

holocanthus Linnaeus 1758, *Diodon hystrix* Linnaeus 1758, *Diodon liturosus* Shaw 1804, and *Diodon nictemerus* Cuvier 1818. Leis (2006) provided a list of synonyms and keys for all species of the Diodontidae. Keys to regional species were also provided by Leis (1986, western Indian Ocean; 2001, eastern Indian Ocean and western central Pacific; 2003, western Atlantic). Accounts and color photographs for species of the eastern Pacific were provided by Allen and Robertson (1994). Australian species were diagnosed and illustrated by Gomon (2008). As pointed out by Leis (2006), taxonomic problems remain for some species, such as *Chilomycterus reticulatus* (Linnaeus 1758) and species of “Atlantic *Chilomycterus*.”

Molidae (Ocean sunfishes, Fig. 1j)

Ocean sunfishes of the family Molidae occur in tropical and other warm seas of the world. They are usually pelagic, descending to a depth of over 200 m. The ocean sunfishes differ externally from other families of Tetraodontiformes by the following combination of characters: body short and deep or oblong, prominently compressed; caudal peduncle and typical caudal fin absent; eyes small; mouth terminal, small; teeth united and beak-like in each jaw without a median suture; no palatine teeth; gill opening small, pore-like, located in front of pectoral-fin base; dorsal and anal fins of similar shape, generally triangular, dorsal fin located opposite anal fin; dorsal and anal fins spineless, each with 15 to 21 soft rays; pectoral fins of small to moderate size, located midlaterally, fitting into a shallow concavity in side of body in some; pelvic fins absent; caudal fin replaced by a leathery, rudder-like lobe known as a pseudocaudal fin or clavus (supported mostly by fin-ray elements originally belonging to dorsal and anal fins); skin leathery, with many small scales (small juveniles may also have some larger scattered spiny scales) (Hutchins 2001b).

Fraser-Brunner (1951) reviewed ocean sunfishes and recognized five species in the Molidae: *Masturus lanceolatus* (Liénard 1840), *Masturus oxyropterus* (Bleeker 1873), *Mola mola* (Linnaeus 1758), *Mola ramsayi* (Giglioli 1883), and *Ranzania laevis* (Pennant 1776). Because species of *Mola* and *Masturus* reach more than 3 m in length and two tons in weight, it is difficult to preserve specimens of adults in museums. It is also difficult for ichthyologists to obtain measurements and counts on large adult ocean sunfishes in the field, and specimens of *Mola* and *Masturus* are not frequently collected and returned to museum collections. *Ranzania laevis* is relatively small, reaching around 80 cm TL, but specimens of *Ranzania* have also been rarely collected. Since ichthyologists have few opportunities to study an adequate number of adult specimens of ocean sunfishes, authors have been unable to agree

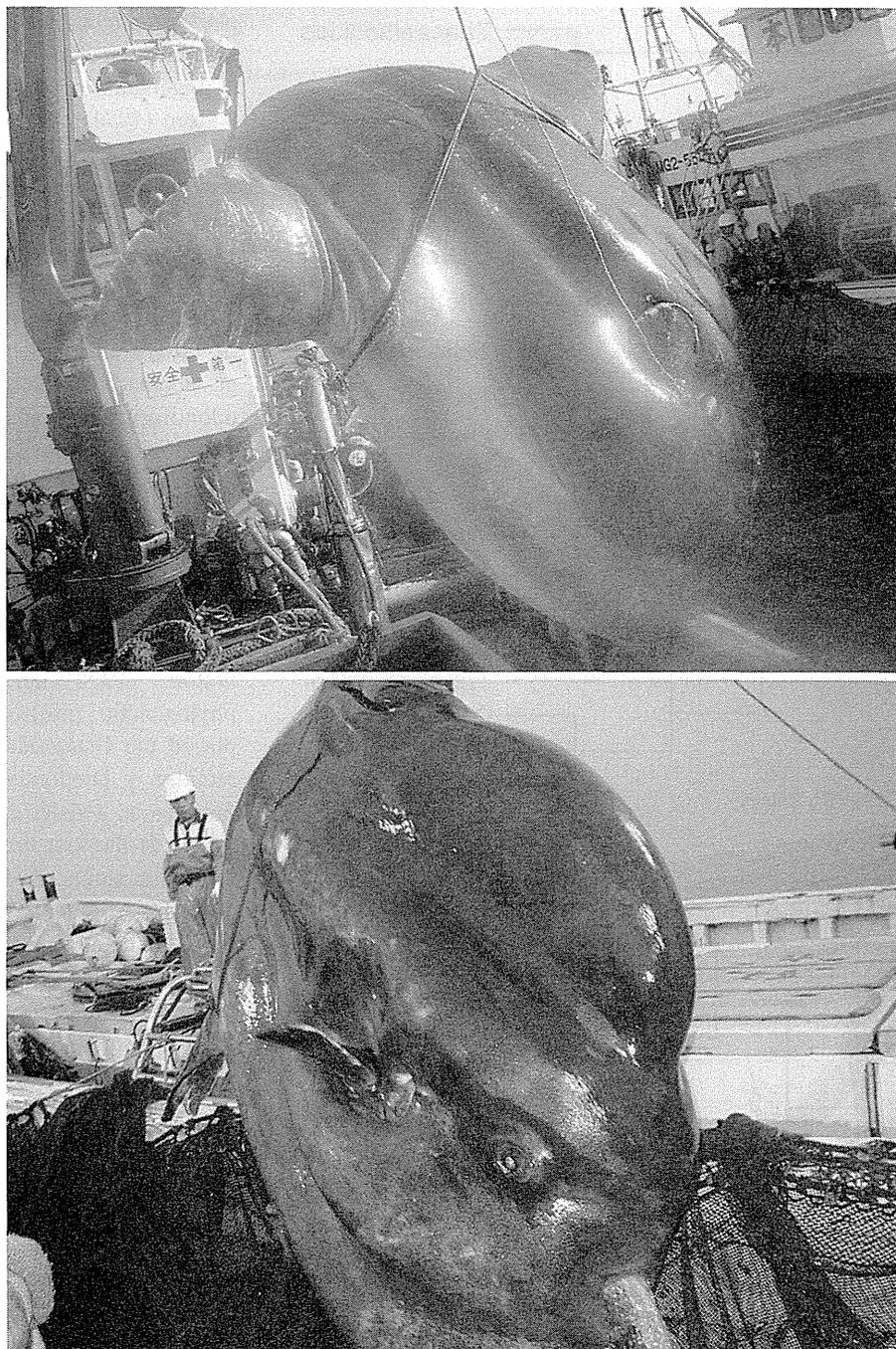
how many species in the family, some believing a single species exists in each genus, and others recognizing two species each in *Mola* and *Masturus* and one species in *Ranzania* (Bray 2008).

Parenti (2003) published a list of nominal species in the Molidae. Bass et al (2005) published a molecular analysis of ocean sunfishes and recognized two clades in *Mola*, *M. mola* and *M. ramsayi*. They demonstrated that *M. ramsayi* occurs in South Africa and Australia, whereas *M. mola* is found in all oceans. However, they were unable to differentiate among specimens of *Masturus* from the West Pacific (Taiwan) and the western Atlantic (Florida). Yoshita et al. (2009) studied ocean sunfishes within the genus *Mola* around Japan. They took measurements and counted 99 specimens of young and adults (maximum size 332 cm TL, Fig. 6). They showed convincingly that there are two species with clear morphological differences: a well-developed head bump (head bump height 12.1 % TL) in group A vs. with no distinct head bump (head bump height 7.8 % TL) in group B, number of clavus fin rays 14–17 in group A vs 10–13 in group B, number of clavus ossicles 8–15 in group A vs. 8–9 in group B, and edge of clavus not wavy in group A vs. wavy in group B. Yoshita et al. (2009) suggested strongly that their group A was *M. ramsayi* and group B was *M. mola*. However, a clearer view of intra- and interspecific relationships of *Mola* must await the availability of more specimens from other regions of the world’s oceans for study by both morphological and molecular methods.

Systematics

Cuvier (1816) pioneered the classification of tetraodontiform fishes by placing them in the order Plectognathi based on his detailed anatomical studies. Since Cuvier’s (1816) work was published, there have been various arrangements of tetraodontiform classification (see Tyler 1980 for a history of tetraodontiform classification), but the Plectognathi or Tetraodontiformes has nearly always been considered a monophyletic group, except for Le Danois (1955, 1959, 1961). As appropriately criticized by Tyler (1963), Yseult Le Danois tried to destroy the order Tetraodontiformes. She stated that the triacanthoids and balisoidts are of acanthurid origin and that the other plectognaths (her Orbiculati) are not even of percoid derivation, being related to the isospondylous fishes, and that *Canthigaster* is related to the ostracioids rather than the tetraodontids. However, her statements were based on erroneous observations and interpretations of the osteological and myological characters of tetraodontiforms (Tyler 1963; Winterbottom 1974). No comprehensive phylogenetic studies of tetraodontiforms appeared prior to studies by Winterbottom (1974) and Tyler

Fig. 6 A large specimen of *Mola ramsayi* (330 cm TL) captured with a set net along the Pacific coast of northern Honshu, Japan



(1980). Morphological synapomorphies of tetraodontiforms have been provided by Winterbottom (1974), Tyler (1980), Rosen (1984), Tyler and Sorbini (1996), and Santini and Tyler (2003). In their review of the interrelationships of actinopterygian fishes, Lauder and Liem (1983) supported the monophyly of Tetraodontiformes by adding to the already substantial list of synapomorphies. In addition, Wiley and Johnson (2010) provided a list of 10 synapomorphies for fossil and extant tetraodontiforms.

On the basis of a comprehensive myological study, Winterbottom (1974) analyzed relationships of Tetraodontiformes using cladistic methods. He recognized three major clades: (1) Triacanthodidae + Triacanthidae, (2) (Balistidae + Monacanthidae) + (Araucanidae + Ostraciidae), and (3) Triodontidae + [(Tetraodontidae + Diodontidae) + Molidae] (Fig. 7). The first clade, including the Triacanthodidae and Triacanthidae, was considered to be the sister group of all other tetraodontiforms. Tyler

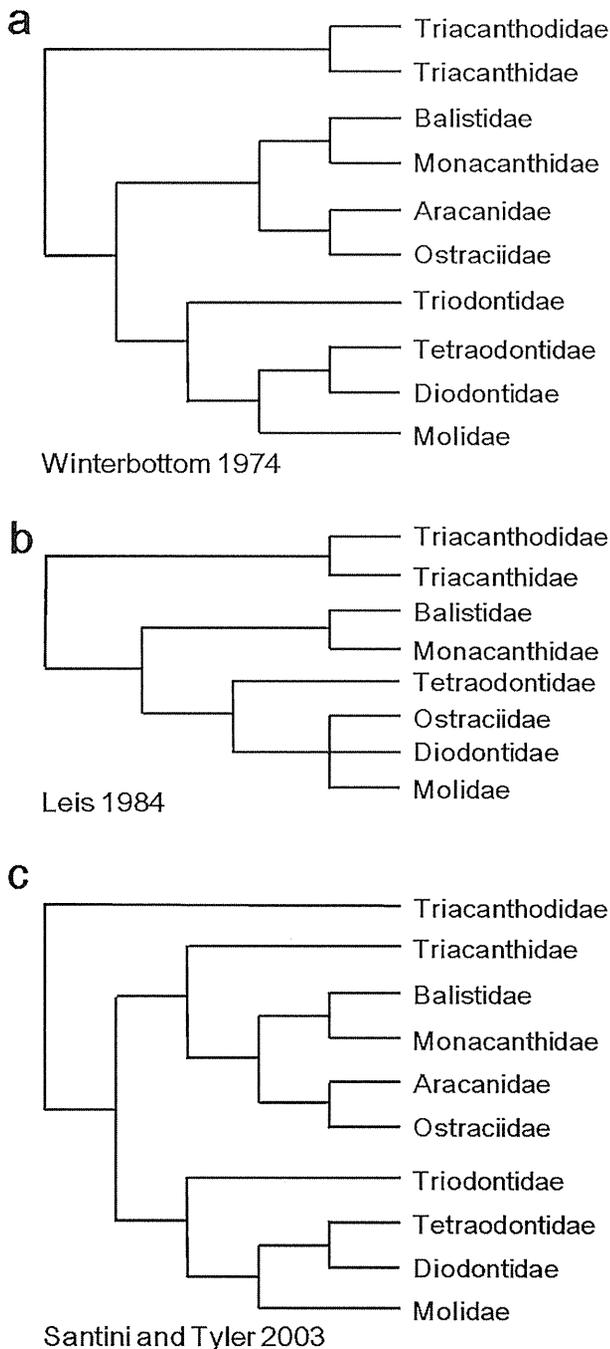


Fig. 7 Phylogenetic relationships of the extant families of Tetraodontiformes inferred from cladistic analyses of morphological characters. **a** Winterbottom 1974; **b** Leis 1984 (larvae of the Aracaniidae and Triodontidae not available for Leis); **c** Santini and Tyler 2003

(1980) studied tetraodontiforms extensively and provided a huge number of osteological descriptions, comparative diagnoses, and illustrations for all extant families, major representatives of extant genera, and most of the known fossil taxa of the Tetraodontiformes. Tyler (1980) analyzed

phylogenetic relationships of the Tetraodontiformes by an evolutionary (traditional) method and his systematic arrangements of families are similar to those of Winterbottom (1974), except for placing the superfamily Triacanthoidea (Triacanthodidae + Triacanthidae) as the basal sister group to the two superfamilies, the Balistoidea (Balistidae and Monacanthidae) and the Ostracioidea (Aracaniidae and Ostraciidae).

Winterbottom (1974) and Tyler (1980) stated that tetraodontiforms were probably related to acanthuroid fishes of the Perciformes, although Winterbottom (1974) suggested that some zeiforms might also be related to tetraodontiforms. Rosen (1984) proposed on the basis of his osteological analysis that zeoids have a sister-group relationship with tetraodontiforms and the two groups are sister to the caproids. Leis (1984) used characters of eggs and larvae to investigate tetraodontiform relationships. Although no aracanid and triodontid larvae were available for his study, Leis (1984) showed relationships of tetraodontiform families that were similar to those of Winterbottom (1974) and Tyler (1980), except for the phylogenetic position of the Ostraciidae. Leis (1984) placed the Ostraciidae in an unresolved trichotomy, Ostraciidae + Diodontidae + Molidae, and placed the three families as a sister clade to the Tetraodontidae (Fig. 7b). This was the first time that the Ostraciidae was placed in the gymnodonts (Triodontidae, Tetraodontidae, Diodontidae, and Molidae). Winterbottom and Tyler (1983) also provided many synapomorphies involving osteological and myological characters that supported a sister-group relationship of balistoids and ostracioids. Klassen (1995) similarly supported the relationship of the two groups.

James C. Tyler and other authors published many papers on fossil tetraodontiforms (e.g., Tyler and Patterson 1991; Tyler and Banikov 1992, 1994, 2011, 2012; Tyler et al. 1992, 1993, 2000, 2003, 2006; Tyler and Sorbini 1996, 1998; Tyler and Winterbottom 1999; Tyler and Santini 2001, 2002; Sorbini and Tyler 2004; Bannikov and Tyler 2008a, b; Gregorova et al. 2009; Carnevale and Tyler 2010; Tyler and Kriznar 2013; Miyajima et al. 2014).

Santini and Tyler (2003) used osteological data on fossil and extant tetraodontiform fishes accumulated by previous contributions to generate a new classification of all known families represented by fossil and extant forms. For extant families, Santini and Tyler (2003) placed the Triacanthodidae as a sister group to all other families of the Tetraodontiformes (Fig. 7). They arranged the other families into two suborders, the Balistoidei and Tetraodontoidei. The former is composed of the Triacanthidae + [(Balistidae + Monacanthidae) + (Aracaniidae + Ostraciidae)]. The latter suborder is composed of the Triodontidae + [(Tetraodontidae + Diodontidae) + Molidae]. This

classification is similar to those of Winterbottom (1974) and Tyler (1980).

Miya et al. (2003) analyzed molecular data for 100 species of higher teleosts. Their study was the first to hypothesize close relationships among lophiiforms, tetraodontiforms, and caproids. They retrieved phylogenetic topologies placing caproids as a sister group with tetraodontiforms and the two groups as sister to lophiiforms. However, they used few taxa: one species of Caproidae, two species of Tetraodontiformes, and six species of Lophiiformes. Yamanoue et al. (2007) analyzed more species of the three groups and provided a robust phylogenetic topology that placed the Caproidei as sister to the Lophiiformes, and the two groups as a clade that is sister to the Tetraodontiformes.

Nakae and Sasaki (2010) studied the lateral-line system and its innervations of nine species of tetraodontiforms (representing all families examined except for the Molidae) and a single species each from the Lophiidae, Zeidae, Caproidae, and Siganidae. Their analysis supported a close relationship of the Tetraodontiformes with the Lophiidae, but not with the Zeidae, Caproidae, or Siganidae. Recently, Chanet et al. (2013) presented synapomorphies of tetraodontiforms and lophiiforms involving soft anatomical characters: rounded and anteriorly disposed kidneys, a compact thyroid included in a blood sinus, an abbreviated spinal cord, an asymmetric liver, and clusters of supradullary neurons in the rostral part of the spinal cord. Baldwin (2013) also provided a putative synapomorphy of some tetraodontiforms and lophiiforms: they are strikingly similar in having the trunk enclosed in an inflated sac covered with xanthophores. Although Nakae and Sasaki (2010), Chanet et al. (2013), and Baldwin (2013) did not study many species of tetraodontiform and outgroup fishes, and the relationship between the Tetraodontiformes and Lophiiformes is now supported both by molecular and morphological characters.

Molecular studies by various authors have generally supported the monophyly of tetraodontiform families (Holcroft 2005; Alfaro et al. 2007; Yamanoue et al. 2007, 2008), although conflicts exist between the constructed topologies of familial relationships by morphological and molecular analyses (Figs. 7, 8). In the morphological studies by Winterbottom (1974), Tyler (1980), and Santini and Tyler (2003), the Triodontidae, Tetraodontidae, Diodontidae, and Molidae form a monophyletic group, whereas Holcroft (2005) placed the Molidae with Aracanidae + Ostraciidae, treating them as subfamilies. Alfaro et al. (2007) placed the Molidae as the basal sister group to Triodontidae + (Aracanidae + Ostraciidae). Britz and Johnson (2005) and Johnson and Britz (2005a) found the fusion of anterior vertebral centra in the occipital region and a thick band of cartilage on the side of the pterygiophores of the vertical fins in an ostraciid and molids

suggestive of a close relationship between the Ostraciidae and Molidae. However, because they studied only one species of Ostraciidae and two species of Molidae, it seems premature to hypothesize a close relationship of the two families until further support for it may be forthcoming. In contrast, the Molidae was recovered as the sister group to a clade comprising the Tetraodontidae and Diodontidae by Santini et al. (2013c) as previously indicated by morphological studies. The Triodontidae was considered to be close to the Tetraodontidae, Diodontidae, and Molidae by morphological studies (Winterbottom 1974; Tyler 1980; Santini and Tyler 2003), whereas molecular studies recovered close relationship of the Triodontidae with the Aracanidae and Ostraciidae (Alfaro et al. 2007; Yamanoue et al. 2008; Santini et al. 2013c).

Despite differences in molecular trees of familial relationships among authors, several sister group relationships are generally supported by molecular studies (Holcroft 2005; Alfaro et al. 2007; Yamanoue et al. 2007; Santini et al. 2013c) as follows: Triacanthodidae + Triacanthidae, Balistidae + Monacanthidae, Aracanidae + Ostraciidae, and Tetraodontidae + Diodontidae, as previously seen in morphological studies. On the basis of whole mitochondrial genome sequences, Yamanoue et al. (2008) documented different phylogenetic relationships from those of other authors. Whereas the Triacanthidae was usually placed close to the Triacanthodidae, Balistidae, and Monacanthidae in other studies (Winterbottom 1974; Tyler 1980; Leis 1984; Santini and Tyler 2003; Holcroft 2005; Alfaro et al. 2007; Santini et al. 2013c), Yamanoue et al. (2008) recovered a relationship of the Triacanthidae with the Tetraodontidae and Diodontidae.

Phylogenetic relationships of genera and species were studied by various authors in the Triacanthidae, Balistidae, Monacanthidae, Aracanidae, Ostraciidae, Tetraodontidae, and Molidae, but the numbers of taxa studied differed greatly and resulted in different resolutions of phylogenetic analyses. Santini and Tyler (2002b) analyzed phylogenetic relationships of species and genera of the Triacanthidae using morphological characters. They found two clades, one composed of two species of *Triacanthus* Oken 1817, and the other composed of three species of *Tripodichthys* Tyler 1968 and one species each of *Pseudotriacanthus* Fraser-Brunner 1941b and *Trixiphichthys* Fraser-Brunner 1941b. Matsuura (1979, 1981) analyzed cladistic relationships of all extant genera of the Balistidae and 22 genera of the Monacanthidae using osteological characters. Although many balistid genera showed no significant differences in osteological characters, Matsuura (1979) found that a derived condition of the interhyal was shared by *Rhinecanthus* and *Sufflamen*. He also recovered *Canthidermis* as sister to all other balistid genera based on a scale bone in the posterior part of the skull. However, Tyler and

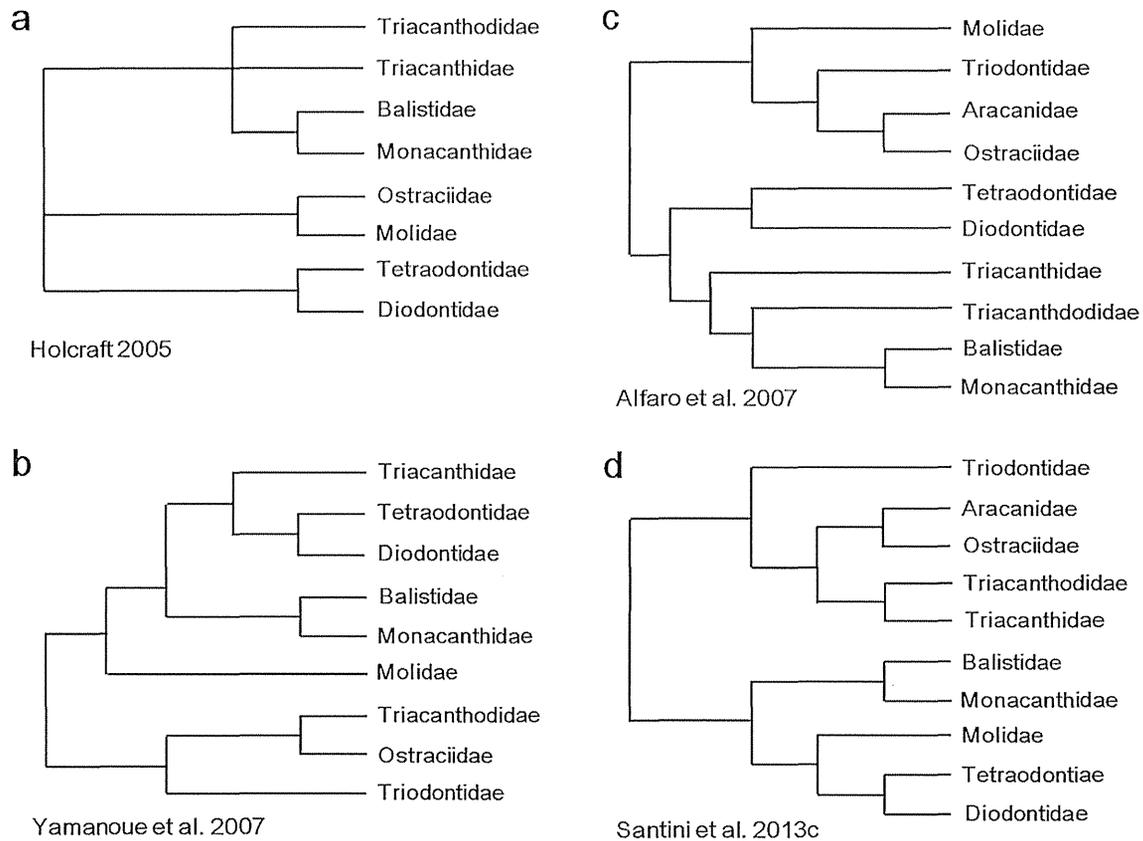


Fig. 8 Phylogenetic relationships of the Tetraodontiformes inferred from molecular analyses. **a** Holcroft 2005; **b** Alfaro et al. 2007; **c** Yamanoue et al. 2007; **d** Santini et al. 2013c. The Triodontidae was not included in Holcroft (2005), and the Ostraciidae of Holcroft

(2005) and Yamanoue et al. (2007) included two subfamilies the Aracaninae and Ostraciinae, which were classified as families in the other papers

Matsuura (1981) revealed Matsuura's (1979) "scale bone" to be the posterior part of the sphenotic that appears separated from the major portion of the sphenotic. Matsuura (1981) found derived conditions of the pectoral girdle and the skull in *Xenobalistes*, making it a sister group to all other balistid genera. Matsuura (1979) recognized two clades in the Monacanthidae: the first composed of *Arotrolepis* Fraser-Brunner 1941c, *Paramonacanthus*, *Monacanthus*, *Stephanolepis* Gill 1861, *Chaetodermis*, *Acreichthys*, and *Pervagor*; the second *Cantherhines*, *Eubalichthys* Whitley 1930b, *Thamnaconus* (= *Navodon* Whitley 1930b of Matsuura 1979), *Pseudomonacanthus*, *Scobinichthys* Whitley 1931, *Nelusetta* Whitley 1939, *Meuschenia* Whitley 1929, *Rudarius*, *Aluterus*, *Oxymonacanthus* Bleeker 1865, *Pseudalutarius*, *Brachaluteres*, *Paraluteres*, and *Anacanthus*. The second clade possesses more advanced characters than the first clade and is composed of three subclades: (1) *Amanses* and *Cantherhines*, (2) *Eubalichthys*, *Thamnaconus*, *Pseudomonacanthus*, *Scobinichthys*, *Nelusetta*, *Meuschenia* and *Rudarius*, and (3) *Aluterus*, *Oxymonacanthus*, *Pseudalutarius*, *Brachaluteres*, *Paraluteres*, and *Anacanthus*.

In her molecular analyses of tetraodontiforms, Holcroft (2005) also recovered the close relationship of *Rhinecanthus* and *Sufflamen* found by Matsuura (1979). She further showed that three species of *Balistes* form a sister group to *Pseudobalistes fuscus* (Bloch and Schneider 1801) and that *Xanthichthys auromarginatus* (Bennett 1832) is sister to *Balistoides viridescens*. Her analysis revealed that *Balistoides conspicillum* is sister to other balistids, including *Balistes*, *Pseudobalistes*, *Rhinecanthus*, *Sufflamen*, *Abalistes*, *Canthidermis*, *Xanthichthys*, and *Balistoides viridescens*. In addition, she found *Melichthys niger* (Bloch 1786) to be the first lineage to diverge in the Balistidae. Although Holcroft (2005) studied phylogenetic relationships of nine genera of Monacanthidae, her study covered relatively small numbers of monacanthid genera making it difficult to compare her phylogenetic tree with that constructed by Matsuura (1979). Yamanoue et al. (2009) studied the phylogenetic relationships of 12 species of Balistidae and 21 genera of Monacanthidae, involving one species each from 33 genera of the two families. The molecular analysis placed *Balistes* as sister to all other balistid genera that were separated into two clades, the first comprising

Canthidermis, *Abalistes*, *Rhinecanthus*, and *Sufflamen*, and the second *Pseudobalistes*, *Xanthichthys*, *Xenobalistes*, *Odonus*, *Balistapus*, *Balistoides*, and *Melichthys*. In the Monacanthidae they found the clade that included two genera, *Oxymonacanthus* and *Pseudalutarius*, form a sister group to other genera that are divisible into two major clades, the first composed of *Rudarius*, *Brachaluteres*, *Paraluteres*, *Pervagor*, *Stephanolepis*, *Acreichthys*, *Chaetodermis*, *Monacanthus*, and *Paramonacanthus*, and the second *Aluterus*, *Pseudomonacanthus*, *Amaneses*, *Cantherhines*, *Eubalichthys*, *Thamnaconus*, *Nelusetta*, *Scobinichthys*, *Meuschenia*, and *Acanthaluteres*.

Santini et al. (2013a) provided the largest molecular dataset for the Balistidae and Monacanthidae based on two mitochondrial and three nuclear loci of 33 species of Balistidae and 53 species of Monacanthidae. The molecular analysis supported monophylies of the following genera: *Odonus*, *Balistapus*, *Melichthys*, *Xanthichthys*, *Canthidermis*, *Balistes*, *Abalistes*, *Rhinecanthus*, and *Sufflamen*. Species of *Balistoides* and *Pseudobalistes* were recovered in separate clades with *Balistoides conspicillum* sister to *Melichthys*, and *B. viridescens* forming a clade with *P. flavimarginatus*. The latter two species share at least two morphological characters, a small naked area on the cheek just behind the mouth, and a large maximum size, reaching over 60 cm TL. In the balistid tree *Xenobalistes tumidipectoris* was deeply nested in a clade composed of five species of *Xanthichthys*, strongly supporting *Xenobalistes* as a junior synonym of *Xanthichthys* (see Santini et al. 2013b). Santini et al. (2013b) recovered virtually all of the subclades of Yamanoue et al. (2009), except for *Chaetodermis* and *Acreichthys* relationships. In the phylogenetic topology of Santini et al. (2013b), *Chaetodermis* and *Acreichthys* are sequential sister taxa to the clade composed of three species of *Paramonacanthus* and *Monacanthus chinensis*, whereas Yamanoue et al. (2009) presented sister-group relationships of *Chaetodermis* and *Acreichthys*. Santini et al. (2013b) supported monophylies or close relationships of most genera, but species of *Monacanthus* and *Paramonacanthus* were separated into different clades suggesting strongly that these genera require revision.

A cladistic analysis of the external characters, osteology, and myology of all genera of Aracnidae led Winterbottom and Tyler (1983) to recognize two clades in the Aracnidae, the first composed of *Kentrocapros* and *Polyplacapropros*, and the second *Aracana*, *Strophurichthys* Fraser-Brunner 1935b, *Anoplocapros*, *Caprichthys*, and *Capropygia*. In the second clade *Aracana* was sister to the remaining genera, *Strophurichthys* and *Anoplocapros* diverged sequentially, and *Caprichthys* and *Capropygia* were placed in a small terminal clade. Santini et al. (2013a) studied the phylogenetic relationships of *Kentrocapros*

(two species), *Caprichthys* (monotypic), *Capropygia* (monotypic), *Aracana* (two species), and *Anoplocapros* (three species), with *Polyplacapropros* (monotypic). The two monotypic genera *Caprichthys* and *Capropygia* were found to represent a clade to other genera. *Kentrocapros* was placed as sister to the subclade composed of *Aracana* and *Anoplocapros*.

Klassen (1995) studied the osteological characters of 19 species of the Ostraciidae extensively. His phylogenetic analysis found two clades in the Ostraciidae, the first composed of *Acanthostracion* and *Lactophrys* Swainson 1839, and the second *Ostracion* and *Lactoria*, having synonymized *Rhynchostracion* with *Ostracion* and *Tetrosomus* with *Lactoria*. Santini et al. (2013a) studied the phylogenetic relationships of 17 species of Ostraciidae by molecular analysis. The resultant phylogenetic tree closely resembled that of Klassen (1995), but where Klassen (1995) found *Rhynchostracion nasus* (Bloch 1785) deeply nested within *Ostracion*, Santini et al. (2013a) presented it as sister to *Ostracion*.

On the basis of many osteological characters, nasal organ, and lateral-line system, Tyler (1980) inferred three groups of pufferfish genera: (1) *Lagocephalus*, *Colomesus*, *Guentheridia* Gilbert and Starks 1904, and *Sphoeroides*; (2) *Amblyrhynchote*, *Torquigener*, and *Fugu* (= *Takifugu*); and (3) all other genera. Holcroft (2005) and Alfaro et al. (2007) analyzed the phylogenetic relationships of 19 species of 10 genera (*Arothron*, *Canthigaster*, *Lagocephalus*, *Marilyna*, *Monotreta*, *Sphoeroides*, *Takifugu*, *Tetractenos*, *Tetraodon*, and *Torquigener*). Their results are similar, placing *Lagocephalus* at the base of the topologies. Yamanoue et al. (2011) studied the phylogenetic relationships of 50 species of Tetraodontidae by molecular analysis. The study found four major clades, the first composed of species of *Lagocephalus*, the second *Colomesus* and three species of *Sphoeroides*, the third *Marilyna*, *Tetractenos*, *Tylerirus*, *Polyspina*, *Torquigener*, and *Takifugu*, and the fourth and the largest clade *Carinotetraodon*, *Tetraodon*, *Auriglobus*, *Pelagocephalus*, *Canthigaster*, *Chelonodon*, *Omegophora*, and *Arothron*. The phylogenetic tree of Yamanoue et al. (2011) recognized many monophyletic lineages, but *Colomesus* and species of *Tetraodon* fell into distantly related clades. A relaxed molecular-clock Bayesian divergence time estimation calculated three invasions to freshwater by pufferfishes during their evolution: the first 48–78 million years ago in Southeast Asia, the second 17–38 million years ago in Africa, and the third 0–10 million years ago in South America.

Igarashi et al. (2013) studied the phylogenetic relationships of 17 species of *Tetraodon* by molecular analysis. The study clearly showed that they did not form a monophyletic group. Except for *T. cutcutia*, 16 species

were placed into three major clades: an Asian freshwater group composed of *T. leiurus*, *Tetraodon palembangensis* Bleeker 1850b, *T. abei*, *Tetraodon baileyi* Sontirat 1985, *Tetraodon cochinchinensis* Steindachner 1866, *T. suvattii*, and *Tetraodon turgidus* Mitchill 1815; an Asian brackish water group of *Tetraodon erythrotaenia* Bleeker 1853, *Tetraodon biocellatus* Tirant 1885, *T. fluviatilis*, and *Tetraodon nigroviridis* Marion de Procé 1822; and an African freshwater group of *Tetraodon lineatus* Linnaeus 1758, *Tetraodon pustulatus* Murray 1857, *Tetraodon mbu* Boulenger 1899, *Tetraodon miurus* Boulenger 1902, and *Tetraodon duboisi* Poll 1959. Two molecular studies by Yamanoue et al. (2011) and Igarashi et al. (2013) produced essentially the same phylogenetic tree for freshwater pufferfishes.

In his review of ocean sunfishes, Fraser-Brunner (1951) found *Masturus* Gill 1884 and *Mola* to be more closely related to each other than to *Ranzania*. Tyler's (1980) extensive surveys of osteological characters supported the phylogenetic tree of Fraser-Brunner (1951). Santini and Tyler (2002a) performed the first cladistic analysis of the phylogenetic relationships of ocean sunfishes, using 48 morphological characters. Their study supported the results of the previous studies. Yamanoue et al. (2004) used mitochondrial genomes to analyze the phylogenetic relationships of ocean sunfishes. Their study resulted in the same phylogenetic tree as recovered by previous morphological studies. Molecular studies on tetraodontiform relationships by Alfaro et al. (2007) also produced the same result. Bass et al. (2005) examined many specimens of ocean sunfishes captured from various localities worldwide. The molecular analysis found that *M. ramsayi* is distributed in the Southern Hemisphere and *M. mola* in both the Northern and Southern hemispheres. Yoshita et al. (2009) studied ocean sunfishes of *Mola* around Japan employing both morphological and molecular characters. As discussed in the section of Molidae, the study clearly showed two species of *Mola* around Japan, probably identifiable as *M. mola* and *M. ramsayi*.

Concluding remarks

The taxonomy of tetraodontiforms has progressed greatly since the mid-1960s. On the basis of contributions to date, this paper identifies 412 extant species in the 10 living families of Tetraodontiformes, with an allocation of species and genera as follows: Triacanthodidae including 23 species in 11 genera, Triacanthidae with seven species in four genera, Balistidae with 37 species in 12 genera, Monacanthidae with 102 species in 27 genera, Aracanidae with 13 species in six genera, Ostraciidae with 22 species in five genera, monotypic Triodontidae, Tetraodontidae with 184

species in 27 genera, Diodontidae with 18 species in seven genera, and Molidae with five species in three genera. However, many taxonomic problems involving species and genera of various families still remain. In particular, taxonomic anomalies exist in the Monacanthidae and Tetraodontidae, which have the greatest number of species and diversity within the order. Studies of spikefishes of the Triacanthodidae reveal clarity on the number of genera and species, but poorly surveyed deep areas of the world's oceans exist where new species may occur. Several genera of Balistidae, Aracanidae, and Ostraciidae require study both by morphological and molecular analyses to clarify generic and species limits. The large size attained by ocean sunfishes has made it difficult for us to have a clear understanding of species limits, although a combination of molecular and morphological approaches have clarified that the presence of several populations probably represent species of *Mola* (see Bass et al. 2005; Yoshita et al. 2009). When the taxonomic levels of these populations are established, difficult nomenclatural challenges still remain: many nominal species of ocean sunfishes were published in the old days without type specimens.

With regard to the systematics of the Tetraodontiformes overall, familial relationships have been clarified by morphological and molecular analyses, providing us with a firm understanding of the sister relationships of the following family groups: Triacanthodidae and Triacanthidae, Balistidae and Monacanthidae, and Tetraodontidae and Diodontidae. However, the phylogenetic positions of the Triodontidae and Molidae remain unclear because of conflicts about their positions in morphological and molecular studies (the position of Molidae differs even among molecular studies). More taxon sampling is needed for molecular analyses to produce more robust phylogenetic topologies. Although generic and specific phylogenetic relationships for the families Triacanthidae, Balistidae, Monacanthidae, Aracanidae, Ostraciidae, and Molidae have been studied using morphological and/or molecular analyses, the genera and species of the Triacanthodidae and Diodontidae have never been studied cladistically and await future studies.

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Appendix

Specimens of *Triodon macropterus* examined in this study. Twenty eight specimens, 87.6–488 mm SL. INDIAN OCEAN: Saya de Malha Bank, HUMZ 73183 (281 mm SL), HUMZ 73927 (178 mm SL), HUMZ 74281 (HUMZ 229 mm SL); Chagos Archipelago, HUMZ 87242 (488 mm SL), HUMZ 89466 (386 mm SL), HUMZ 89467 (384 mm SL), HUMZ 89468 (367 mm SL), HUMZ 89469 (345 mm SL); Seychelles, NSMT-P 117608 (165 mm SL). WEST PACIFIC: Shikoku Island, Tosa Bay, BSKU 2279 (351 mm SL), BSKU 22422 (306 mm SL), BSKU 22423 (254 mm SL), BSKU 60657 (307 mm SL), HUMZ 39151 (334 mm SL); Ryukyu Islands, Amami-oshima Island, HUMZ 38975 (240 mm SL), HUMZ 41444 (353 mm SL), HUMZ 49825 (223 mm SL); Ryukyu Islands, Ishigaki-jima Island, HUMZ 38716 (388 mm SL), HUMZ 38731 (398 mm SL); Kyushu-Palau Ridge, BSKU 29011 (374 mm SL), BSKU 29016 (402 mm SL); east of Ogasawara Islands, HUMZ 71886 (426 mm SL); Queensland, north of Townsville, AMS-I. 25811-002 (94.3 mm SL), AMS-I. 25812-002 (87.6 mm SL), AMS-I. 258820-002 (97.5 mm SL); New South Wales, Sawtell, AMS-I. 38286-001 (378 mm SL); New Caledonia, MNHN 1994-592 (235 mm SL), MNHN 1994-853 (377 mm SL).

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A new pufferfish of the genus *Torquigener* that builds “mystery circles” on sandy bottoms in the Ryukyu Islands, Japan (Actinopterygii: Tetraodontiformes: Tetraodontidae)

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Abstract *Torquigener albomaculosus* sp. nov. is described based on two specimens collected from sandy bottoms at depths of 15 and 18 m along the south coast of Amami-oshima Island in the Ryukyu Islands. This new species is distinguished from all other species of *Torquigener* by the following unique combination of characters: dorsal-fin rays 9 (10); anal-fin rays 6; pectoral-fin rays 16 (dorsalmost ray nubbin-like and rudimentary); vertebrae 8 + 11 = 19; no solid, dark, longitudinal stripe nor longitudinal rows of dark spots on the mid-side of body from behind pectoral fin to caudal-fin base; no vertical markings on cheek; dorsal half of head and body covered with fine brown reticulations and many white spots; ventral half of head and body silvery white covered by many white spots from chin to above anal-fin origin; dorsal rim of eye light yellow; and many two-rooted spinules on head and body. Males of *T. albomaculosus* build unique circles as spawning nests, these being 2 m in diameter on sandy bottoms at depths from 10 to 30 m at Amami-oshima Island.

Keywords New pufferfish · *Torquigener* · Tetraodontiformes · mystery circles · Ryukyu Islands

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Introduction

Strange circles have been found on sandy bottoms at depths from 10 to 27 m along the south coast of Amami-oshima Island of the Ryukyu Islands over the past 20 years. These “mystery circles” on the sea floor are relatively large, being about 2 m in diameter, and characterized by having double edges and radiating troughs giving a spoke-like appearance, which have long been a mystery to local SCUBA divers. How are these mystery circles constructed and who builds them? Three years ago, an underwater photographer, Yoji Okata, observed a pufferfish of the genus *Torquigener* Whitley (1930) building the circles. Following his observation, a team comprising TV staff and ichthyologists including the author visited Amami-oshima Island to record the behavior of this pufferfish for about four weeks in July 2012. This field survey and additional observations resulted in a TV program and a publication on the reproductive behavior of this pufferfish (Kawase et al. 2013). Although specimens were not collected at that time, excellent underwater photographs of the pufferfish taken by Yoji Okata documented that this is a new species clearly distinguished from all other species of *Torquigener* by its color pattern. In May 2014, a research team of the National Museum of Nature and Science visited the south coast of Amami-oshima Island to seek specimens of this new pufferfish. They succeeded in collecting a male and a female of the new pufferfish that is described herein as *Torquigener albomaculosus*.

Materials and methods

The two specimens of *Torquigener albomaculosus* sp. nov. were collected by dip net on the sandy bottom along the

Fig. 1 Maps showing collection localities of *Torquigener albomaculosus* sp. nov. along the south coast of Amami-oshima Island in the Ryukyu Islands

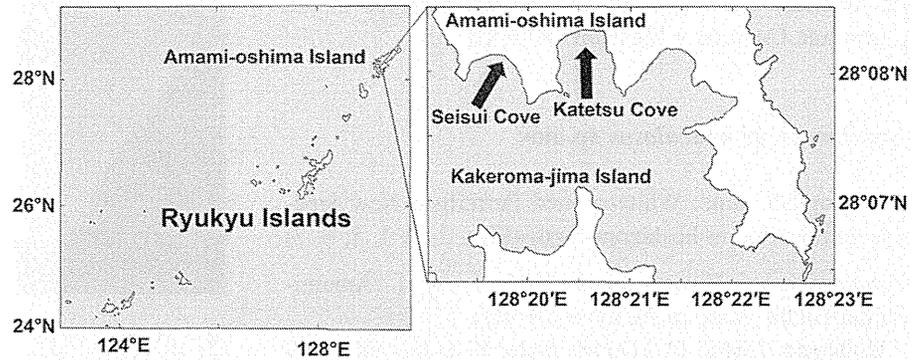
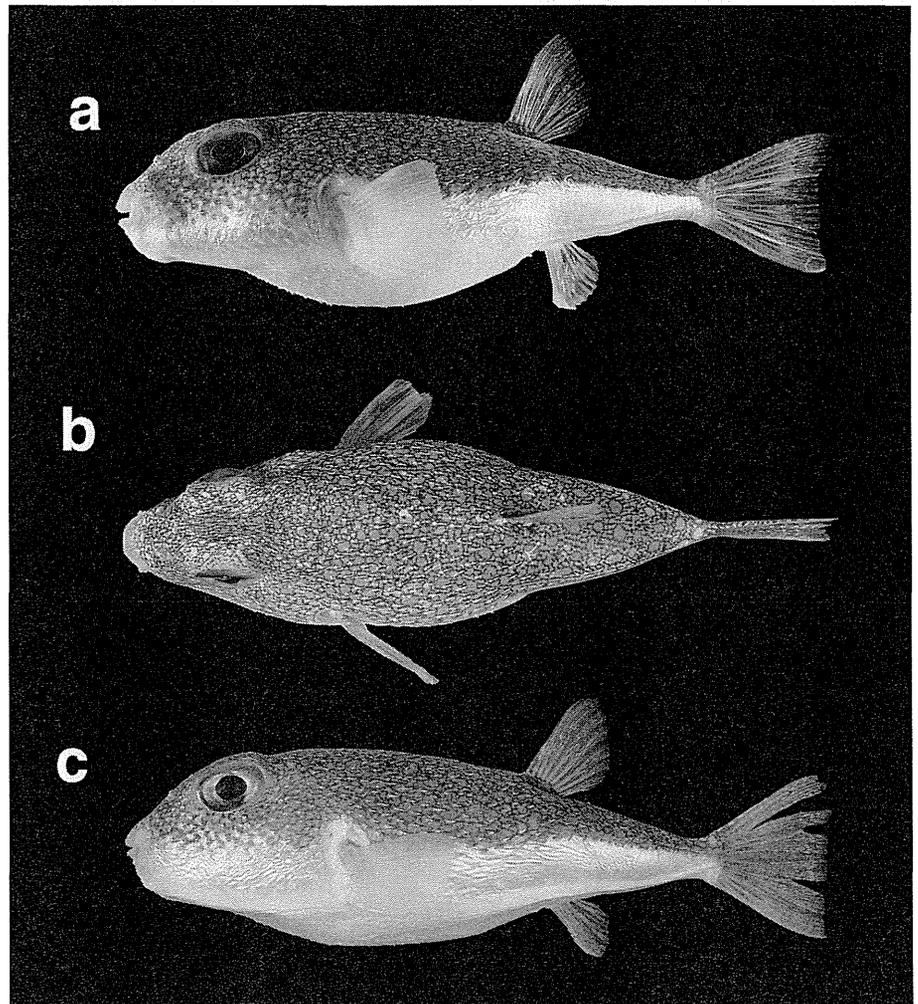


Fig. 2 Type specimens of *Torquigener albomaculosus* sp. nov. **a** Lateral view of holotype, NSMT-P 118118, male, 87.8 mm SL; **b** dorsal view of holotype; **c** lateral view of paratype, KAUM-I. 61100, female, 90.5 mm SL.

Photographs by Satoru N. Chiba



south coast of Amami-oshima Island in the northern part of the Ryukyu Islands (Fig. 1). Methods for counts and measurements followed Dekkers (1975). Fin-ray counts include all visible rays, both branched and unbranched, and fin-ray lengths were determined by measurement from the embedded base. Radiographs were used to count the number of vertebrae. The osteological characters of the

skull and associated bones were observed from three-dimensional images constructed from X-ray CT scanning equipment, LCT 100 (Aloka, Tokyo). Paratype data are shown in parentheses when different from those of the holotype. Standard, total and head lengths are abbreviated as SL, TL and HL, respectively. The holotype is deposited at the Department of Zoology, National Museum of Nature