Phylogenetic position of the family Trichodontidae (Teleostei: Perciformes), with a revised classification of the perciform suborder Cottoidei

Hisashi Imamura[1]✉, Shigeru M. Shirai[2], and Mamoru Yabe[3]

[1] *The Hokkaido University Museum, 3-1-1 Minato-cho, Hakodate, Hokkaido 041-8611, Japan (e-mail: imamura@museum.hokudai.ac.jp)*
[2] *Japan Sea National Fisheries Research Institute, Fisheries Research Agency, 1-5939-22 Suido-cho, Niigata 950-8121, Japan (e-mail: sigra@affrc.go.jp)*
[3] *Laboratory of Marine Biodiversity, Graduate School of Fisheries Sciences, Hokkaido University, 3-1-1 Minato-cho, Hakodate, Hokkaido 041-8611, Japan (e-mail: myabe@fish.hokudai.ac.jp)*

Received: July 29, 2004 / Revised: March 4, 2005 / Accepted: March 14, 2005

Ichthyological Research

Ichthyol Res (2005) 52: 264–274
DOI 10.1007/s10228-005-0282-6

Abstract The phylogenetic relationships of the family Trichodontidae and suborder Cottoidei (and zoarcoid Bathymasteridae) are reconstructed morphologically. The monophyly of the Trichodontidae, Cottoidei, and Zoarcoidei is unambiguously supported by 14 synapomorphies, including 1 newly recognized (and also 4 synapomorphies when ACCTRAN is accepted). It is assumed that the Trichodontidae is deeply nested within the Cottoidei, and the family and Cottoidea plus Cyclopteroidea have a sister relationship, supporting a previously inferred molecular phylogenetic hypothesis. We propose that the Trichodontidae is placed into the cottoid superfamily Trichodontoidea.

Key words Trichodontidae · Phylogenetic position · Cottoidei · Monophyly · Classification

The family Trichodontidae, which comprises only two species, *Trichodon trichodon* (von Tilesius, 1813) and *Arctoscopus japonicus* (Steindachner, 1881), has been variously classified. For example, Greenwood et al. (1966) placed the family in the perciform suborder Trachinoidei, whereas Gosline (1968) put it into the percoid superfamily Trichodontoidae. Pietsch (1989) and Pietsch and Zabetian (1990), however, excluded the family from the Trachinoidei, supporting the monophyly of the suborder by two characters, small, short, and wide pectoral radials and the presence of a pelvic spur; but they did not provide taxonomic comments on the excluded Trichodontidae. Later, Nelson (1994) returned the Trichodontidae to the Trachinoidei. Recently, the family was placed into the perciform suborder Trichodontoidei by Nazarkin and Voskoboinikova (2000) based on comparative osteology. Such taxonomic disagreements have been caused by the lack of a comprehensive phylogenetic analysis, including the Trichodontidae and candidates as its closely related taxa.

At the 35th Annual Meeting of the Ichthyological Society of Japan on 13 October 2002, the authors presented the phylogenetic relationships of the "Scorpaeniformes" (sensu Nelson, 1994) and related taxa analyzed from mitochondrial *COI* and *Cyt b* sequences having ca. 2.7 kbp with M. Miya (Natural History Museum and Institute, Chiba) and M. Nishida (University of Tokyo), and it was put forward that the Trichodontidae is nested within the perciform Cottoidei (sensu Imamura and Yabe, 2002). More recently, Smith and Wheeler (2004) also demonstrated that the Trichodontidae is closely related to the Cottoidei, having as sister-relationship with a monophyletic clade including the Cottoidea and Cyclopteroidea, from a phylogenetic analysis based on both mitochondrial and nuclear sequence data. Although the Trichodontidae lacks the distinct suborbital stay (Fig. 1), which had been regarded as a synapomorphy of the former "Scorpaeniformes" (e.g., Gill, 1888; Matsubara, 1943; Shinohara, 1994; Yabe and Uyeno, 1996), the posterior margin of the third infraorbital is slightly pointed in the family. Additionally, there are several osteological similarities, which had been regarded as homoplasies a priori, in the previous descriptions of Trichodontidae and Cottoidei (Starks, 1930; Mooi and Johnson, 1997; Nazarkin and Voskoboinikova, 2000; Imamura and Yabe, 2002).

In this article, we examine the morphological characters of the Trichodontidae in detail and analyze the phylogenetic relationships of the family and Cottoidei to test the phylogenetic hypothesis from the molecular analysis and reconsider its phylogenetic position morphologically, to clarify the synapomorphies of the family and cottoid taxa, and to reconstruct the classification based on the inferred relationships.

Materials and Methods

Terminology generally follows recent studies for osteology (e.g., Baldwin and Johnson, 1993; Imamura and Yabe, 2002) and follows Winterbottom (1974) for myology, except

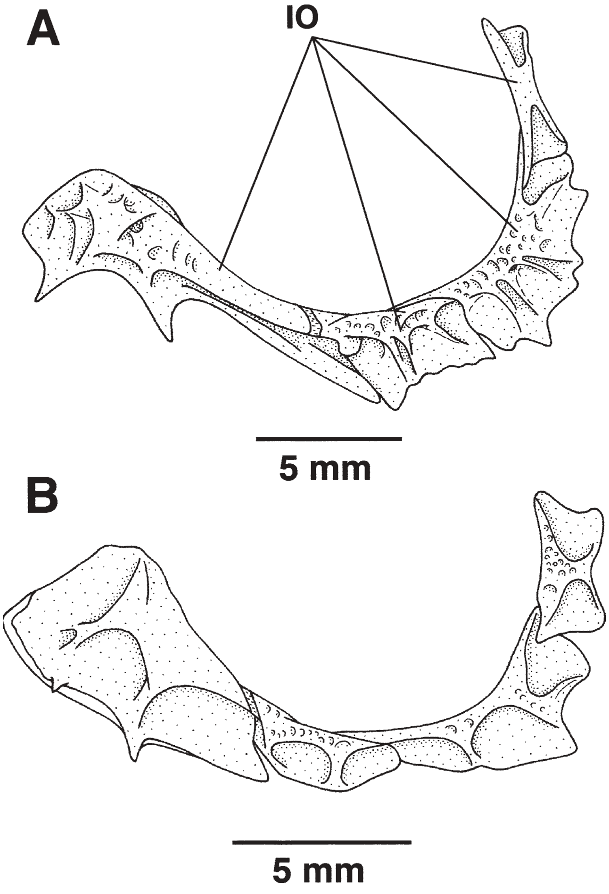

Fig. 1. Lateral view of infraorbitals (*IO*) of **A** *Trichodon trichodon*, HUMZ 88978, 179 mm and **B** *Arctoscopus japonicus*, HUMZ 45194, 142 mm

for the extrinsic swimbladder muscle, and transversus epibranchialis 2 and transversus pharyngobranchial 2, which follow Hallacher (1974) and Springer and Johnson (2004), respectively. Institutional abbreviations follow Leviton et al. (1985). Standard length (SL, mm) is used throughout. The Zoarcoidei is also included in the phylogenetic analysis to confirm the Trichodontidae is nested within the Cottoidei as shown by Smith and Wheeler (2004); if the family is not closely related with Cottoidei, it is inferred being branched off from the Cottoidei earlier than the Zoarcoidei. The family Bathymasteridae is used as a representation of the Zoarcoidei, because the family has many more plesiomorphic characters than the other zoarcoids and was assumed to have branched off from other zoarcoids initially although the relationships of the latter are still unknown (Anderson, 1994; Imamura and Yabe, 2002; this study). The Percoidei (sensu Nelson, 1994), which has been considered as the most primitive group within the Perciformes, was employed as the outgoup, and its typical or primitive conditions are coded as “0,” although the monophyly of the Percoidei is unclear (e.g., Nelson, 1994). The data were analyzed using PAUP *4.0b10 (Swofford, 2002), including an exhaustive search option. Character evolution was assumed as “ordered” (Wagner parsimony) or “unordered” (Fitch parsimony) when the transformation series contained a derived “loss” or character order was equivocal owing to many modifications. The character optimization was examined by both ACCTRAN and DELTRAN. The definition of the five cottoid superfamilies follows Imamura and Yabe (2002), and the superfamilies, Trichodontidae, and Bathymasteridae are used as operational taxonomic units. Dark areas in the figures indicate the cartilage throughout.

Materials examined. Trichodontidae: *Arctoscopus japonicus*, HUMZ 45194, 87857 (2 specimens, 142–147 mm, dissected), HUMZ 49987, 82477, 87845, 99629, 149737 (5, 128–187 mm, examined external morphology and osteology from radiographs); *Trichodon trichodon*, HUMZ 88978, 189048 (2, 150–179 mm, dissected), HUMZ 19942, 20621–20622, 124748–124749 (5, 154–196 mm, examined external morphology and osteology from radiographs). Anoplopomatoidea: *Anoplopoma fimbria*, HUMZ 130803 (240 mm); *Erilepis zonifer*, HUMZ 88050 (240 mm). Zaniolepidoidea: *Oxylebius pictus*, CAS 2010183 (124 mm). Hexagrammoidea: *Hexagrammos lagocephalus*, HUMZ 104878 (152 mm). Cottoidea: *Enophrys diceraus*, HUMZ uncat. (122 mm); *Hemitripterus villosus*, HUMZ uncat. (101 mm); *Malacocottus zonurus*, HUMZ 83016 (158 mm); *Marukawichthys ambulator*, HUMZ uncat. (123 mm); *Rhamphocottus richardsonii*, HUMZ uncat. (59 mm). Cyclopteroidea: *Eumicrotremus birulai*, HUMZ 67949 (101 mm); *Liparis agassizii*, HUMZ 80745 (150 mm). Bathymasteridae: *Bathymaster signatus*, HUMZ 46589 (250 mm) and 1 uncatalogued specimen (248 mm).

In addition, another 89 cottoids, 36 percoids, and 7 zoarcoid species were examined as listed by Yabe (1985), Imamura (2000), and Imamura and Yabe (2002), respectively.

Results

Character argumentation. The following characters belonging to 44 transformation series (TS) were recognized to be valuable to infer the phylogenetic relationships of the Trichodontidae, Cottoidei, and Bathymasiteridae.

TS 1. Distinct suborbital stay (Fig. 1).—0: absent or obscure; 1: present. The suborbital stay had been considered as a synapomorphpy of the “Scorpaenifromes.” All cottoid members bear this stay in the third infraorbital (e.g., Yabe, 1985; Kido, 1988; Shinohara, 1994; Imamura and Yabe, 2002). In the Trichodontidae, the posterior margin of the third infraorbital is slightly pointed and the suborbital stay is obscure.

TS 2. Bony parietal structure supporting sensory canal (Fig. 2).—0: absent; 1: present, lacking spines; 2: present, having spine(s) (unordered). The Trichodontidae has a bony parietal structure supporting sensory canal lacking spines, as pointed out previously (e.g., Mooi and Johnson, 1997; Imamura and Yabe, 2002). This character was regarded as a synapomorphy of the Cottoidei and Zoarcoidei by Imamura and Yabe (2002); it is reversely absent in the Cyclopteryidae among the Cottoidei, as well as in many percoids; and the canal bears spine(s) in many cottoids (e.g., Shinohara, 1994; Imamura and Yabe, 2002; this study).

TS 3. Lachryopalatine articulation.—0: absent; 1: present. An inner projection of the first infraorbital (=lachrymal;

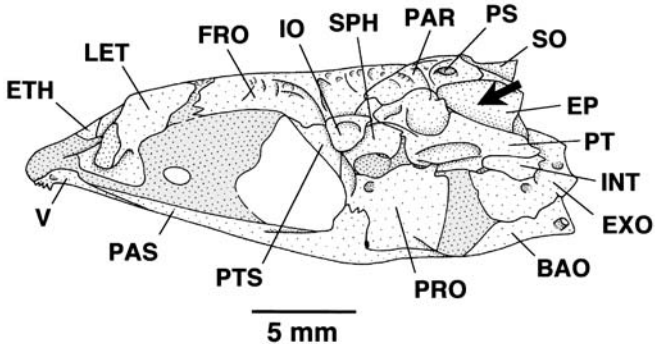

Fig. 2. Lateral view of neurocranium of *Arctoscopus japonicus*, HUMZ 45194, 142 mm. *BAO*, basioccipital; *ETH*, ethmoid; *EP*, epiotic; *EXO*, exoocipital; *FRO*, frontal; *IO*, 5th infraorbital; *INT*, intercalar; *LET*, lateral ethmoid; *PAS*, parasphenoid; *PAR*, parietal; *PRO*, prootic; *PS*, parietal sensory canal; *PT*, pterotic; *PTS*, pterosphenoid; *SO*, supraoccipital; *SPH*, sphenotic; *V*, vomer. *Arrow* indicates posttemporal fossa

Yabe, 1985) for the articulation with the palatine providing a firm attachment with the latter (=lachryopalatine articulation) has been known in the Cottoidei except for the Anoplopomatoidea (e.g., Yabe, 1985; Shinohara, 1994). Such an articulation is not recognized in the Percoidei, as well as in the Trichodontidae and Zoarcoidei including the Bathymasteridae (Yabe, 1985; Shinohara, 1994; this study).

TS 4. Intercalar (Fig. 2).—0: attached to prootic; 1: separated from prootic; 2: absent (unordered). The intercalary is typically attached to the prootic in the Percoidei, as well as in the Bathymasteridae (e.g., Yabe, 1985; Imamura, 1996; this study), whereas this connection is absent in the Trichodontidae (Nazarkin and Voskoboinikova, 2000; this study). Such a separation is also found in the Cottoidea and some liparids (*Careproctus reinhardti* and *Crystallichthys matsushimae*); the intercalar is absent in the other liparids and examined cyclopterid (e.g., Regan, 1913; Quast, 1965; Yabe, 1985; Kido, 1988; Shinohara, 1994; this study).

TS 5. Parasphenoid-pterosphenoid connection (Fig. 2).—0: absent; 1: present; 2 pterosphenoid absent (unordered). The parasphenoid and pterosphenoid is typically separated in the Percoidei (Quast, 1965; Yabe, 1985; Shinohara, 1994; this study). The parasphenoid-pterosphenoid connection is recognized in the zoarcoid Bathymasteridae and most cottoids. The connection is absent in the cottoid Ereuniidae, Psychrolutidae, and Cyclopteroidea, as well as in the Trichodontidae (Yabe, 1985; Imamura and Yabe, 2002). In the cyclopteroid Liparidae, the connection is absent or the pterosphenoid is absent (Kido, 1988; this study).

TS 6. Basisphenoid (Fig. 2).—0: present; 1: absent. The basisphenoid is a basic element of the neurocranium in the Percoidei (e.g., Yabe, 1985; Shinohara, 1994). As pointed out by Nazarkin and Voskoboinikova (2000), the Trichodontidae lacks the basisphenoid. This bone is also absent in the Cottoidea and Cyclopteroidea, as well as in the Zoarcoidei, including the Bathymasteridae (e.g., Taranetz, 1941; Yabe, 1985; Kido, 1988; Anderson, 1994; Shinohara, 1994; this study).

TS 7. Posttemporal fossa (Fig. 2).—0: present; 1: shallow or absent. The posttemporal fossa is shallow or absent in the Cottoidea and Cyclopteroidea (Yabe, 1985; Kido, 1988). Kido (1988) regarded this derived character as a synapomorphy of these groups. The Trichodontidae has well-developed posttemporal fossa inserted by the epaxialis, as well as in the Percoidei and Zoarcoidei, including the Bathymasteridae (Yabe, 1985; this study).

TS 8. Palatine teeth.—0: present; 1 absent. The palatine teeth are typically present in the Percoidei (e.g., Imamura, 1996). Among the ingroup, the palatine teeth are absent in the Trichodontidae, Cyclopteroidea, and a part of the Cottoidea (e.g., Taranetz, 1941; Yabe, 1985; Kido, 1988; Nazarkin and Voskoboinikova, 2000; this study).

TS 9. Connection between preopercle and temporal sensory canals.—0: present; 1: absent. As pointed out by Imamura (1996), the preopercular and temporal sensory canals are usually continuous at the pterotic in the Percoidei. These canals are separated in the trichodontid *Trichodon*, as well as in the Cottoidei, except for the Anoplopomatoidea, and Zoarcoidei, including the Bathymasteridae; on the other hand, they are continuous in the trichodontid *Arctoscopus* and Anoplopomatoidea.

TS 10. Branchiostegal rays.—0: seven; 1: six; 2: five (order as 0–1–2). Typical percoids have seven branchiostegal rays (e.g., Yabe, 1985; Shinohara, 1994; Imamura, 1996). The Psychrolutidae has seven branchiostegal rays and liparid *Paraliparis nanus* five, whereas other ingroup members, including the Trichodontidae, bear six rays (Taranetz, 1941; Quast, 1965; Yabe, 1985; Kido, 1985; Shinohara, 1994; Nazarkin and Voskoboinikova, 2000; Imamura and Yabe, 2002; this study).

TS 11. Basihyal (Fig. 3).—0: ossified; 1: cartilaginous; 2: absent (unordered). The basihyal is an ossified element in the Percoidei (Yabe, 1985; Imamura, 1996) and Trichodontidae (Nazarkin and Voskoboinikova, 2000; this study). The cartilaginous basihyal is found in the cottoid *Rhamphocottus*. The element is absent in the Cyclopteroidea and Cottoidea, except in *Jordania*, which has a tiny ossified basihyal, and *Rhamphocottus* (Yabe, 1985; this study).

TS 12. Urohyal and first basibranchial (Fig. 3).—0: loosely attached; 1: firmly attached. Imamura (1996) described the urohyal as being loosely attached to the first basibranchial in the Percoidei. Kido (1988) reported the Liparidae and Cyclopteridae share a derived character, these bones being firmly attached. Such a condition is also present in the Trichodontidae. These bones are loosely attached in other ingroup members.

TS 13. First epibranchial.—0: with two processes medially; 1: with single process medially. In the Percoidei, the first epibranchial bears two processes medially: one connected with the first pharyngobranchial, and another with the second pharyngobranchial via the interarcual cartilage. Such a condition is recognized in the Trichodontidae, as well as in the Zaniolepidoidea, Hexagrammoidea, Cottoidea, and Cyclopteridae (Kido, 1988: fig. 12E; this study). A single medial process (=uncinate process, see Imamura and Yabe, 2002: 119) is found in the Anoplopomatoidea and Liparidae,

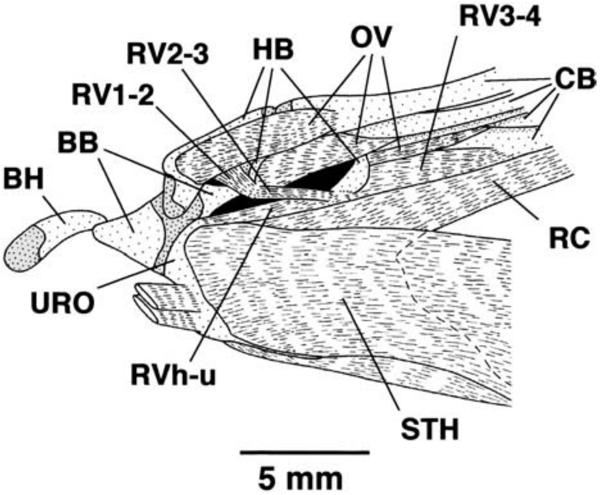

Fig. 3. Ventrolateral view of lower gill arch of *Trichodon trichodon*, HUMZ 88978, 179 mm. *BB*, basibranchial; *BH*, basihyal; *RV1–2, RV2–3 and RV3–4*, rectus ventralis connecting first and hypobranchials, second and third hypobranchial, and third hypobranchial and fourth ceratobranchial, respectively; *HB*, hypobranchial; *OV*, obliquus ventralis; *CB*, ceratobranchial; *RC*, rectus communis; *STH*, sternohyoideus; *URO*, urohyal; *RVh-u*, rectus ventralis connecting third hypobranchial and urohyal

and also Zoarcoidei including the Bathymasteridae (Kido, 1988: fig. 12A–D; Imamura and Yabe, 2002).

TS 14. Tooth plate on third epibranchial.—0: present; 1: absent. A tooth plate is typically present on the third epibranchial in the Percoidei (e.g., Shinohara, 1994; Imamura, 1996). The Trichodontidae lacks the tooth plate, as well as the Cottoidei, except for the cottoid *Hemitripterus*, hexagrammoid *Ophiodon*, and Zoarcoidei including the Bathymasteridae (e.g., Yabe, 1985; Shinohara, 1994; Nazarkin and Voskoboinikova, 2000: fig. 8; Imamura and Yabe, 2002; this study).

TS 15. Second to fourth pharyngobranchials.—0: separated; 1: third and fourth continuous; 2: second to fourth continuous (ordered as 0–1–2). The Trichodontidae bears the second to fourth pharyngobranchials separated from each other, as well as the Percoidei and Bathymasteridae (Imamura, 1994; this study). Both characters 15-1 and 15-2 are recognized in the Cottoidea and Cyclopteroidea (Yabe, 1985; Kido, 1988: fig. 12; this study).

TS 16. Scapula foramen (Fig. 4).—0: closed; 1: with crack anteriorly; 2: widely opened anteriorly (ordered as 0–1–2). The scapula foramen is completely closed in the typical percoids (e.g., Yabe, 1985; this study). In the Trichodontidae, the foramen is widely opened anteriorly (Nazarkin and Voskoboinikova, 2000; this study). Such a condition is also recognized in the Cottoidea, except for the rhamphocottid *Rhamphocottus* and cottid *Jordania* having a crack anteriorly, and Cyclopteroidea, whereas the foramen is closed in the other ingroup members (e.g., Yabe, 1985; Kido, 1988; this study).

TS 17. Lateral extrascapular (Fig. 5).—0: composed of single element with three openings; 1: composed of two elements with two openings, respectively; 2: composed of a single horizontal element with two openings; 3: composed of single longitudinal element with two openings; 4: absent (unordered). Imamura and Yabe (2002) inferred the lateral extrascapular composed of a single element with three openings as being primitive, because it was inferred the bone is made by the fusion of two elements with two openings, respectively. The trichodontid *Arctoscopus* has the lateral extrascapular composed of two elements with two openings. Although *Trichodon* has three elements, it is assumed from the comparison with *Arctoscopus* that the horizontal element is divided into two; this condition is an autapomorphy of the genus. The condition of *Arctoscopus* is also recognized in most ingroup members. However, among the Cottoidei, the lateral extrascapular consisting of a single element with three openings is found in the zaniolepidoid *Oxylebius* (right side of a single specimen only) and Hexagrammoidea, except for *Ophiodon* having the bone comprised of two elements with two openings, respectively. It is composed of a single horizontal element with two openings in the Psychrolutidae, except for *Dasycottus* and *Eurymen* having a single element with three openings. In the Cyclopteroidea, a single longitudinal element has two openings or the lateral extrascapular is absent (see also Imamura and Yabe, 2002).

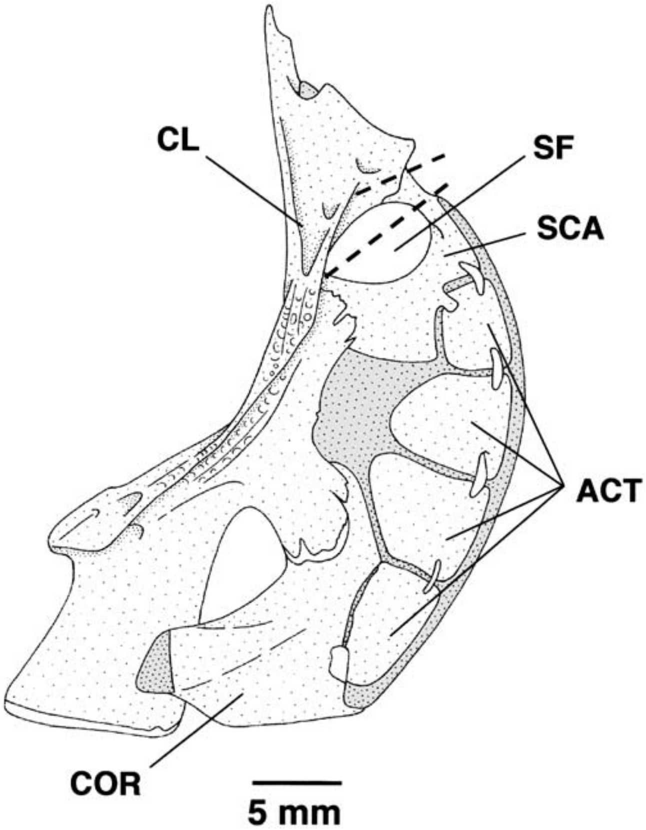

Fig. 4. Lateral view of shoulder girdle of *Trichodon trichodon*, HUMZ 88978, 179 mm. *ACT*, actinost; *CL*, cleithrum; *COR*, coracoid; *SCA*, scapula; *SF*, scapula foramen. *Broken lines* indicate upper and lower borders of arrector ventralis

TS 18. Number of supraneurals (Fig. 6).—0: three; 1: one; 2: zero (ordered as 0–1–2). Three supraneurals constitute the basic condition in the Percoidei (e.g., Smith and Bailey, 1961; Johnson, 1980, 1984; Sasaki, 1989). Two specimens of the trichodontid *Arctoscopus* (HUMZ 49987 and 82477) bear a single rodlike element without fin rays between the third and fourth neural spines, whereas three specimens of the genus (HUMZ 87845, 99629, and 149737) have the first dorsal fin pterygiophore with a fin ray within the same interneural space. Although a single specimen of *Arctoscopus* (HUMZ 45194) bears a single rodlike element without fin rays and one dorsal fin pterygiophore with a fin ray between the fourth and fifth neural spines (Fig. 6B), *Trichodon* has two dorsal fin pterygiophores with a fin ray, respectively, between the same interneural space (Fig. 6A). Therefore, we identified the rayless element in *Arctoscopus* with the first dorsal fin pterygiophore lacking a dorsal fin ray, and regarded the presence and absence of the fin ray as an intraspecific variation of *Arctoscopus*. Thus, Trichodontidae completely lacks the supraneurals, as well as other ingroup members, except for the hexagrammoid *Ophiodon* having a single element (see Shinohara, 1994; Imamura and Yabe, 2002).

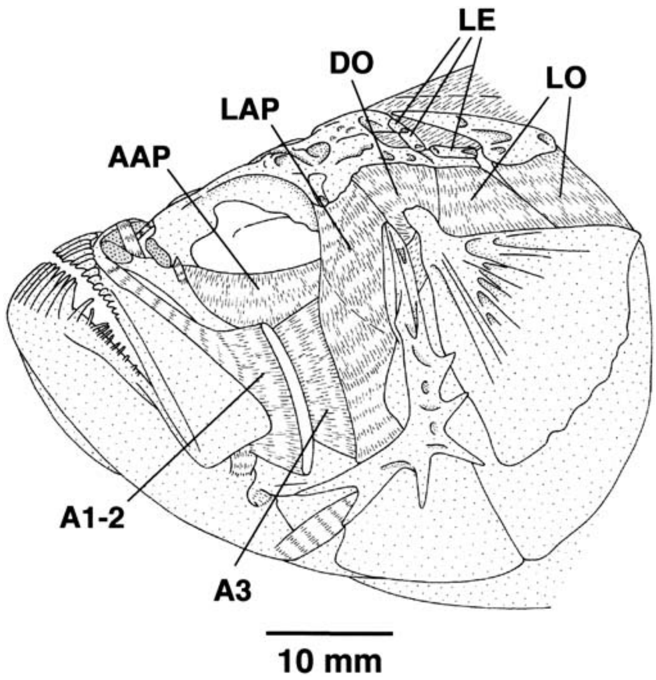

Fig. 5. Lateral view of head of *Trichodon trichodon*, HUMZ 88978, 179 mm. *A1–2* and *A3*, adductor mandibulae section 1–2 and 3; *AAP*, adductor arcus palatini; *DO*, dilator operculi; *LAP*, levator arcus palatini; *LE*, lateral extrascapular; *LO*, levator operculi

TS 19. Dorsal fin pterygiophores (Fig. 6).—0: two elements inserted into single interneural space anteriorly; 1: single element arranged singly in each interneural space. The anterior interneural space (second or third interneural space) typically receives two dorsal fin pterygiophores in the Percoidei (Imamura and Yabe, 2002). *Trichodon* and a single specimen of *Arctoscopus* (HUMZ 45194) also have the fourth interneural space receiving two dorsal fin pterygiophores, whereas the first and second dorsal fin pterygiohpores insert into the third and fourth interneural spaces, respectively, in other *Arctoscopus* specimens (see TS 18 for the identification of spineless bony element in *Arctoscopus*). On the other hand, a single pterygiophore element is arranged singly in each interneural space in all ingroup members, except for the anoplopomatoid *Erilepis* (Shinohara, 1994; Imamura and Yabe, 2002).

TS 20. Anal fin spines with robust anterior pterygiophore.—0: present; 1: absent. Both anal fin spines and robust anterior pterygiophore are usually found in the Percoidei (Shinohara, 1994; this study), whereas they are absent in the Trichodontidae, Cottoidei (except for the Zaniolepidoidea), and Zoarcoidei, including the Bathymasteridae (Imamura and Yabe, 2002; this study).

TS 21. Number of anal fin rays associated with first anal pterygiophore ventrally.—0: two; 1: one; 2: zero (ordered as 0–1–2). Two anal fin rays are associated with the ventral

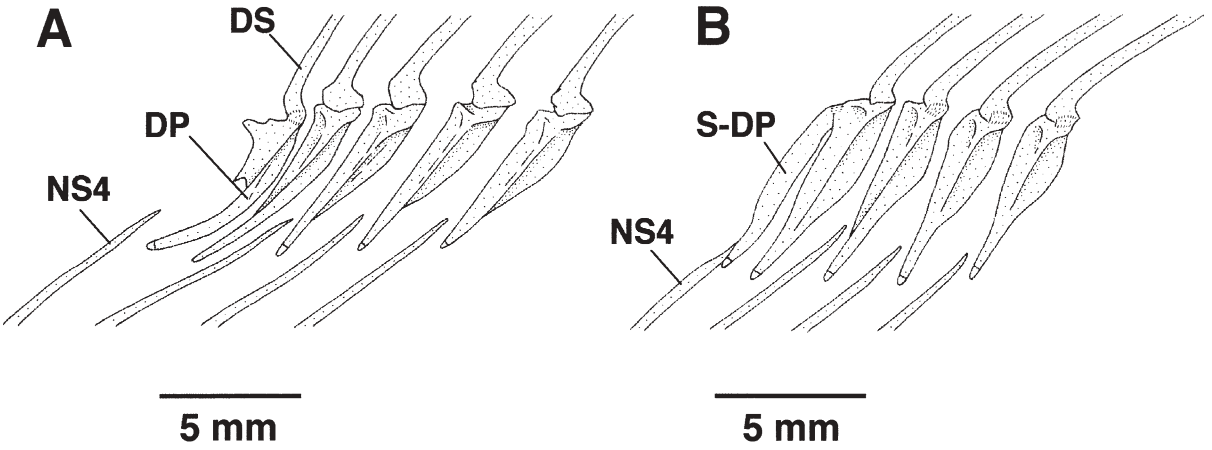

Fig. 6. Lateral view of anterior vertebrae and associated bones of **A** *Trichodon trichodon*, HUMZ 88978, 179 mm and **B** *Arctoscopus japonicus*, HUMZ 45194, 142 mm. *DP*, dorsal fin pterygiophore; *DS*, dorsal fin spine; *NS4*, fourth neural spine; *S-DP*, spineless dorsal fin pterygiophore

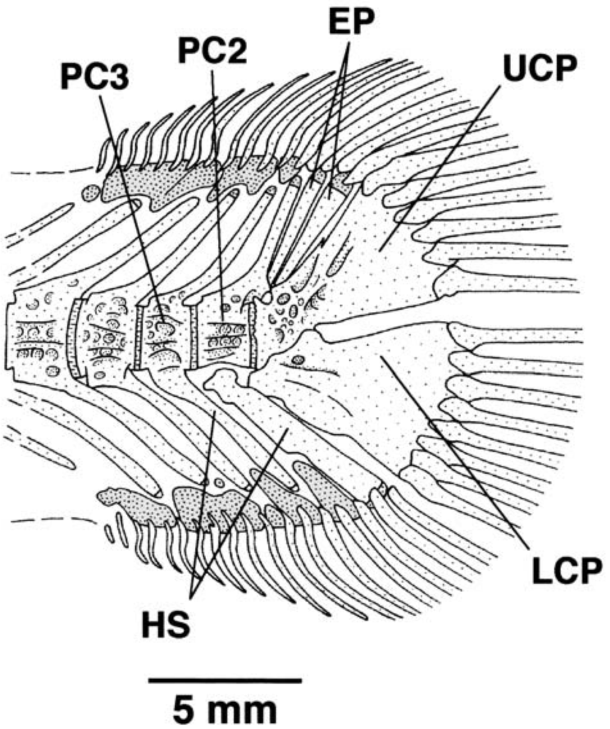

Fig. 7. Lateral view of caudal skeleton of *Trichodon trichodon*, HUMZ 88978, 179 mm. *PC2 and PC3*, second and third preural centra, respectively; *UCP*, upper caudal plate composed of third and fourth hypurals, uroneural, and urostyle; *LCP*, lower caudal plate composed of first and second hypurals and parhypural; *EP*, epurals; *HS*, hemal spine

edge of the first anal pterygiophore typically in percoids. Such a condition is recognized in the trichodontid *Arctoscopus*, as well as in the several ingroup members (Anoplopomatoidea, Zaniolepidoidea, hexagrammoid *Pleurogrammus*, and Bathymasteridae). A single ray is supported in the trichodontid *Trichodon*, hexagrammoid *Hexagrammos*, and Cyclopteroidea, and no rays in the Cottoidea (e.g., Shinohara, 1994: fig. 31; this study).

TS 22. Dorsal and anal fin stays.—0: present; 1: absent. The dorsal and anal fin stays are typically present in the Percoidei (e.g., Shinohara, 1994; Imamura, 1996). They are completely absent in the Trichodontidae, as well as in the Hexagrammoidea, most cottoids, Cyclopteroidea, and Zoarcoidei, including the Bathymasteridae (Yabe, 1985; Shinohara, 1994; Imamura and Yabe, 2002; this study). Among the Cottoidea, stays are present in the Rhamphocottidae and Ereuniidae (Yabe, 1985; this study).

TS 23. Second preural centrum and hemal spine (Fig. 7).—0: autogenous; 1:fused. In the typical percoid caudal skeleton, the following autogenous elements are recognized: five hypurals, parhypural with the hypurapophysis, hemal spines on the second and third preural centra, three epurals, urostyle, and one or two uroneurals (e.g., Yabe, 1985; Shinohara, 1994; Imamura, 1996). The second preural centrum and hemal spine are separated in the Trichodontidae, which is contrary to the description of Nazarkin and Voskoboiniskova (2000). They are fused in the Cottoidea and several liparid *Liparis* among the ingroup (Yabe, 1985; Kido, 1988).

TS 24. Third preural centrum and hemal spine (Fig. 7).—0: autogenous; 1: fused. The third preural centrum and hemal spine are fused in the Trichodontidae, as well as in the Cottoidei, except for the Zaniolepidoidea and Hexagrammoidea, and zoarcoid Bathymasteridae (Yabe, 1985; Kido, 1988; Shinohara, 1994; this study). See comment under TS 23 for the character polarity.

TS 25. First and second hypurals (Fig. 7).—0: autogenous; 1: fused. In all ingroup members, including the Trichodontidae, the first and second hypurals are fused to form a lower hypurals plate (Shinohara, 1994; this study). See comment under TS 23 for the character polarity.

TS 26. Third and fourth hypurals (Fig. 7).—0: autogenous; 1: fused. In all ingroup members, except for the cottoid Anoplopomatoidea and zoarcoid Bathymaiteridae, the third and fourth hypurals are fused to form an upper hypural plate (Shinohara, 1994; this study). See comment under TS 23 for the character polarity.

TS 27. Fifth hypural (Fig. 7).—0: present; 1: absent. The fifth hypural is absent in the Trichodontidae, as well as in the Anoplopomatoidea, zaniolepidoid *Oxylebius*, Hexagrammoidea, Cottoidea, and Cyclopteroidea, whereas it is present in the other ingroup members (Yabe, 1985; Kido, 1988; Shinohara, 1994; Nazarkin and Voskoboinikova, 2000; this study). See comment under TS 23 for the character polarity.

TS 28. Urostyle and upper hypural plate (Fig. 7).—0: autogenous; 1: fused. In the Trichodontidae, zaniolepidoid *Zaniolepis*, Cottoidea, and Cyclopteroidea except for the liparid *Liparis* and some *Crystallichthys*, the urostyle and upper hypural plate are fused (Yabe, 1985; Shinohara, 1994; Kido, 1988; this study). See comment under TS 23 for the character polarity.

TS 29. Parhypural and lower hypural plate (Fig. 7).—0: autogenous; 1: fused. All ingroup members, except for the Anoplopomatoidea and hexagrammoid *Ophiodon*, have the fused parhypural and lower hypural plate (e.g., Yabe, 1985; Shinohara, 1994; this study). See comment under TS 23 for the character polarity.

TS 30. Hypurapophysis (Fig. 7).—0: present; 1: absent. The hypurapophysis is absent in the Trichonotidae, Hexagrammoidea, Cottoidea, and Cyclopteroidea among ingroup taxa (Yabe, 1985; Shinohara, 1994; this study). See comment under TS 23 for the character polarity.

TS 31. Number of epurals (Fig. 7).—0: three; 1: two; 2: one; 3: zero (ordered as 0–1–2–3). Both trichodontid genera *Arctoscopus* and *Trihcodon* have three or two epurals, respectively (Nazarkin and Voskoboinikova, 2000; this study). The number of epurals varies from three to one in the Cottoidea and from two to zero in the Cyclopteroidea (e.g., Yabe, 1985; Kido, 1988). The other ingroup members have three epurals (Yabe, 1985; Shinohara, 1994; this study). See comment under TS 23 for the character polarity.

TS 32. Uroneural (Fig. 7).—0: present; 1: absent. There are no autogenous uroneurals in the Trichodontidae, as well as in the Cyclopteroidea and several cottoids (e.g., *Altediellus*

Myoxocephalus), whereas other ingroup members have a single element (Yabe, 1985; Kido, 1988; Shinohara, 1994; Nazarkin and Voskoboinikova, 2000; this study). See comment under TS 23 for the character polarity.

TS 33. Posterior nostril.—0: present; 1: absent. In the Percoidei, anterior and posterior nostrils are typically present. Among the ingroup, the posterior nostril is absent in the Trichodontidae and Zoarcoidei, including the Bathymasteridae (Anderson, 1994; Nazarkin and Voskoboinikova, 2000; this study).

TS 34. Adductor mandibulae section 3 (Fig. 5).—0: absent; 1: present, located on medial surface of levator arcus palatini; 2: present, not associated with levator arcus palatini (unordered). A well-separated adductor mandibulae section 3 is usually absent in the Percoidei. The muscle element located on the medial surface of the levator arcus palatini (LAP) is recognized in the Trichodontidae. Such a condition was regarded as a synapomorphy of the Cottoidei and Zoarcoidei by Imamura and Yabe (2002), although the muscle element is absent in the cyclopteroid Liparidae and it is not associated with LAP in the Cyclopteridae (Imamura and Yabe, 2002).

TS 35. Number of elements of levator operculi (Fig. 5).—0: one; 1: two. As pointed out by Imamura and Yabe (2002), typical percoids have a single levator operculi originating from the pterotic. Most ingroup members, including the Trichodontidae, bear a levator operculi composed of two elements, although a single element is present in the Liparidae (Imamura and Yabe, 2002).

TS 36. Transversus pharyngobranchialis 2 (Fig. 8).—0: present, mostly straight; 1: present, circular; 2: absent (unordered). Imamura and Yabe (2002) recognized that the circular element of the transversus dorsalis anterior is a derived condition in the "Scorpaeniformes." Recently, Springer and Johnson (2004) regarded that this circular element is homologous with the transversus pharyngobranchialis 2 (TPB2) (sensu Springer and Johnson, 2004). The circular TPB2 is found in all ingroup taxa, except for the trichodontid *Arctoscopus*, Cyclopteroidea, and several cottoids (see Imamura and Yabe, 2002), in which TPB2 is absent. On the other hand, TPB2 is mostly straight in the typical percoids (this study).

TS 37. Levator externus III (Fig. 8).—0: present; 1: absent. The Percoidei has typically four levatores externi, extending from the cranium to epibranchials, as well as the Trichodontidae (Yabe, 1985; Shinohara, 1994; Imamura, 1996; this study). On the other hand, the third element, inserted onto the third epibranchial, is absent in the Cottoidea and Cyclopteroidea among the ingroup (Yabe, 1985; Shinohara, 1994; Springer and Johnson, 2004; this study).

TS 38. Adductores I–III (Fig. 8).—0: absent; 1: present. Imamura and Yabe (2002) inferred the absence of adductores I–III, muscles between the ceratobranchials and epibranchials, as being a primitive character in the Percoidei. These elements are also absent in the Trichodontidae, whereas they are present in all other ingroup members, except for the Cyclopteroidea and several Cottoidea (Imamura and Yabe, 2002; this study).

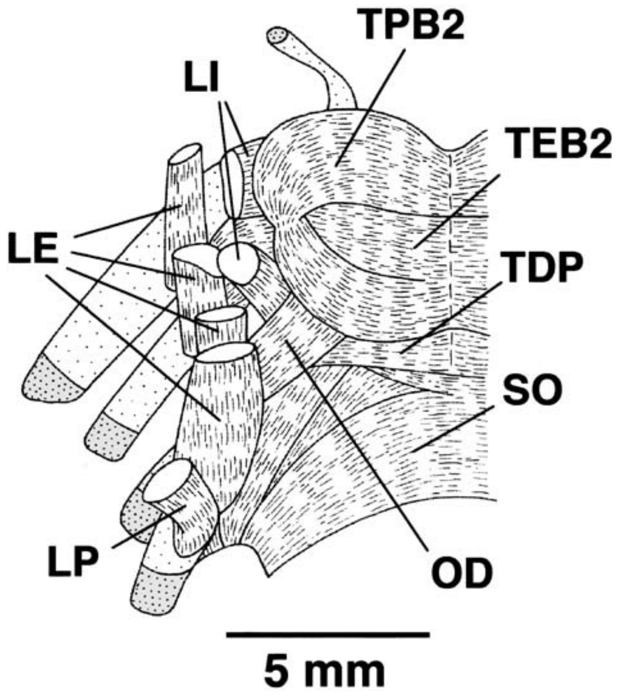

Fig. 8. Dorsal view of upper gill arch of *Trichodon trichodon*, HUMZ 88978, 179 mm. *LE*, levator externus; *LI*, levator internus; *LP*, levator posterior; *OD*, obliquus dorsalis; *SO*, sphincter oesophagi; *TEB2*, transversus epibranchials 2; *TPB2*, transversus pharyngobranchialis 2; *TDP*, transversus dorsalis posterior

TS 39. Number of rectus ventralis muscles between gill arches (Fig. 3).—0: one; 1: two; 2: three (ordered as 0–1–2). In the Percoidei, there is a rectus ventralis muscle between the third hypobranchial and fourth ceratobranchial (e.g., Yabe, 1985; Sasaki, 1989). The Trichodontidae has an additional two elements: one connects the first and second hypobranchials; and the other connects the second and third hypobranchials. Such elements have been reported in an agonid *Podthecus* (between the second and third hypobranchials) and the liparid *Liparis* (between the first and second, and second and third hypobranchials) among the Cottoidei (Yabe, 1985). Additionally, we newly found an element between the second and third hypobranchials in the hemitripterid *Hemitripterus*. These unique elements were not found in the other ingroup members.

TS 40. Number of rectus ventralis muscles between hypobranchial and urohyal (Fig. 3).—0: zero; 1: one; 2: two (ordered as 0–1–2). There are no rectus ventralis muscles connecting the hypobranchial and urohyal in typical percoids (e.g., Yabe, 1985). There is a single rectus ventralis between the third hypobranchial and urohyal in the Trichodontidae. Such an element was described in all cottoids except for the Ereuniidae and Rhamphocottidae by Yabe (1985). On the other hand, two elements, situated between the second hypobranchial and urohyal, and the third hypobranchial and urohyal, are restricted to the cyclopteroid Liparidae (Yabe, 1985; this study). The other ingroup members (e.g., Hexagrammoidea, cottoid Rhamphocottidae, cyclopteroid Cyclopteridae, and zoarcoid

Bathymasteridae) lack these muscular elements (Yabe, 1985; Shinohara, 1994; this study).

TS 41. Arrector ventralis (Fig. 4).—0: well developed; 1: reduced. The arrector ventralis of the pectoral fin muscular element is well developed in the Percoidei (Shinohara, 1994; this study). A reduced arrector ventralis is found in the Trichodontidae, Hexagrammoidea, Cottoidea, and Cyclopteroidea among the ingroup (Shinohara, 1994; this study).

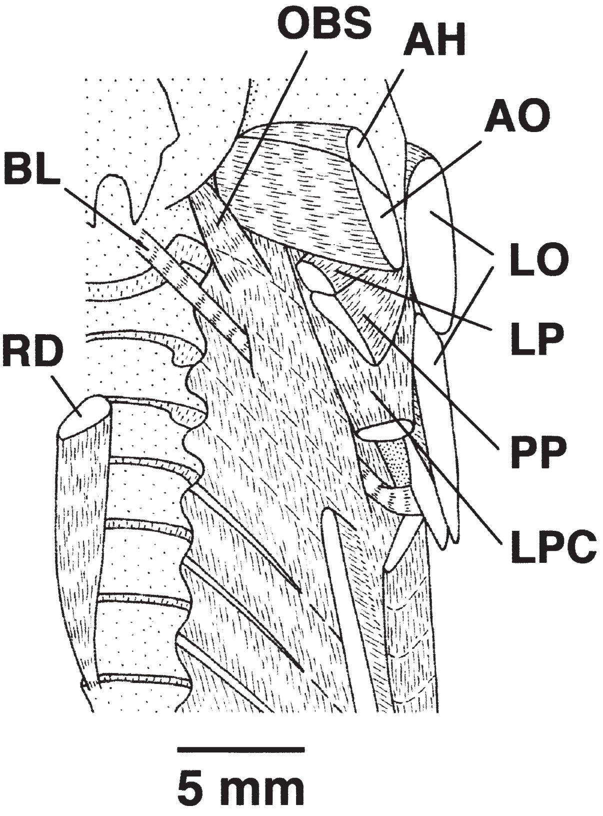

Fig. 9. Ventral view of body cavity of *Trichodon trichodon*, HUMZ 88978, 179 mm. *AH*, adductor hyomandibulae; *AO*, adductor operculi; *BL*, Baudelot's ligament; *LO*, levator operculi; *LP*, levator posterior; *LPC*, levator pectoralis; *OBS*, obliquus superioris; *PP*, protractor pectoralis; *RD*, retractor dorsalis

TS 42. Extensor proprius.—0: present; 1: absent. The extensor proprius of the pelvic fin muscular element is typically present in the Percoidei (Shinohara, 1994; this study). This element is absent in the Trichodontidae, and also in the Hexagrammoidea, Cottoidea, and Cyclopteroidea (Yabe, 1985; Shinohara, 1994; this study).

TS 43. Obliquus superioris (Fig. 9).—0: not connected with cleithrum; 1: connected with cleithrum. In the Cottoidea and Cyclopteroidea, the extrinsic muscle originates from the otolith chamber of the neurocranium, and is inserted on the anteroventral process of the cleithrum (Yabe, 1985; this study). However, the extrinsic muscle originates mainly from the posttemporal fossa of the neurocranium, and is situated on the dorsal portion of the body in the other members of the Cottoidei (Imamura, 1996; this study). Such a muscle was also found in the Cottoidea and Cyclopteroidea. We consider that the extrinsic muscle (sensu Yabe, 1985) of the Cottoidea is not homologous with that of the other members of the Cottoidei, because the extrinsic muscle is situated on the dorsal portion of body in the latter. On the other hand, the obliquus superioris originates from the otolith chamber and its posterior portion is nested within the body muscle in the Cottoidei except for Cottoidea and Cyclopteroidea, as well as in the Percoidei. Therefore, we conclude that Yabe's (1985) extrinsic muscle is homologous with the obliquus superioris connecting with the cleithrum, which is considered to be a derived condition. The obliquus dorsalis superioris is not connected with the cleithrum in the Trichodontidae and Zoarcoidei including the Bathymasteridae.

TS 44. Extrinsic muscle derived from epaxialis.—0: absent; 1: present. Presence of the extrinsic muscle derived from the epaxialis has been recognized as a synapomorphy of the Cottoidei, finding its absence in the Percoidei (Imamura, 1996, 2000; Imamura and Yabe, 2002) (see also comments on TS 43). This muscle element is absent in the Trichodontidae and Zoarcoidei, including the Bathymasteridae.

Phylogenetic position of Trichodontidae. The phylogenetic relationships of the Trichodontidae, Cottoidei, and Bathymasiteridae were analyzed based on the characters found in 44 transformation series (Table 1). The autapomorphies of a sole operational taxonomic unit were not

Table 1. Character matrix of Trichodontidae, five superfamilies of Cottoidei, and Bathymasteridae

	Transformation series								
Taxon	1–5	6–10	11–15	16–20	21–25	26–30	31–35	36–40	41–44
Outgroup	00000	00000	00000	00000	00000	00000	00000	00000	0000
Trichodontidae	01010	101A1	01010	212A1	A1011	11111	A1111	C0021	1100
Anoplopomatoidea	11001	00001	00110	012A1	00011	01000	00011	10100	0001
Zaniolepidoidea	11101	00011	00010	0A210	00001	1AA10	00011	10100	0001
Hexagrammoidea	11101	00011	000A0	0AC11	A1001	110A1	00011	10100	1101
Cottoidea	1C11A	11A1A	E00AC	CE211	2A111	11111	EA011	C1AAA	1111
Cyclopteroidea	101CB	1111C	21A1C	2D211	11A11	11A11	F10BA	210BB	1111
Bathymasteridae	01001	10011	00110	01211	01011	00010	00111	10100	0000

Numbers of transformation series and characters correspond to those in the text

Polymorphic characters as follows: A, 0 and 1; B, 0 and 2; C, 1 and 2; D, 3 and 4; E, 0, 1 and 2; F, 1, 2 and 3

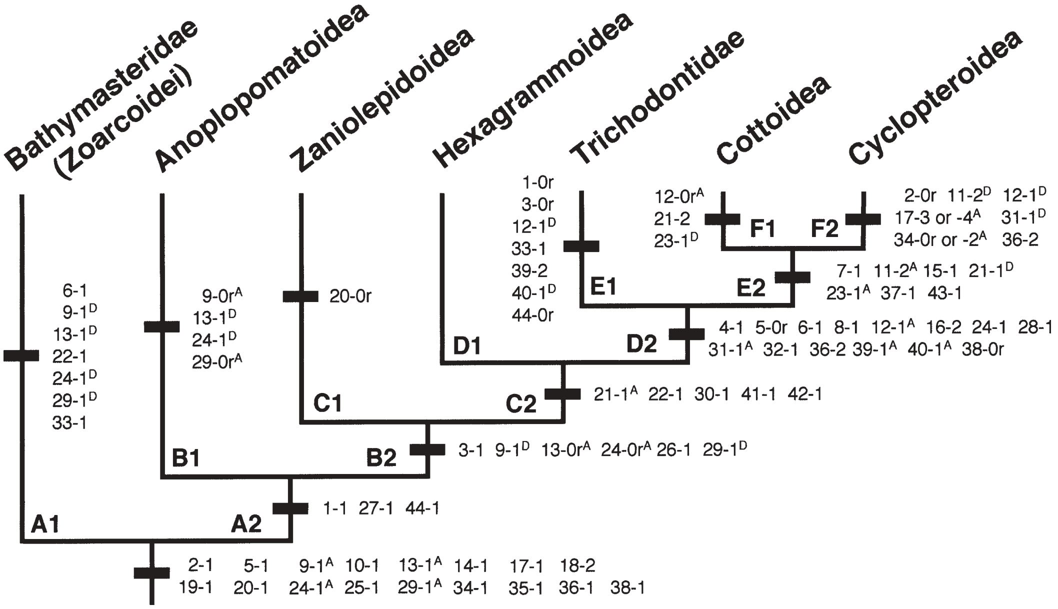

Fig. 10. Phylogenetic relationships of the Trichodontidae, five superfamilies of Cottoidei, and Bathymasteridae. Character numbers correspond to those in the text and Table 1. *A*, ACCTRAN; *D*, DELTRAN; *r*, reversal

included in the analysis because they have no effect on the determination of relationships (these characters are commented with the characters supporting each clade). After the analysis, a single most parsimonious tree (TL = 67, CI = 0.75) was obtained (Fig. 10), and the Trichodontidae was inferred to be the sister-group of the Cottoidea plus Cyclopteroidea. The interrelationships among the Cottoidei agree well with those proposed by Shinohara (1994).

Monophyly of Trichodontidae + Cottoidei + Zoarcoidei. Imamura and Yabe (2002) supported the monophyly of the Cottoidei and Zoarcoidei by 13 derived characters: (1) parasphenoid connected with the pterosphenoid (character 5-1 of this study); (2) six branchiostegal rays (character 10-1); (3) absence of a toothed plate on the third epibranchial (character 14-1); (4) lateral extrascapular composed of two elements (character 17-1); (5) absence of supraneurals (character 18-2); (6) dorsal pterygiophores arranged singly in each interneural space (character 19-1); (7) absence of anal spines with robust pterygiophore (character 20-1); (8) adductor mandibulae section 3 located medial surface of the levator arcus palatini (character 34-1); (9) levator operculi comprised of two elements (character 35-1); (10) presence of a circular TDA (=presence of a circular TPB2 of this study, character 36-1); (11) presence of adductores I–III (character 38-1); (12) absence of the swimbladder; and (13) presence of the parietal sensory canal without spines (character 2-1). Among them, the characters of the swimbladder (its presence or absence) were not included in the phylogenetic analysis because it is commonly absent in the ingroup. Other 12 characters are confirmed here as the valid for the synapomorphy of Trichodontidae, Cottoidei, and Zoarcoidei when analyzed using both ACCTRAN and DELTRAN. After the analysis, character 25-1 (the first and second hypurals fused) is also unambiguously inferred to be a synapomorphy of the ingroup. Thus, the monophyly of the Trichodontidae, Cottoidei, and Zoarcoidei is supported by 14 synapomorphies in total, including the absence of the swimbladder. In addition, when ACCTRAN is employed, characters 9-1 (preoperclar and temporal sensory canals separated), 13-1 (first epibranchial with single process medially), 24-1 (third preural centrum and hemal spine fused), and 29-1 (parhypural and lower hypural plate fused) also support the monophyly of these groups.

Phylogenetic relationships and characters supporting clades. After the phylogenetic analysis, 12 clades were recognized in the most parsimonious tree (Fig. 10). Both the unambiguous characters, which do not change the evolutionary interpretation, and the ambiguous characters, in which the interpretation is changed when different character optimization (ACCTRAN or DELTRAN) is employed, are listed below.

Clade A1.—Includes Bathymasteridae (Zoarcoidei). Clade A1 is unambiguously supported by characters 6-1, 22-1, and 33-1. Characters 9-1, 13-1, 24-1, and 29-1 also support this clade according to DELTRAN.

Clade A2.—Includes Trichodontidae and Cottoidei. This clade is unambiguously supported by 1-1, 27-1, and 44-1.

Clade B1.—Includes Anoplopomatoidea. This superfamily is supported by characters 9-0r and 29-0r according to ACCTRAN, whereas by 13-1 and 24-1 according to DELTRAN. According to Shinohara (1994), the Anoplopomatoidea bears the following autapomorphic characters: robust hypurapohysis and presence of ramus lateralis accesorius facialis pattern 7(?) (sensu Freihofer, 1963).

Clade B2.—Includes Trichodontidae and Cottoidei minus Anoplopomatoidea. Clade B2 is supported by unambiguous characters 3-1 and 26-1. It is also supported by 13-0r and 24-0r according to ACCTRAN and by 9-1 and 29-1 according to DELTRAN.

Clade C1.—Includes Zaniolepidoidea. This clade is unambiguously supported by character 20-0r. The Zaniolepidoidea also bears an autapomorphy, reduction of the ascending process of anguloarticular (Shinohara, 1994).

Clade C2.—Includes Trichodontidae, Hexagrammoidea, Cottoidea, and Cyclopteroidea. Clade C2 is unambiguously supported by characters 22-1, 30-1, 41-1, and 42-1. This clade is also supported by character 21-1 according to ACCTRAN.

Clade D1.—Includes Hexagrammoidea. Clade D1 has no characters after present analysis. However, the Hexagrammoidea possesses three derived characters according to Shinohara (1994): presence of primary tubes on second infraorbital (=his first infraorbital); presence of relatively thin rounded supraoccipital crest; and operculomandibular canal region of preopercle covered by adductor mandibulae.

Clade D2.—Includes Trichodontidae, Cottoidea, and Cyclopteroidea. This clade is supported by unambiguous characters 4-1, 5-0r, 6-1, 8-1, 16-2, 24-1, 28-1, 32-1, and 38-0r. It is also supported by characters 12-1, 31-1, 36-2, 39-1, and 40-1 according to ACCTRAN.

Clade E1.—Includes Trichodontidae. Clade E1 is unambiguously supported by characters 1-0r, 3-0r, 33-1, 39-2, and 44-0r. This clade also supported by 12-1 and 40-1 according to DELTRAN. The family Trichodontidae possesses the autapomorphic characters, the lips with long (*Trichonodon*) or short (*Arctoscopus*) papillae (Nazarkin and Voskoboinikova, 2000; this study) and A1 and A2 not separated (Fig. 7).

Clade E2.—Includes Cottoidea and Cyclopteroidea. The Cottoidea and Cyclopteroidea commonly bear unambiguous characters 7-1, 15-1, 37-1, and 43-1. This clade is also supported by characters 11-2 and 23-1 according to ACCTRAN, whereas by 21-1 according to DELTRAN.

Clade F1.—Includes Cottoidea. Clade F1 is unambiguously supported by character 21-2. It is also supported by character 12-0r according to ACCTRAN, whereas by 23-1 according to DELTRAN.

Clade F2.—Includes Cyclopteroidea. The Cyclopteroidea is supported by an unambiguous character 2-0r. This clade is also supported by characters 17-3 or 17-4 (not determined) and 34-or or 34-2 (not determined) according to ACCTRAN, whereas by 11-2 12-1, 31-1, and 36-2 according to DELTRAN. According to Kido (1988), this superfamily also possesses the following derived characters: epaxialis reaching almost above middle of orbit; absence of myodome; entopterygoid and ectopterygoid fused; second and third basibranchials cartilaginous; all actinosts located between scapula and coracoid; and ethmoid cartilage forming a keel projecting anteriorly on dorsal midline.

Discussion and Classification

Smith and Wheeler (2004) hypothesized that the family Trichodontidae is deeply nested within the suborder Cottoidei based on their molecular phylogenetic analysis. The morphological phylogenetic analysis of the Trichodontidae, Cottoidei, and Bathymasteridae presented here supports their hypothesis. As pointed out by Smith and Wheeler (2004), Starks (1930), and Mooi and Johnson (1997) previously suggested a close relationship of the Trichodontidae and Cottoidei; i.e., from the similarity of the shoulder girdle and parietal sensory canal morphologies, respectively. Imamura and Yabe (2002) did not support the close relationship of the Trichodontidae and Cottoidei because *Arctoscopus* lacks the following three synamorphies of the Cottoidei and Zoarcoidei: the parasphenoid connected with pterosphenoid (character 5-1 of this study); presence of a circular TPB2 (35-1); and presence of adductors I–III (38-1). However, it was newly found that the trichodontid *Trichodon* has a circular TPB2 (Fig. 8). After the phylogenetic analysis, it was assumed the absence of these characters in the family (or *Arctoscopus*) is a reversal.

Imamura and Yabe (2002) supported the monophyly of the Cottoidei by two derived characters: presence of the homoplasic suborbital stay (character 1-1 in this study) and extrinsic muscle derived from the epaxialis (44-1). Although the Trichodontidae lacks a distinct suborbital stay and the extrinsic muscle, it was reconfirmed here that they are synapomophies of the Cottoidei (plus Trichodontidae), and absence of these characters in the family were regarded as reversals. In addition, it was newly inferred here that character 27-1 (absence of fifth hypural) also unambiguously support the monophyly of the Trichodontidae and Cottoidei in this study.

Smith and Wheeler (2004) assumed the family Trichodontidae to be a sister group of the monophyletic Cottoidea plus Cyclopteroidea. They also suggested six synapomorphies (e.g., loss of basisphenoid, intercalary not reaching anteriorly to prootic) to support the monophyly of these three taxa. Smith and Wheeler's (2004) results are well supported by our findings based on morphological characters. Morphologically, the monophyly of Trichodontidae, Cottoidea, and Cyclopteroidea is supported by nine unambiguous derived characters, including two characters being consistent with Smith and Wheeler's (2004) characters mentioned previously, plus five characters when ACCTRAN is employed.

Shinohara (1994) optimized the larval and egg characters on the reconstructed relationships of the Cottoidei (sensu Imamura and Yabe, 2002) and inferred the monophyly of the superfamilies Zaniolepidoidea, Hexagrammoidea, and Cottoidea as being supported by a derived character, the spawning of dermal egg mass. It is known the Trichodontidae also spawns such an egg mass (e.g., Watson et al. 1984). We regard this character as support for the close relationship of the Trichodontidae and Cottoidei minus Anoplopomatoidea.

Imamura and Yabe (2002) recognized five superfamilies among the Cottoidei: the Anoplopomatoidea, Zaniolepidoidea, Hexagrammoidea, Cottoidea, and Cyclopteroidea. In this study, we propose to provide the superfamilial rank to six terminal clades B1, C1, D1, E1, F1, and F2, all of which have one or more autapomorphies, to avoid changing the previous cottoid classification. Therefore, the family Trichodontidae is newly placed within the cottoid superfamily Trichodontoidea as follows:

- Suborder Cottoidei (Perciformes)
  - Superfamily Anoplopomatoidea
    - Family Anoplopomatidae
  - Superfamily Zaniolepidoidea
    - Family Zaniolepididea
  - Superfamily Hexagrammoidea
    - Family Hexagrammidae
  - Superfamily Trichodontoidea
    - Family Trichodontidae
  - Superfamily Cottoidea
    - Includes nine families (see Nelson, 1994)
  - Superfamily Cyclopteroidea
    - Family Cyclopteridae
    - Family Liparidae

Acknowledgments We express our sincere thanks to T.W. Pietsch (UW) for providing critical comments on the draft manuscript and M. Miya (Natural History Museum and Institution, Chiba) and W.L. Smith (AMNH) for providing the most recent information on the molecular phylogeny of the Trichodontidae. We are grateful to T. Iwamoto (CAS) for providing materials.

Literature Cited

Anderson ME (1994) Systematics and osteology of the Zoarcidae (Teleostei: Perciformes). Ichthyol Bull JLB Smith Inst Ichthyol (60): 1–120

Baldwin CC, Johnson GD (1993) Phylogeny of the Epinephelinae (Teleostei: Serranidae). Bull Mar Sci 52:240–283

Freihofer WC (1963) Pattern of the ramus lateralis accessorius and their systematic significance in teleostean fishes. Stanford Ichthyol Bull 8:80–189

Gill T (1888) On the classification of the mail-cheeked fishes. Proc US Nat Mus 11:567–592

Gosline WA (1968) The suborders of perciform fishes. Proc US Nat Mus 124:1–78

Greenwood PH, Rosen DN, Weitzman SH, Myers GS (1966) Phyletic studies of teleostean fishes, with a provisional classification of living forms. Bull Am Mus Nat Hist 131:339–455

Hallacher LE (1974) The comparative morphology of the extrinsic gasbladder musculature in the scorpionfish genus *Sebastes* (Pisces: Scorpaeniformes). Proc Calif Acad Sci 15:59–84

Imamura H (1996) Phylogeny of the family Platycephalidae and related taxa (Pisces: Scorpaeniformes). Species Divers 1: 123–233

Imamura H (2000) An alternative hypothesis on the phylogenetic position of the family Dactylopteridae (Pisces: Teleostei), with a proposed new classification. Ichthyol Res 47:203–222

Imamura H, Yabe M (2002) Demise of the Scorpaeniformes (Actinopterygii: Percomorpha): an alternative phylogenetic hypothesis. Bull Fish Sci Hokkaido Univ 53:107–128

Johnson GD (1980) The limits and relationships of the Lutjanidae and associated families. Bull Scripps Inst Oceanogr Univ Calif 24:1–114

Johnson GD (1984) Percoidei: development and relationships. In: Moser HG, Richards WJ, Cohen DM, Fahay MP, Kendall AW Jr, Richardson SL (eds) Ontogeny and systematics of fishes. Allen Press, Lawrence, KS, pp 438–447

Kido K (1988) Phylogeny of the family Liparididae, with the taxonomy of the species found around Japan. Mem Fac Fish Hokkaido Univ 35:125–256

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 1985:802–832

Matsubara K (1943) Studies on the scorpaenoid fishes from Japan. Anatomy, phylogeny and taxonomy (I). Trans Sigenkagaku Kenkyusyo 1:1–170

Mooi RD, Johnson GD (1997) Dismantling the Trachinoidei: evidence of a relationship for the Champsodontidae. Ichthyol Res 44:143–176

Nazarkin MV, Voskoboinikova OS (2000) New fossil genus and species of Trichodontidae and the position of this family in the order Perciformes (in Russian). Vopr Iktiol 40:725–742

Nelson JS (1994) Fishes of the world, third edn. Wiley, New York

Pietsch TW (1989) Phylogenetic relationships of trachinoid fishes of the family Uranoscopidae. Copeia 1989:253–303

Pietsch TW, Zabetian CP (1990) Osteology and interrelationships of the sand lances (Teleostei: Ammodytidae). Copeia 1990:78–100

Quast JC (1965) Osteological characters and affinities of the hexagrammid fishes with a synopsis. Proc Calif Acad Sci 31:563–600

Regan CT (1913) The osteology and classification of the teleostean fishes of the order Scleroparei. Ann Mag Nat Hist Ser 8 11:169–184

Sasaki K (1989) Phylogeny of the family Sciaenidae, with notes on its zoogeography (Teleostei, Perciformes). Mem Fac Fish Hokkaido Univ 36:1–137

Shinohara G (1994) Comparative morphology and phylogeny of the suborder Hexagrammoidei and related taxa (Pisces: Scorpaeniformes). Mem Fac Fish Hokkaido Univ 41:1–97

Smith CL, Bailey RM (1961) Evolution of the dorsal fin supports of percoid fishes. Mich Acad 46:345–362

Smith WL, Wheeler WC (2004) Polyphyly of the mail-cheeked fishes (Teleostei: Scorpaeniformes): evidence from mitochondrial and nuclear sequence data. Mol Phylogenet Evol 32:627–646

Springer VG, Johnson GD (2004) Study of the dorsal gill-arch musculature of teleostome fishes, with special reference to the Actinopterygii. Bull Biol Soc Wash (11):i–vi + 1–260, 205 pls

Starks EC (1930) The primary shoulder girdle of the bony fishes. Stanford Univ Publ Univ Ser Biol Sci 6:147–239

Steindachner F (1881) Ichthyologische Beiträe (X). Sitzungsber Akad Wiss Wien 83:179–219, pls 1–8

Swofford DL (2002) PAUP*. Phylogenetic analysis using parsimony (*and other methods). Version 4. Sinauer Associates, Sunderland, MA

Taranetz AY (1941) On the classification and origin of the family Cottidae. Inst Fish Univ BC Mus Contrib 5:1–28

von Tilesius WG (1813) Iconum et descriptionum piscium Camtschaticorum continuatio tertia tentamen monographiae generis Agoni blochiani sistens. Mem Acad Imp Sci St Petersb 4:406–478, pls 11–16

Watson W, Matarese AC, Stevens EG (1984) Trachinoidea: development and relationships. In: Moser HG, Richards WJ, Cohen DM, Fahay MP, Kendall AW Jr, Richardson SL (eds) Ontogeny and systematics of fishes. Allen Press, Lawrence, KS, pp 554–561

Winterbottom R (1974) A descriptive synonymy of the striated muscles of the Teleostei. Pros Acad Nat Sci Phila 125:225-317

Yabe M (1985) Comparative osteology and myology of the superfamily Cottoidea (Pisces: Scorpaeniformes), and its phylogenetic classification. Mem Fac Fish Hokkaido Univ 32:1–130

Yabe M, Uyeno T (1996) Anatomical description of *Normanichthys crockeri* (Scorpaeniformes, *incertae sedis*: family Normanichthyidae). Bull Mar Sci 58:494–510