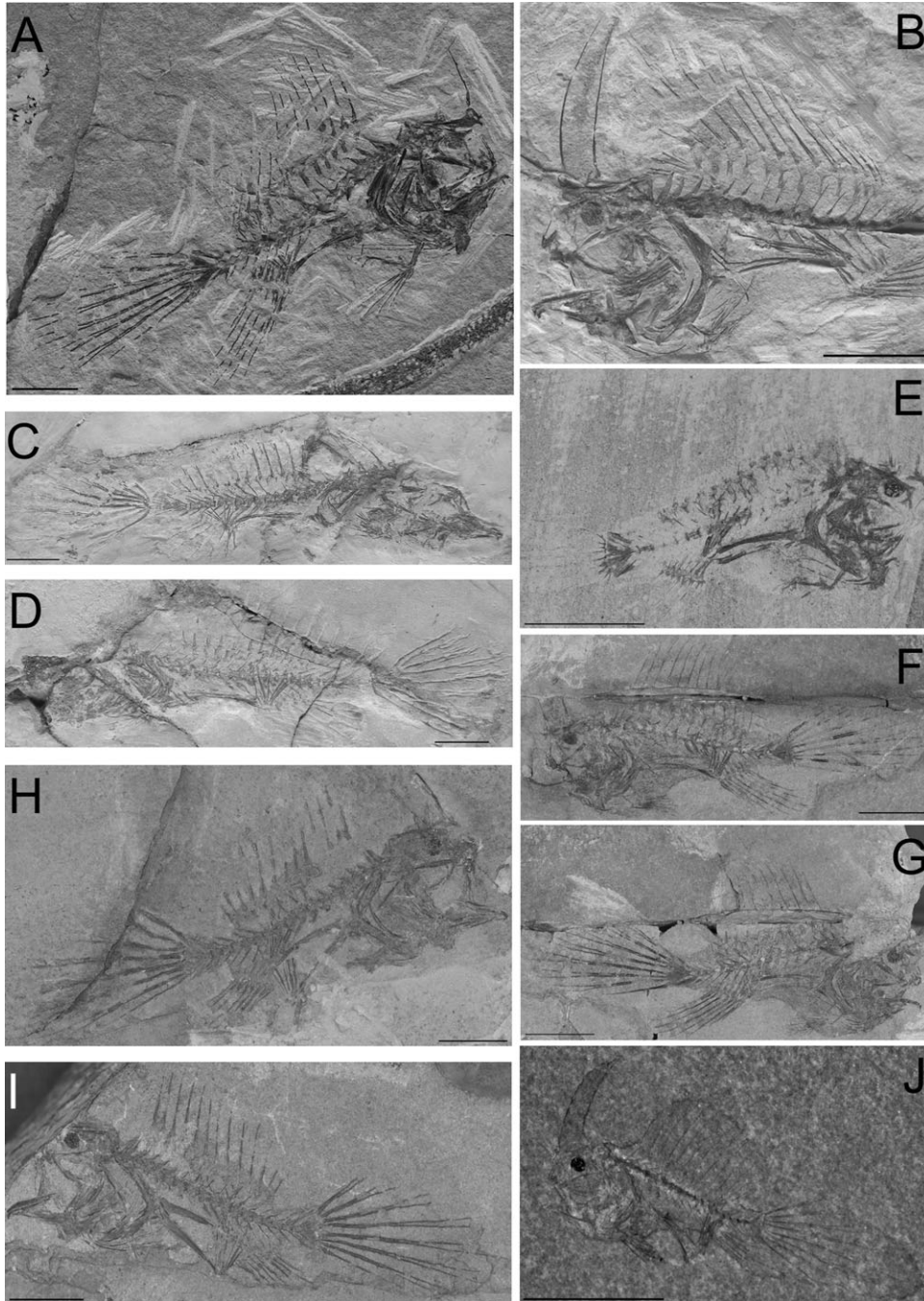
*Diagnosis:* As given for the genus.

*Description:* The body is moderately elongate and slightly compressed (Figs 1–3). The dorsal and ventral profile of the anterior part of the body is convex. The abdomen is expanded (Fig. 2B, F–G). The eyeball (based on preserved pigment) is close to the

dorsal margin of the head. The caudal peduncle is well developed, its average length greater than 16% SL (see Table 1). The head is short, contained more than three times in standard length. The snout is short (10.1–14.6% SL). The eyeball is relatively small (5.9–8.5% SL). The mouth is nearly horizontal, terminal, and relatively small. The illicium is slender and terminal on the snout. The second and third dorsal-fin spines are interconnected by a membrane (Fig. 2J). A membrane also connects the third spine with the dorsal mid-line of the body. The soft-dorsal fin is extremely well developed, sail-like. The central rays of the soft dorsal and anal fins are longer than the others; for this reason the posterior portion of the anal fin appears to be orientated vertically. The anal-fin base is relatively short (15.5% SL). The arm-like pectoral fins are characterized by extremely elongate radials (31.5–41.4% SL), bearing slender filamentous soft rays. The pelvic fin is elongate, with a short anterior spine and slender delicate soft rays. The caudal fin is sharply pointed (Fig. 3A), elongate (as long as 63.7% SL). For additional counts and measurements, see Table 1.

The neurocranium is relatively deep and robust (Fig. 4). The frontals are the largest bones of the skull roof, each relatively wide posteriorly, tapering anteriorly to form a prominent rostral process. The parietals are probably separated from each other. The mesethmoid, which forms a sort of interorbital septum, is columnar, with a broadly expanded ventral portion and a moderately constricted middle portion; the dorsal end of this bone articulates with the central extensions of the frontals. There is an evident gap between the mesethmoid and the vomer and parasphenoid that was probably occupied originally by the ethmoid cartilage. The lateral ethmoid is poorly preserved in all specimens examined; this bone appears to be thin and delicate, of irregular shape. The vomer is toothless, with a flattened ventral surface. The parasphenoid is a stout shaft throughout most of its length. The sphenotic (preserved in part only in MCSNV I.G. 23163) forms a prominent flange that extends laterally. The limits of the pterotic, prootic, epioccipital, and basioccipital are difficult to recognize as a result of inadequate preservation.

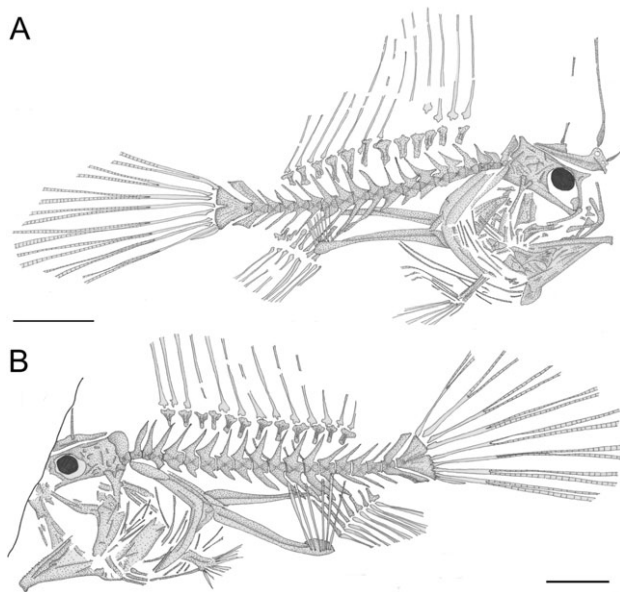
The premaxilla bears a long slender ascending process, a laminar well-developed articular process, and a thin spatulate postmaxillary process; the ascending and articular processes form an obtuse angle at their junctions. Minute granular teeth arranged in many irregular rows can be observed along the ventral surface of the alveolar process (Figs 3, 4). The morphology of the maxilla is rather difficult to recognize, often fragmented; the main axis of this bone appears to be slightly curved. The outer mandibular surface is sculptured, ornamented with



**Figure 2.** †*Histionotophorus bassani* (De Zigno, 1887). A, MCSNV G.23163; B, MCSNV T.358; C, D, MCSNV T.162/163; E, CM 5237; F, G, MCZ 5177a/b; H, I, MCZ 5176a/b; J, NHM 19060. Scale bars = 10 mm.

delicate striae. The dentary is relatively large, with a distinct pointed symphyseal spine; the alveolar process of this bone bears minute granular teeth similar to those of the premaxilla. The articular bears a stout coronoid process and a rounded posteroventral bony lamina. The angular is poorly preserved in the material examined.

The suspensorium (Figs 3, 4) consists of the ectopterygoid, endopterygoid, hyomandibula, metapterygoid, palatine, quadrate, and symplectic. The hyomandibula is forked dorsally, producing two articular heads; the main shaft of this bone is stout; a short opercular process arises along the upper sector of the posterior margin. The quadrate is



**Figure 3.** †*Histonotophorus bassani* (De Zigno, 1887). A, MCSNV G.23163, right lateral view of the entire skeleton; B, MCZ 5176b, left lateral view of the entire skeleton. Scale bars = 10 mm.

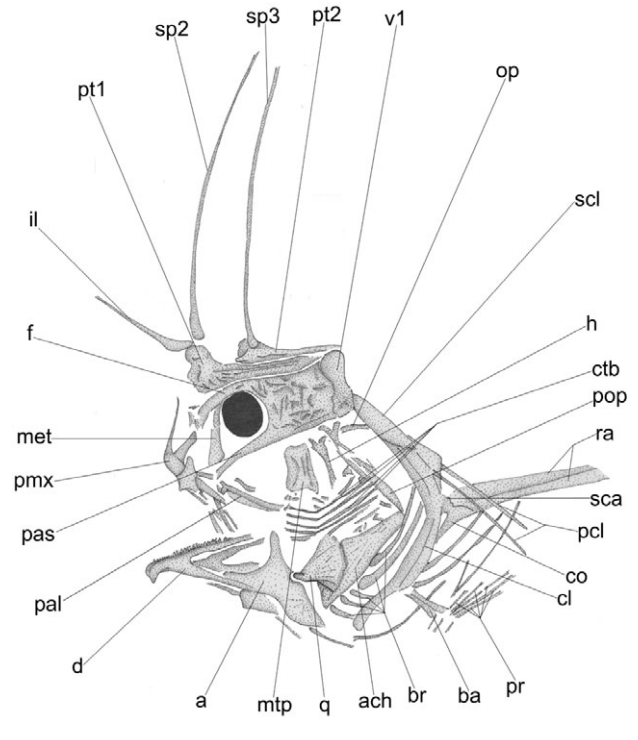
approximately triangular, with a wide dorsal head. The structure of the symplectic is not clear. The metapterygoid appears to be subrectangular in shape. The anterior portion of the palatine is curved and expanded; there is no evidence of palatine teeth or a dorsal articular head. The ectopterygoid is thick, well-ossified, and expanded posteroventrally.

The bones of the opercular series (Figs 3, 4) are, in many cases, extensively fragmented because of their delicate, papery structure. The preopercle is crescent-shaped. The opercle consists of a number of bony striae that radiate from the anterior condyle. The exact structure of the subopercle is difficult to determine.

The hyoid bar (Figs 3, 4) is robust and strongly elongate. The anterior ceratohyal is subrectangular, with a central constricted area. The posterior ceratohyal is nearly triangular in outline. There are five, slender, pointed branchiostegal rays.

The bones of the branchial arches are often fragmented. The ceratobranchials are slender and curved medially (Fig. 4). The epibranchials are thin and short; these bones can be observed exclusively in CM 5237. Sparse branchial teeth, possibly belonging to the second and third pharyngobranchials and fifth ceratobranchial can be also observed in some specimens (MGPD 68487; MCZ 5177a, b).

The vertebral column (Fig. 3) is relatively linear and straight. There are 19 (or rarely 20) vertebrae,



**Figure 4.** †*Histonotophorus bassani* (De Zigno, 1887). MCSNV T. 358, left lateral view of the head. Abbreviations: a, articular; ach, anterior ceratohyal; ba, basiptyergium; br, branchiostegal rays; cl, cleithrum; co, coracoid; ctb, ceratobranchial; d, dentary; f, frontal; h, hyomandibula; il, illicium; met, mesethmoid; mtp, metapterygoid; op, opercle; pal, palatine; pas, parasphenoid; pcl, postcleithrum; pmx, premaxilla; pop, preopercle; pr, pelvic-fin rays; pt1, illicial pterygiophore; pt2, second pterygiophore of the spinous dorsal fin; q, quadrate; ra, pectoral-fin radials; sca, scapula; scl, supracleithrum; sp2, second dorsal-fin spine; sp3, third dorsal-fin spine; v1, first vertebra. Scale bar = 10 mm.

including the last half-centrum fused to the hypural plate. The centra are rectangular, slightly longer than high. The anterior-most vertebra is closely associated with the posterior margin of the neurocranium. The neural spines of the second to fifth anterior-most vertebrae are greatly expanded anteroposteriorly. The vertebrae bear prominent neural prezygapophyses. The abdominal vertebral centra (five) six to nine (ten) bear well-developed posteriorly directed haemal spines progressively increasing in size. The haemal spines of the caudal portion of the body are robust and slender. The neural and haemal spines of the penultimate centrum (second preural centrum) are spatulate and broadly expanded anteroposteriorly. The hypural plate is large, triangular in outline, with a short median notch on the posterior margin (Fig. 3).



**Table 1.** Measurements of †*Histonotophorus bassani* (De Zigno, 1887)

	MCSNV I.G. 23163	MCSNV T358	MGPD 68487	MCZ 5177	MCZ 5176	NHM P19060
Standard length	50.5	38.5	55.1	38.4	34.5	16.4
Total length	77.1	?	80.2	60.1	53.2	28.8
Dorsal fin base	24.6 (48.7)	20.4 (52.9)	26.9 (48.8)	20.7 (53.9)	17.3 (50.1)	8.8 (53.6)
Snout to soft dorsal fin origin	20.0 (39.6)	14.5 (37.6)	21.4 (38.8)	14.9 (38.8)	15.3 (44.3)	5.9 (35.9)
Anal fin base	6.6 (13.0)	5.4 (14.0)	8.2 (14.8)	6.8 (17.7)	6.3 (18.2)	2.3 (14.0)
Snout to anal fin origin	43.4 (85.9)	26.0 (67.5)	38.5 (69.8)	23.9 (62.2)	26.8 (76.8)	11.8 (71.9)
Head length	18.1 (35.8)	13.2 (34.2)	21.4 (38.8)	12.3 (32.0)	8.9 (25.7)	5.0 (30.4)
Length of pectoral fin radials	18.7 (37.0)	13.9 (36.1)	18.3 (33.2)	13.7 (35.6)	10.9 (31.5)	6.8 (41.4)
Length of pelvic fin rays	10.7 (21.1)	6.7 (17.4)	?	8.4 (21.8)	?	4.6 (28.0)
Length of pectoral fin rays	11.8 (23.3)	?	10.2 (18.5)	?	9.5 (27.5)	4.9 (29.8)
Body depth at dorsal fin origin	21.0 (41.5)	17.7 (45.9)	20.4 (37.0)	17.5 (45.5)	15.0 (43.4)	8.2 (50.0)
Body depth at anal fin origin	14.5 (28.7)	11.6 (30.1)	14.3 (25.9)	14.8 (38.5)	11.2 (32.4)	3.9 (23.7)
Eyeball diameter	3.0 (5.9)	2.5 (6.4)	?	3.3 (8.5)	2.3 (6.6)	1.4 (8.5)
Orbit diameter	4.0 (7.9)	3.0 (7.7)	4.7 (8.5)	4.3 (11.2)	3.0 (8.6)	2.2 (13.4)
Snout length	7.1 (14.0)	3.9 (10.1)	7.1 (12.8)	4.5 (11.7)	4.2 (12.1)	2.4 (14.6)
Maxillary length	?	?	?	5.7 (14.8)	4.0 (11.5)	?
Length of bony illicium	2.0 (3.9)	?	?	?	?	2.0 (12.1)
Length of 2nd dorsal spine	9.8 (19.4)	14.5 (37.6)	12.6 (22.8)	?	?	8.2 (50.0)
Length of 3rd dorsal spine	12.9 (25.5)	15.8 (41.0)	?	?	?	8.8 (53.6)
Longest dorsal fin ray	16.1 (31.8)	13.7 (35.5)	14.1 (25.5)	9.9 (25.7)	?	5.8 (35.3)
Longest anal fin ray	17.6 (34.8)	?	15.1 (27.4)	12.1 (31.5)	?	5.1 (31.0)
Length of caudal peduncle	8.3 (16.4)	6.9 (17.9)	7.7 (13.9)	6.9 (17.9)	5.2 (15.0)	3.0 (18.2)
Depth of caudal peduncle	8.1 (16.0)	7.3 (18.9)	10.9 (19.7)	6.2 (16.1)	5.0 (14.5)	3.4 (20.7)
Longest caudal fin ray	29.4 (58.2)	?	29.1 (52.8)	21.2 (55.2)	22.0 (63.7)	7.2 (43.9)

All values are in millimetres. Values in parentheses are in per cent of standard length.

There is no trace of an epural. There are nine (four + five) caudal-fin rays, all segmented and branched, except the ventral-most, which is reduced to a small unsegmented splint.

All three dorsal-fin spines are well developed (Figs 3A, 4). The illicium and second dorsal-fin spine are situated anterodorsal to the neurocranium. The anterior-most (illicial) pterygiophore, which supports the illicium and second dorsal-fin spine, is hypertrophied, with a greatly enlarged, blade-like ventral margin; the anterior margin of this bone is irregular, characterized by a small process and two closely spaced foramina for the articulation of the two spines. The ventral blade-like bony lamina of this pterygiophore shows thick striations and alternating furrows that radiate approximately from the anterior margin of the bone. The illicial bone is slender and delicate, whereas the second and third dorsal-fin spines are elongate and relatively robust. The pterygiophore of the third dorsal-fin spine partially overlaps the posterior end of the preceding pterygiophore. The soft dorsal fin consists of 12–13 rays supported by 12 pterygiophores (Fig. 3). The pterygiophores are short, massive, and laterally compressed, with a proximal fan-like articular portion. Proximally, the posterior-most pterygiophore bears an enlarged rounded posterior process. The main axis of the five anterior-most pterygiophores of the soft dorsal fin is short and does not interdigitate with the neural spines of the underlying vertebrae. The anal fin is extremely short, containing eight or nine rays supported by seven pterygiophores (Fig. 3). All the pterygiophores are obliquely orientated, with their proximal portion directed posteriorly. The two posterior anal-fin pterygiophores insert between the haemal spines of the 14th and 15th vertebrae. Proximally, the posterior-most anal-fin pterygiophore bears an enlarged, rounded posterior process, similar to that of the opposite pterygiophore of the soft dorsal fin.

The pectoral fin originates just above the anal-fin origin and contains six or seven filamentous rays (Fig. 3). The extreme posterior displacement of the pectoral-fin origin is related to the enormous elongation of the two pectoral radials (as long as 41.4% SL). The post-temporal is difficult to recognize. The supracleithrum is a blade-like ovoid bone, with rounded margins. A large part of the medial surface of the supracleithrum is bound to the lateral surface of the dorsal arm of a large, crescent-shaped cleithrum. There is a single rod-like postcleithrum. The coracoid and scapula are laminar, laterally compressed. The pelvic fin consists of a single spine and five unbranched rays (Figs 3, 4). The basipterygium is stout, with an expanded articular head. The skin is naked.

*Remarks:* As discussed above, the relationships and familial placement of †*Histionotophorus bassani* were actively debated (Woodward, 1901; Eastman, 1904, 1905; Gill, 1904; Regan, 1912; Le Danois, 1964; Rosen & Patterson, 1969) until Pietsch (1981) conclusively demonstrated its alignment with the Brachionichthyidae. Our morphological investigation revealed a number of characters that unquestionably support the independent status of this taxon. Yet, at the same time, †*Histionotophorus bassani* is easily distinguished from all other members of the family in the conspicuous development of the spinous dorsal fin and the soft rays of the dorsal, anal, and caudal fins, making it look superficially similar to certain genera of the family Callionymidae, for example, *Bathycallionymus*, *Calliurichthys*, *Dactylopus*, *Diplogrammus*, *Foetorepus*, *Orbonymus*, and *Pseudocalliurichthys* (see Nakabo, 1982).

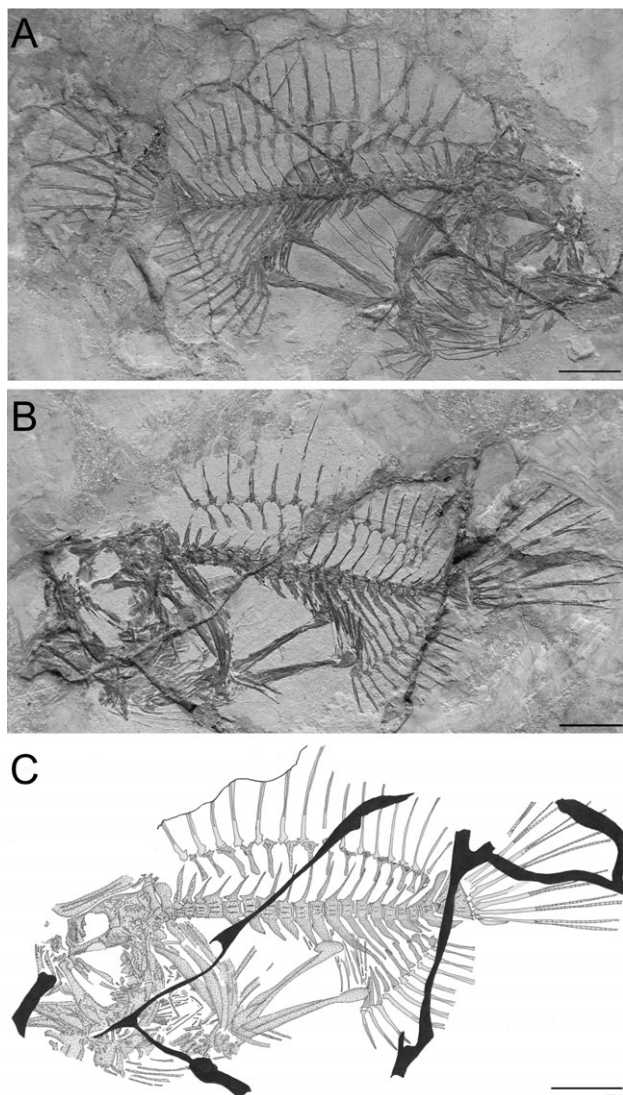
#### †ORRICHTHYS GEN. NOV.

†*Histionotophorus* Eastman, 1904: 32 (in part; replacement name for *Histiocephalus* De Zigno, 1887: 31, preoccupied by *Histiocephalus* Diesing, 1851, therefore taking the same type species, *Histiocephalus bassani* De Zigno, 1887: 31). Sorbini, 1972: 120, pl. 6, fig. 1 (misidentification).

*Type species:* *Orrichthys longimanus* sp. nov., by original designation and monotypy.

*Diagnosis:* A brachionichthyid genus unique and derived in having the maxilla strongly developed, length nearly 20% SL; haemal spines of the caudal vertebrae enlarged anteroposteriorly; and anterior-most anal-fin pterygiophores directed anteroventrally. The genus is further distinguished from all other brachionichthyid genera in having the following combination of character states: jaw teeth relatively large and caniniform; vertebrae 21 or 22; neural spines of abdominal vertebrae simple, not spatulate; haemal spines of abdominal vertebrae posteroventrally directed; neural spine of second vertebra anteroposteriorly enlarged; first dorsal-fin pterygiophore hypertrophied; pectoral radials extremely elongate; body depth at origin of dorsal fin nearly 42% SL; body depth at origin of anal fin nearly 35% SL; dorsal-fin rays 16 or 17; anal-fin rays 11; pectoral-fin rays eight or nine; pelvic fin one spine and five rays; caudal-fin rays nine, ventral-most ray reduced to a small splint; skin naked, without dermal spinules.

*Etymology:* Named after James Wilder Orr, Affiliate Associate Professor, University of Washington; and Research Fisheries Biologist, Alaska Fisheries Science Center, National Marine Fisheries Service,



**Figure 5.** †*Orrichthys longimanus* gen. et sp. nov. A, B, holotype, MCSNV T.160/161; C, MCSNV T.161, left lateral view of the entire skeleton. Scale bars = 10 mm.

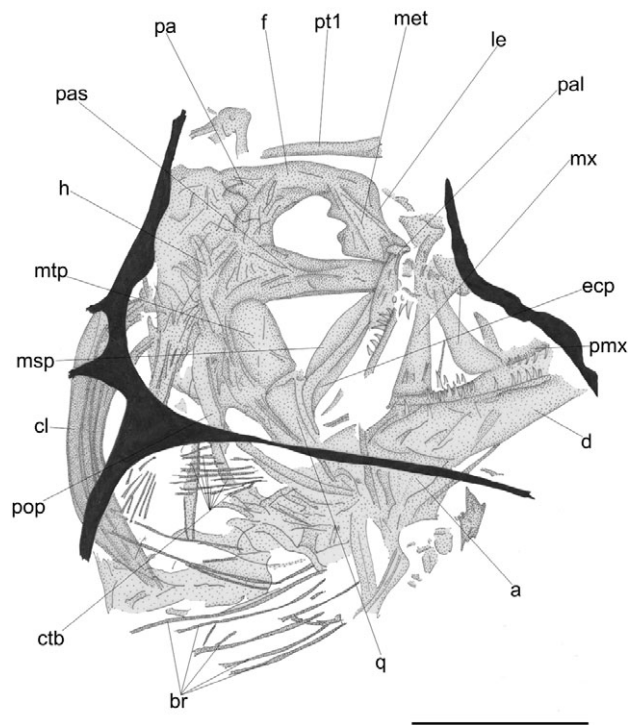
Seattle, for his generous help with the present research, and for his many significant contributions to ichthyology.

†*ORRICHTHYS LONGIMANUS* SP. NOV. (FIGS 5–7)

†*Histionotophorus bassani* Sorbini, 1972: pl. 6, fig. 1 (misidentification).

*Holotype*: MCSNV T.160/161, nearly complete skeleton in part and counterpart, 63 mm SL; late early Eocene, Ypresian; Monte Bolca, Pesciara cave site.

*Paratype*: MCSNV T.164/165, nearly complete skeleton in part and counterpart, 54.1 mm SL; from the type locality.

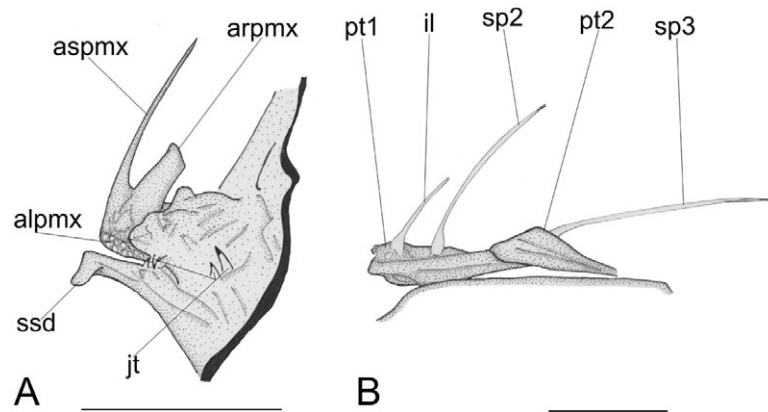


**Figure 6.** †*Orrichthys longimanus* gen. et sp. nov. Holotype, MCSNV T.160, right lateral view of the head. Abbreviations: a, articular; br, branchiostegal rays; cl, cleithrum; ctb, ceratobranchial; d, dentary; ecp, ectopterygoid; f, frontal; h, hyomandibula; le, lateral ethmoid; met, mesethmoid; msp, mesopterygoid; mtp, metapterygoid; mx, maxilla; pa, parietal; pal, palatine; pas, parasphenoid; pmx, premaxilla; pop, preopercle; pt1, illicial pterygiophore; q, quadrate. Scale bar = 10 mm.

*Diagnosis*: As given for the genus.

*Description*: The body is short and globose (depth as great as 52.5% SL) (Fig. 5). The caudal peduncle is short and deep. The head is compressed, relatively large (about 37% SL). The snout is short, the orbital diameter moderately large. The neurocranium is slightly oblique in position. The mouth is nearly horizontal and extremely large (Figs 5, 6). There is a membrane between the second and third dorsal-fin spines and between the third spine and the dorsal mid-line of the body. The dorsal-fin rays are broadly elongate. The external margins of the dorsal and anal fins are characterized by a gently curved profile. The arm-like pectoral fin is supported by greatly elongate pectoral radials. The pelvic-fin rays are also relatively long (24.9% SL). The caudal fin is rounded. Additional counts and measurements are given in Table 2.

The neurocranium is massive, moderately high, and subrectangular in outline (Figs 5, 6). The bones are well ossified and thickened (Fig. 6). The frontals



**Figure 7.** †*Orrichthys longimanus* gen. et sp. nov. Paratype MCSNV T.165. A, left lateral view of the jaws; B, left lateral view of the spinous dorsal fin. Abbreviations: alpmx, alveolar process of the premaxilla; arpmx, articular process of the premaxilla; aspmx, ascending process of the premaxilla; il, illicium; jt, jaw teeth; pt1, illicial pterygiophore; pt2, second pterygiophore of the spinous dorsal fin; sp2, second dorsal-fin spine; sp3, third dorsal-fin spine; ssd, symphyseal spine of the dentary. Scale bars = 5 mm.

**Table 2.** Measurements of †*Orrichthys longimanus* gen. et sp. nov.

	MCSNV T.160/T.161	MCSNV T.164/T.165
Standard length	63.0	54.1
Total length	86.2	77.4
Dorsal fin base	36.0 (57.1)	30.5 (56.3)
Snout to soft dorsal fin origin	23.1 (36.6)	20.8 (38.4)
Anal fin base	15.9 (25.2)	16.4 (30.3)
Snout to anal fin origin	40.6 (64.4)	35.9 (66.3)
Head length	24.2 (38.4)	19.6 (36.2)
Length of pectoral fin radials	21.8 (34.6)	14.9 (27.5)
Length of pelvic fin rays	9.5 (15.0)	18.9 (34.9)
Length of pectoral fin rays	18.3 (29.0)	16.8 (31.0)
Body depth at dorsal fin origin	33.1 (52.5)	18.0 (33.2)
Body depth at anal fin origin	24.0 (38.0)	17.3 (31.9)
Eyeball diameter	3.0 (4.7)	3.7 (6.8)
Orbit diameter	4.7 (7.4)	4.9 (9.0)
Snout length	5.0 (7.9)	5.7 (10.5)
Maxillary length	11.8 (18.7)	10.9 (20.1)
Length of bony illicium	?	4.9 (8.5)
Length of 2nd dorsal spine	?	> 14.9
Length of 3rd dorsal spine	?	16.8 (31.0)
Longest dorsal fin ray	16.9 (26.8)	17.2 (31.7)
Longest anal fin ray	15.1 (23.9)	15.7 (29.0)
Length of caudal peduncle	7.0 (11.1)	7.5 (13.8)
Depth of caudal peduncle	10.3 (16.3)	8.3 (15.3)
Longest caudal fin ray	24.1 (38.2)	22.0 (40.6)

All values are in millimetres. Values in parentheses are in per cent of standard length.

are large and robust. The parietal appears to be characterized by a nearly rounded profile; the parietals are separated from each other by the supraoccipital. The mesethmoid is thick, with an irregular posterior profile. What appear to be the lateral eth-

moids partially cover the anterior portion of the mesethmoid. The bones of the ethmoid block are separated from the basicranial elements by a very small gap, which was probably filled originally by the ethmoid cartilage. The vomer is toothless, with a

flattened ventral surface. The parasphenoid is extremely thick, dorsoventrally expanded, with a median lateral ridge. The bones of the otic and occipital regions are difficult to determine.

The premaxilla bears a slender elongate ascending process and a flattened spatulate articular process (Fig. 7A). There are a few rows of large depressible caniniform teeth with recurved tips. The maxilla is greatly elongate and robust, with an enlarged flattened posterior end, its length contained approximately five times in SL (see Table 2). The dentary is massive and thick, with a prominent symphyseal spine; the mandibular teeth are identical to those of the upper jaw (Fig. 7A). The articular bears a posteroverentral bony lamina, with a rounded profile.

The bones of the suspensorium (Fig. 6) are fragmented in both specimens examined. The hyomandibula has a slender primary shaft, two articular heads, and a short opercular process. The quadrate is roughly triangular and dorsoventrally expanded. The symplectic is difficult to recognize. The metapterygoid is flat and nearly rectangular in shape, with a convex dorsal margin and two diagonal ridges. The ectopterygoid is greatly elongate, crescent-shaped, and posteriorly expanded. The endopterygoid consists of an elongate thin plate, with a rounded dorsal profile. The palatine has an enlarged robust articular head.

What appears to be the preopercle is elongate and slightly curved (Fig. 6). The opercle cannot be determined. The subopercle is crescent-shaped, apparently without a spine along the anterior margin.

The hyoid bar is difficult to recognize as a result of inadequate preservation. There are five slender and elongate branchiostegal rays (Fig. 6). The bones of the branchial skeleton are badly fragmented. The ceratobranchials appear to be slightly curved. Large caniniform pharyngobranchial teeth are recognizable.

The vertebral column is slightly curved (Fig. 5). There are 21–22 vertebrae, 12–13 abdominal and nine caudal. The anterior-most vertebra is strongly associated with the occipital region of the neurocranium. With the exception of the anterior-most four vertebrae, which are nearly square in shape, the centra are massive, subrectangular, and higher than long. The four anterior-most vertebrae bear anteroposteriorly enlarged neural spines; the two anterior-most are characterized by having a rounded profile, whereas those of the third and fourth are stout and pointed. The neural spines of the fifth to eighth vertebrae are shorter, not clearly interdigitating with the dorsal-fin pterygiophores situated above. Well-developed neural prezygapophyses characterize all the vertebral centra. Vertebrae 7 (8) to 20 (21) bear flattened, anteroposteriorly enlarged and posteroverentrally directed haemal spines, each with a pointed tip (Fig. 5C).

The penultimate vertebra bears enlarged spatulate neural and haemal spines. The hypural plate is roughly triangular, with a small median notch along its posterior margin (Fig. 5C). There are no epurals. The caudal fin consists of nine rays, four in the upper lobe and five in the lower one. The lowest ray is reduced to a small splint of bone; the remaining rays are bifurcated distally.

The spinous dorsal fin is well preserved in the paratype (Fig. 7B); the illicium and two following spines are slender. The first pterygiophore is greatly enlarged; it consists of an elongate anteriorly expanded bony lamina, with a thick median ridge. The second pterygiophore is rather large, blade-like, with an elongate lateral bony crest. The soft dorsal fin contains 16–17 rays, supported by 15–16 pterygiophores (Fig. 5). These pterygiophores are characterized by having an elongate primary shaft and an enlarged, fan-like distal end. The four anterior pterygiophores are obliquely orientated with posteroverentrally directed shafts. The two posterior pterygiophores lie in the interneural space between the 17th (or 18th) and 18th (or 19th) vertebrae. The posterior-most dorsal-fin pterygiophore (as well as its counterpart in the anal fin) bears a posteriorly directed process on the posterior margin of its distal end.

The anal fin consists of 11 rays supported by ten pterygiophores (Fig. 5). The proximal shaft of the two anterior pterygiophores is bent posteriorly. The four anterior pterygiophores lie in the interhaemal space between the 17th (or 18th) and 18th (or 19th) vertebrae.

The pectoral fin inserts above the anal-fin origin (Fig. 5). It contains eight or nine elongate rays. The supracleithrum is elongate and laterally flattened. The cleithrum is rather large and crescent shaped. The scapula and coracoid are poorly preserved and difficult to interpret. There is a single elongate postcleithrum. The two radials are strongly elongate; the ventral-most has a distally expanded portion and bears the bases of the pectoral-fin rays. The pelvic fin contains one spine and five rays (Fig. 5A). The basipterygium is stout with an expanded distal end. The skin is naked.

*Etymology:* The specific name is derived from the Latin *longus*, meaning 'long'; and *manus*, 'hand,' in allusion to the exceptionally long, hand-like, pectoral-fin lobe of this species.

*Remarks:* The first documentation of this new handfish genus and species was provided by Sorbini (1972), who figured the holotype (MCSNV T.161) but misidentified it as †*Histionotophorus bassani*. The information obtained in this study indicates that †*Orrichthys longimanus* is defined by three

autapomorphies, plus many other features that are found in various combinations in other brachionichthyid or antennarioid fishes. Some of these diagnostic features, including large caniniform jaw teeth, an enlarged maxilla, dorsoventrally developed anterior part of the body, and anteroventrally directed anterior-most anal-fin pterygiophores, can all be considered trophic adaptations. In particular, these characters clearly reflect an increased development of the oro-pharyngeal cavity (i.e. an expansion of the throat and abdomen) for engulfing large prey. Although a similar strong development of feeding adaptations is not evident in †*Histionotophorus bassani*, it should be noted that the mouth and abdomen of the latter are still comparatively enlarged with respect to those of extant brachionichthyids. Therefore, the microphagous habits characteristic of extant handfishes can be interpreted as a specialization amongst lophiiforms, whereas the functional adaptations of the trophic-related structures of †*Orrichthys longimanus* and, to a lesser extent, of †*Histionotophorus bassani*, seem to be consistent with those of other antennarioids, and more generally of other lophiiform fishes (e.g. see Gregory, 1933; Gregory & Conrad, 1936; Pietsch, 2009).

#### GENUS *BRACHIONICHTHYS* BLEEKER, 1855

*Lophius* Linnaeus, 1758: 236 (in part; type species *Lophius piscatorius* Linnaeus, 1758: 236, by subsequent designation of Jordan & Gilbert, 1883: 844). *Brachionichthys* Bleeker, 1855: 12, 21 [in part; type species *Cheironectes hirsutus* (= *Lophius hirsutus* Lacepède, 1804: 210), by subsequent designation of Bleeker, 1865: 5].

**Diagnosis:** A brachionichthyid genus unique and derived in having the posterior part of the body extremely long and slender, body depth at origin of anal fin approximately 21% SL, palatine with a prominent dorsal head; symphysial spine of dentary absent; articular without posteroventral flange; and skin covered with close-set unicuspid dermal spinules. The genus is further distinguished from all other brachionichthyid genera in having the following combination of character states: jaw teeth small and villiform; vertebrae 22–26; neural spines of sixth to ninth abdominal vertebrae spatulate; haemal spines of anterior-most abdominal vertebrae anteroventrally directed, becoming progressively directed posteroventrally; hypural notch absent; supernumerary ray of dorsal and anal fins absent; dorsal-fin rays 16–19; anal-fin rays 8–11; pectoral-fin rays seven; pelvic fin one spine and four rays; ninth (ventral-most) caudal-fin ray relatively well developed.

**Recognized species:** *Brachionichthys hirsutus* (Lacepède, 1804): lectotype, MNHN A.4627, 76 mm SL, 'Côtes du sud de l'Australie, Voyage de Péron' (see Pietsch *et al.*, 1986: 142). *Brachionichthys australis* Last, Gledhill, & Holmes, 2007: holotype, CSIRO H.4451–02, 46 mm SL, east of Disaster Bay, New South Wales, 37°18'S, 150°17'E, 125 m, 7.xii.1996.

**Remarks:** Bleeker (1855) distinguished the genus *Brachionichthys* from antennariid fishes primarily on the basis of characters of the spinous dorsal fin, jaw teeth, gill openings, pelvic fins, and gill arches. He also incorrectly reported the presence of six rather than five branchiostegal rays. The subsequent diagnoses of Gill (1863, 1878) were based primarily on the structure and extension of the membranous connection of the dorsal-fin spines. A recent attempt to define the genus *Brachionichthys* (Last *et al.*, 2007) by a unique combination of morphometric, meristic, and external features, none of which have any phylogenetic relevance, is rejected.

#### GENUS *SYMPTERICHTHYS* GILL, 1878

*Lophius* Linnaeus, 1758: 236 (in part; type species *Lophius piscatorius* Linnaeus, 1758: 236, by subsequent designation of Jordan & Gilbert, 1883: 844). *Brachionichthys* Bleeker, 1855: 12, 21 [in part; type species *Cheironectes hirsutus* (= *Lophius hirsutus* Lacepède, 1804: 210), by subsequent designation of Bleeker, 1865: 5]. *Sympterichthys* Gill, 1878: 222 [type species *Lophius laevis* Lacepède, 1804: 210 (= *Chironectes unipennis* Cuvier, 1817), by original designation and monotypy].

**Diagnosis:** A brachionichthyid genus unique and derived in having dorsal- and anal-fin rays deeply embedded within the skin; dorsal fin-base long, greater than 60% SL; hyomandibular foramen present; mesopterygoid and ectopterygoid absent; and posterior margin of opercle fimbriated. The genus is further distinguished from all other brachionichthyid genera in having the following combination of character states: neural spine of second anterior-most vertebra expanded anteroposteriorly; neural spines of sixth to tenth abdominal vertebrae spatulate; haemal spines of anterior-most abdominal vertebrae anteroventrally directed, becoming progressively directed posteroventrally; hypural notch absent; supernumerary rays of dorsal and anal fins absent; dorsal-fin rays 13–17; anal-fin rays six to ten; pectoral-fin rays six to nine; pelvic fin one spine and four rays; ninth (ventral-most) caudal-fin ray relatively well developed; skin naked, without dermal spinules.

*Recognized species:* *Sympterichthys unipennis* (Cuvier, 1817): holotype MNHN A.4630, 43.5 mm SL, 'Mer de l'Australie, Voyage de Péron' (Pietsch *et al.*, 1986: 142). *Sympterichthys politus* (Richardson, 1844): holotype, about 42 mm SL, apparently lost (see Eschmeyer, 1998), Port Arthur, Tasmania, Australia. *Sympterichthys verrucosus* McCulloch & Waite, 1918: holotype SAMA F626, 33 mm SL, St. Vincent Gulf, South Australia.

*Remarks:* The original diagnosis of *Sympterichthys* was based on a single erroneous character, a connection of the spinous- and soft-dorsal fins by an incised membrane (Gill, 1878). McCulloch & Waite (1918) redefined the genus based on several external and meristic features, some of which, however, are not unique to *Sympterichthys* (e.g. the possession of small depressible teeth, position of the gill opening, structure of the membrane of the spinous dorsal fin, etc.). In this study, *Sympterichthys* is diagnosed for the first time on the basis of derived external and osteological features.

#### PHYLOGENETIC RELATIONSHIPS

The present analysis is based on an examination of seven antennarioid genera (*Antennarius*, *Brachionichthys*, †*Histionotophorus*, *Lophichthys*, †*Orrichthys*, *Sympterichthys*, and *Tetrabrachium*), representing all known antennarioid families (Antennariidae, Brachionichthyidae, Lophichthyidae, and Tetrabrachyidae; see Pietsch, 2009: 175–179, fig. 188), plus the basal lophiid genus *Sladenia* (see Caruso, 1985). The purpose of this section is to place the extinct genera †*Histionotophorus* and †*Orrichthys* and the extant *Brachionichthys* and *Sympterichthys* in a phylogenetic framework of the family Brachionichthyidae and more generally of the Antennarioidei. A data matrix of eight taxa and 36 characters was constructed. Character polarity was determined by outgroup comparison. All characters were treated as unordered and unweighted. All characters except numbers 5 and 32 (see below) were binary. Character states that could not be determined from the fossils because of inadequate preservation are coded as unknown, and indicated in the data matrix by a question mark (Appendix). The matrix was analysed with PAUP (v. 4.0b10; Swofford, 2002), using the branch and bound algorithm, with accelerated transformation (ACCTRAN) to optimize characters. To evaluate branch support, a heuristic bootstrap analysis of 1000 replicates was conducted, with simple addition sequence and tree bisection-reconnection (TBR) branch-swapping options. Bremer decay values (Bremer, 1988) were calculated using TREEROT (v. 2; Sorenson, 1999).

*Characters and character states:* Descriptions of phylogenetically informative characters for the taxa examined in this analysis are arranged below by discrete anatomical complexes. A description of each character is followed by a summary of the recognized character state of each character. Consistency and retention indices (CI and RI) were produced as a whole and for each character individually. Both CI and RI are given after each character description. A brief discussion of the condition of the feature in the genera included in the phylogenetic study is also provided.

#### CRANIUM

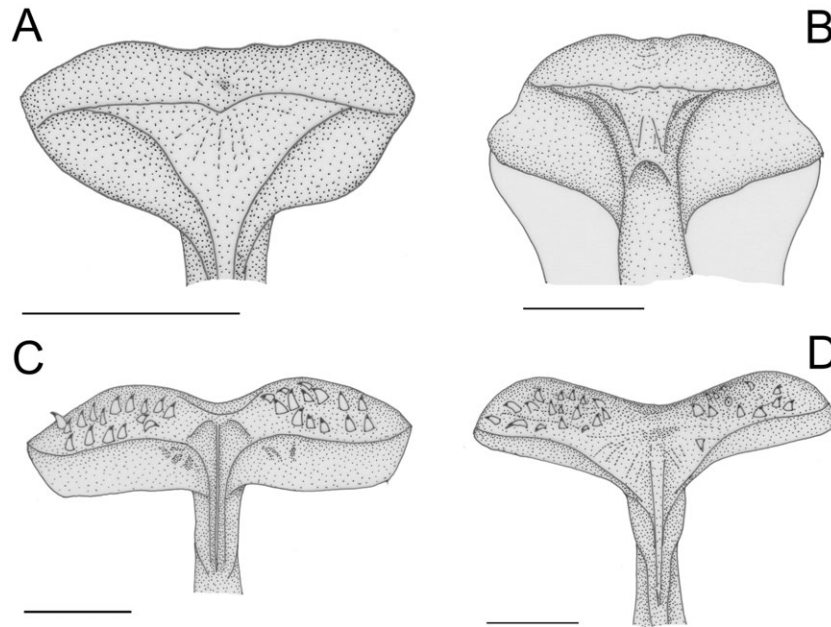
1. The ventral surface of the vomer is flat in *Sladenia*, *Lophichthys*, and all brachionichthyids (Fig. 8) (0), but deeply concave in *Tetrabrachium* and *Antennarius* (Fig. 8C; Pietsch, 1981: fig. 6) (1) (CI 1.00, RI 1.00).
2. Vomerine teeth are present in *Sladenia*, *Lophichthys*, *Tetrabrachium*, and *Antennarius* (Fig. 8; Pietsch, 1981: fig. 6) (0), but absent in all brachionichthyids (Figs 4, 6, 8) (1) (CI 1.00, RI 1.00).

#### SUSPENSORIUM

3. A hyomandibular foramen is absent in all taxa (Figs 4, 6, 9A; Pietsch, 1981: figs 9, 21–23) (0), except *Sympterichthys* (Fig. 10A) (1) (CI 1.00, RI 0.00).
4. The articular head of the quadrate is wide in all taxa (Pietsch, 1981: figs 22, 23) (0), except *Tetrabrachium* and *Antennarius* (Pietsch, 1981, figs 9, 21) (1) (CI 1.00, RI 1.00).
5. The ectopterygoid is posteroventrally expanded in *Sladenia*, *Brachionichthys*, and in both fossil taxa (Figs 3, 6, 9B) (0); T-shaped in *Lophichthys*, *Tetrabrachium*, and *Antennarius* (Pietsch, 1981: figs 9, 21, 22) (1); but absent in *Sympterichthys* (Fig. 10A) (2) (CI 1.00, RI 1.00).
6. The mesopterygoid is present in *Sladenia*, *Brachionichthys*, both fossil taxa, and *Antennarius* (Figs 3, 6, 9A, B) (0), but absent in *Sympterichthys*, *Lophichthys*, and *Tetrabrachium* (Fig. 10A; Pietsch, 1981: figs 9, 22) (1) (CI 0.33, RI 0.00).
7. A dorsal head of the palatine is absent in all taxa (Figs 4, 6, 10A; Pietsch, 1981: figs 9, 21, 22) (0), except *Brachionichthys* (Fig. 9A) (1) (CI 1.00, RI 0.00).
8. Palatine teeth are present in *Sladenia*, *Lophichthys*, and *Antennarius* (Pietsch, 1981: figs 21, 22) (0), but absent in all other taxa (Figs 4, 6, 9A, 10A; Pietsch, 1981: figs 9, 23) (1) (CI 0.00, RI 0.00).

#### JAWS

9. A prominent symphyseal spine of the dentary is present in all taxa (Figs 4, 6, 10A; Pietsch, 1981:



**Figure 8.** Ventral view of the vomer. A, *Sympterichthys unipennis*, UW 116854. Scale bar = 1 mm. B, *Brachionichthys hirsutus*, NMV A.19954. Scale bar = 2 mm. C, *Antennarius striatus*, UW 20768. Scale bar = 2 mm. D, *Lophichthys boschmai*, UW 20773. Scale bar = 2 mm.

figs 9, 21, 22) (0), except *Brachionichthys* (Fig. 9A) (1) (CI 0.50, RI 0.67).

10. The articular has a broad posteroventral flange in all taxa (Figs 4, 6, 10A; Pietsch, 1981: figs 9, 21, 22) (0), except *Brachionichthys* (Fig. 9A) (1) (CI 1.00, RI 0.00).
11. The jaw teeth are caniniform and well developed in all taxa (Figs 6, 7A; Pietsch, 1981: figs 9, 21, 22) (0); the teeth are small, granular or villiform in *Brachionichthys*, *Sympterichthys*, and †*Hisionotophorus* (Figs 3, 4, 9A, 9E, 10A, B) (1) (CI 0.50, RI 0.50).

#### HYOID APPARATUS AND GILL ARCHES

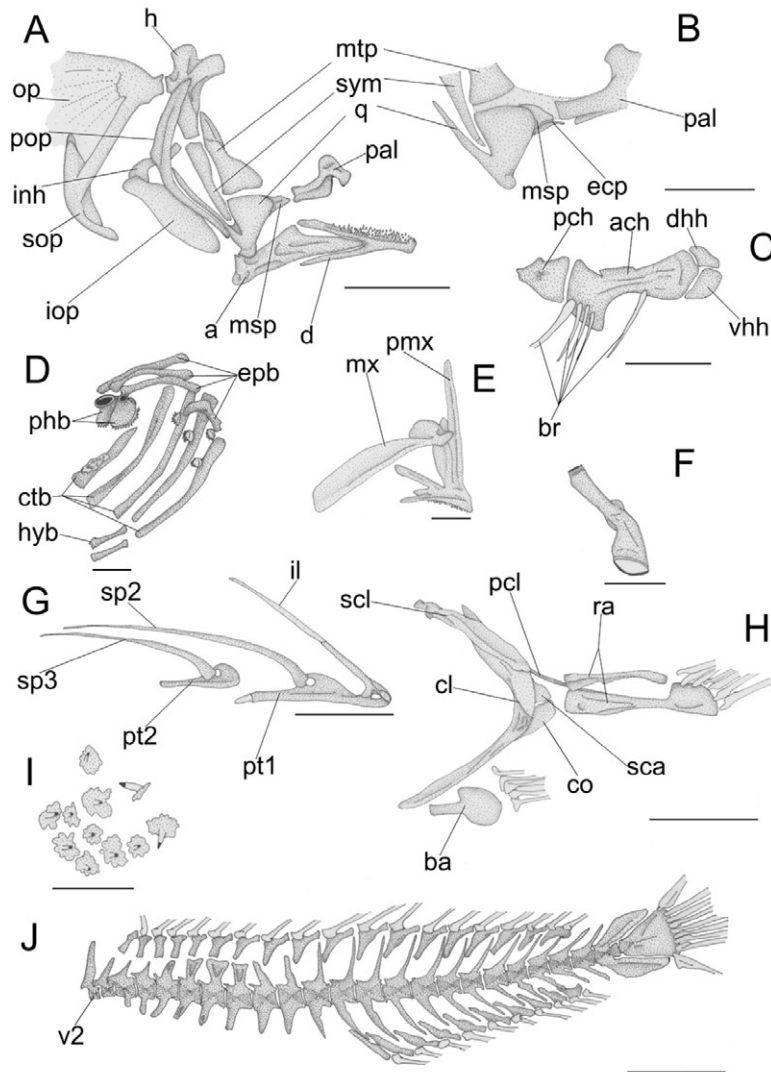
12. The interhyal is simple in *Sladenia* (0), but bears a prominent medial posterolaterally directed process in all other extant taxa (Figs 9F, 10C; Pietsch, 1981: fig. 26) (1); the morphology of the interhyal is unknown in the fossil taxa (CI 1.00, RI 1.00).
13. There are six branchiostegal rays in *Sladenia*, *Lophichthys*, *Tetrabrachium*, and *Antennarius* (0), but only five in all brachionichthyids (Figs 4, 6, 9C, 10D; Table 3) (1) (CI 1.00, RI 1.00).
14. The third hypobranchial is present in *Sladenia*, *Lophichthys*, *Tetrabrachium*, and *Antennarius* (0), but absent in *Brachionichthys* and *Sympterichthys* (Figs 9D, 10F) (1); the condition is unknown in the fossil taxa (CI 1.00, RI 1.00).

15. The ceratobranchials are simple and slightly curved in all taxa (Pietsch, 1981: figs 11, 28, 29) (0), but strongly curved in all brachionichthyids (Figs 4, 9D, 10F; Pietsch, 1981: fig. 31) (1) (CI 1.00, RI 1.00).
16. Teeth are present on the first epibranchial in all taxa (Figs 9D, 10F; Pietsch, 1981: figs 29, 30) (0), but absent in *Tetrabrachium* and *Antennarius* (Pietsch, 1981: figs 11, 28) (1); the condition is unknown in the fossil taxa (CI 1.00, RI 1.00).
17. There are three pharyngobranchials in *Sladenia* (0), but only two in all remaining taxa (Figs 9D, 10F; Pietsch, 1981: figs 11, 28–30) (1) (CI 1.00, RI 1.00).

#### AXIAL SKELETON AND CAUDAL FIN

18. The vertebral column is straight or only slightly curved in all taxa (Figs 1–3, 5, 9J, 10J; Pietsch, 1981: fig. 34) (0), but sigmoid in *Tetrabrachium* and *Antennarius* (Pietsch, 1981: figs 12, 33) (1) (CI 1.00, RI 1.00).
19. The number of vertebral centra is 19 (rarely 20) or fewer in *Sladenia* (Caruso, 1985), *Lophichthys*, *Antennarius* (Pietsch, 1981: table 2), and †*Hisionotophorus* (Table 3) (0); but 21 or more in *Sympterichthys*, *Brachionichthys*, *Tetrabrachium*, and †*Orrichthys* (Table 3; Pietsch, 1981: table 2) (1) (CI 0.50, RI 0.50).

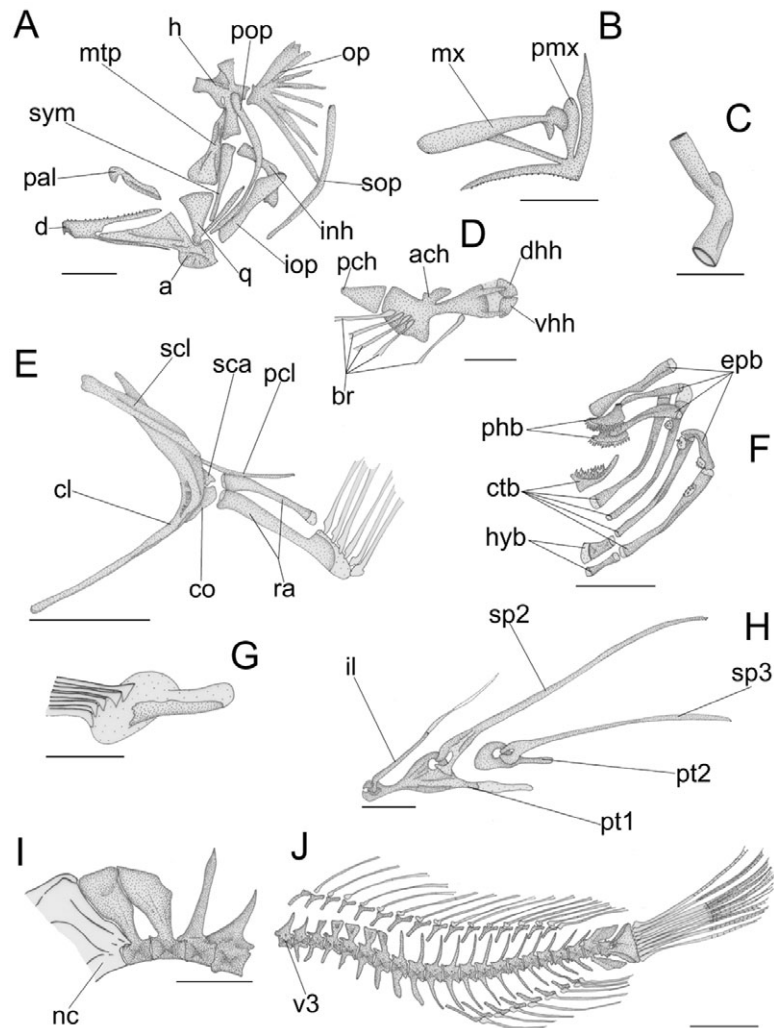




**Figure 9.** *Brachionichthys hirsutus*, NMV A.19954. A, right lateral view of lower jaw, suspensorium, interhyal, and opercular apparatus. Scale bar = 5 mm. C, right lateral view of the hyoid apparatus. Scale bar = 5 mm. D, branchial arches. Scale bar = 2 mm. E, right lateral view of the upper jaw. Scale bar = 2 mm. F, right medial view of the interhyal. Scale bar = 2 mm. H, left lateral view of the pectoral and pelvic girdles. Scale bar = 10 mm. I, dermal spinules. Scale bar = 1 mm. J, left lateral view of the axial skeleton. Scale bar = 10 mm. *Brachionichthys australis*. B, UW 116842, right lateral view of the suspensorium. Scale bar = 2 mm. G, UW 116843, right lateral view of the spinous dorsal fin. Scale bar = 5 mm. Abbreviations: a, articular; ach, anterior ceratohyal; ba, basiptyrgium; br, branchiostegal rays; cl, cleithrum; co, coracoid; ctb, ceratobranchial; d, dentary; dhh, dorsal hypohyal; ecp, ectopterygoid; epb, epibranchial; h, hyomandibula; hyb, hypobranchial; inh, interhyal; il, illicium; iop, interopercle; msp, mesopterygoid; mtp, metapterygoid; mx, maxilla; op, opercle; pal, palatine; pch, posterior ceratohyal; pcl, postcleithrum; phb, pharyngobranchial; pmx, premaxilla; pop, preopercle; pt1, illicial pterygiophore; pt2, second pterygiophore of the spinous dorsal fin; q, quadrate; ra, pectoral-fin radials; sca, scapula; scl, supracleithrum; sop, subopercle; sp2, second dorsal-fin spine; sp3, third dorsal-fin spine; sym, symplectic; v2, second vertebra; vhh, ventral hypohyal.

20. The neural spine of the second abdominal vertebra is simple in all taxa (see Figs 3, 9J) (0), but anteroposteriorly expanded in *Sympterichthys* and †*Orrichthys* (Figs 5C, 10I) (1) (CI 0.50, RI 0.00).

21. The neural spines of the abdominal vertebrae are simple in *Sladenia* and both fossil taxa (Figs 3, 5C) (0), but the fifth (or sixth) to the eighth (or ninth and tenth) abdominal vertebrae are spatulate in all other taxa (Figs 9J, 10J;



**Figure 10.** *Sympterichthys unipennis*. A, UW 116845, left lateral view of lower jaw, suspensorium, interhyal, and opercular apparatus. Scale bar = 2 mm. B, UW 116845, right lateral view of the upper jaw. Scale bar = 2 mm. C, UW 116845, right medial view of the interhyal. Scale bar = 1 mm. D, UW 116845, right lateral view of the hyoid apparatus. Scale bar = 2 mm. E, UW 116845, left lateral view of the pectoral girdle. Scale bar = 5 mm. F, UW 116845, branchial arches. Scale bar = 2 mm. G, UW 116845, right lateral view of the basipterygium. Scale bar = 2 mm. H, UW 116845, left lateral view of the spinous dorsal fin. Scale bar = 2 mm. I, UW 116844, left lateral view of the anterior portion of the vertebral column. Scale bar = 2 mm. J, UW 116845, left lateral view of the axial skeleton. Scale bar = 5 mm. Abbreviations: a, articular; ach, anterior ceratohyal; br, branchiostegal rays; cl, cleithrum; co, coracoid; ctb, ceratobranchial; d, dentary; dhh, dorsal hypohyal; epb, epibranchial; h, hyomandibula; hyb, hypobranchial; il, illicium; inh, interhyal; iop, interopercle; mtp, metapterygoid; mx, maxilla; nc, neurocranium; op, opercle; pal, palatine; pch, posterior ceratohyal; pcl, postcleithrum; phb, pharyngobranchial; pmx, premaxilla; pop, preopercle; pt1, illicial pterygiophore; pt2, second pterygiophore of the spinous dorsal fin; q, quadrate; ra, pectoral-fin radials; sca, scapula; scl, supracleithrum; sop, subopercle; sp2, second dorsal-fin spine; sp3, third dorsal-fin spine; sym, symplectic; v3, third vertebra; vhh, ventral hypohyal.

Pietsch, 1981: figs 12, 33, 34) (1) (CI 0.50, RI 0.67).

22. The haemal spines of the anterior-most abdominal vertebrae are anteroventrally directed, becoming progressively posteroventrally directed in all taxa (Figs 9J, 10J; Pietsch, 1981: figs 12, 33, 34) (0), except †*Histionotopho-*

*rus* and †*Orrichthys* (Figs 3, 5C) (1) (CI 1.00, RI 1.00).

23. The haemal spines of the caudal vertebrae are slender in all taxa (Figs 3, 9J, 10J; Pietsch, 1981: figs 12, 33, 34) (0), but anteroposteriorly expanded in †*Orrichthys* (Fig. 5C) (1) (CI 1.00, RI 0.00).

**Table 3.** Counts and measurements (in per cent of standard length) of representatives of fossil and extant taxa of the Brachionichthyidae

	<i>Orrichthys longimanus</i>	<i>Histionotophorus bassani</i>	<i>Brachionichthys australis</i>	<i>Sympterichthys verrucosus</i>	<i>Sympterichthys unipennis</i>	<i>Sympterichthys</i> sp.
Dorsal fin base	56.3–57.1 (56.7)	48.7–53.9 (51.3)	52.5–55.5 (54.0)	?	61.1	60.0
Snout to soft dorsal fin origin	36.6–38.4 (37.5)	35.9–44.3 (39.1)	38.1–38.2 (38.1)	44.4	36.3	40.5
Anal fin base	25.2–30.3 (27.7)	13.0–18.2 (15.2)	26.8–28.0 (27.4)	?	26.8	30.4
Snout to anal fin origin	64.4–66.3 (65.3)	62.2–85.9 (72.3)	57.6–61.2 (59.4)	64.2	72.1	65.6
Head length	36.2–38.4 (37.3)	25.7–38.8 (32.7)	26.8–31.2 (29.0)	30.5	32.2	27.3
Length of pectoral fin radials	27.5–34.6 (31.0)	31.5–41.4 (35.8)	25.6–27.6 (26.6)	27.9	26.5	25.5
Length of pelvic fin rays	15.0–34.9 (24.9)	17.4–28.0 (22.0)	14.2–16.9 (15.5)	9.4	16.1	16.2
Length of pectoral fin rays	29.0–31.0 (30.0)	18.5–29.8 (24.7)	18.8–24.0 (21.4)	18.8	19.9	19.2
Body depth at dorsal fin origin	33.0–52.5 (42.8)	37.0–50.0 (43.8)	31.2–31.5 (31.3)	39.6	46.2	28.5
Body depth at anal fin origin	31.9–38 (34.9)	23.7–38.5 (29.8)	21.2–21.9 (21.5)	25.4	29.4	24.6
Eyeball diameter	4.7–6.8 (5.7)	5.9–8.5 (7.1)	9.0–12.6 (10.8)	9.8	12.9	6.5
Snout length	7.9–10.5 (9.2)	10.1–14.6 (12.5)	8.2–8.7 (8.4)	9.4	10.1	9.3
Maxillary length	18.7–20.1 (19.4)	11.5–14.8 (13.1)	14.0–17.5 (15.7)	19.2	16.7	11.9
Length of bony illicium	8.5	3.9–12.1 (8.0)	9.5–10.1 (9.8)	13.7	12.9	10.7
Length of 2nd dorsal spine	?	19.4–50.0 (32.4)	32.1–34.8 (33.4)	30.2	27.8	25.2
Length of 3rd dorsal spine	31.0	25.5–53.6 (40.0)	22.7–25.5 (24.1)	23.8	20.2	22.0
Longest dorsal fin ray	26.8–31.7 (29.2)	25.5–35.5 (37.1)	21.2–21.9 (21.5)	?	15.8	19.0
Longest anal fin ray	23.9–29.0 (26.4)	27.4–34.8 (31.1)	18.7–18.9 (18.8)	?	14.2	13.6
Length of caudal peduncle	11.1–13.0 (12.4)	13.9–18.2 (16.5)	11.6–13.4 (12.5)	11.4	13.2	8.7
Depth of caudal peduncle	15.3–16.3 (15.8)	14.5–20.7 (17.6)	11.2–12.1 (11.6)	12.3	12.6	8.9
Longest caudal fin ray	38.2–40.6 (39.4)	43.9–63.7 (54.7)	30.7–31.8 (31.2)	16.5	26.8	18.7
Dorsal-fin rays	16–17	12–13	17 (16–19)	?	16	16
Anal-fin rays	11	8–9	10 (8–11)	?	8	8
Pectoral-fin rays	8.9	7	7	8	8	9
Pelvic-fin rays	I+5	I+5	I+4	I+4	I+4	I+4
Vertebrae	21–22	19–20	22–26	?	23	?
Branchiostegal rays	5	5	5	5	5	5

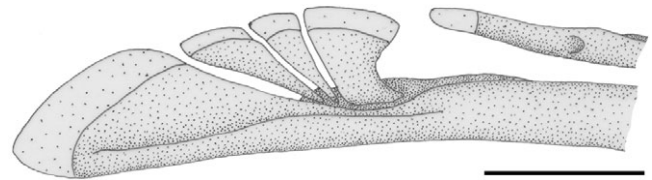
24. A median posterior notch is present in the hypural plate in all taxa (Figs 3, 5C; Pietsch, 1981: figs 12, 33, 34) (0), except *Brachionichthys* and *Sympterichthys* (Figs 9J, 10J) (1) (CI 1.00, RI 1.00).
25. An epural is present in *Sladenia*, *Lophichthys*, and *Antennarius* (Pietsch, 1981: figs 33, 34) (0), but absent in all other taxa (Figs 3, 5C, 9J, 10J; Pietsch, 1981: fig. 12) (1) (CI 0.50, RI 0.67).
26. The caudal is slightly rounded in all taxa (Pietsch, 1981: fig. 1A; Pietsch & Grobecker, 1987) (0), but elongate and pointed in †*Histionotophorus* (Figs 1–3) and *Lophichthys* (Boeseman, 1964) (1) (CI 0.50, RI 0.00).
27. The ventral-most caudal-fin ray is well developed in all taxa (see Figs 9J, 10J) (0), but reduced to a small splint of bone in †*Histionotophorus* and †*Orrichthys* (Figs 3, 5C) (1) (CI 1.00, RI 1.00).

#### DORSAL AND ANAL FINS

28. There are more than three dorsal-fin spines in *Sladenia* (as well as in other lophioids; Caruso, 1985; Pietsch, 1981, 1984a) (0), but only three in all other taxa (Figs 3, 9G, 10H; Pietsch, 1981: figs 13, 36, 37) (1) (CI 1.00, RI 1.00).
29. The shaft of the illicial pterygiophore is relatively narrow in all taxa (Figs 9G, 10H; Pietsch, 1981: figs 13, 36, 37) (0), but hypertrophied in †*Histionotophorus* and †*Orrichthys* (Figs 3, 4, 5C) (1) (CI 1.00, RI 1.00).
30. The foramina of the illicial pterygiophore are relatively far apart in nearly all taxa (Fig. 9G, 10H; Pietsch, 1981: figs 13, 36, 37) (0), but very closely spaced in †*Histionotophorus* (Fig. 3A) (1) (CI 1.00, RI 0.00).
31. The second and third dorsal-fin spines are free in nearly all taxa (0), but connected along their entire length by a cutaneous membrane in brachionichthyids (see Fig. 2) (1) (CI 1.00, RI 1.00).
32. A supernumerary ray is present in the soft dorsal and anal fins of nearly all taxa (Figs 3, 5C; Pietsch, 1981: figs 12, 33) (0), but there is a one-to-one ratio of rays to pterygiophores in *Brachionichthys* and *Sympterichthys* (Figs 9J, 10J) (1) (CI 1.00, RI 1.00).
33. The anterior-most anal-fin pterygiophores are posteroventrally directed in nearly all taxa (Figs 3, 9J, 10J; Pietsch, 1981: figs 12, 33) (0), but anteroventrally directed in †*Orrichthys* (Fig. 5C) (1) (CI 1.00, RI 0.00).

#### PECTORAL FINS

34. There are five pectoral-fin radials in *Sladenia* (Fig. 11) (0), three in *Lophichthys*, *Tetra-*



**Figure 11.** *Sladenia* sp., CSIRO H.2559–02, left medial view of the pectoral-fin radials. Scale bar = 5 mm.

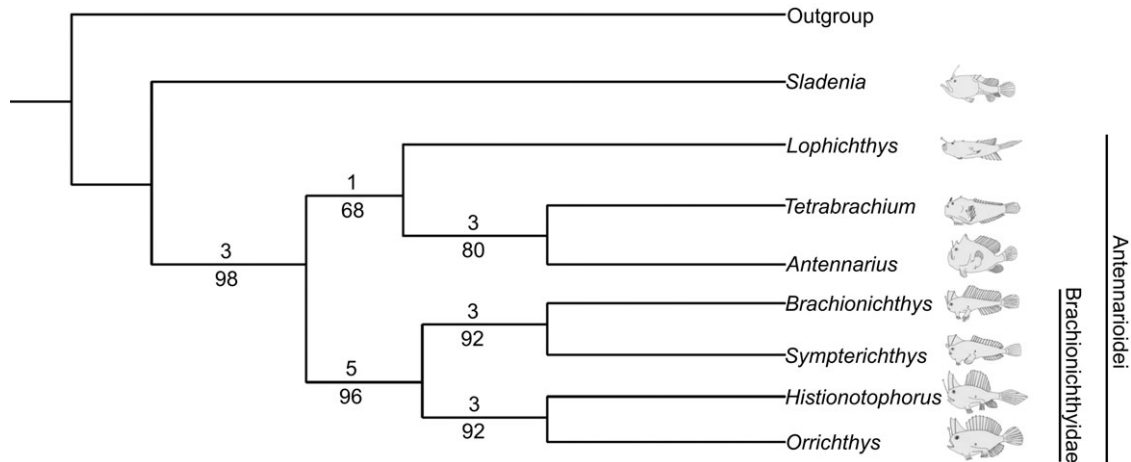
- brachium*, and *Antennarius* (Monod, 1960; Pietsch, 1981: figs 14, 40) (1), but only two in brachionichthyids (Figs 3, 5C, 9H, 10E) (2) (CI 1.00, RI 1.00).
35. The pectoral radials are short to moderately elongate, less than 25% SL, in nearly all taxa (Table 3; Pietsch, 1981: figs 14, 40) (0), but extremely elongated, more than 30% SL, in †*Histionotophorus* and †*Orrichthys* (Tables 1–3) (1) (CI 1.00, RI 1.00).

#### SKIN SPINES

36. The skin is naked in nearly all taxa (0), but covered with simple close-set spinules in *Brachionichthys* (Fig. 9I) and *Lophichthys* (1), and with bifurcated spinules in *Antennarius* (Pietsch, 1981, 1984b: fig. 1; Pietsch & Grobecker, 1987: fig. 16) (2) (CI 0.67, RI 0.00).

#### RESULTS

The phylogenetic analysis produced a single tree, with a total length of 49, a CI of 0.7959, and a RI of 0.7959 (Fig. 12). Monophyly of the Antennarioidei was reconfirmed as recognized by Pietsch (1984a, 2009) and Pietsch & Grobecker (1987) (with bootstrap support of 98% and a Bremer value of 3). Four characters without homoplasy (unique and unreversed within the Antennarioidei) support antennarioid monophyly: interhyal with medial process (character 12, state 1), pharyngobranchials two (17, 1), dorsal-fin spines three (28, 1), and pectoral radials three or fewer (34, 1 and 2). Monophyly of the Brachionichthyidae was established (with bootstrap support of 96% and a Bremer value of 5) and its relationship to other antennarioids confirmed, again as proposed by Pietsch (1984a, 2009) and Pietsch & Grobecker (1987). Monophyly of the Brachionichthyidae is supported by six characters: vomerine teeth absent (2, 1), branchiostegal rays five (13, 1), third hypobranchial absent (14, 1), ceratobranchials strongly curved (15, 1), dorsal-fin spines two and three connected by membrane (31, 1), and pectoral radials two (34, 2). The clade with the weakest support comprises the Lophichthyidae as the sister group of the Tetrabrachiidae

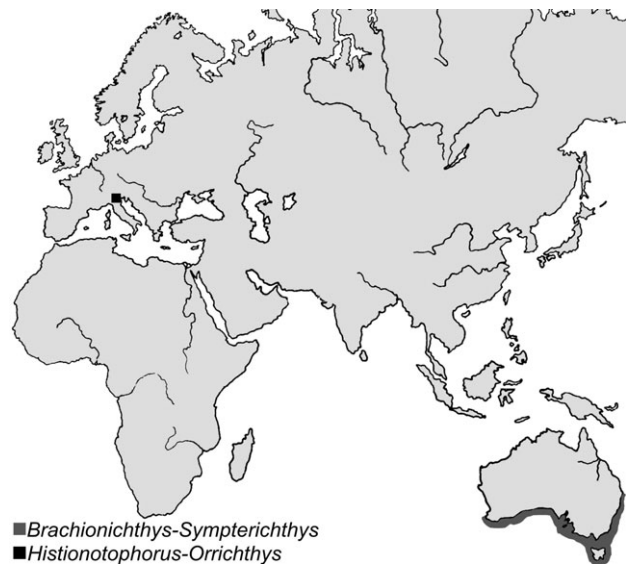


**Figure 12.** Cladogram of hypothesized relationships of the Brachionichthyidae and four lophiiform outgroups. The number above the base of a node is the Bremer value, and the number below the node indicates bootstrap support for the respective node.

and Antennariidae. The clade is supported by a single character: ectopterygoid T-shaped (5, 1). However, the sister-group relationship of Tetrabrachiidae and Antennariidae is supported by four characters: ventral surface of vomer deeply concave (1, 1), quadrate head narrow (4, 1), epibranchial teeth absent (16, 1), and vertebral column sigmoid (18, 1). These three families together form the sister group of the Brachionichthyidae. Within the Brachionichthyidae, the two extant genera *Brachionichthys* and *Sympterichthys* form a sister pair, supported by the absence of a hypural notch (24, 1) and a one-to-one ratio of dorsal- and anal-fin rays and pterygiophores (32, 1); as do the two extinct genera †*Histionotophorus* and †*Orrichthys* (both clades with bootstrap support of 92% and a Bremer value of 3), supported by posteroventrally directed haemal spines of the anterior-most abdominal vertebrae (22, 1), ventral-most caudal-fin ray reduced to a small splint (27, 1), illicial pterygiophore hypertrophied (29, 1), and extremely long pectoral-fin radials (35, 1).

**BIOGEOGRAPHICAL IMPLICATIONS**

Fossils provide the only direct record for morphological and genetic change through time, and greatly contribute to biogeography in providing additional taxa that can increase the known biogeographical range of a particular group and provide absolute times of first appearance (Grande, 1985; Smith, 1998). Moreover, the combination of phylogenetic analysis and the fossil record provides a powerful tool for understanding the dynamics leading to current biodiversity patterns. Therefore, the brachionichthyid



**Figure 13.** Known distribution of fossil and extant brachionichthyids.

phylogeny presented in this study allows for some consideration of handfish distribution through time.

Unlike other antennarioids that are primarily restricted to tropical biotopes (Pietsch & Grobecker, 1987), extant species of the family Brachionichthyidae are endemic to subtropical and temperate waters of southern and eastern Australia (Fig. 13), with the bulk of diversity concentrated in Tasmania, where no fewer than five taxa have been reported (see Edgar *et al.*, 1982; Last *et al.*, 1983). Endemicity, the exclusive occurrence of a taxon in a particular locality or region, is certainly the most significant feature of distribution patterns. Most biogeographers agree that

endemism may result in two ways, either because taxa originate in a particular geographical location and never disperse or because they now survive in only a small part of their former range (Brown & Lomolino, 1998). Following a more dynamic perspective, however, endemism may also result from a progressive and continuous shift in time and space of a determinate taxon range. Considering the phylogenetic relationships hypothesized within the brachionichthyids (Fig. 12), the Eocene record of the †*Histionotophorus*–†*Orrichthys* lineage necessarily implies that the lineage leading to the extant genera also existed at that time, even though there is no evidence that such a lineage occupied the inner shelf biotopes of southern and eastern Australia during the Eocene. Palaeontological evidence clearly indicates that during the Eocene southern Australia was characterized by a peculiar biota remarkably different from those of the Indian Ocean and Mediterranean Sea (Rosen & Smith, 1988). As for many other taxa, this suggests that the Australian *Brachionichthys*–*Symptericthys* lineage had a West Tethyan origin (e.g. Wallace & Rosen, 2006). A recent comprehensive analysis of Cenozoic global biodiversity patterns (Renema *et al.*, 2008) has revealed the presence of spatially and temporally distinct biodiversity hotspots, with different biotic and environmental histories over the past 50 Myr. During the Eocene, a West Tethyan hotspot originated in response to the wide enlargement of shallow marine platforms in southern Europe because of the progressive northern migration of the African plate. At the same time, the Australian–New Guinea block was separated from South-East Asia by a deep-water Indo-Pacific gateway (see Hall, 1998); this gap was progressively reduced in width by the northward subduction of the Indian–Australian lithosphere beneath the Sunda–Java–Sulawesi arcs, and closed in the Miocene by the collision of the Australia with Pacific arcs and the South-East Asian margin. The West Tethyan hotspot progressively vanished with the closure of the so-called Atlantic–Indian Ocean seaway in response to the rotation of the Afro–Arabian plate that eventually resulted in the collision with the Anatolian plate, approximately 18 Mya (Rögl, 1998). As a result of the closure of the Tethys in the Middle East and the huge increase in the availability of tropical shallow-water habitats in the region of convergence between Eurasia, Australia, and the Pacific–Philippine Sea plates, the modern Indo–Australian Archipelago hotspot originated with a dramatic rise in the number of tropical shallow marine organisms (e.g. Rosen, 1988; Pandolfi, 1992; Crame & Rosen, 2002; Renema *et al.*, 2008). Therefore, a progressive spatial shift of component taxa between West Tethyan and Indo–Australian Archipelago hotspots occurred synchronously

with the northward migration of the Afro–Arabian and Australian plates (see Wallace & Rosen, 2006). Handfishes probably were involved in this eastward biogeographical shift and eventually became established in Australia. A different scenario, concerning a possible south Australian or Tasmanian origin of brachionichthyids, is unlikely. Despite several indications that the Tasmanian region represents one of the primary evolutionary centres of modern life, with an extraordinary number of basal endemic taxa of Mesozoic origin that have survived *in situ* (Heads, 2009), the fossil record and the extremely reduced dispersal capability of handfishes across deep-water seaways (not to mention the lack of a dispersive larval stage; Bruce *et al.*, 1999) evidently contrast with such an hypothesis.

Based on their derived morphology and feeding adaptation, it is reasonable to hypothesize that the emergence of extant brachionichthyids occurred in subtropical and temperate biotopes of Tasmania and southern and eastern Australia. This area is peripheral to the high diversity centres of the Indo–Australian Archipelago, representing a region where new taxa of Tethyan ancestry may have originated during the Cenozoic (Pandolfi, 1992). Handfishes probably became extinct in the domain of the Indo–Australian Archipelago biodiversity hotspot and their present distribution can be considered the residual range of a temporally and spatially dynamic range shift.

As a final note, it is interesting to observe that the origin of a subtropical–temperate handfish lineage within a large primarily tropical antennarioid clade (including the tropical Eocene brachionichthyids †*Histionotophorus* and †*Orrichthys*) represents a further example of the so-called ‘out of the tropics’ model in which taxa preferentially originated in the tropics and then expanded in extra-tropical areas, being more successful at invading temperate zones than temperate taxa are at invading the tropics (see Jablonski, 1993; Vermeij, 2004; Jablonski *et al.*, 2006). The tropics are the source of many evolutionary novelties and have provided a pool of taxa from which high latitudes were populated through geological time (see also Crame, 2000). However, in the case of brachionichthyids, their latitudinal expansion can be regarded as a latitudinal shift that coincided with the loss of their presence in tropical waters.

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APPENDIX  
 Character matrix of 36 morphological characters for species of the Brachionichthyidae and four lophiiform outgroups.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36			
<i>Sladenia</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>Brachionichthys</i>	0	1	0	0	0	0	0	0	0	1	1	1	1	1	1	0	1	0	1	0	1	0	0	1	1	0	0	1	0	0	1	1	0	2	0	1	0	1	
<i>Sympierichthys</i>	0	1	1	0	2	1	0	1	0	0	1	1	1	1	1	0	1	0	1	1	1	0	0	1	1	0	0	1	0	0	1	1	0	2	0	0	0	0	
† <i>Histonotophorus</i>	0	1	0	0	0	0	0	1	0	0	1	?	1	?	1	?	1	0	0	0	0	1	0	0	1	1	1	1	1	1	1	0	0	2	1	0	0		
† <i>Orrichthys</i>	0	1	0	0	0	0	0	1	0	0	0	?	1	?	1	?	1	0	1	1	0	1	0	1	0	1	1	1	1	0	1	0	1	2	1	0	0		
<i>Lophichthys</i>	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	1	2	1	0	1	0	
<i>Tetrabrachium</i>	1	0	0	1	1	1	1	0	0	0	0	1	0	0	0	1	1	1	1	0	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	1	0	0
<i>Antennarius</i>	1	0	0	1	1	0	0	0	0	0	0	1	0	0	0	1	1	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	2	0