

Taxonomy and systematics of tetraodontiform fishes: a review focusing primarily on progress in the period from 1980 to 2014

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Abstract When the first Indo-Pacific Fish Conference (IPFC1) was held in Sydney in 1981, there were still many problems in the generic- and species-level taxonomy of all tetraodontiform families except for the recently reviewed Triacanthodidae and Triacanthidae. The period from IPFC1 to IPFC9 (1981–2013) was a time of great progress in the taxonomy and systematics of the Tetraodontiformes: many review and revisional papers have been published for various genera and species, with descriptions of many new taxa occurring mainly on coral reefs and in tropical freshwaters; and cladistic analyses of morphological characters have been performed to clarify phylogenetic relationships of various families and molecular analyses have greatly progressed to provide detailed phylogenetic relationships of families, genera, and even species. The purpose of this paper is to provide a review on developments in the taxonomy and systematics of the Tetraodontiformes, focusing primarily on contributions since 1980 (when James C. Tyler's monumental work was published) through the period of IPFCs, including pertinent publications before 1980. This paper recognizes 412 extant species in the 10 families of living Tetraodontiformes, with the allocation of species and genera as follows: Triacanthodidae including 23 species in 11 genera, Triacanthidae seven

species in four genera, Balistidae 37 species in 12 genera, Monacanthidae 102 species in 27 genera, Aracanthidae 13 species in six genera, Ostraciidae 22 species in five genera, Triodontidae monotypic, Tetraodontidae 184 species in 27 genera, Diodontidae 18 species in seven genera, and Molidae five species in three genera. Phylogenetic relationships of the families have been clarified by morphological and molecular analyses and have provided well-supported sister relationships of the families: Triacanthodidae and Triacanthidae, Balistidae and Monacanthidae, and Tetraodontidae and Diodontidae. However, there remain problems with the phylogenetic positions of the Triodontidae and Molidae due to conflicts of differing positions in morphological and molecular studies (e.g., Molidae has been placed differently among molecular studies).

Keywords Tetraodontiformes · Classification · Morphology · Molecular · Phylogenetic relationships

Introduction

Tetraodontiform fishes are distributed in tropical to temperate seas and freshwaters of the world. They show a remarkable diversity in shape, size, and way of life (Fig. 1). A small filefish of the genus *Rudarius* Jordan and Fowler 1902 and a small pufferfish of the genus *Carinotetraodon* Benl 1957 mature at about 2 cm in total length (TL) (Lim and Kottelat 1995; Tyler 1970), whereas ocean sunfishes of the genus *Mola* Koelreuter 1766 attain over 300 cm TL (Yoshita et al. 2009). Tetraodontiform fishes are characterized by a small mouth with either relatively few teeth that are often enlarged or massive beak-like tooth plates, a small gill opening restricted to the side of the body, scales usually modified as spines, enlarged plates, or

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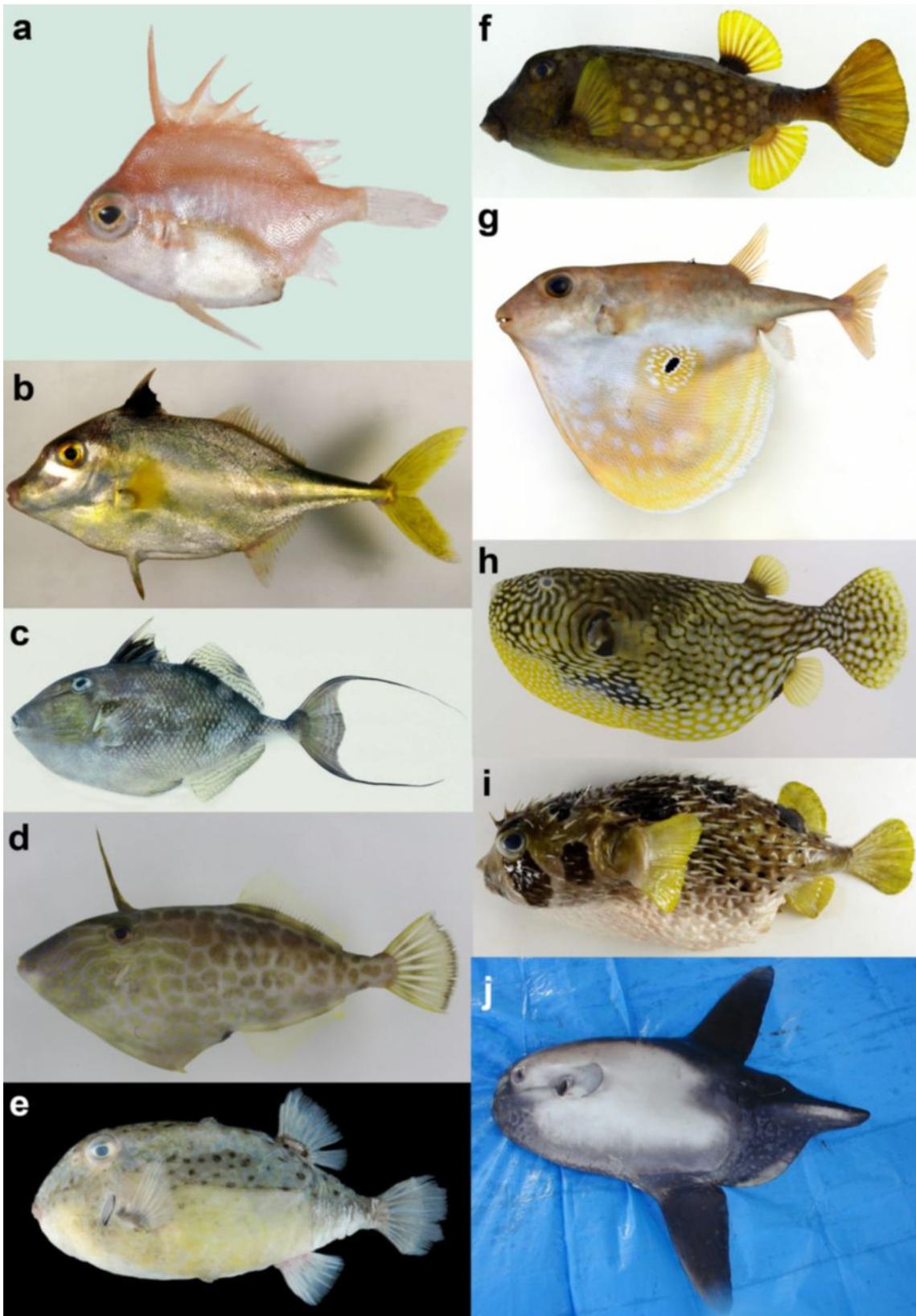


Fig. 1 Representatives of the 10 extant families of Tetraodontiformes. **a** Triacanthodidae, *Triacanthodes anomalus*; **b** Triacanthidae, *Triacanthus biaculeatus*; **c** Balistidae, *Abalistes filamentosus*; **d** Monacanthidae, *Thamnaconus hypargyreus*; **e** Aracanidae, *Kentrocopros aculeatus*; **f** Ostraciidae, *Ostracion immaculatus*; **g** Triodontidae, *Triodon macropterus*; **h** Tetraodontitidae, *Arothron mappa*; **i** Diodontidae, *Diodon liturosus*; **j** Molidae, *Masturus lanceolatus*. Photographs of **a** and **e** provided by BSKU; **b**, **d**, **f**, **h**, and **i** by KAUM; **c** and **g** by NSMT; **j** by Hideki Sugiyama

a carapace, and pelvic fins that are reduced or absent (Tyler 1980; Nelson 2006). In addition, many pufferfishes are characterized by having a strong toxin in the viscera and skin, and even in the musculature of some species of *Lagocephalus* Swainson 1839 (Matsuura 1984). Because of their peculiar morphological characters, tetraodontiforms have long attracted the attention of ichthyologists and biologists.

Since Cuvier (1816) classified tetraodontiforms in the order Plectognathi, tetraodontiforms were usually considered to form a monophyletic group among the advanced percomorph fishes (Nelson 2006). Although the taxonomy of tetraodontiform fishes progressed greatly in the nineteenth century (see Tyler 1980, for a history of the classification of the order), information about tetraodontiform taxonomy was scattered in many articles, making it difficult to understand the taxonomic relationships of tetraodontiforms overall. Alec Fraser-Brunner published an important series of articles on various groups of tetraodontiforms as reviews of genera and families during the mid-1930s to early 1950s: however, many parts of his publications were based on cursory examinations of relatively few specimens. There were no comprehensive phylogenetic studies until Winterbottom (1974) and Tyler (1980) provided their interpretations of the phylogenetic relationships of tetraodontiforms based on myology and osteology, respectively.

When the first Indo-Pacific Fish Conference (IPFC1) was held in Sydney in 1981, many problems remained in the generic- and species-level taxonomy of all tetraodontiform families, except for the Triacanthodidae and Triacanthidae for which Tyler (1968) had provided a monographic revision. The period from IPFC1 to IPFC9 (1981–2013) was a time of great progress in the taxonomy and systematics of tetraodontiforms. Many review and revisional papers have been published for various genera and species, with descriptions of new taxa found mainly in coral reefs and tropical freshwaters; and cladistic analyses of morphological characters have clarified phylogenetic relationships of a number of families and molecular analyses greatly assisted our understanding of the detailed phylogenetic relationships of families, genera, and even species. The purpose of this paper is to present a review of the developments in the taxonomy and

systematics of the Tetraodontiformes, focusing primarily on contributions from 1980 (when James C. Tyler's monumental work was published) through the period of IPFCs, but including pertinent publications before 1980. This paper is composed of two parts, the first reviewing taxonomic studies and the second focusing of studies on systematics. Institutional abbreviations follow Fricke and Eschmeyer (2014).

Triacanthodidae (Spikefishes, Fig. 1a; Table 1)

Spikefishes of the family Triacanthodidae are usually found in depths of 100–600 m on continental shelves and slopes (Tyler 1968; Matsuura and Tyler 1997). They are easily distinguished externally from other families of the order Tetraodontiformes by the following combination of characters: body deep and slightly compressed, covered by moderately thick skin with numerous small scales not readily distinguishable to the unaided eye, with each scale bearing upright spinules and having a roughly shagreen-like appearance; two separate dorsal fins, six spines in the first dorsal fin and 12–18 soft rays in the second dorsal fin; caudal fin rounded to almost truncate, not forked; most dorsal-, anal-, and pectoral-fin rays branched; pelvic fins with a large spine and one or two inconspicuous and rudimentary soft rays; mouth small and usually terminal; teeth of moderate size, usually conical, 10 or more in an outer series in each jaw; caudal peduncle compressed, deeper than wide, not distinctly tapered (Matsuura 2001).

Spikefishes are still relatively poorly known in terms of taxonomy and biology among tetraodontiform families, although Tyler (1968) published an excellent monograph on the superfamily Triacanthoidea including the Triacanthodidae and Triacanthidae. He recognized 19 triacanthodid species in 11 genera (Table 1): *Atrophacanthus* Fraser-Brunner 1950 (one species), *Bathyphylax* Myers 1934 (two species), *Halimochirurgus* Alcock 1899 (two species), *Hollardia* Poey 1861 (three species), *Johnsonina* Myers 1934 (one species), *Macrorhamphosodes* Fowler 1934 (two species), *Mephisto* Tyler 1966b (one species), *Parahollardia* Fraser-Brunner 1941b (two species), *Paratriacanthodes* Fowler 1934 (two species), *Triacanthodes* Bleeker 1857 (two species), and *Tydemanina* Weber 1913 (one species). Because all these genera and species were described in detail by Tyler (1968), their taxonomic features are not repeated here, except for new information that provides a better understanding of taxa.

Many species of the Triacanthodidae are known from the tropical and warm regions of the Indo-Pacific. However, five species are distributed in the western Atlantic: *Hollardia hollardi* Poey 1861, *Hollardia meadi* Tyler 1966a, *Johnsonina eriomma* Myers 1934, *Parahollardia*

Table 1 A list of 23 species of the Triacanthodidae in the world

Subfamily	Species	Distribution
Hollardiinae	<i>Hollardia goslinei</i> Tyler 1968	Hawaii
	<i>Hollardia hollardi</i> Poey 1861	Bermuda and Florida Keys southward to Gulf of Mexico and Caribbean Sea
	<i>Hollardia meadi</i> Tyler 1966a	Bahamas, Cuba, and Barbados
	<i>Parahollardia lineata</i> (Longley 1935)	Atlantic coast of the USA from Virginia to Florida; Gulf of Mexico from Florida to Yucatan
	<i>Parahollardia schmidti</i> Woods 1959	Honduras to Panama in the western Caribbean Sea
Triacanthodinae	<i>Atrophacanthus japonicus</i> (Kamohara 1941)	Off Tanzania, Maldive Islands, Japan, and Celebes Sea
	<i>Bathyphylax bombfrons</i> Myers 1934	Off Kenya, China Sea (off Hong Kong), Australia, and New Caledonia
	<i>Bathyphylax omen</i> Tyler 1966c	Off Kenya
	<i>Bathyphylax pruvosti</i> Santini 2006	Marquesas Islands
	<i>Halimochirurgus alcocki</i> Weber 1913	Arabian Sea, Japan, Mariana Islands, Australia, and New Caledonia
	<i>Halimochirurgus centriscoides</i> Alcock 1899	Arabian Sea and Australia
	<i>Johnsonia eriomma</i> Myers 1934	Bahamas to Greater and Lesser Antilles and western Caribbean Sea
	<i>Macrorhamphosodes platycheilus</i> Fowler 1934	Bay of Bengal, Philippines, and Australia
	<i>Macrorhamphosodes uradoi</i> (Kamohara 1933)	South Africa, off Kenya, Japan, Korea, East China Sea, South China Sea, Australia, New Caledonia, and New Zealand
	<i>Mephisto fraserbrunneri</i> Tyler 1966b	Somalia, Arabian Sea, and Andaman Sea
	<i>Paratriacanthodes abei</i> Tyler 1997	South China Sea
	<i>Paratriacanthodes herrei</i> Myers 1934	Philippines
	<i>Paratriacanthodes retrospinis</i> Fowler 1934	East Africa, Japan, Kyushu-Palau Ridge, South China Sea, Australia, and New Caledonia
	<i>Triacanthodes anomalus</i> (Temminck and Schlegel 1850)	Japan, Korea, East China Sea, South China Sea
	<i>Triacanthodes ethiops</i> Alcock 1894	East Africa, Maldive Islands, Japan, East China Sea, Philippines, Indonesia, New Caledonia, and Australia
	<i>Triacanthodes indicus</i> Matsuura 1982	Saya de Malha Bank (western Indian Ocean)
	<i>Triacanthodes intermedius</i> Matsuura and Fourmanoir 1984	New Caledonia
	<i>Tydemanina navigatoris</i> Weber 1913	East Africa, Bay of Bengal, Japan, China, Philippines, Indonesia, and Australia

lineata (Longley 1935), and *Parahollardia schmidti* Woods 1959. *Hollardia goslinei* Tyler 1968 are known only from nine specimens collected from the Hawaiian Islands.

Little information about the Atlantic and Hawaiian spikefishes has been published since Tyler's (1968) monograph. Matsuura (1983) provided a brief morphological account of *Hollardia hollardi* with a color photograph based on specimens collected from off Surinam. McEachran and Fechhelm (2005) also provided a brief account and line drawing of *Hollardia hollardi* and *Hollardia meadi* from the Gulf of Mexico. McEachran and Fechhelm (2005) and Hartel et al. (2008) reported briefly *Parahollardia lineata* from the Gulf of Mexico and off greater New England, respectively. Tyler et al. (2013) documented a large northern range extension for *Hollardia hollardi* to the northeast coast of the USA off

Massachusetts, whereas this species had previously only been known from the Florida Keys, Bahamas, Bermuda, Gulf of Mexico, Caribbean, and south to Brazil, with the new northern occurrence perhaps associated with warming currents along the east coast of North America.

In contrast to the Atlantic spikefishes, many papers on Indo-Pacific spikefishes were published after 1980. Matsuura (1982) described *Triacanthodes indicus* based on 13 specimens collected from the western Indian Ocean. This species is characterized by relatively large nasal organs compared to other species of *Triacanthodes*. Matsuura and Fourmanoir (1984) described *Triacanthodes intermedius* based on two specimens collected from New Caledonia. *Triacanthodes intermedius* is unique among spikefishes in having several intermediate characters between *Paratriacanthodes* and *Triacanthodes*. Tyler (1997) described *Paratriacanthodes abei* based on a single

specimen collected in the South China Sea. Santini (2006) described *Bathyphylax pruvosti* based on 25 specimens collected from the Marquesas Islands. In addition to these contributions, papers and books on taxonomic and zoogeographical studies of spikefishes were published by authors from various countries including Australia, China, Japan, Korea, Russia, Taiwan, Ukraine, and the USA.

Amaoka (1982) reported *Halimochirurgus alcocki* Weber 1913, *Macrorhamphosodes uradoi* (Kamohara 1933), and *Paratriacanthodes retrospinis* Fowler 1934 with detailed descriptions and color photographs of fresh specimens collected from the Kyushu-Palau Ridge. Matsuura (1984) provided brief accounts and color photographs of tetraodontiform fishes found in the Japanese Archipelago, including *Atrophacanthus japonicus* Kamohara 1941, *Halimochirurgus alcocki*, *Macrorhamphosodes uradoi*, *Triacanthodes anomalus* (Temminck and Schlegel 1850), and *Triacanthodes ethiops* Alcock 1894. In the following year, Matsuura (1985) provided detailed accounts and a color photograph of *Triacanthodes anomalus* collected from the Okinawa Trough. Matsuura (1987) and Stewart and Clark (1988) recorded *Macrorhamphosodes uradoi* from New Zealand, a species previously known only from Japan (Kamohara 1933; Tyler 1968; Matsuura 1984), Kenya (Tyler 1983) and South Africa (Hulley 1972). Matsuura and Tyler (1997) reported *Bathyphylax bombifrons* Myers 1934, *Halimochirurgus alcocki*, *Macrorhamphosodes uradoi*, *Paratriacanthodes retrospinis*, *Triacanthodes ethiops*, and *Triacanthodes intermedius* based on many specimens collected from New Caledonia. Except for *Triacanthodes intermedius*, these are the first records for the species from New Caledonia. Chen et al. (1997) recorded *Triacanthodes anomalus* from the South China Sea. Matsuura (2000) compiled a checklist of Tetraodontiformes from the South China Sea including eight species of spikefishes: *A. japonicus*, *B. bombifrons*, *Halimochirurgus alcocki*, *Macrorhamphosodes platycheilus* Fowler 1934, *Paratriacanthodes retrospinis*, *Triacanthodes anomalus*, *Triacanthodes ethiops*, and *Tydemanian navigatoris* Weber 1913.

Myers and Donaldson (2003) published a checklist of fishes from the Mariana Islands including a record of *Halimochirurgus alcocki*. Kim et al. (2005) provided brief accounts and color photographs of *Triacanthodes anomalus* and *Macrorhamphosodes uradoi* from Korea. Hoese et al. (2006) recorded eight species of spikefishes for the first time from Australia: *B. bombifrons* (New South Wales and Queensland), *Halimochirurgus alcocki* (New South Wales, Queensland and Western Australia), *Halimochirurgus centriscoides* (Western Australia), *Macrorhamphosodes platycheilus* (Northern Territory and Western Australia), *Macrorhamphosodes uradoi* (New South Wales and Queensland), *Paratriacanthodes retrospinis* (New

South Wales and Western Australia), *Triacanthodes ethiops* (Northern Territory, Queensland, Western Australia), and *Tydemanian navigatoris* (Western Australia). Shao et al. (2008) recorded seven species of spikefishes from off southern Taiwan in the South China Sea: *B. bombifrons*, *Halimochirurgus alcocki*, *Halimochirurgus centriscoides*, *Macrorhamphosodes uradoi* (first record from the South China Sea), *Paratriacanthodes retrospinis*, *Triacanthodes anomalus*, and *Tydemanian navigatoris*. All species records of Shao et al. (2008) were based on specimens deposited at museums and institutions in Taiwan and the USA. Larson et al. (2013) published an annotated checklist of the fishes of the Northern Territory, Australia, in which they recorded *Halimochirurgus centriscoides*, *Macrorhamphosodes platycheilus*, *Triacanthodes ethiops*, and *Tydemanian navigatoris*.

Tyler (1983) reported four spikefishes from off Kenya in the western Indian Ocean: *B. bombifrons*, *Bathyphylax omen* Tyler 1966c, *Macrorhamphosodes uradoi*, and *Macrorhamphosodes platycheilus*. When Tyler (1968) compared *B. bombifrons* and *B. omen*, the main differences were that *B. bombifrons* has a narrower pelvis, a shorter postorbital length, a less distinctly supraterminal mouth, and a more concave snout profile. Because the holotype of *B. omen* (37.5 mm in standard length, SL) from the western Indian Ocean is much smaller than that of *B. bombifrons* (77.6 mm SL) from off Hong Kong in the South China Sea, some of these differences were considered to be due in part to the size differences of the holotypes (Tyler 1968). Based on four additional, newly collected specimens of *B. bombifrons* (80.9–84.0 mm SL) and two specimens of *B. omen* (67.0–93.5 mm SL), Tyler (1983) concluded that the most reliable character separating the two species is the degree of concavity of the snout. The depth of the snout in the middle of its length is 10.8–13.4 % SL (average 12.0) in *B. bombifrons* and 12.5–15.5 % SL (average 13.9) in *B. omen*. Matsuura and Tyler (1997) confirmed this difference in three specimens (86.2–93.0 mm SL) of *B. bombifrons* collected off New Caledonia.

Tyler (1986) provided keys to the genera and species of spikefishes known from South and East Africa. He recognized 11 species in this region: *A. japonicus*, *B. bombifrons*, *B. omen*, *Halimochirurgus alcocki*, *Halimochirurgus centriscoides*, *Macrorhamphosodes platycheilus*, *Macrorhamphosodes uradoi*, *Mephisto fraserbrunneri*, *Paratriacanthodes retrospinis*, *Triacanthodes ethiops*, and *Tydemanian navigatoris*. Adam et al. (1998) recorded *A. japonicus* and *Triacanthodes ethiops* for the first time from the Maldives Islands in the central Indian Ocean. *Atrophacanthus japonicus* had previously been recorded only from southern Japan, the Celebes Sea, and off Tanzania (Kamohara 1941; Fraser-Brunner 1950; Tyler 1968; Matsuura 1984). Although *T. ethiops* is relatively common

Table 2 A list of 7 species of the Triacanthidae in the world

Species	Distribution
<i>Pseudotriacanthus strigilifer</i> (Cantor 1849)	Persian Gulf, Gulf of Oman, Arabian Sea, Bay of Bengal, Philippines, South China Sea including Gulf of Thailand, Indonesia, and northern Australia
<i>Triacanthus biaculeatus</i> (Bloch 1786)	Persian Gulf, Gulf of Oman, Arabian Sea, Bay of Bengal, and Japan (north to central Honshu), China, South China Sea including Gulf of Thailand, Indonesia, northern Australia
<i>Triacanthus nieuhoftii</i> Bleeker 1852b	Arabian Sea, Bay of Bengal, Andaman Sea, Indonesia, South China Sea, northern Australia
<i>Tripodichthys angustifrons</i> (Hollard 1854)	Indonesia and northern Australia
<i>Tripodichthys blochii</i> (Bleeker 1852b)	Arabian Sea, Japan (stray), China (stray), South China Sea including Gulf of Thailand, and Indonesia
<i>Tripodichthys oxycephalus</i> (Bleeker 1851c)	Bay of Bengal, South China Sea including Gulf of Thailand, and Arafura Sea
<i>Trixiphichthys weberi</i> (Chaudhuri 1910)	Bay of Bengal, South China Sea including Gulf of Thailand, and Indonesia

in the West Pacific and New Caledonia (Tyler 1968; Matsuura and Tyler 1997), it had previously been known only from East Africa in the Indian Ocean (Tyler 1968, 1986). Manilo and Bogorodsky (2003) studied coastal fishes of the Arabian Sea based on specimens collected by research vessels of Russia and Ukraine from 1967 to 1991. They also examined specimens collected by the German *RV Meteor*, which are deposited at the Zoological Museum of Hamburg University. The two authors recorded *Hali-mochirurgus centriscoides* and *Mephisto fraserbrunneri* Tyler 1966b (previously known only from the holotype, 52.2 mm SL from the Andaman Sea and a non-type specimen, 66.0 mm SL from off Somalia in the western Indian Ocean), but did not provide descriptions of the two species. The specimens they studied are deposited at the National Museum of Natural History, National Academy of Sciences, Ukraine, the Zoological Museum of the Russian Academy of Sciences, and the Zoological Museum of Moscow State University. In addition to these, Venkatar-amanujam et al. (1993) erroneously described a new solenostomid species, *Solenostomus tuticoriensis* based on a specimen of *Macrorhamphosodes platycheilus* from southern India (see Orr and Fritzsche 1997).

This brief historical review clearly shows that there are many collection lacunae with respect to the distribution and diversity of spikefishes in the world oceans. New Caledonia is one example of how collection efforts could provide us with better understanding of spikefish diversity. When Matsuura and Fourmanoir (1984) described *Triacanthodes intermedius* from New Caledonia, only two type specimens were available for their study. Long-term deep-water surveys by ORSTOM around New Caledonia added six species of spikefishes including 16 specimens of *Triacanthodes intermedius* to a taxonomic study on tetraodontiform fishes of this region by Matsuura and Tyler (1997). Many regions of the world oceans need to be surveyed, but the most promising areas would be waters in French Polynesia and the Indian Ocean coast of Sumatra and Java in Indonesia. Japanese and Indonesian fisheries

agencies have recently implemented a joint survey along the Indian Ocean coast of Sumatra and Java. Their surveys have resulted in many interesting spikefishes, including two undescribed species and several rarely collected species, which will be published elsewhere (Matsuura and Kawai in preparation).

Triacanthidae (Triplespines, Fig. 1b; Table 2)

Triplespines of the family Triacanthidae are found on continental shelves in the Indo-West Pacific, usually just below the sea surface to 60 m depth (Tyler 1968). They clearly differ from other families of the order Tetraodontiformes in having the following combination of characters: moderately elongate, strongly compressed body; skin moderately thick with numerous scales not easily discernible to the unaided eye, with each scale bearing upright spinules and having a rough, shagreen-like appearance; two separate dorsal fins, six spines (usually only five spines visible, the sixth rudimentary) in the first dorsal fin and 20–26 soft rays in the second dorsal fin; pelvic fin with a large spine and no visible soft rays; mouth small and usually terminal; teeth in jaws with an outer series of about 10 heavy incisors and an internal series of several molars, usually four in the upper jaw and two in the lower jaw; caudal fin deeply forked; caudal peduncle distinctly tapering to a narrow transversely indented region just in front of the caudal-fin base where the peduncle is wider than deep (Matsuura 2001).

In his monograph of the superfamily Triacanthoidea, Tyler (1968) recognized seven species (Table 2): *Pseudotriacanthus strigilifer* (Cantor 1849), *Triacanthus biaculeatus* (Bloch 1786), *Triacanthus nieuhoftii* Bleeker 1852b, *Tripodichthys blochii* (Bleeker 1852a), *Tripodichthys angustifrons* (Hollard 1854), *Tripodichthys oxycephalus* (Bleeker 1851c), and *Trixiphichthys weberi* (Chaudhuri 1910). He appeared to have resolved all taxonomic problems in the Triacanthidae, except for two unusual

Table 3 A list of 37 species of the Balistidae in the world

Species	Distribution
<i>Abalistes filamentosus</i> Matsuura and Yoshino 2004	Ryukyu Islands, North West Shelf of Australia, and Timor Sea
<i>Abalistes stellatus</i> (Anonymous 1798)	Red Sea, East Africa eastward through northern Australia to Fiji, northward to southern Japan
<i>Balistapus undulates</i> (Park 1797)	Red Sea, East Africa eastward through northern Australia to Tuamotu Islands, northward to southern Japan
<i>Balistes capriscus</i> Gmelin 1789	Tropical western and eastern Atlantic
<i>Balistes polylepis</i> Steindachner 1876	Eastern Pacific from northern California to Chile and Hawaiian Islands
<i>Balistes punctatus</i> Gmelin 1789	Eastern Atlantic from Madeira to Angola
<i>Balistes vetula</i> Linnaeus 1758	Tropical western and eastern Atlantic
<i>Balistoides conspicillum</i> (Bloch and Schneider 1801)	East Africa eastward through northern Australia to Samoa, northward to southern Japan
<i>Balistoides viridescens</i> (Bloch and Schneider 1801)	Red Sea, East Africa eastward through northern Australia to Line and Tuamotu islands, northward to southern Japan
<i>Canthidermis macrolepis</i> (Boulenger 1888)	Red Sea, Gulf of Oman, and Arabian Sea
<i>Canthidermis maculata</i> (Bloch 1786)	Circumgloba in warm and tropical seas
<i>Canthidermis sufflamen</i> (Mitchill 1815)	Western Atlantic from Massachusetts through Gulf of Mexico to Lesser Antilles, Bermuda
<i>Melichthys indicus</i> (Randall and Klauswitz 1973)	Red Sea, East Africa eastward to western Thailand and Sumatra, southern Java, and Bali
<i>Melichthys niger</i> (Bloch 1786)	Circumglobal in tropical seas
<i>Melichthys vidua</i> (Richardson 1845)	East Africa eastward through northern Australia to Hawaiian and Tuamotu islands, northward to southern Japan
<i>Odonus niger</i> (Rüppell 1836)	Red Sea, East Africa eastward through northern Australia to Line, Marquesas and Society islands, northward to southern Japan
<i>Pseudobalistes flavimarginatus</i> (Rüppell 1829)	Red Sea, East Africa eastward through northern Australia to Tuamotu Islands, northward to southern Japan
<i>Pseudobalistes fuscus</i> (Bloch and Schneider 1801)	Red Sea, East Africa eastward through northern Australia to Society Islands, northward to southern Japan
<i>Pseudobaliste naufragium</i> (Jordan and Starks 1895)	Eastern Pacific from Baja California to Ecuador
<i>Rhinecanthus abyssus</i> Matsuura and Shiobara 1989	Known only from Kume-jima Island, Ryukyu Islands
<i>Rhinecanthus aculeatus</i> (Linnaeus 1758)	East Africa eastward through northern Australia to Hawaiian, Marquesas and Tuamotu islands, northward to southern Japan
<i>Rhinecanthus assasi</i> (Forsskål 1775)	Red Sea and Gulf of Oman
<i>Rhinecanthus cinereus</i> (Bonnaterre 1788)	Mauritius and Reunion
<i>Rhinecanthus lumula</i> Randall and Steene 1983	Queensland to Pitcairn Islands
<i>Rhinecanthus rectangulus</i> (Bloch and Schneider 1801)	Red Sea, East Africa eastward through northern Australia to Hawaiian and Pitcairn islands, northward to southern Japan
<i>Rhinecanthus verrucosus</i> (Linnaeus 1758)	Seychelles, Chagos Archipelago eastward through northern Australia to Vanuatu, northward to southern Japan
<i>Sufflamen albicaudatum</i> (Rüppell 1829)	Red Sea, Gulf of Oman, and Arabian Sea
<i>Sufflamen bursa</i> (Bloch and Schneider 1801)	East Africa eastward through northern Australia to Hawaiian, Marquesas and Pitcairn islands, northward to southern Japan
<i>Sufflamen chrysopterum</i> (Bloch and Schneider 1801)	East Africa eastward through northern Australia to Samoa, northward to southern Japan
<i>Sufflamen fraenatum</i> (Latreille 1804)	Red Sea, East Africa eastward through northern Australia to Hawaiian, Marquesas and Tuamotu islands, northward to southern Japan
<i>Sufflamen verres</i> (Gilbert and Starks 1904)	Eastern Pacific from Baja California to Ecuador
<i>Xanthichthys auromarginatus</i> (Bennett 1832)	Mauritius eastward through northern Australia to Hawaiian and Society islands, northward to southern Japan
<i>Xanthichthys caeruleolineatus</i> Randall, Matsuura and Zama 1978	Angela Islands in western Indian Ocean eastward through Indonesia to Galapagos Islands, northward to southern Japan

Table 3 continued

Species	Distribution
<i>Xanthichthys lineopunctatus</i> (Hollard 1854)	South Africa eastward through northern Australia to New Guinea, northward to southern Japan
<i>Xanthichthys mento</i> (Jordan and Gilbert 1882)	Antitropical in Pacific, southern Japan, Hawaiian Islands, Clipperton Island, Revillagigedo Islands, southern California, Easter Island, and Pitcairn Islands
<i>Xanthichthys ringens</i> (Linnaeus 1758)	Western Atlantic from South Carolina through Gulf of Mexico to Lesser Antilles
<i>Xenobalistes punctatus</i> Heemstra and Smith 1983	South Africa
<i>Xenobalistes tumidipectoris</i> Matsuura 1981	Mariana Islands

specimens of *Triacanthus biaculeatus* collected from the Gulf of Thailand. Tyler (1968) reported that four specimens from the Gulf of Thailand near Paknam have differences in eye size and the width of the interorbital space. Two of these specimens (111.5 mm SL and 113.9 mm SL) have exceptionally large eyes (10.4 % SL) and the other two (105.6 mm SL and 107.9 mm SL) have a normal eye size (7.8 and 8.5 % SL). The two large-eye specimens have eyes that are also larger than those of any other specimens of equivalent size. The large-eye specimens have a wider interorbital space (10.2–10.5 % SL vs. 6.3–10.0 % SL in many other specimens). Tyler (1968) stated that they could be an undescribed species, but tentatively considered them as abnormal *Tiracanthus biaculeatus*. Although I have been to the Gulf of Thailand many times and examined local collections in Thailand, I have not seen specimens of *Triacanthus* with such large eyes.

Tyler (1968) provided color descriptions of *P. strigilifer*, *Triacanthus biaculeatus*, and *Triphichthys weberi* based on color notes or color photographs of fresh specimens, but neither was available for the other species. Matsuura (2009) included a color photograph of a juvenile specimen (50 mm SL) of *Triacanthus nieuhofii* collected from Phuket in the Andaman Sea: body silvery white with light brown tinge on dorsal half of body; first dorsal spine silvery white with a black membrane between the first and third dorsal spines; second dorsal, anal, and pectoral fins with light yellowish rays; caudal fin dark yellow. Matsuura (2013) provided brief accounts and a color photograph of *Tripodichthys blochii* collected from the northern Gulf of Thailand: body silvery white with several irregular golden brownish markings on head and body; basal half of first dorsal spine silvery white and proximal half black with yellowish orange first dorsal fin membrane; second dorsal, anal, and pectoral fins with light yellowish rays; caudal fin dusky yellow.

Distribution ranges of triplespines were well documented by Tyler (1968). After his monograph appeared, many publications on fish faunas, field guides and checklists have provided additional information on triplespine

distributions (e.g., Matsuura 1984, 2003a, 2009, 2011, 2013; Allen and Swainston 1988; Talwar and Jhingran 1991; Kottelat et al. 1993; Randall 1995; Allen 1997; Chen et al. 1997; Fricke 1999; Johnson 1999; Matsuura and Peristiwady 2000; Hutchins 2001b; Hoese et al. 2006; Kottelat 2013; Larson et al. 2013). Although most of these publications did not greatly extend the previously reported distributions of triplespines, Fricke (1999) recorded *Triacanthus biaculeatus* from the Mascarene Islands and Kottelat et al. (1993) reported a 60-mm SL specimen of this species from freshwater in Indonesia.

Balistidae (Triggerfishes, Fig. 1c; Table 3)

Triggerfishes of the family Balistidae occur in shallow waters, mainly on coral reefs around the world usually from just below the sea surface to 50 m depth. They differ externally from other families of the order Tetraodontiformes by the following combination of characters: body deep, moderately compressed, encased in very thick, tough skin with large scales easily discernible as individual units; scales above pectoral-fin base in many species enlarged, forming a flexible tympanum; mouth small and terminal, or almost terminal; teeth strong, eight in the outer series of both jaws; gill opening, a moderately short, vertical to oblique slit in front of pectoral-fin base; two dorsal fins, first dorsal fin with three visible spines, the second spine more than 1/2 length of first spine; first spine capable of being locked in an erect position by second spine; second dorsal and anal fin similar in shape; most dorsal-, anal-, and pectoral-fin rays branched; pelvic fins rudimentary, represented by a series of four pairs of enlarged scales encasing posterior end of pelvis (Matsuura 2001).

Triggerfishes of the Balistidae have not yet been comprehensively reviewed, but Matsuura (1979) described the osteology of family and its generic relationships, and Matsuura (1980) diagnosed and illustrated the 20 species of 10 genera found in Japanese waters. His latter paper covered many of the 25 species that were known from the

Indo-Pacific before 1980. Prior to this publication two papers reviewed triggerfishes in the eastern Pacific (Berry and Baldwin 1966) and those of the western Atlantic (Moore 1967a). In addition, Randall and Klausewitz (1973) reviewed *Melichthys* Swainson 1839, with a description of *Melichthys indicus*, and Randall et al. (1978) revised *Xanthichthys* Kaup in Richardson 1856 with a description of *Xanthichthys caeruleolineatus*. These were important contributions about the taxonomy of triggerfishes up to and including 1980. A brief historical review of triggerfish taxonomy follows.

Fraser-Brunner (1935a) published a review of the Balistidae, one of his series of taxonomic studies of tetraodontiform fishes. He recognized 13 genera in the Balistidae and provided a platform for triggerfish taxonomy. Although de Beaufort and Briggs (1962) lumped Fraser-Brunner's 11 genera into the single genus *Balistes* Linnaeus 1758, they relegated all 11 genera to subgenera. Berry and Baldwin (1966) reviewed triggerfishes of the eastern Pacific with comments on Fraser-Brunner's classification. They pointed out that Fraser-Brunner (1935a) recognized *Nematobalistes* Fraser-Brunner 1935a and *Verrunculus* Jordan 1924 on trivial differences of squamation and the anterior few soft rays of the dorsal fin. Berry and Baldwin (1966) examined many individuals of the eastern Pacific triggerfishes, which diminished differences among *Balistes*, *Nematobalistes*, and *Verrunculus*. It led Berry and Baldwin (1966) to conclude that the latter two are junior synonyms of *Balistes*. They partially accepted Fraser-Brunner's system by recognizing six genera: *Balistes*, *Canthidermis* Swainson 1839, *Melichthys*, *Pseudobalistes* Bleeker 1865–1869, *Sufflamen* Jordan 1916, and *Xanthichthys*, but they left the other five genera, *Abalistes* Jordan and Seale 1906, *Balistapus* Tilesius 1820, *Balistoides* Fraser-Brunner 1935a, *Odonus* Gistel 1848, and *Rhinecanthus* Swainson 1839 to the deliberations of subsequent authors. Just after Berry and Baldwin's (1966) paper appeared, Moore (1967a) published a review of the triggerfishes of the western Atlantic and recognized four genera, *Balistes*, *Canthidermis*, *Melichthys*, and *Xanthichthys* (i.e., triggerfishes of other genera not occurring in the western Atlantic). Just after his review of the western Atlantic triggerfishes, Moore (1967b) clarified the taxonomic status of *Balistes punctatus* Gmelin 1789, stating that it occurs only in the eastern Atlantic.

Matsuura (1980) provided keys to genera and species, and taxonomic accounts of 20 Japanese species that he classified in 10 genera, *Abalistes*, *Balistapus*, *Balistoides*, *Canthidermis*, *Melichthys*, *Odonus*, *Pseudobalistes*, *Rhinecanthus*, *Sufflamen*, and *Xanthichthys*. He also addressed a taxonomic problem in the genus *Hemibalistes*. *Hemibalistes* as proposed by Fraser-Brunner (1935a) was not an available name because two species, *Sufflamen bursa*

(Bloch and Schneider 1801) and *Sufflamen chrysopteryum* (Bloch and Schneider 1801), were included and neither was designated type species. Smith (1949b) subsequently designated *Balistes bursa* Bloch and Schneider 1801 as the type species of the genus *Hemibalistes*. However, the diagnostic character of *Hemibalistes*, all scales on cheek smaller than those on body, is not adequate to differentiate it from other triggerfish genera because squamation on the cheek of *Sufflamen* and *Hemibalistes* is variable (Matsuura 1980). As stated above, the papers of Berry and Baldwin (1966), Moore (1967a), Randall and Klausewitz (1973), Randall et al. (1978), and Matsuura (1980) contributed to the proper recognition of 11 genera, *Abalistes*, *Balistapus*, *Balistes*, *Balistoides*, *Canthidermis*, *Melichthys*, *Odonus*, *Pseudobalistes*, *Rhinecanthus*, *Sufflamen*, and *Xanthichthys*. Tyler (1980) also accepted these 11 genera in his phylogenetic study on tetraodontiform fishes. The osteologically based phylogenies of balistoids given by Matsuura (1979) and Tyler (1980) were largely in agreement, as were the majority of their morphological description; the few conflicts between their respective accounts were clarified by Tyler and Matsuura (1981) as an aid to subsequent workers.

Matsuura (1981) described *Xenobalistes tumidipectoris* as a new genus and species based on a small juvenile collected from stomach contents of a marlinfish, *Makaira mazara* (Jordan and Snyder 1901), captured in the Mariana Islands. Although the holotype of *Xenobalistes tumidipectoris* was partially damaged by digestion, it differs clearly from other triggerfishes by its possession of a number of unique characters, such as there is a large lateral expansion protruding laterally just below the pectoral fin, the supraorbital ridge is well developed and convex dorsolaterally, and the mid-lateral portion of the coracoid is greatly expanded to form a disk-like bone. Two years later, Heemstra and Smith (1983) described *Xenobalistes punctatus* as a new species, based on a small juvenile washed up on a beach at the mouth of the Van Stadens River, South Africa.

Randall and Steene (1983) described *Rhinecanthus lunula* and provided brief comments about the other five species, *Rhinecanthus aculeatus* (Linnaeus 1758), *Rhinecanthus assasi* (Forsskål 1775), *Rhinecanthus cinereus* (Bonnaterre 1788), *Rhinecanthus rectangulus* (Bloch and Schneider 1801), and *Rhinecanthus verrucosus* (Linnaeus 1758). Matsuura and Shiobara (1989) described *Rhinecanthus abyssus* on the basis of two specimens collected off the northeast coast of Kume-jima in the Ryukyu Islands, at depths of 120–150 m, which is quite deep for triggerfishes. Matsuura and Yoshino (2004) studied the monotypic genus *Abalistes* and recognized two species, *Abalistes stellatus* (Anonymous 1798) and a new species, *Abalistes filamentosus*.

Taxonomic studies of triggerfishes continued during the period from Berry and Baldwin (1966) to Matsuura and Yoshino (2004), resulting in the classification shown in Table 3, which recognizes 37 species of triggerfishes in 11 genera. In addition to the above contributions, many checklists and illustrated books on shallow-water fishes also provided taxonomic and zoogeographical information of the Balistidae and other tetraodontiforms (Böhlke and Chaplin 1968; Jones and Kumaran 1980; Kyushin et al. 1982; Gloerfelt-Tarp and Kailola 1984; Matsuura 1984, 2000, 2001, 2002, 2003a, 2009, 2011, 2013; Sainsbury et al. 1984; Smith and Heemstra 1986; Tortonese 1986; Allen and Swainston 1988; Winterbottom et al. 1989; Kuitert 1993; Allen and Robertson 1994; Randall 1995, 1996, 2005, 2010; Kyushin et al. 1977; Randall et al. 1997, 2004; Fricke 1999; Myers 1999; Manilo and Bogorodsky 2003; Munday 2005; Shao et al. 2008; Fricke et al. 2009; Allen and Erdman 2012). Still, taxonomic challenges remain. *Sufflamen verres* (Gilbert and Starks 1904) in the eastern Pacific is said to be different from the Indo-West Pacific species, *Sufflamen fraenatum* (Latreille 1804), in having higher counts of fin rays of the second dorsal and anal fins (Berry and Baldwin 1966). According to their study, *S. verres* has 30–33 dorsal rays and 27–30 anal rays, while *S. fraenatum* has 28–30 dorsal rays and 24–26 anal rays. However, Berry and Baldwin (1966) also noted that a specimen of *S. fraenatum* from South Africa with 31 dorsal rays and 27 anal rays, overlapping the counts of *S. verres*. Matsuura (1980) showed on the basis of 22 specimens of *S. fraenatum* from Japan that dorsal rays range from 27 to 30 and anal rays from 24 to 27. Randall (2010) stated that the Hawaiian population of *S. fraenatum* has 27–31 dorsal rays and 24–28 anal rays. These data strongly suggest that *S. verres* is a junior synonym of *S. fraenatum*. Molecular comparisons of *S. verres* and *S. fraenatum* may help clarify their relationships. Fricke (1999) stated that *Xanthichthys lineopunctatus* (Hollard 1854) is a synonym of *Xanthichthys lima* (Bennett 1832). However, the original description of *Balistes lima* by Bennett (1832) comprised only 50 words with fin ray counts “D. 1?, A. 26, P. 13.” Because the poor original description fits several species of the Balistidae, it is impossible to verify that *Balistes lima* is conspecific with *Xanthichthys lineopunctatus*. As no type specimens are known for *Balistes lima*, I conclude that *Balistes lima* should be treated as a nomen dubium.

Santini et al. (2013a) showed *Xenobalistes tumidipectoris* to be deeply nested among five species of *Xanthichthys* in a phylogenetic tree of the Balistidae based on molecular analysis. Their molecular analysis suggests that *Xenobalistes* is a junior synonym of *Xanthichthys*. I am currently comparing larger specimens of *Xenobalistes tumidipectoris* and *Xenobalistes punctatus* with those of

Xanthichthys to clarify the relationships of the two species of *Xenobalistes* with the five species of *Xanthichthys*. This study will be published elsewhere to resolve the taxonomic status of *Xenobalistes*. Santini et al. (2013a) also mentioned that *Balistoides* and *Pseudobalistes* are not monophyletic: *Balistoides conspicillum* (Bloch and Schneider 1801) is sister to *Melichthys*, and *Pseudobalistes flavimarginatus* (Rüppell 1829) forms a clade with *Balistoides viridescens* (Bloch and Schneider 1801), whereas *Pseudobalistes fuscus* (Bloch and Schneider 1801) and *Pseudobalistes naufragium* (Jordan and Starks in Jordan 1895) represent a single clade. These species should be revisited with detailed morphological examinations.

Monacanthidae (Filefishes, Fig. 1d; Table 4)

Filefishes of the family Monacanthidae occur on coral and rocky reefs and in sea grass beds, shallower than 200 m, but some species are found at depths reaching almost 300 m (Matsuura and Tyler 1997; Hutchins 2001b). They differ externally from other families of the order Tetraodontiformes by the following combination of characters: body usually deep, strongly compressed, body shape varying from oblong to almost circular; skin smooth to rough, shagreen-like, with minute to small scales armed with one to many fine spinules, spinules enlarged in some species forming bristles or spines on the posterior portion of the body; scales on head of some species with strong flattened spinules; mouth small, generally terminal, non-protractile; teeth pointed and not fused together, central pair usually the largest in each jaw; gill opening, a short vertical to oblique slit in front of, or above, pectoral-fin base; two dorsal fins, first dorsal fin consisting of a prominent spine, which can be locked upright by a second very small spine, second dorsal fin with 22 to 52 simple (unbranched) soft rays; anal fin with 20 to 62 simple soft rays; pelvic fin and spines rudimentary or absent, represented by a series of three or fewer pairs of enlarged scales encasing the pelvic terminus, or segments of indeterminate number, or entirely absent; pelvis usually capable of vertical movement giving rise to a ventral flap (Hutchins 2001b; Matsuura 2003b).

There are no comprehensive reviews of the Monacanthidae, although in 1988 Barry Hutchins provided taxonomic, morphological, and phylogenetic data for all monacanthid species in the world in his doctoral dissertation. Some parts of his dissertation were published, however, the taxonomic accounts of many species and genera and the phylogenetic analysis of the genera remain unpublished. Hutchins published a series of articles on the Monacanthidae between 1977 and 2002. His first article on Australian filefishes recognized 28 genera in Australia

Table 4 A list of 102 species of the Monacanthidae in the world

Species	Distribution
<i>Acanthaluteres brownii</i> (Richardson 1848)	Southern Western Australia and South Australia
<i>Acanthaluteres spilomelanurus</i> (Quoy and Gaimard 1824)	Southern Western Australia, South Australia, Victoria, Tasmania, and southern New South Wales
<i>Acanthaluteres vittiger</i> (Castelnau 1873)	Southern Western Australia, South Australia, Victoria, Tasmania and southern New South Wales
<i>Acreichthys hajam</i> (Bleeker 1851a)	Indonesia to Papua New Guinea, northward to southern Japan
<i>Acreichthys radiatus</i> (Popta 1900)	Indonesia to Papua New Guinea, northward to southern Japan
<i>Acreichthys tomentosus</i> (Linnaeus 1758)	Sri Lanka eastward thorough Indonesia to New Caledonia, northward to southern Japan
<i>Aluterus heudelotii</i> Hollard 1855	Both sides of Atlantic: in the western Atlantic from Massachusetts and Bermuda to Brazil, in the eastern Atlantic Mauritania to Angola
<i>Aluterus monoceros</i> (Linnaeus 1758)	Circumglobal in warm and tropical seas
<i>Aluterus schoepfii</i> (Walbaum 1792)	Nova Scotia and Bermuda to Brazil
<i>Aluterus scriptus</i> (Osbeck 1765)	Circumglobal in warm and tropical seas
<i>Amanses scopas</i> (Cuvier 1829)	Red Sea, East Africa eastward through northern Australia to Tuamotu Islands, northward to southern Japan
<i>Anacanthus barbatus</i> Gray 1831	India eastward to northern Australia
<i>Artrolepis filicauda</i> (Günther 1880)	Northern Western Australia, Northern Territory, Queensland, New South Wales, eastern Victoria, northern Tasmania, and southern Papua New Guinea
<i>Brachaluteres fahaqa</i> Clark and Gohar 1953	Red Sea
<i>Brachaluteres jacksonianus</i> (Quoy and Gaimard 1824)	Southern Western Australia, South Australia, Victoria, Tasmania, and New South Wales
<i>Brachaluteres taylori</i> Woods in Schultz et al. 1966	Indonesia eastward to Papua New Guinea and eastern Australia, northward to Philippines
<i>Brachaluteres ulvarum</i> Jordan and Fowler 1902	Japan
<i>Cantherhines cerinus</i> Randall 2011	Philippines
<i>Cantherhines dumerilii</i> (Hollard 1854)	East Africa, Mozambique Channel, Comores and Mascarenes, north to southern Japan, Ogasawara Islands and Hawaiian Islands, south to New Caledonia, Lord Howe Island, Rapa and Ducie (Pitcairn Group). East to Central America
<i>Cantherhines fronticinctus</i> (Günther in Playfair and Günther 1867)	East Africa eastward through Indonesia to New Caledonia, northward to southern Japan
<i>Cantherhines longicaudus</i> Hutchins and Randall 1982	Tahiti, Cook Islands, New Caledonia, and Tuamotu Islands
<i>Cantherhines macroceros</i> (Hollard in Guichenot 1853)	Western Atlantic and St. Paul's Rocks, Cape Verde Islands
<i>Cantherhines multilineatus</i> (Tanaka 1918)	Eastern Indian Ocean, South China Sea, and Japan
<i>Cantherhines nukuhiva</i> Randall 2011	Marquesas Islands and Tuamotu Archipelago
<i>Cantherhines pardalis</i> (Rüppell 1837)	Red Sea, East Africa eastward through northern Australia to Marquesas and Pitcairn islands, northward to southern Japan
<i>Cantherhines pullus</i> (Ranzani 1842)	Massachusetts and Bermuda to Brazil, also recorded from West Africa
<i>Cantherhines rapanui</i> (de Buen 1963)	Easter Island
<i>Cantherhines sandwichiensis</i> (Quoy and Gaimard 1824)	Hawaiian Islands, Johnston Island, and Cook Islands
<i>Cantherhines verecundus</i> Jordan 1925	Hawaiian Islands
<i>Cantheschenia grandisquamis</i> Hutchins 1977	Western Australia, New South Wales, and Lor Howe Island
<i>Cantheschenia longipinnis</i> (Fraser-Brunner 1941c)	Southern Western Australia and northern New South Wales
<i>Chaetodermis penicilligerus</i> (Cuvier 1816)	Indonesia east ward to northern Australia, northward to southern Japan
<i>Colurodontis paxmani</i> Hutchins 1977	Northern Australia
<i>Enigmacanthus filamentosus</i> Hutchins 2002	Seychelles and Marshall Islands
<i>Eubalichthys bucephalus</i> (Whitley 1931)	Southern Western Australia, South Australia, Tasmania, and southern New South Wales

Table 4 continued

Species	Distribution
<i>Eubalichthys caeruleoguttatus</i> Hutchins 1977	Northern Western Australia
<i>Eubalichthys cyanoura</i> Hutchins 1987	Southern Western Australia and South Australia
<i>Eubalichthys gunnii</i> (Günther 1870)	Eastern South Australia, Victoria, and Tasmania
<i>Eubalichthys mosaicus</i> (Ramsay and Ogilby 1886)	Southern Western Australia, South Australia, Victoria, Tasmania, New South Wales, and southern Queensland
<i>Eubalichthys quadrispinis</i> Hutchins 1977	Southern Western Australia and South Australia
<i>Lalmohania velutina</i> Hutchins 1994b	Southeastern India
<i>Meuschenia australis</i> (Donovan 1824)	Eastern South Australia, Victoria, and Tasmania
<i>Meuschenia flavolineata</i> Hutchins 1977	Southern Western Australia, South Australia, Victoria, Tasmania, and southern New South Wales
<i>Meuschenia freycineti</i> (Quoy and Gaimard 1824)	Southern Western Australia, South Australia, Tasmania, and southern New South Wales
<i>Meuschenia galii</i> (Waite 1905)	Southern Western Australia, South Australia, and western Victoria
<i>Meuschenia hippocrepis</i> (Quoy and Gaimard 1824)	Southern Western Australia, South Australia, Victoria, and northeastern Tasmania
<i>Meuschenia scaber</i> (Forster in Bloch and Schneider 1801)	Southern Western Australia, South Australia, Tasmania, and southern New South Wales
<i>Meuschenia trachylepis</i> (Günther 1870)	New South Wales and Queensland
<i>Meuschenia venusta</i> Hutchins 1977	Southern Western Australia, South Australia, Tasmania, and southern New South Wales
<i>Monacanthus chinensis</i> (Osbeck 1765)	West Pacific northward to southern Japan and southward to Victoria
<i>Monacanthus ciliates</i> (Mitchill 1818)	Newfoundland and Bermuda to the Antilles
<i>Nelusetta ayraud</i> (Quoy and Gaimard 1824)	Southern Western Australia, South Australia, Victoria, northern Tasmania, New South Wales, and southern Queensland
<i>Oxymonacanthus halli</i> Marshall 1952	Red Sea
<i>Oxymonacanthus longirostris</i> (Bloch and Schneider 1801)	East Africa eastward through northern Australia to Samoa, northward to southern Japan
<i>Paraluteres arqat</i> Clark and Gohar 1953	Red Sea
<i>Paraluteres prionurus</i> (Bleeker 1851b)	East Africa eastward through Indonesia to Nieu, northward to southern Japan
<i>Paramonacanthus arabicus</i> Hutchins 1997	Arabian Gulf
<i>Paramonacanthus choirocephalus</i> (Bleeker 1853)	Thailand eastward through Indonesia to Papua New Guinea
<i>Paramonacanthus frenatus</i> (Peters 1855)	East Africa and Seychelles
<i>Paramonacanthuys lowei</i> Hutchins 1997	Eastern Australia
<i>Paramonacanthus matsuurai</i> Hutchins 1997	Ogasawara Islands
<i>Paramonacanthus nematophorus</i> (Günther 1870)	Red Sea, East Africa, and Seychelles
<i>Paramonacanthus oblongus</i> (Temminck and Schlegel 1850)	Indonesia through northern Australia to New Caledonia, northward to southern Japan
<i>Paramonacanthus otisensis</i> Whitley 1931	Eastern Australia
<i>Paramonacanthus pusillus</i> (Rüppell 1828)	Red Sea, East Africa eastward through Indonesia to northern Australia, northward to southern Japan
<i>Paramonacanthus sulcatus</i> (Hollard 1854)	Malaysia, Indonesia, Thailand, Taiwan, and China
<i>Paramonacanthus tricuspis</i> (Hollard 1854)	India eastward to west coast of Thailand
<i>Pervagor alternans</i> (Ogilby 1899)	Eastern Australia, Lord Howe Island, New Caledonia, and Marshall Islands
<i>Pervagor aspricaudus</i> (Hollard 1854)	Mauritius eastward to Marshall Islands, Hawaiian Islands, and New Caledonia, northward to southern Japan
<i>Pervagor janthinosoma</i> (Bleeker 1854)	East Africa eastward through Indonesia to Fiji and Tonga, northward to southern Japan
<i>Pervagor marginalis</i> Hutchins 1986a	Marquesas Islands and Line Islands
<i>Pervagor melanocephalus</i> (Bleeker 1853)	Indonesia eastward through northern Australia to Samoa, northward to southern Japan
<i>Pervagor nigrolineatus</i> (Herre 1927)	Indonesia eastward through Papua New Guinea to Solomon Islands, northward to southern Japan
<i>Pervagor randalli</i> Hutchins 1986a	Red Sea

Table 4 continued

Species	Distribution
<i>Pervagor pilosoma</i> (Lay and Bennett 1839)	Hawaiian Islands
<i>Pseudalutarius nasicornis</i> (Temminck and Schlegel 1850)	East Africa eastward through northern Australia to New Caledonia, northward to southern Japan
<i>Pseudomonacanthus elongatus</i> Fraser-Brunner 1940	Australia
<i>Pseudomonacanthus macruru</i> (Bleeker 1856)	Singapore, Malaysia, Brunei, Indonesia, Philippines, and Japan
<i>Pseudomonacanthus peroni</i> (Hollard 1854)	Australia and New Guinea
<i>Pseudomonacanthus tweediei</i> Fraser-Brunner 1940	Singapore
<i>Rudarius ercodes</i> Jordan and Fowler 1902	Japan, Korea, and China
<i>Rudarius excelsus</i> Hutchins 1977	Malaysia (Sabah), Papua New Guinea, Queensland, and Ryukyu Islands
<i>Rudarius minutus</i> Tyler 1970	Malaysia (Sabah), Indonesia, Palau, and Great Barrier Reef
<i>Scobinichthys granulatus</i> (Shaw in White 1790)	Southern Western Australia, South Australia, Victoria, northern Tasmania, New South Wales, and southern Queensland
<i>Stephanolepis auratus</i> (Castelnau 1861)	Eastern Western Australia, South Australia, Victoria, and Tasmania
<i>Stephanolepis cirrhifer</i> (Temminck and Schlegel 1850)	Japan, Korea, Taiwan, China, and northern Philippines
<i>Stephanolepis diaspros</i> Fraser-Brunner 1940	Red Sea, Gulf of Oman, and Persian Gulf
<i>Stephanolepis hispidus</i> (Linnaeus 1766)	Both sides of Atlantic: western Atlantic from Nova Scotia and Bermuda to Brazil; eastern Atlantic from Canary Islands to Angola
<i>Stephanolepis setifer</i> (Bennett 1831)	North Carolina and Bermuda to northern South America
<i>Thamnaconus analis</i> (Waite 1904)	Southwestern Pacific
<i>Thamnaconus arenaceus</i> (Barnard 1927)	Western Indian Ocean
<i>Thamnaconus degeni</i> (Regan 1903)	Tasmania, Victoria and South Australia
<i>Thamnaconus fajardoi</i> Smith 1953	Mozambique Channel, Madagascar, western Mascarenes
<i>Thamnaconus fijiensis</i> Hutchins and Matsuura 1984	Fiji
<i>Thamnaconus garretti</i> (Fowler 1928)	Hawaiian Islands
<i>Thamnaconus hypargyreus</i> (Cope 1871)	Western Pacific and southeastern Indian Ocean
<i>Thamnaconus melanoproctes</i> (Boulenger 1889)	Muscat, Oman, Gulf of Oman, Arabian Sea, northwestern Indian Ocean
<i>Thamnaconus modestoides</i> (Barnard 1927)	Red Sea, Indo-West Pacific: East Africa, South Africa, Seychelles, Madagascar and Réunion (Mascarenes) east to Indonesia, north to southern Japan, south to northwestern Australia
<i>Thamnaconus modestus</i> (Günther 1877)	Japan, Korea, China
<i>Thamnaconus paschalis</i> (Regan 1913)	Easter Island and southeastern Pacific
<i>Thamnaconus septentrionalis</i> (Günther 1874)	China, East China Sea, and Japan
<i>Thamnaconus tessellatus</i> (Günther 1880)	Western Pacific and southeastern Indian Ocean

(Hutchins 1977) where the greatest diversity of filefishes is found (Hutchins 2001a).

Before Hutchins' (1977) review of Australian filefishes appeared, Fraser-Brunner (1941a) published a review paper on the Monacanthidae (his Aluteridae), recognizing 22 genera. Although de Beaufort and Briggs (1962) lumped *Amanses* Gray 1835, *Chaetodermis* Swainson 1839, *Paramonacanthus* Bleeker 1865–1869, *Pervagor* Whitley 1930a, and *Pseudomonacanthus* Bleeker 1865 into a single genus, *Monacanthus* Linnaeus 1758, they recognized *Aluterus* Cloquet 1816, *Anacanthus* Gray 1830 (their

Psilocephalus Swainson 1839), *Paraluteres* Bleeker 1865, and *Pseudalutarius* Bleeker 1865 as distinctive genera. Berry and Vogele (1961) reviewed nine species of the Monacanthidae of the western North Atlantic with detailed accounts of *Amanses pullus* (Ranzani 1842), *Aluterus monoceros* (Linnaeus 1758), *Aluterus heudelotii* Hollard 1855, *Aluterus schoepfi* (Walbaum 1792), *Aluterus scriptus* (Osbeck 1765), *Monacanthus ciliatus* (Mitchill 1818), *Monacanthus tuckeri* Bean 1906, *Stephanolepis hispidus* (Linnaeus 1758), and *Stephanolepis setifer* (Bennett 1831). Although Berry and Vogele (1961) placed *Monacanthus*

pullus in the genus *Amanses*, they also pointed out that *M. pullus* should be classified in the subgenus *Cantherhines* Swainson 1839 because *M. pullus* does not have a patch of long spines on the mid-side of the body between the dorsal and anal fins, which is a diagnostic character of *Amanses*. When Randall (1964) reviewed the filefish genera *Amanses* (monotypic) and *Cantherhines*, he recognized 11 species of *Cantherhines* in the tropical seas of the world. He showed that *Amanses* possesses a patch of long stout spines (male) or a dense brushlike mass of long setae (female) on the mid-side of the body, whereas all species of *Cantherhines* lack long spines or long setae on the mid-side of the body. Randall (1964) described *Cantherhines tiki* as a new species based on a single specimen collected from Easter Island. *Cantherhines tiki* was said to be distinguishable from other species of *Cantherhines* by its strongly produced snout (Randall 1964). However, Caldwell and Randall (1967) showed *Cantherhines tiki* to be a junior synonym of *Cantherhines rapanui* (de Buen 1963) because of the considerable variation in the snout shape of *Cantherhines rapanui*.

Hutchins (1977) described three new genera, *Bigener*, *Cantheschenia* and *Colurodontis*, and eight new species from Australia. However, Hutchins (1994a) subsequently placed *Aleuterius brownii* Richardson 1848, the type species of *Bigener*, in *Acanthaluteres* Bleeker 1865, making *Bigener* a junior synonym of *Acanthaluteres*. Hutchins and Randall (1982) reviewed the *Cantherhines fronticinctus* complex and described *Cantherhines longicaudus* as a new species from Tahiti and Rarotonga. Matsuura (1984) provided brief accounts and color photographs of 26 monacanthids found in Japanese waters. Hutchins and Matsuura (1984) described *Thamnaconus fijiensis* from Fiji. In the following year, Hutchins (1985) reviewed the genus *Brachaluteres* Bleeker 1865 and recognized four species with comments on their ability to inflate the abdomen. Hutchins (1986a) published a revision of the genus *Pervagor* and recognized eight species including two new species, *Pervagor randalli* and *Pervagor marginalis*. Hutchins (1986b) provided a key and brief taxonomic accounts for 16 species of filefishes found along South Africa. Hutchins (1987) published *Eubalichthys cyanoura* as a new species from South Australia. Hutchins (1994b) described and illustrated *Lalmohania velutina* from India as a new genus and species. Hutchins (2002) reported another new genus and species, *Enigmacanthus filamentosus*, from the Seychelles and Marshall Islands. *Enigmacanthus filamentosus* is a very small filefish, 27–36 mm SL, resembling in size species of the genus *Rudarius*. Randall (2011) again reviewed the genus *Cantherhines*, recognizing 11 species, including two new species, *Cantherhines cerinus* from the Philippines and *Cantherhines nukuhiva* from the Marquesas Islands.

Based on the contributions shown above, I recognize 102 species in 27 genera worldwide (Table 4). I provisionally place *Pseudomonacanthus multilineatus* Tanaka 1918 in the genus *Cantherhines* following previous authors (Matsuura 1984; Kyushin et al. 1977; Lindberg et al. 1997). Although Randall (1964) placed *Pseudomonacanthus multilineatus* in *Cantherhines*, Hutchins and Randall (1982) said that *Cantherhines multilineatus* should be classified in the genus *Thamnaconus* Smith 1949b. However, they did not provide characters to justify the transfer from *Cantherhines* to *Thamnaconus*. To resolve the taxonomic status of *Cantherhines multilineatus*, a detailed study of diagnostic characters, including encasing scales of the posterior end of the pelvis, is needed. Hutchins suggested in his dissertation that *Thamnaconus melanoproctes* (Boulenger 1889) is a senior synonym of *Pseudomonacanthus multilineatus*. However, an examination of specimens from various localities in the Indo-West Pacific is necessary to properly assess the relationships of the two nominal species. Although Barry Hutchins made great contributions to the better understanding of taxonomy and diversity of filefishes, in particular Australian filefishes, taxonomic problems in several genera such as *Acreichthys* Fraser-Brunner 1941c, *Pseudomonacanthus*, and *Thamnaconus* remain. As in the case of triggerfishes, many checklists and illustrated guidebooks have provided much useful information on the taxonomy, distribution, and biology of filefishes (see the section on the Balistidae).

Aracaniidae (Trunkfishes, Fig. 1e; Table 5)

Trunkfishes of the family Aracaniidae occur in shallow to relatively deep waters in depths from 5 m to 300 m. The species of *Aracana* Gray 1833, *Anoplocapros* Kaup 1855, *Caprichthys* McCulloch and Waite 1915, *Capropygia* Kaup 1855 and *Polyplacapros* Fuji and Uyeno 1979 are found in temperate seas of southern Australia, whereas species of *Kentrocapros* Kaup 1855 are known from deep waters in the warm, tropical regions of the Indo-Pacific (Matsuura and Yamakawa 1982; Matsuura and Tyler 1997; Matsuura 2006, 2008).

Trunkfishes differ externally from other families of Tetraodontiformes by the following combination of characters: body almost completely encased in a bony shell or carapace formed of enlarged, thickened scale plates, usually hexagonal in shape and firmly sutured to one another; isolated bony plates on caudal peduncle; carapace triangular or hexagonal in cross section, with openings for mouth, eyes, gill slit, pectoral, dorsal, and anal fins, and for the flexible caudal peduncle; scale plates often with surface granulations and prolonged in some species into prominent

Table 5 Distributions of 13 species of the Aracnidae in the world

Species	Distribution
<i>Anoplocapros amygdaloides</i> Fraser-Brunner 1941d	Western Australia and South Australia
<i>Anoplocapros inermis</i> (Fraser-Brunner 1935b)	Southern Queensland, New South Wales and Victoria
<i>Anoplocapros lenticularis</i> (Richardson 1841)	Western Australia, South Australia and Victoria
<i>Aracana aurtia</i> (Shaw in Shaw and Nodder 1798)	Western Australia, South Australia, Victoria, Tasmania, and New South Wales
<i>Aracana ornata</i> (Gray 1838)	Western Australia, South Australia, Victoria, and Tasmania
<i>Caprichthys gymnura</i> McCulloch and Waite 1915	Western Australia and South Australia
<i>Capropygia unistriata</i> (Kaup 1855)	Western Australia, South Australia, and Victoria
<i>Kentrocapros aculeatus</i> (Houttuyn 1782)	Japan, Korea, China, and Hawaiian Islands
<i>Kentrocapros eco</i> Phillipps 1932	New Zealand
<i>Kentrocapros flavofasciatus</i> (Kamohara 1938)	Japan, New South Wales, Queensland, and New Caledonia
<i>Kentrocapros rosapinto</i> (Smith 1949a)	Western Indian Ocean
<i>Kentrocapros spilonota</i> (Gilbert 1905)	Hawaiian Islands
<i>Polyplacapros tyleri</i> Fujii and Uyeno 1979	New South Wales and Norfolk Ridge

carapace spines over the eyes or along ventrolateral or dorsolateral angles of the body; mouth small, terminal, with fleshy lips; teeth of moderate size, conical, usually fewer than 15 in each jaw; gill opening moderately short, a vertical to oblique slit in front of pectoral-fin base; spinous dorsal fin absent; most dorsal-, anal-, and pectoral-fin rays branched; caudal fin with nine branched rays; pelvic fins absent (Matsuura 2001).

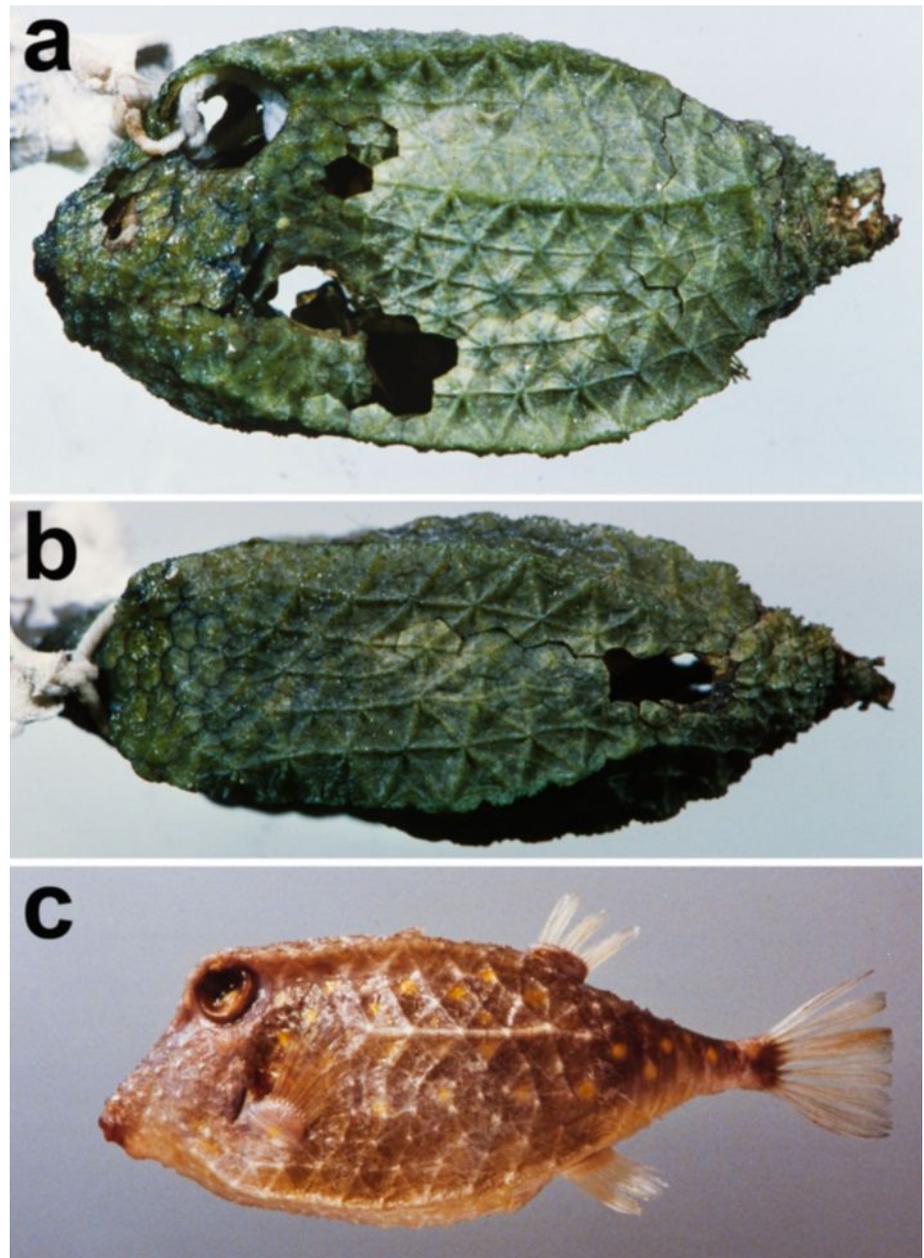
The Aracnidae and Ostraciidae have been placed in separate families by some authors (e.g., Winterbottom 1974; Tyler 1980; Matsuura 1984, 2001), but they have also been treated as two subfamilies of the family Ostraciidae by others (e.g., Winterbottom and Tyler 1983; Klassen 1995; Allen et al. 2006; Nelson 2006; Matsuura 2008). All the above authors recognized the two groups as closely related phylogenetic clades (sister groups), but placed them at different taxonomic ranks. Santini and Tyler (2003) studied fossils and extant members of the Tetraodontiformes extensively and recognized familial groupings for the Aracnidae and Ostraciidae. Recently, Santini et al. (2013a) investigated the phylogenetic relationships of the Aracnidae and Ostraciidae based on molecular analysis of many taxa (nine species of five genera of Aracnidae and 17 species of six genera of Ostraciidae). They demonstrated that the species examined in their studies (Santini and Tyler 2003; Santini et al. 2013a) have adequate characteristics to recognize two separate groups at the family level.

A problem exists with the spelling of the genus *Aracana*. When Gray (1833) published his article on Indian zoology, he used two different spellings for a species of trunkfish. At the beginning of the article, a section titled “Directions for arranging the plates” provided the name of animals in the plates where he presented the name of

the trunkfish as “Many Spined Coffin Fish. *Ostracion* (*Acerana*) *auritus*”; however, the legend of plate 98 spelled the name as “*Ostracion* (*Acarana*) *auritus*.” Plate 98 provided a good illustration of the species showing appropriate characters to identify the species. It is the type species of the subgenus by monotypy. However, in 1838 John E. Gray published another paper in which he described three species, *Ostracion* (*Aracana*) *ornata*, *Ostracion* (*Aracana*) *flavigaster*, and *Ostracion* (*Aracana*) *lineata*. The second species is a junior synonym of *Aracana ornata* and the third *Aracana aurita* (Shaw in Shaw and Nodder 1798). Gray (1838) stated for his three species that “I have formed a subgenus under the name of *Aracana*” indicating his intention to establish the group at the subgeneric level. Although the name *Aracana* has long been used for the trunkfish genus, the two names *Acerana* and *Acarana* were published earlier than *Aracana*, thus creating a nomenclatural problem. If one follows the priority rule of the Code (ICZN 1999), the family name should be Aceranidae or Acaranidae. As *Aracana* has been used almost universally in the literature, with *Acerana* or *Acarana* virtually ignored by taxonomists, *Aracana* should be preserved under Article 33.3.1 of the Code, making the spelling of the family group name Aracnidae preserved under Article 35.4.1.

Trunkfishes have not yet been comprehensively reviewed. Although Fraser-Brunner (1935b, 1941d) provided brief reviews of the family, his accounts of genera and species were cursory as they were based on few specimens and did not provide adequate characteristics for the species treated. Kuitert (1994) and Matsuura (2008) diagnosed and illustrated seven species in four genera of Australian aracnids, covering many representatives of the family except for the genera *Kentrocapros* and

Fig. 2 *Kentrocapros eco* (NMNZ P.903, 102 mm TL, from Pahia, Bay of Islands, New Zealand; **a** lateral view; **b** dorsal view) and an undescribed species of *Kentrocapros* (c NSMT-P 43344, 104 mm SL) collected from New Zealand



Polyplacapros. *Polyplacapros tyleri* Fujii and Uyeno 1979 is unique in having a fusiform body and the caudal peduncle nearly completely covered by discrete bony plates. In addition to Australian genera of Aracanidae, detailed descriptions and illustrations of all four known species of *Kentrocapros* were provided by Matsuura and Yamakawa (1982), Matsuura and Tyler (1997), and Matsuura (2006). Matsuura (1990) provided brief accounts and a color photograph of a species of *Kentrocapros* collected from the Tasman Sea (32°43'S, 167°30'E) under the name *Kentrocapros eco* (Phillipps 1932). However, an examination of the holotype (102 mm TL) of *Ostracion eco*

(NMNZ P. 903) revealed Matsuura's (1990) Tasman Sea material to be an undescribed species (Fig. 2). This undescribed species has a spine on the dorsolateral ridge midway between the eye and the dorsal-fin origin, whereas the holotype of *O. eco* lacks this spine. This new species will be described and published elsewhere.

As discussed above, no major taxonomic problems remain in the Aracanidae. However, there still remains a need to clarify the nomenclature of some species of *Anoplocapros* as well as the intraspecific variation of morphological characters related to ontogenetic development of *Kentrocapros*.

Table 6 Distributions of 22 species of the Ostraciidae in the world

Species	Distribution
<i>Acanthostracion guineensis</i> Bleeker 1865	Eastern Atlantic on West Coast of Africa from Guinea to Gabon
<i>Acanthostracion notacanthus</i> Bleeker 1863	Eastern Atlantic from St. Helena, Ascension and Azores islands, Ghana and Angola
<i>Acanthostracion polygonius</i> Poey 1876	Western Atlantic from New Jersey and Bermuda to Brazil
<i>Acanthostracion quadricornis</i> (Linnaeus 1758)	Western Atlantic from Massachusetts and Bermuda to Brazil
<i>Lactophrys bicaudalis</i> (Linnaeus 1758)	Western Atlantic from Florida to Brazil
<i>Lactophrys trigonus</i> (Linnaeus 1758)	Western Atlantic from Massachusetts and Bermuda to Brazil
<i>Lactophrys triqueter</i> (Linnaeus 1758)	Western Atlantic from Massachusetts and Bermuda to Brazil
<i>Lactoria cornuta</i> (Linnaeus 1758)	Red Sea, East Africa eastward through northern Australia to Marquesas Islands, northward to southern Japan
<i>Lactoria diaphana</i> (Bloch and Schneider 1801)	East Africa eastward through northern Australia to Hawaiian and Marquesas islands, northward to southern Japan
<i>Lactoria fornasini</i> (Bianconi 1846)	East Africa through Indonesia to Easter Island, southward to New South Wales, northward to southern Japan
<i>Ostracion cubicus</i> Linnaeus 1758	Red Sea, East Africa eastward through northern Australia to Tuamotu Islands (stray found in Hawaiian Islands), northward to southern Japan
<i>Ostracion cyanurus</i> Rüppell 1828	Red Sea, Gulf of Oman, and Arabian Sea
<i>Ostracion immaculatus</i> Temminck and Schelgel 1850	Japan, Korea, China, and East China Sea
<i>Ostracion meleagris</i> Shaw in Shaw and Nodder 1796	East Africa eastward through Indonesia to Hawaiian and Pitcairn islands, northward to southern Japan
<i>Ostracion nasus</i> Bloch 1785	India eastward through Indonesia to Papua New Guinea, northward to Philippines
<i>Ostracion rhinorhynchus</i> Bleeker 1851a	Sri Lanka eastward through Indonesia to Queensland, northward to southern Japan
<i>Ostracion solorensis</i> Bleeker 1853	Philippines through Indonesia to Great Barrier Reef
<i>Ostracion trachys</i> Randall 1975	Réunion and Mauritius
<i>Ostracion whitleyi</i> Fowler 1931	Hawaiian, Society, Marquesas, and Tuamotu islands
<i>Tetrosomus concatenatus</i> (Bloch 1785)	East Africa through Indonesia to New South Wales, northward to southern Japan
<i>Tetrosomus gibbosus</i> (Linnaeus 1758)	Red Sea, East Africa eastward through northern Australia to New Caledonia, northward to southern Japan
<i>Tetrosomus reipublicae</i> (Ogilby 1913)	East Africa through Indonesia to New South Wales, northward to southern Japan

Ostraciidae (Boxfishes, Fig. 1f; Table 6)

Boxfishes of the family Ostraciidae occur in shallow tropical and warm seas of the world. Boxfishes differ externally from other families of Tetraodontiformes by the following combination of characters: body almost completely encased in a bony shell or carapace formed of enlarged, thickened scale plates, usually hexagonal in shape and firmly sutured to one another; no isolated bony plates on caudal peduncle; carapace triangular, rectangular, or pentangular in cross section, with openings for mouth, eyes, gill slits, pectoral, dorsal, and anal fins, and for the flexible caudal peduncle; scale-plates often with surface granulations, which are prolonged in some species into prominent carapace spines over the eye or along the ventrolateral or dorsal angles of the body; mouth small, terminal, with fleshy lips; teeth moderate, conical, usually fewer than 15 in each jaw; gill opening, a moderately short, vertical to oblique slit in front of pectoral-fin base; spinous dorsal fin absent; most dorsal-, anal-, and pectoral-fin rays

branched; caudal fin with eight branched rays; pelvic fins absent (Matsuura 2001).

Fraser-Brunner (1935b) published a brief review of the Aracaniidae and Ostraciidae, recognizing six genera in the Ostraciidae: *Acanthostracion* Bleeker 1865, *Lactophrys* Swainson 1839, *Lactoria* Jordan and Fowler 1902, *Ostracion* Linnaeus 1758, *Rhinesomus* Swainson 1839, and *Rhynchostracion* Fraser-Brunner 1935b. Boxfishes found in the Indo-Australian Archipelago were studied by de Beaufort and Briggs (1962) who lumped Fraser-Brunner's (1935b) Indo-Pacific genera into the genus *Ostracion*. However, they recognized five subgenera in *Ostracion*: *Lactoria*, *Ostracion*, *Rhynchostracion*, *Tetrosomus* Swainson 1839, and *Triorus* Jordan and Hubbs 1925. *Triorus* is a junior synonym of *Tetrosomus* because the type species of the former, *Lactophrys tritropis* Snyder 1911, is a junior synonym of *Tetrosomus concatenatus* (Bloch 1786) (see Randall et al. 1997). Although *Ostracion nasus* Bloch 1785 and *Ostracion rhinorhynchus* Bleeker 1851a have been placed in the genus *Rhynchostracion* by some authors

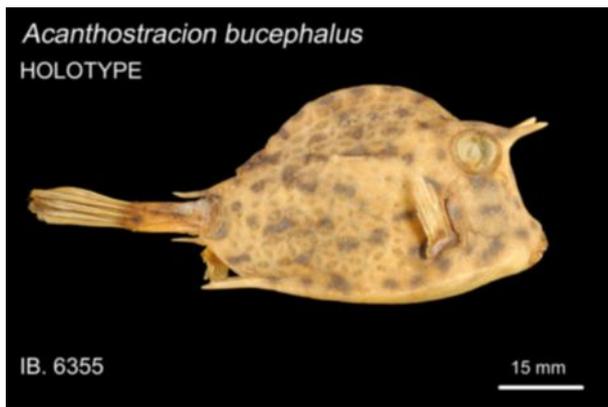


Fig. 3 Holotype of *Acanthostracion bucephalus* (AMS IB.6355) collected from Queensland, Australia. Photograph provided by Mark McGrouther

(Kyushin et al. 1982; Gloerfelt-Tarp and Kailola 1984; Sainsbury et al. 1984; Mohsin and Ambak 1996; Randall et al. 1997; Allen et al. 2006), they were classified in the genus *Ostracion* by other authors (Klassen 1995; Matsuura 2001; Hayashi and Hagiwara 2013). When Fraser-Brunner (1935b) established *Rhynchostracion*, he differentiated it from other ostraciid genera by the degree of the development of the dorsal ridge, the convexity of the dorsal surface of the carapace, and the projection of the snout anterior to the mouth. However, the two characters involving the carapace do not clearly differentiate *Rhynchostracion* from other ostraciids and the snout of *Ostracion nasus*, the type species of *Rhynchostracion*, protrudes anteriorly beyond the mouth in adults but not juveniles. In addition, large adults of *Ostracion cubicus* Linnaeus 1758 have a snout protruding to some extent beyond the mouth. These factors led Matsuura (2001) to place *O. nasus* and *O. rhinorhynchos* in their own genus in his key and brief accounts of ostraciids found in the western central Pacific. Klassen (1995) studied osteological characters of many species of the Ostraciidae extensively and provided evidence that *Rhynchostracion* is a junior synonym of *Ostracion*. Klassen (1995) also regarded *Tetrosomus* as a junior synonym of *Lactoria* because all species of *Lactoria* and *Tetrosomus* examined by him formed a single clade. If Klassen's (1995) proposal is accepted, *Lactoria* should be a junior synonym of *Tetrosomus* because the latter has priority over the former. However, it seems premature to accept his proposal because there are species-level taxonomic problems in several species of *Tetrosomus* (Allen and Erdman 2012).

Tyler (1965) revised the genus *Acanthostracion* in the Atlantic and recognized four species, *Acanthostracion guineensis* Bleeker 1865, *Acanthostracion notacanthus* (Bleeker 1863), *Acanthostracion polygonus* Poey 1876, and *Acanthostracion quadricornis* (Linnaeus 1758).

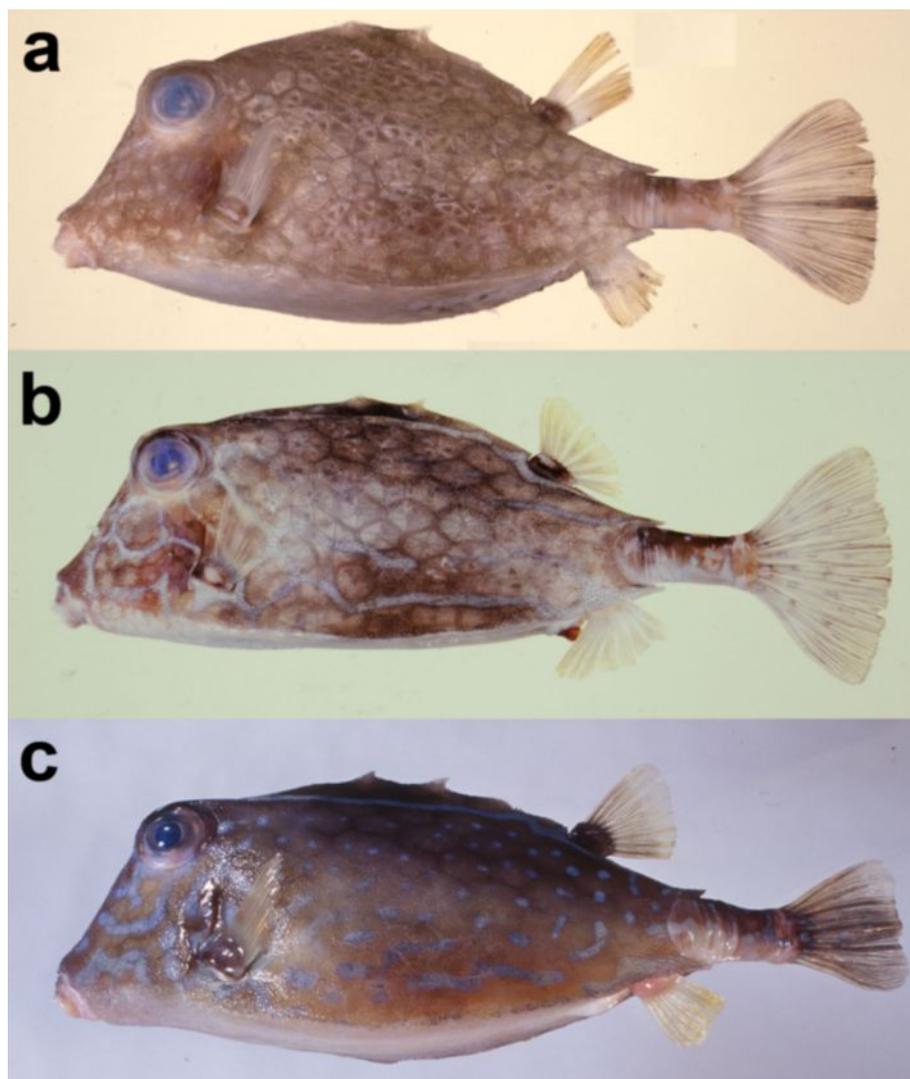
Böhlke and Chaplin (1968) provided keys and accounts accompanied by illustrations to boxfishes found in the western Atlantic. They recognized five species, *A. polygonus*, *A. quadricornis*, *Lactophrys bicaudalis* (Linnaeus 1758), *Lactophrys trigonus* (Linnaeus 1758), *Lactophrys triqueter* (Linnaeus 1758). *Lactophrys bicaudalis* and *L. triqueter* were placed in the genus *Rhinesomus* by Matsuura (2003b) and McEachran and Fechhelm (2005). However, Klassen (1995) argued that *L. bicaudalis*, *L. triqueter*, and *L. trigonus* are nested in a single clade on the basis of his extensive osteological analysis; I agree with this. *Acanthostracion quadricornis* is common in the western Atlantic, but strays were recorded from waters off South Africa (Tyler 1965). Whitley (1965) described *Acanthostracion bucephalus* on the basis of a specimen from Queensland, Australia. However, there seems little doubt that it is actually *A. quadricornis* (Fig. 3). The record of *A. quadricornis* from Australia may suggest that the specimen was transferred by ballast water from a ship or released from an aquarium. As with the Balistidae, many checklists and illustrated guidebooks have provided a great deal of information on the taxonomy, distribution, and biology of boxfishes (see the section on the Balistidae). On the basis of the above overview, I recognize 22 species in the Ostraciidae (Table 6). However the relationships of *T. concatenatus* and *T. reipublicae* need to be examined in detail based on a comparison of a large selection of specimens including the types from various localities of the Indo-West Pacific to better understand the morphological variations observed in *T. reipublicae* (Fig. 4).

Triodontidae (Threetooth puffer, Fig. 1g)

The family Triodontidae is represented by a single extant species, *Triodon macropterus* Lesson 1831, but several fossil taxa referred to this genus date back to the Eocene (see Tyler and Patterson 1991). The family differs externally from others of the order Tetraodontiformes by the following combination of characters: body moderately elongate and moderately compressed, with a very large ventral flap that may be extended downward by a rotation of the long, shaft-like pelvis; jaws modified to form a beak of three heavy, massive teeth, two on the upper jaw and one on the lower jaw; two rudimentary dorsal-fin spines present or absent; and caudal fin deeply forked (Matsuura 2001).

Triodon macropterus is rare in museum collections and poorly known. It is a deep-water species collected at depths of 50–377 m (Kyushin et al. 1977; Matsuura and Tyler 1997). When Tyler (1967) redescribed *T. macropterus* in detail, only 20 specimens were available for his study: five from the Indian Ocean (Mauritius, Reunion and India) and 15 from the West Pacific (Indonesia, Philippines and

Fig. 4 Two forms of *Tetrosomus reipublicae* collected from the Ryukyu Islands (**a, b**) and Kochi, Japan (**c**). **a** Deep body with no blue lines (BSKU 29663); **b**, **c** slender body with wavy blue lines (**b** BSKU 29697; **c** BSKU 59588)



Japan). Due to the poor condition of two specimens, Tyler (1967) used 18 specimens to determine whether the first dorsal fin, composed of one or two spines, is present or absent. His examination revealed 12 specimens from the West Pacific to have a first dorsal fin, and five Indian Ocean specimens and a specimen from the West Pacific to lack a

Table 7 Presence or absence of first dorsal fin (two spines) in *Tridodon macropterus*. Tyler (1967) showed that a specimen (448.3 mm SL) collected from the Volcano Islands, south of the Ogasawara Islands, had a single spine

First dorsal fin		
	Present	Absent
Indian Ocean		9 + 5* = 14
West-Pacific	19 + 12* = 31	1*

* Data from Tyler (1967)

first dorsal fin (Table 7). However, he did not find other differences between the Indian Ocean specimens and those from the West Pacific. This led him to recognize the two groups as being conspecific. I have recently had the opportunity of examining 28 specimens of *T. macropterus*, nine from the Indian Ocean and 19 from the West Pacific (see Appendix). My examination revealed that the first dorsal fin to be absent in the nine specimens from the Indian Ocean, and present in the 19 specimens from the West Pacific (Table 7). Tyler (1967) also provided frequency distributions of fin-ray counts. My examination of 28 specimens produced almost the same frequency distributions of fin-ray counts as those of Tyler (1967), except for a count of 17 fin rays on the right side pectoral fin in a single specimen (Table 8).

Since Tyler's (1967) redescription was published, *T. macropterus* was reported (with color photographs) from several areas in the Indo-West Pacific: the Chagos

Table 8 Frequency distributions of fin-ray counts in *Triodon macropterus*. Counts of fin rays of damaged or abnormal fins are excluded. Counts of pectoral-fin rays were obtained from fins on both sides

Dorsal-fin rays				
	10	11	12	
This study	3	24	1	
Tyler (1967)	2	14	1	
Total	5	38	2	
Anal-fin rays				
	9	10		
This study	8	19		
Tyler (1967)	3	12		
Total	11	31		
Pectoral-fin rays				
	14	15	16	17
This study	1	12	41	1
Tyler (1967)	2	7	17	
Total	3	19	58	1

Archipelago (Kyushin et al. 1977), the South China Sea (Kyushin et al. 1982), the Kyushu-Palau Ridge (Okamura et al. 1985), the Timor Sea (Gloerfelt-Tarp and Kailola 1984), and the Japanese Archipelago (Matsuura 1984). Color photographs taken by research staff of the National Museum of Nature and Science show *T. macropterus* to have the following coloration: body yellowish brown dorsally, becoming white ventrally; ventral flap yellow in the ventral four-fifths and white in the proximal one-fifth; a large black ocellus with a narrow white edge in the proximal part of the ventral flap; second dorsal, anal, pectoral, and caudal fins yellow or yellowish brown; when present, membrane of first dorsal fin black (Fig. 1g). In addition to the above reports, *T. macropterus* has been recorded in checklists of fishes from several areas in the West Pacific: the Mariana Islands (Myers and Donaldson 2003), Tonga (Randall et al. 2004), off southern Taiwan (Shao et al. 2008), Northern Territory of Australia (Larson et al. 2013), and northern half of Australia (Hoese et al. 2006). Kim et al. (2005) provided a brief account and a color illustration of *T. macropterus* from Korea.

Johnson and Britz (2005b) reported the smallest known *T. macropterus* (20 mm SL), collected at Wallis and Futuna at a depth of 245–440 m. They provided detailed characters and the visceral anatomy of the early juvenile that differs from adults in having a huge head (45 % SL vs 28.5–32.7 % SL in adults), no ventral flap, and different scale structure. Juveniles also differ from adults in having a very large distended stomach.

Table 9 A list of 27 genera of the Tetraodontidae in the world

Genus	Number of species
<i>Amblyrhynchote</i> Bibron in Duméril 1855	1
<i>Arothron</i> Müller 1841	11
<i>Auriglobus</i> Kottelat 1999	5
<i>Canthigaster</i> Swainson 1839	36
<i>Carinotetraodon</i> Benl 1957	5
<i>Chelonodontops</i> Smith 1958	2
<i>Colomesus</i> Gill 1884	3
<i>Contusus</i> Whitley 1947	2
<i>Dichomyctere</i> Duméril 1855	6
<i>Ephippion</i> Bibron in Duméril 1855	1
<i>Feroxodon</i> Su, Hardy and Tyler 1986	1
<i>Guentheridia</i> Gilbert and Starks 1904	1
<i>Javichthys</i> Hardy 1985	1
<i>Lagocephalus</i> Swainson 1839	11
<i>Leiodon</i> Swainson 1839	1
<i>Marilyna</i> Hardy 1982a	3
<i>Omegophora</i> Whitley 1934	2
<i>Pao</i> Kottelat 2013	14
<i>Pelagocephalus</i> Tyler and Paxton 1979	2
<i>Polyspina</i> Hardy 1983a	1
<i>Reicheltia</i> Hardy 1982a	1
<i>Sphoeroides</i> Anonymous 1798	20
<i>Takifugu</i> Abe 1949c	25
<i>Tetractenos</i> Hardy 1983a	2
<i>Tetraodon</i> Linnaeus 1758	6
<i>Torquigener</i> Whitley 1930a	20
<i>Tylerius</i> Hardy 1984a	1
Total number of species	184

Tetraodontidae (Pufferfishes, Fig. 1h, Table 9)

Pufferfishes of the family Tetraodontidae usually occur in shallow warm, tropical seas, and freshwaters of the world, although some species may be found at depths over 350 m (Matsuura 1982; Tyler and Matsuura 1997). They differ externally from other families of the order Tetraodontiformes by the following combination of characters: head large and blunt; jaws modified to form a beak of four heavy, powerful teeth, two above and two below; eyes high on head; gill opening, a simple slit in front of pectoral fins; dorsal and anal fins located far posteriorly, containing seven to 15 soft rays; caudal fin truncate, rounded, or emarginate to somewhat lunate; pelvic fins absent; lateral line (when present) often indistinct, forming an interconnected pattern on sides of the head and body, but quite distinct in some genera (e.g., *Lagocephalus* and *Torquigener* Whitley 1930c); typical scales absent, but many spinules often present on back and/or belly, and sometimes on sides (Matsuura 2001).

The Tetraodontidae is the most speciose family in the Tetraodontiformes, including 184 species (Table 9). Because pufferfishes possess very few external characters useful for taxonomy and specimens are easily distorted when they are fixed in formalin and preserved in ethanol, it is often not easy for ichthyologists to recognize species limits and classify them into natural groups. Consequently, they have been poorly studied and taxonomic confusion remains. Although the Tetraodontidae has never been comprehensively reviewed, the taxonomy of pufferfishes has progressed since Fraser-Brunner's (1943) brief review of tetraodontid genera. He classified pufferfishes into 11 genera, *Canthigaster* Swainson 1839, *Lagocephalus*, *Sphoeroides* Anonymus 1798, *Amblyrhynchote* Bibron in Duméril 1855, *Torquigener*, *Colomesus* Gill 1884, *Ephippion* Bibron in Duméril 1855, *Tetraodon* Linnaeus 1758, *Arothron* Müller 1841, *Chonerhinos* Bleeker 1854, *Xenoptere* Bibron in Duméril 1855, based on osteological characters of the skull, the lateral-line system on the head and body, a skin fold on the ventrolateral side of the body, and spinule distributions on the body. Although Fraser-Brunner (1943) used the spellings *Amblyrhynchotes* and *Xenopterus*, I follow Kottelat's (2001, 2013) *Amblyrhynchote* and *Xenoptere* because Kottelat (2001) showed that *Amblyrhynchotes* and *Xenopterus* of Troschel (1856) are incorrect spellings.

When Alec Fraser-Brunner studied pufferfishes during World War II, Abe (1939, 1942, 1944, 1949a, b, c, 1950, 1952, 1954) independently studied pufferfishes found in Japan and adjacent regions. Abe (1949c) provided keys and accounts of pufferfishes in the seas around Japan. Subsequently, Abe (1952) proposed *Fugu* as a new genus to include five subgenera *Akamefugu*, *Higanfugu*, *Shosai-fugu*, *Takifugu*, and *Torafugu*, which had been previously proposed and made available by Abe (1949c, 1950). However, the genus *Fugu* is an objective synonym of the subgenus *Torafugu* Abe 1950, because the type species of these genus group names is *Tetraodon rubripes* Temminck and Schlegel 1850. Matsuura (1990) clarified the nomenclatural problems concerning the genus group names proposed by Abe (1949c, 1950, 1952) and showed that *Takifugu* Abe 1949c is the appropriate generic name for warmwater pufferfishes found mainly around Japan, Korea, and China. As with other tetraodontiform families, de Beaufort and Briggs (1962) lumped Fraser-Brunner's (1943) Indo-Pacific genera, *Amblyrhynchote*, *Lagocephalus*, and *Torquigener* into the genus *Sphoeroides* although they recognized *Canthigaster*, *Chelonodon* Müller 1841, *Chonerhinos*, and *Tetraodon*. As shown by subsequent authors, *Amblyrhynchote*, *Lagocephalus*, and *Torquigener* are distinctive genera.

Marine pufferfishes occurring in warm and tropical regions of the world were studied by many authors from the

1970s to present. Allen and Randall (1977) reviewed *Canthigaster* and described seven new species, bringing the total number of species to 22. Since Allen and Randall's (1977) revisionary study was published, six Indo-Pacific species have been described as new as follows: *Canthigaster leoparda* Lubbock and Allen 1979 from the Indo-West Pacific, *Canthigaster flavoreticulata* Matsuura 1986 from the Tonga Submarine Ridge, South Pacific, *Canthigaster cyanetron* Randall and Cea-Egaña 1989 from Easter Island, *Canthigaster punctata* Matsuura 1992 from the Mascarene Submarine Ridge in the western Indian Ocean, *Canthigaster cyanospilota* Randall, Williams and Rocha 2008 from the Red Sea, and *Canthigaster criobe* Williams, Delrieu-Trottin, Planes 2012 from the Gambier Archipelago in French Polynesia. In addition, Randall et al. (2008) reviewed *Canthigaster coronata* (Vaillant and Sauvage 1875) and recognized *Canthigaster axiologa* Whitley 1931 as a separate species. Although Allen and Randall (1977) synonymized *Canthigaster papua* (Bleeker 1848) with *Canthigaster solandri* (Richardson 1845), Randall (1995) and Allen and Erdman (2012) recognized it as a distinctive species. Moura and Castro (2002) reviewed *Canthigaster* in the Atlantic where many authors recognized only a single species *Canthigaster rostrata* (Bloch 1786). Moura and Castro (2002) extensively studied specimens collected from various localities from both sides of the Atlantic and recognized six species, three of which they described as new: *Canthigaster figueiredoi* from the east coast of South America, *Canthigaster jamestyleri* from the southeast coast of the United States and the Gulf of Mexico, and *Canthigaster supramaculata* from the west coast of Africa. The above studies bring the total number of species of *Canthigaster* to 36, making it the largest genus in the Tetraodontidae.

Shipp (1974) reviewed pufferfishes of the Atlantic belonging to *Canthigaster*, *Colomesus* Gill 1884, *Ephippion* Bibron in Duméril 1855, *Lagocephalus*, and *Sphoeroides*. Prior to Shipp's (1974) publication, Tyler (1964) reviewed two species of *Colomesus*, *Colomesus asellus* (Müller and Troschel 1848), and *Colomesus psittacus* (Bloch and Schneider 1801) in detail. Amaral et al. (2013) described *Colomesus tocantinensis* from the Tocantins River, Brazil. Shipp (1974) recognized 13 species of *Sphoeroides* in the Atlantic and provided a key to the species, along with detailed accounts of all Atlantic species. Walker and Bussing (1996) described the eastern Pacific *Sphoeroides lispus* Walker in Walker and Bussing 1996 and *Sphoeroides rosenblatti* Bussing in Walker and Bussing 1996 as new species. Prior to Shipp (1974) and Walker and Bussing (1996), five species of *Sphoeroides* had already been reported from the eastern Pacific. With 20 species, *Sphoeroides* is the third largest genus in the Tetraodontidae. Most species of *Sphoeroides* occur in shallow waters of the Atlantic and the eastern Pacific, but *Sphoeroides pachygaster* (Müller and

Troschel *in* Schomburgk 1848) is found in deep waters exceeding 350 m in all oceans.

Shipp (1974) also provided detailed accounts and photographs of *Lagocephalus laevigatus* (Linnaeus 1766) and *Lagocephalus lagocephalus* (Linnaeus 1758). The former is endemic to the Atlantic and the latter is distributed in tropical and other warm seas of the world. Abe and Tabeta (1983) described *Lagocephalus gloveri* as a new species from Japan. Abe et al. (1984) described another new species, *Lagocephalus wheeleri*, from Japan, but Matsuura (2010) showed it to be a junior synonym of *Lagocephalus spadiceus* (Richardson 1845). Matsuura et al. (2011) re-described *Lagocephalus guentheri* (Miranda Ribeiro 1915) based on an examination of the holotype and many specimens from the Red Sea. Although the genus *Lagocephalus* has not been comprehensively reviewed, an ongoing study by the author has revealed 11 valid species in the genus. This study will be published elsewhere.

Although Abe (1949a, b, c, 1950, 1952, 1954) made progress on the taxonomy of *Takifugu*, many species found along the coast of China were not included in his articles. Cheng et al. (1975) reviewed pufferfishes found in Chinese waters and described *Takifugu flavidus* (Li, Wang and Wang *in* Cheng et al. 1975) and *Takifugu reticularis* (Tian, Cheng and Wang *in* Cheng et al. 1975). Subsequently, Chinese authors described four species of *Takifugu* from China: *Takifugu orbimaculatus* Kuang, Li and Liang 1984 from a creek in Lianhuashan, Guangdong; *Takifugu coronoides* Ni and Li 1992 from an estuary of Chang Jiang; *Takifugu plagiocellatus* Li *in* Su and Li 2002 from the coast of Hainan Island; and *Takifugu variomaculatus* Li *in* Su and Li 2002 from brackish waters of Modaomen Zhuhai, Guangdong. These Chinese and Japanese authors increased the number of *Takifugu* species making it the second largest genus in the Tetraodontidae, with 25 species. However, taxonomic problems still remain in *Takifugu*, such as *Takifugu basilevskianus* (Basilevsky 1855) and *Takifugu pseudommus* (Chu 1935), which show significant variation in morphological features including ontogenetic color changes.

Benl (1957) described *Carinotetraodon chlupaty* as a new genus and species from Thailand. However, Dekkers (1975) synonymized *Carinotetraodon chlupaty* with *Carinotetraodon lorteti* (Tirant 1885), making that species the type of the genus. *Carinotetraodon* is similar to *Canthigaster* in having a laterally compressed body and several derived osteological features, as well as a shared derived behavioral peculiarity in their skin ridge-lifting along the midline of the body (Tyler 1978, 1980). Additional new species of *Carinotetraodon* were described: *Carinotetraodon salvator* Lim and Kottelat 1995 from Sarawak, *Carinotetraodon irrubesco* Tan 1999 from Sumatra, and *Carinotetraodon imitator* Britz and Kottelat 1999 from India.

Tyler and Paxton (1979) described *Pelagocephalus coheni* as a new genus and species based on a single specimen collected at Norfolk Island. *Pelagocephalus* is externally distinguished from other pufferfishes by its nasal apparatus in the form of an open, flat, and relatively unornamented disk. Heemstra and Smith (1981) described a second species of *Pelagocephalus*, *Pelagocephalus marki* from South Africa. Hardy (1982b) recorded *P. marki* from New Zealand.

In the period from 1980 to 1989, Graham S. Hardy published a series of papers on the taxonomy of pufferfishes that are distributed mainly in the Southern Hemisphere. Hardy (1980) reviewed the antitropical species *Arothron firmamentum* (Temminck and Schlegel 1850) indicating that it should be classified in *Arothron*, whereas it had previously been classified in *Boesemanichthys* by Abe (1952). The monotypic genus *Contusus* Whitley 1947 was reviewed by Hardy (1981), who described a second species *Contusus brevicaudus* restricted to southern Australia. Hardy and Hutchins (1981) recognized the validity of *Omegophora* Whitley 1934 with the description of *Omegophora cyanopunctata* from the southwestern part of Australia. Hardy (1982a) erected two new genera, *Marilyna* and *Reichelitia*, based on detailed morphological comparisons including skull osteology. Hardy (1983a) reviewed the Australian species of *Torquigener* and established two new generic names, *Polyspina* with one species and *Tetractenos* with two species. He recognized 12 species of *Torquigener*, including five new species from Australia. Hardy and Randall (1983) described *Torquigener flavomaculosus* as a new species from the Red Sea. Hardy described *Torquigener randalli* Hardy 1983b from the Hawaiian Islands and *Torquigener gloerfelti* Hardy 1984b from Indonesia. Hardy (1989) described *Torquigener balteus* as a new species from South Africa and provided a key to 19 species of *Torquigener*, although he overlooked *Sphoeroides marleyi* Fowler 1929, which is a member of *Torquigener*. My examination of the holotypes of *Torquigener balteus* and *S. marleyi* from South Africa revealed them to be conspecific, making the former a junior synonym of the latter. Matsuura (2014) recently described *Torquigener albomaculosus* as a new species from Amami-oshima Island, Ryukyu Islands. *Torquigener albomaculosus* is unique in building large spawning nests, called “mystery circles” by local SCUBA divers. Thus, the above studies of *Torquigener* bring the total number of species of *Torquigener* to 20, the co-equal third largest genus in the Tetraodontidae along with *Sphoeroides*. Hardy (1984a) recognized *Sphoeroides spinosissimus* Regan 1908 as being distinctive from other genera of the Tetraodontidae and established a new genus *Tylerius* for it. Hardy (1985) described *Javichthys kailolae* as a new genus and species from Indonesia. Su et al. (1986) established a new genus,

Feroxodon, for *Anchisomus multistriatus* Richardson 1854 from Australia.

The taxonomy of freshwater pufferfishes in Asia was in a confused state until Dekkers (1975) reviewed the genus *Tetraodon*. Subsequently, Sontirat and Soonthornsatit (1985) described *Tetraodon suvattii* as a new species from Thailand, and Roberts (1988) described *Tetraodon abei* as a new species from Laos. Roberts (1982) reviewed the genus *Chonerhinos* Bleeker 1854 and described three species from Borneo, *Chonerhinos amabilis*, *Chonerhinos nefastus*, and *Chonerhinos silus*. Still, complex nomenclatural problems involving *Chonerhinos* and *Xenoptere* remained until Kottelat (1999) proposed the new genus, *Auriglobus*, to rectify these problems. Kottelat (2013) discussed nomenclatural issues of the Tetraodontidae found in Southeast Asia in detail. He established the new genus *Pao* (type species, *Tetraodon leiurus* Bleeker 1850a) that includes 13 species previously placed in *Tetraodon* and *Monotretete*, but differentiated from other pufferfishes by their unique color pattern and a very elongate premaxillary pedicel that creates a greatly enlarged open space between their dorsomedial edges. Thus, the generic name *Tetraodon* is now applied to only six species of African freshwater pufferfishes. Kottelat (2013) also recognized *Leiodon* Swainson 1839 as a valid genus that includes *Tetrodon cutcutia* Hamilton 1822 distributed in freshwaters of southern Asia. Kottelat (2013) recognized *Dichotomyctere* Duméril 1855 for six species: *Dichotomyctere erythrotaenia* (Bleeker 1853), *Dichotomyctere fluviatilis* (Hamilton 1822), *Dichotomyctere kremamensis* (Inger 1953), *Dichotomyctere nigroviridis* (Marion de Procé 1822), *Dichotomyctere ocellatus* (Steindachner 1870), and *Dichotomyctere sabahensis* (Dekkers 1975). Saenjudaeng et al. (2013) described *Tetraodon palustris* as a new species from the Mekong basin of Thailand. Because of its publication date, July 2013, the authors were unaware of Kottelat's (2013) article proposing the genus *Pao*. However, it is clear from the original description of *Tetraodon palustris*, that it is a species of *Pao*, bringing the total number of species in that genus to 14.

Kottelat (2013) also commented on genera of marine pufferfishes. Although *Tetrodon patoca* Hamilton 1822 has long been placed in *Chelonodon* Müller 1841, Kottelat (2013) pointed out that *Tetrodon cutcutia* Hamilton 1822, the type species of *Chelonodon*, had been placed in the same genus as *Tetraodon fluviatilis* Hamilton 1822 and related species by Tyler (1980). Tyler (1980) called this group *Chelonodon* but Kottelat (2013) stated that the oldest available name for a genus including *Tetraodon fluviatilis* is *Dichotomyctere*. *Tetrodon patoca* and *Tetraodon fluviatilis* have a sufficient number of character differences to warrant being placed in separate genera. The type species of *Chelonodontops* Smith 1958 is *Chelonodontops pulchellus* Smith 1958, a junior synonym of *Chelonodon*

pleurospilus (Regan 1919) and congeneric with *Tetraodon patoca* (see Smith 1986). Thus, *Tetraodon patoca* is a species of *Chelonodontops* (Kottelat 2013). Matsuura (2002) reviewed two species of *Chelonodon*, *Chelonodon laticeps* Smith 1948, and *Chelonodon patoca*, both of which belong in *Chelonodontops*. Kottelat (2013) showed that *Gastrophysus* Müller 1843 is an objective synonym of *Takifugu* Abe 1949, as the type species of both genus group names is *Tetrodon oblongus* Bloch 1786. However, this is likely to cause confusion not only in pufferfish taxonomy, but also in the fisheries of East Asia where pufferfishes are treated as important and expensive fishes (e.g., several species of *Takifugu* cost about US\$100 per kilogram at fish markets). In addition, because pufferfishes have fatal poison in their viscera, scientific names are very important for food security management in East Asia. As suggested by Kottelat (2013), *Gastrophysus* can be suppressed under the International Code of Zoological Nomenclature (ICZN 1999). I will ask the International Commission on Zoological Nomenclature to suppress *Gastrophysus*.

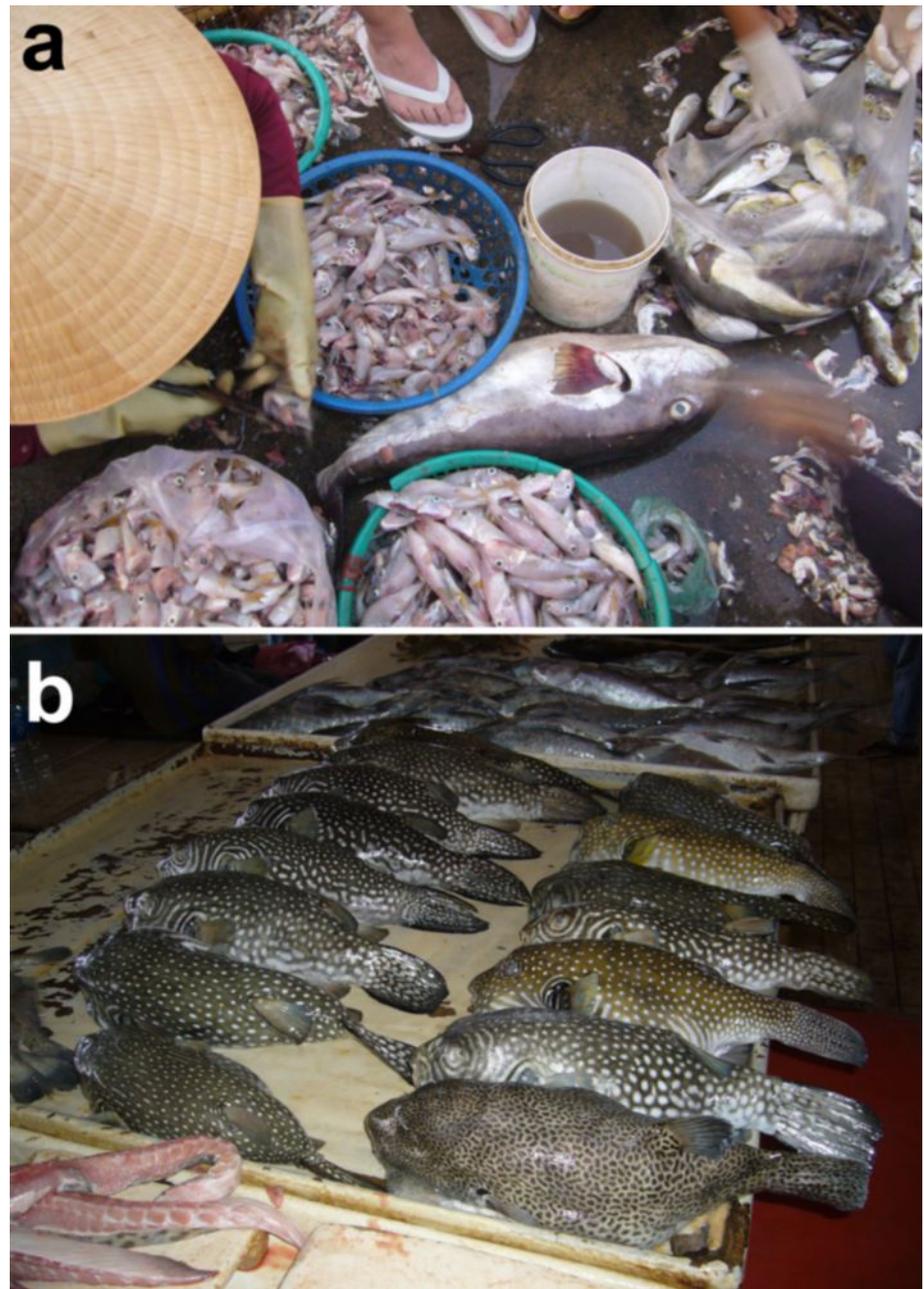
Matsuura and Okuno (1991) redescribed a rare pufferfish, *Arothron carduus* (Cantor 1849), on the basis of the holotype from Penang and two additional specimens from the West Pacific. Matsuura (1994) described *Arothron caeruleopunctatus* as a new species from the tropical region of the Indo-West Pacific. Matsuura (1999) briefly reviewed *Arothron* with a key to species and accounts of all members of the genus including two undescribed species.

As indicated above, there has been a great deal of progress in taxonomy of the Tetraodontidae during the past several decades, especially in the period from the mid-1970s to the present. However, there remain taxonomic problems in genera such as *Arothron*, *Chelonodontops*, *Lagocephalus*, *Pao*, *Takifugu*, and *Torquigener* where many species await description and detailed morphological and molecular comparisons to classify them into appropriate groups. The taxonomy of pufferfishes in Southeast Asia is important not only for the understanding of fish diversity of the region, but also for the welfare and food management for humans. Dao et al. (2012) reported that the number of victims of food poisoning by eating pufferfishes reached 737, with 127 mortalities from 1999 to 2003. Due to the lack of knowledge about pufferfishes and their toxicity, pufferfishes are still found in Southeast Asian fish markets (Fig. 5), although local and state governments in countries around the South China Sea have prohibited the sale of pufferfishes for food.

Diodontidae (Porcupinefishes, Fig. 1i)

Many species of the family Diodontidae are benthic inhabitants around coral or rocky reefs, but some occur

Fig. 5 Pufferfishes found in a fish landing place 60 km north of Nha Trang in southern Vietnam (**a**) and a fish market in Sabah, Malaysia (**b**): **a** many small pufferfishes of *Lagocephalus* and a large specimen of *L. inermis* in the center; **b** large specimens of *Arothron hispidus*, *A. reticularis*, and *A. stellatus*



frequently in seagrass beds and on sand or mud bottom to depths of 150 m, with one species being found in pelagic waters. They differ externally from other families of the order Tetraodontiformes by the following combination of characters: body wide and capable of great inflation, covered with massive spines, which may be quite long; spines with large bases or roots, which are beneath the skin; long spines that are usually erectile and double-rooted, or short spines fixed in an erect position by their triple-rooted bases; head broad and blunt; nasal organ usually appearing as small tentacles located in front of the large eyes; mouth large, wide, and terminal, teeth fused to

form a strong, beak-like crushing structure without a median suture dividing the upper and lower jaws into left and right halves; gill opening, a relatively small, vertical slit immediately preceding the pectoral-fin base; short-based dorsal and anal fins with soft rays, set far back on body, and like caudal fin, generally rounded; most fin rays branched; bases of fins often thick and fleshy; no pelvic fins (Leis 2001).

Porcupinefishes were well studied by Leis (1978, 1986, 2001, 2003, 2006). Leis (1978) reviewed *Diodon* Linnaeus 1758 and provided detailed accounts of five species: *Diodon eydouxi* Brisout de Barneville 1846, *Diodon*

holocanthus Linnaeus 1758, *Diodon hystrix* Linnaeus 1758, *Diodon liturosus* Shaw 1804, and *Diodon niche-merus* 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

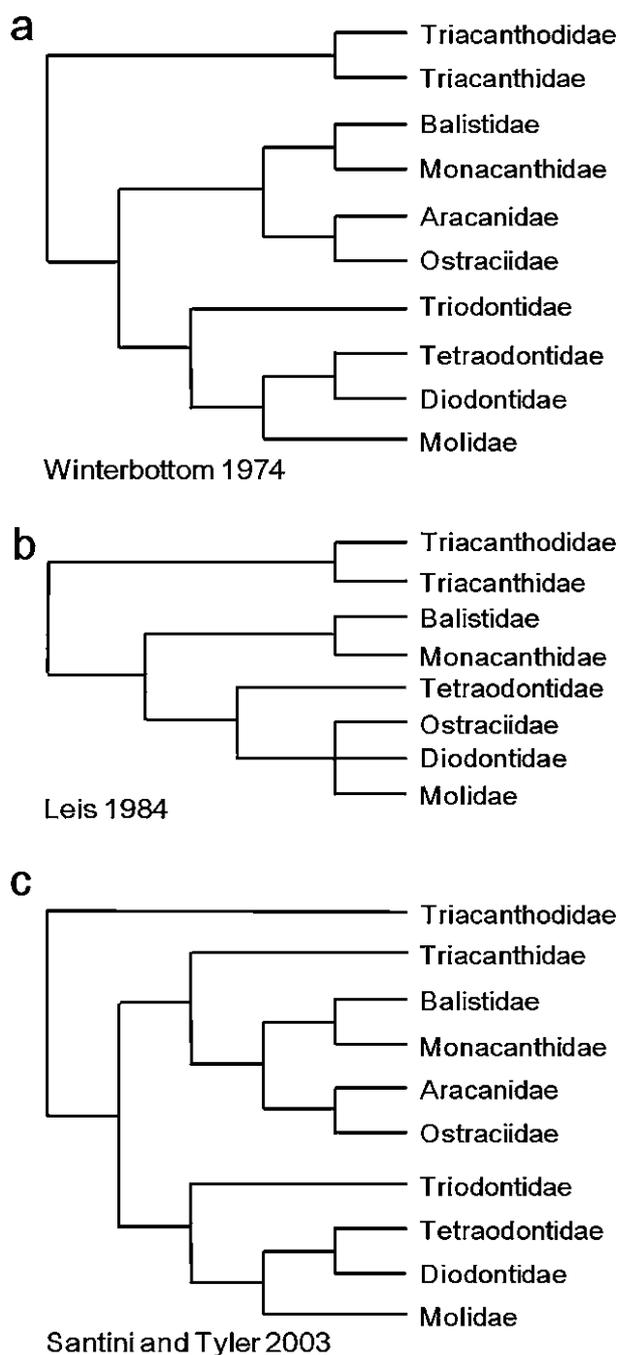


Fig. 7 Phylogenetic relationships of the extant families of Tetraodontiformes inferred from cladistic analyses of morphological characters. **a** Winterbottom 1974; **b** Leis 1984 (larvae of the Aracanidae and Triodontidae not available for Leis); **c** Santini and Tyler 2003

(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 (Aracanidae 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) + (Aracanidae + 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 supramedullary 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 Aracnidae + Ostraciidae, treating them as subfamilies. Alfaro et al. (2007) placed the Molidae as the basal sister group to Triodontidae + (Aracnidae + 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 Aracnidae 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, Aracnidae + 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, Aracnidae, 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

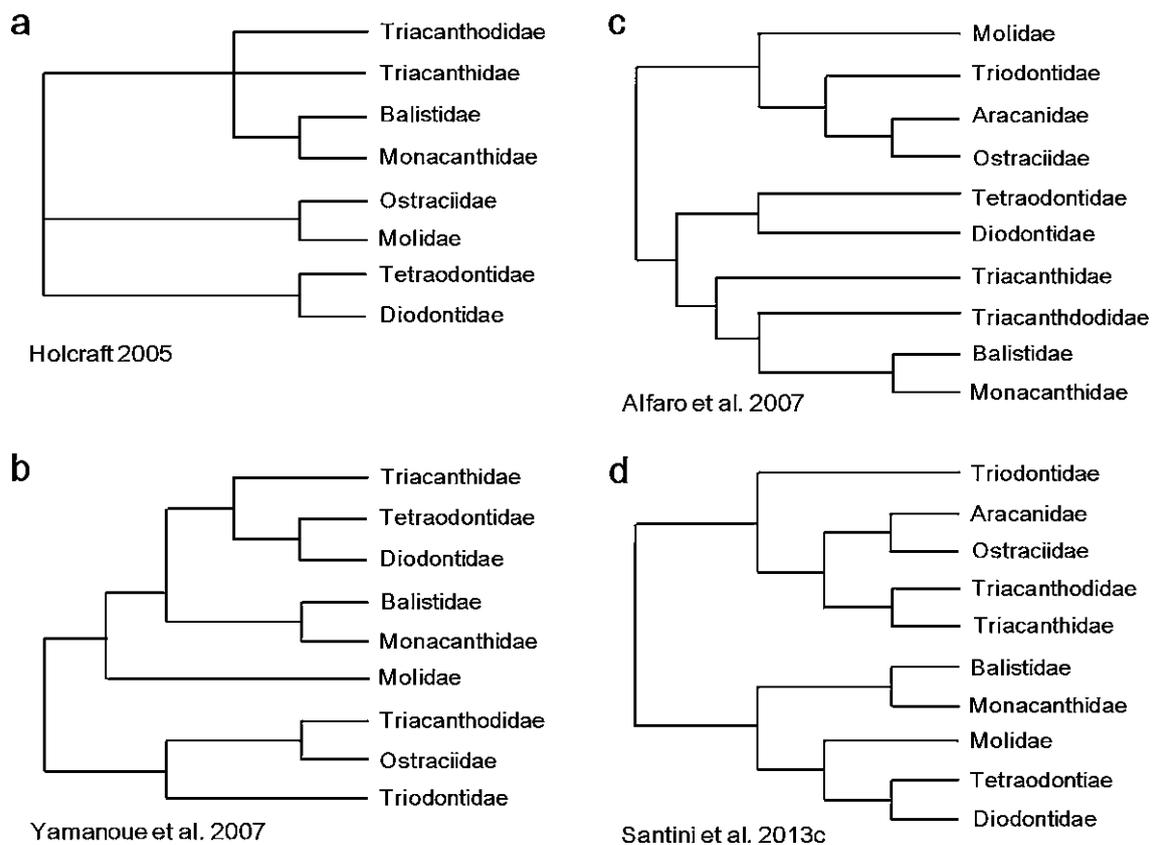


Fig. 8 Phylogenetic relationships of the Tetraodontiformes inferred from molecular analyses. **a** Holcroft 2005; **b** Alfaro et al. 2007; **c** Yamanoue et al. 2007; **d** Santini et al. 2013c. The Triodontidae was not included in Holcroft (2005), and the Ostraciidae of Holcroft

(2005) and Yamanoue et al. (2007) included two subfamilies the Aracanineae 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* Mitchell 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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