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REGULAR PAPER

Life history, distribution and molecular phylogenetics of the Upward-Mouth Spikefish *Atrophacanthus japonicus* (Teleostei: Tetraodontiformes: Triacanthodidae)

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Ninety-six juvenile specimens (37–54 mm standard length; L_S) of the rarely collected Upward-Mouth Spikefish *Atrophacanthus japonicus* (Triacanthodidae) were obtained from the stomachs of three Yellowfin Tuna *Thunnus albacares* collected off Guam in the Mariana Islands in the central Pacific Ocean. These specimens extend the range of *A. japonicus* eastward into Oceania. We review the systematic characters of the monotypic genus *Atrophacanthus* and present colour photographs of freshly collected specimens. The diet of the juvenile specimens of *A. japonicus* consisted of thecosome pteropods and foraminiferans. We present a range map of *A. japonicus* based on all known specimens and show that specimen size is related to whether specimens were collected in the pelagic zone or on the bottom. Our results support that, compared to all other Triacanthodidae, *A. japonicus* has an unusually extended pelagic larval and juvenile period, up to 54 mm L_S, before settling to the bottom as adults. Lastly, we provide a multilocus phylogeny addressing the phylogenetic placement of *Atrophacanthus* based on eight of 11 triacanthodid genera and six genetic markers. Our results reveal that *Atrophacanthus* is the sister group of *Macrorhamphosodes* and they provide new insights about the evolutionary history of the family.

KEYWORDS
Atrophacanthus japonicus, biogeography, Guam, Mariana Islands, Oceania, systematics

1 | INTRODUCTION

The rarely collected Upward-Mouth Spikefish *Atrophacanthus japonicus* (Kamohara 1941) is the only species of its triacanthodid spikefish genus. Unlike all other triacanthodids, which settle into benthic habitats at small sizes, larval and juvenile *A. japonicus* have longer pelagic periods (Tyler, 1968). Most known specimens are larval or juvenile stages that were collected pelagically by the *Dana* Expedition in the early 1900s and only six benthic adult specimens are known. Herein, we report on 96 new juvenile specimens collected from the stomachs of three Yellowfin Tuna *Thunnus albacares* (Bonnaterre 1788) caught off Guam in the western Pacific Ocean. We provide a review of the systematic characters of the genus, diet data, colour photographs of the fresh new specimens from Guam and a distribution map based on all known specimens. We also present a molecular phylogeny of the eight genera of Triacanthodidae for which genetic data presently is available.

2 | MATERIALS AND METHODS

2.1 | Collection and curation of new specimens from Guam

Ninety-six juvenile specimens of *A. japonicus* were collected off Guam, Mariana Islands (Figure 1). The specimens were taken from the stomachs of three *T. albacares* weighing 12.2 to 20.4 kg. The *T. albacares* were caught by trolling surface lures from the F.V. *Stonefish* (Captains

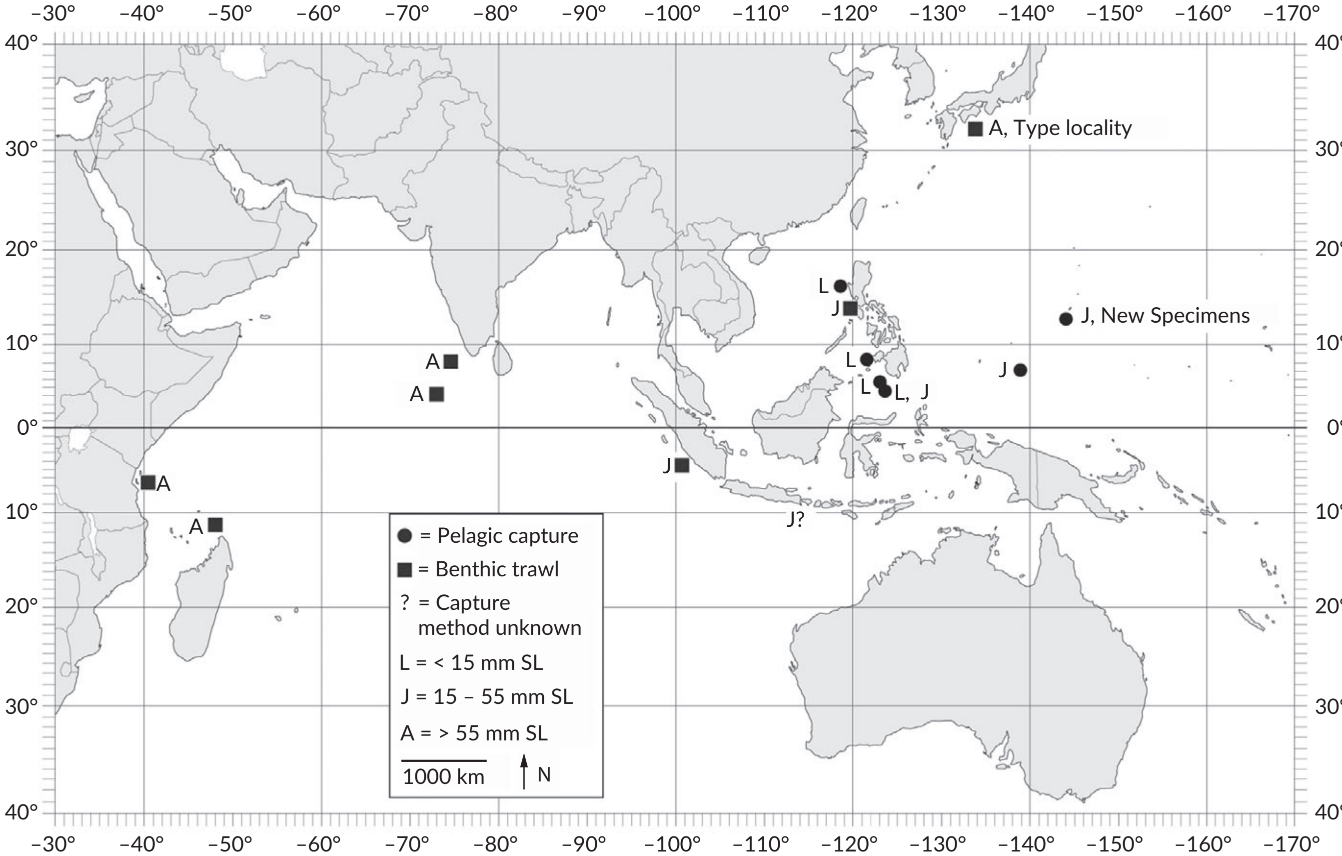

FIGURE 1 Map showing distribution of examined specimens of *Atrophacanthus japonicus* in this study and Tyler (1968, 1970a). L = Larvae, J = Juveniles, A = Adult. Most larvae and juveniles were collected in the pelagic zone, whereas adults were collected using benthic gear. The new specimens collected off Guam represent the most eastward occurrence of *A. japonicus*. All lengths standard length

James and Ken Borja) about 2.4 km offshore from the southeast coast of Guam at 13° 12.829′ N, 144° 43.178′ E, depth *c.* 850 m on 16 April 2016.

Many of the specimens from the *T. albacares* stomachs were in relatively good condition and were photographed on the deck worktable (Figure 2) before the specimens were frozen aboard the ship. During freezing, the specimens became crowded together in a bundle, whereupon many of the slender dorsal and pelvic spines were broken and fin rays and regions of the bodies became distorted in alignment. The frozen fish were sent to the Division of Fishes, National Museum of Natural History, Smithsonian Institution, by B. Mundy, NOAA National Marine Fisheries Service, Hawaii, and his cooperating colleagues, the Captains J. and K. Borja and K. Kawamoto, M. Mitsuyasu, E. Cruz, C. Tam and R. Humphreys. The specimens were thawed and preserved in 95% ethanol by D. Pitassy. Eighteen specimens (38–54 mm standard length; L_S) in relatively good condition were selected for individual cataloguing (USNM 440413–440430) as vouchers for tissue samples. These 18 voucher specimens were individually radiographed by S. Raredon. The remaining 78 specimens (37–50 mm L_S) were placed in one jar as a lot catalogued as USNM 440431. All specimens were stored in 95% ethanol.

We recorded meristic and morphological data for the 18 individually catalogued voucher specimens from Guam to compare with the large dataset presented in Tyler (1968) for *A. japonicus* (larval, juvenile and adults), with emphasis on diagnostic features. We report L_S for

FIGURE 2 (a) Anterior right and (b) Anterior left views of *Atrophacanthus japonicus* from the stomachs of three *Thunnus albacares* caught near the surface 2.4 km off the southeast coast of Guam (13° 12.829′ N, 144°, 43.178′ E) in about 850 m of water on 16 April 2016. Specimens are unspecified individuals photographed on the deck of the F.V. *Stonefish* and catalogued among USNM 440413–440431

the Guam specimens rounded to the nearest millimetre because many specimens sustained length distortion and other damage.

2.2 | Stomach contents of new specimens from Guam

Stomach contents were initially surveyed for the 18 individually catalogued specimens (USNM 440413–440430) using radiographs. We removed the stomach contents from four of these specimens (USNM 440413, USNM 440416, USNM 440418 and USNM 440419) for study under a dissecting microscope to confirm initial identifications made from the radiographs.

2.3 | Other material

Institutional abbreviations follow Sabaj (2016). In addition to the new specimens from Guam, we studied 10 specimens of *A. japonicus* from the ANSP, BMNH, MNHN and USNM collected since Tyler (1968). This material included juveniles and adults (Figure 3). The localities of all records of *A. japonicus* are summarized in Figure 1.

2.4 | Tissue samples and DNA extractions

Tissue samples were collected from two of the new specimens of *A. japonicus* (USNM 440413 and USNM 440414). DNA was extracted using the DNeasy tissue kit (Qiagen; www.qiagen.com) according to the manufacturer's protocol. Double-stranded DNA was synthesized *via* PCR using universal primers for the mitochondrial *16 s* subunit (Kocher *et al*., 1989) marker. The PCR products were electrophoresed in 1.5% low-melting-point agarose gels using a Tris-acetate buffer for

FIGURE 3 (a) Alcohol preserved and (b) Radiograph of adult *Atrophacanthus japonicus* ANSP 103654, 88.0 mm standard length, collected in a benthic trawl off the coast of Tanzania (06° 48′ S, 39° 51′ E), bottom depth 300–400 m, by the R.V. *Anton Bruun* on 20 November 1964

quality control and submitted for purification and sequencing in both directions to the sequencing and genomics facility of the University of Puerto Rico (www.sgf.hpcf.upr.edu). Sequences were assembled and aligned manually with Geneious 10.0.9 (www.geneious.com).

2.5 | Taxon sampling and phylogenetic methods

Molecular data were newly generated only for *A. japonicus*. Additional sequence data for 224 tetraodontiform species were retrieved from the National Center for Biotechnology Information (NCBI) database, including nine of the 24 valid species of Triacanthodidae. Valid species of triacanthodids are summarized in Matsuura (2015: table 1), except that there are only 23 species in that table because *Mephisto albomaculosus* Matsuura, Psomadakis & Than Tun 2018 was described subsequently by Matsuura *et al*. (2018). One taxon included, *Triacanthodes* sp., presumably is one of the two species of this genus not included in our dataset; *i.e.*, *Triacanthodes indicus* Matsuura 1982 or *Triacanthodes intermedius* Matsuura & Fourmanoir 1984. Our dataset includes eight of the 11 valid genera in Triacanthodidae (all except *Hollardia* Poey 1861, *Johnsonina* Myers 1934 and *Mephisto* Tyler 1966). Six genetic markers were examined: two mitochondrial genes (*coI* and *16 s*) and four nuclear markers (ENC1, GLYT, MYH6 and PLAGL2). The data for each species and marker are summarised in Supporting Information Table S1. We analysed the concatenated dataset using maximum likelihood (ML) in RAxML 8.2.10 (Stamatakis, 2006) partitioning by codon position and selecting the best tree inferred from 10 independent replicates generated by the GTRGAMMA model. We assessed branch support using 1000 replicates using RAxML's rapid bootstrapping algorithm, with the collection of sample trees used to draw the bipartition frequencies on the optimal tree. We performed all RAxML analyses using CIPRES portal 3.3. Sequence data produced by this study are deposited in GenBank (MH796904).

3 | RESULTS

3.1 | Synonomy

Atrophacanthus japonicus (Kamohara 1941)
Ukeguchi-kawamuki (Japanese name)
Upward-Mouth Spikefish (new English name based upon that of Kamohara, 1941)

Tydemania japonica Kamohara, 1941: p. 166 (original description; Japanese name: Ukeguchi-kawamuki; type locality: Kochi Prefecture, Shikoku, Japan, on the bottom at > 100 fathoms (c. 183 m); illustration). Kamohara, 1952: p. 60 (description; illustration; type locality given as Mimase (Kochi Prefecture)). Tomiyama and Abe, 1958: p. 30 (description; colour illustration; Kochi Prefecture).

Atrophacanthus danae Fraser-Brunner, 1950: p. 3 (original description; type species of *Atrophacanthus*; illustration; type localities: several *Dana* stations in the Celebes Sea, bathypelagic nets between 600 and 5000 m of wire out over depths of 2160–4950 m). de Beaufort and Briggs, 1962: pp. 262, 266–268 (included in key; illustrations and description after Fraser-Brunner, 1950). George and Dayanandan, 1966: pp. 220-221 (description and illustration of

CMFRI-F.179/497, 98 mm total length (L_T), caught in bottom trawl off southwest coast of India). Murty, 1969: p. 34 (listing of CMFRI-F.179/497 at Central Marine Fisheries Institute, India).

***Astrophacanthus* [sic] *japonicus*.** Kamohara, 1958: p. 51 (listed with *danae* as synonym; Kochi Prefecture, Japan to Celebes). Kamohara, 1961: p. 5 (synonymy; references; type destroyed and no other specimens available for neotype designation). Kamohara, 1964: p. 67 (listed with *danae* as synonym; illustration; Kochi Prefecture to Celebes).

***Atrophacanthus japonicus*.** Tyler, 1968: pp. 163–175 (synonymy; description; illustration; photograph; drawing of lateral view of entire skeleton; discussion of relationships; discussion and figure about depth range). Tyler, 1970a: p. 3 (description of an adult specimen from a bottom trawl in Arabian Sea off India (CMFRI-F.179/497) and of four juvenile specimens from 07° 00′ N, 139° 56′ E). Tyler, 1970b: pp. 8-9, 43 (description and illustration of caudal skeleton). Tyler, 1980: pp. 70–72 (illustration of bones of head; discussion of relationships condensed from Tyler, 1968). Aboussouan and Leis, 1984: pp. 452–454, fig. 247 (eggs unknown; larvae probably unpigmented; composite illustration of specimens 2.6–2.7 mm L_T). Gloerfelt-Tarp and Kailola, 1984: pp. 281 (colour photo and description of 48 mm standard length (L_S) specimen, USNM 265190, from Sumatra, Indonesia). Matsuura, 1984: p. 357 (listed; illustration; distribution from Kochi Prefecture to Philippines, Celebes Sea, and east coast of Africa). Tyler, 1986: p. 887 (description; distribution includes Tanzania). Adam et al., 1998: p. 16 (62 mm L_T specimen, BMNH 1996.9.25.1, from the Maldive Islands, 04° 05′ N, 73° 20′ E). Matsuura, 2000: p. 647 (listed; South China Sea). Shinohara et al., 2001: p. 337 (listed; Tosa Bay, Japan (off Kochi Prefecture, near type locality); Japanese name: Ukeguchi-kawamuki). Bijukumar and Deepthi, 2009: p. 153 (caught in trawl bycatch off Kerala, India; size range of specimens of *A. japonicus* 54–97 mm L_T). Konstantinidis and Johnson, 2012a: pp. 98–114, fig. 3C–F (photographs of cleared and stained specimens and descriptions of caudal skeleton in three specimens, 14.5 mm, 18 mm and 58 mm L_S). Konstantinidis and Johnson, 2012: pp. 351–366, fig. 1C, D (photographs of cleared and stained specimens and descriptions of jaw and suspensorium of two specimens, 18 mm and 58 mm L_S). Matsuura, 2015: pp. 74–76 (valid species; distribution given as off Tanzania, Maldive Islands, Japan and Celebes Sea).

3.2 | Colouration of new specimens from Guam

The new specimens of *A. japonicus* from Guam have pinkish red bodies except for strong silvery overtones in the abdominal region and lower half of the head, beginning at about the middle of the eye and continuing ventrally (Figure 2). In alcohol, the new specimens are uniformly light in colour except for the webbing between the first, second and third dorsal-fin spines, where there are small dark spots (not visible in Figure 3).

3.3 | Diagnostic features of new specimens from Guam

The following 12 features are diagnostic for *A. japonicus* and present in the new specimens from Guam. Average values for the 18 individually catalogued specimens from Guam are given in parentheses where applicable: (1) only the first three dorsal-fin spines well developed and prominently exposed, with the fourth spine much shorter than the first three but frequently exposed and easily seen externally and the fifth and sixth spines reduced in size and barely protruding to the surface or not protruding at all; (2) first dorsal-fin spine relatively short, not reaching much beyond fourth spine when depressed; (3) dorsal-fin rays 13 or 14 (14.0); (4) anal-fin rays 11–13 (12.8); (5) pectoral-fin rays 13–15 (14.0); (6) a single, short pelvic-fin ray protruding to the exterior just behind the locking flange on the posterior region of the pelvic-fin-spine base (single, short pelvic ray present); (7) short conical teeth in a single row, 19–23 in upper jaw and 22–27 in lower jaw (short conical teeth in a single row, 22 in upper jaw and 24 in lower jaw); (8) profile of head straight; (9) mouth distinctly supraterminal; (10) snout short, about equal to or somewhat longer than the postorbital distance, snout length 9.4%–12% L_S (10.9% L_S); (11) gill opening moderately long, usually extending down about one-half to four-fifths of the pectoral-fin base, gill-opening length 6.1%–8.0% L_S (7.2% L_S); and (12) pelvis narrow, basin-like, being flat ventrally with low dorsally upturned lateral edges, usually about five times in pelvic length, width into length 4.6–5.7 times (5.1 times).

3.4 | Diet

The stomach contents of the new juvenile specimens from Guam contained predominantly two species of pelagic thecosome pteropods and undetermined species of foraminiferans. Among the 18 radiographed specimens, only one individual had an empty stomach, whereas one individual had more than 40 pelagic thecosome pteropods and foraminiferans in its stomach and intestine (Figure 4).

3.5 | Molecular phylogeny

Our analysis (Figure 5) suggests that there are three major lineages among triacanthodids: (1) a clade composed of *Parahollardia* Fraser-Brunner 1941; (2) a clade including *Halimochirurgus* Alcock 1899, *Tydemania* Weber 1913, *Paratriacanthodes* Fowler 1934 and

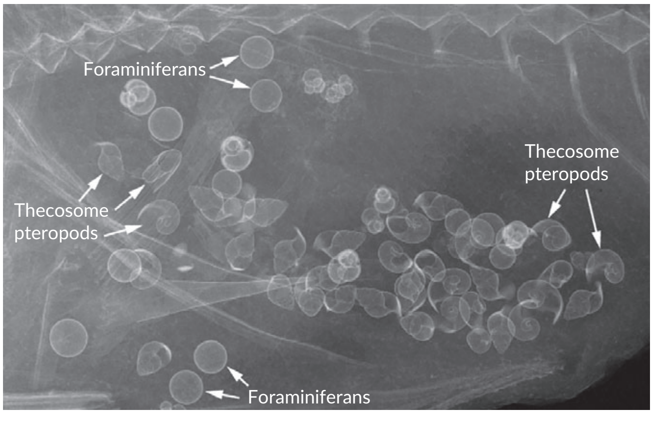

FIGURE 4 Radiograph of the gut of *Atrophacanthus japonicus* USNM 440416, containing more than 40 pelagic thecosome pteropods and foraminiferans

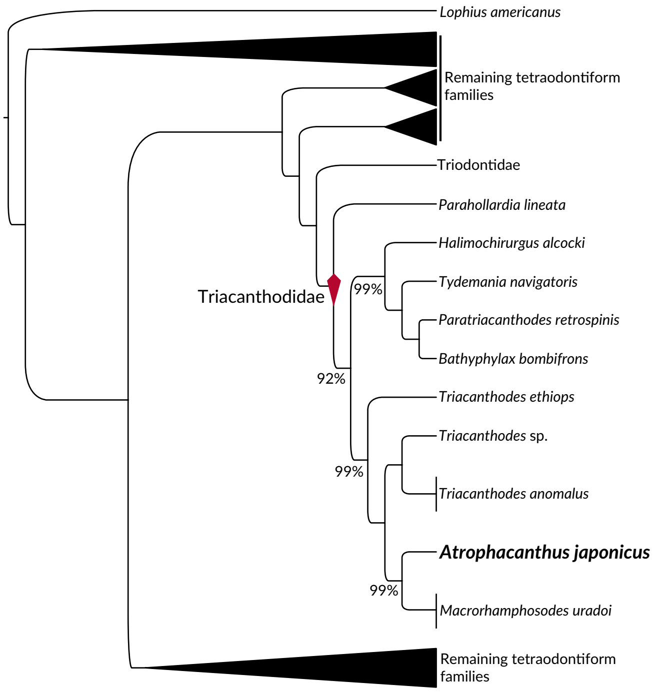

FIGURE 5 Molecular phylogenetic relationships among genera of Triacanthodidae for which tissue samples are available (no tissue samples available for *Hollardia*, *Mephisto*, and *Johnsonina*)

Bathyphylax Myers 1934; and (3) a clade including *Triacanthodes* Bleeker 1857, *Atrophacanthus* and *Macrorhamphosodes* Fowler 1934. Of the 10 triacanthodid species (including *Triacanthodes* sp.) included in this analysis, *A. japonicus* is most closely related to *Macrorhamphosodes uradoi* (Kamohara 1933).

4 | DISCUSSION

4.1 | Distribution

The new specimens from Guam are conspecific with *A. japonicus* from Japan, Indonesia, the Philippines (Celebes Sea), Maldives, India and East Africa (Figure 1; for locality records see: Adam *et al*., 1998; Matsuura, 1984, 2000, 2015; Murty, 1969; Shinohara *et al*., 2001; Tyler, 1968, 1970a). The specimens of *A. japonicus* from Guam represent a range extension eastward into Oceania from a station sampled by the R.V. *Vityaz* between the Caroline Islands and New Guinea (7° 00′ N, 139° 56′E (Tyler, 1970a: p. 3).

4.2 | Depth records of life stages

Atrophacanthus japonicus has been collected infrequently but occasionally in large numbers and more than 250 specimens are now available. Larval and juvenile stages (≤ *c.* 55 mm L_S) are bathy and mesopelagic and have been collected at depths of c. 200–2500 m (Tyler, 1968: p. 171); *n.b.*, depth provided is depth collected in water column, not bottom depth. Juvenile stages have twice been taken in relatively large numbers: (1) in the fine mesh nets of many stations of the *Dana* Expedition in the Celebes Sea, with one station (3739 VI) obtaining 145 specimens (Tyler, 1968: p. 174); and (2) the new 96 specimens from the stomachs of three *Thunnus albacares* (Bonnaterre 1788) off Guam that we describe herein. Based upon *Dana* Expedition material, Fraser-Brunner (1950) noted that the majority of *A. japonicus* were collected in water with a bottom depth of 4000 m and no specimens were collected in water less than 2000 m deep; however, none of the *A. japonicus* studied by Fraser-Brunner were adults. Only six adult specimens of *A. japonicus* (*c.* 60 mm to 117.2 mm L_S) are known; all were collected from benthic bottom trawls at relatively shallower depths of 121–491 m (all collected as single individuals except the holotype and paratype of *Tydemania japonica* (Kamohara 1941), which were collected together). Juveniles that have been collected benthically range from 46.9 to 54.9 mm L_S, so while there is some variation in the size at which *A. japonicus* settle, only large juveniles have been collected benthically. This suggests that larvae and juveniles have an extended pelagic period over deep water and subsequently settle as young adults into shallower benthic shelf and slope habitats.

We interpret that the juvenile specimens of *A. japonicus* from the *T. albacares* stomachs had been ingested recently because of their bright coloration and only superficial digestion. *Thunnus albacares* usually feed in the top 100 m of the water column, so it is likely that they encountered the specimens of *A. japonicus* in the pelagic zone; however, *T. albacares* are known to dive occasionally to > 1000 m (Schaefer *et al*., 2007), so it is possible, albeit unlikely, that the new specimens had settled into benthic habitats when the *T. albacares* ate them. We emphasize that the gut contents of the specimens of *A. japonicus* from Guam contained prey that included pelagic taxa (two species of thecosome pteropods and undetermined foraminiferans). These observations strongly suggest to us that the *T. albacares* ingested these large juvenile *A. japonicus* in the pelagic environment. Fraser-Brunner (1950) reported a similar diet for the *A. japonicus* he studied (pteropods and foraminiferans, as well as ostracods and *Sagitta* spp.) that were collected in the water column by the *Dana* Expedition.

4.3 | Other Triacanthodidae known from the Mariana Islands

Two other species of triacanthodids are known from the Mariana Islands: *Halimochirurgus alcocki* Weber 1913 (Myers, 1988; Myers & Donaldson, 2003; Tenorio, 2014) and, based upon underwater photographs taken aboard the NOAA R.V. *Okeanos Explorer*, *Hollardia* cf. *goslinei* Tyler 1968 also occurs in the region. The photographs show *H.* cf. *goslinei* feeding on the bottom at depths of 359–525 m on the Zealandia Bank of the Marianas on 21, 22 April and 3 May 2016 (photographs available through NOAA Office of Ocean Exploration and Research (OER), 2016 Deepwater Exploration of the Marianas: D2-EX1605-L1, images 01–01:51:17, 02–00:47:53, 12–00:22:48 and 12–00:23:36. Four photographs taken at locations between 12° 43′ 57" N to 16° 54′ 06" N and 144° 16′ 21" E to 145° 53′ 53" E). R.V. *Okeanos Explorer* subsequently photographed another individual of *H.* cf. *goslinei* on the bottom at 448 m on 13 August 2016 off Wake Island (see NOAA OER Deepwater Wonders of Wake: Exploring the Pacific Remote Islands Marine National Monument: D2-EX1606-11, image 03:00:31. The photo was taken at 19° 17′ 21.0" N, 166° 39′

55.5" E). *Hollardia goslinei* is known from nine specimens and *in situ* observations from the Hawaiian Archipelago (Chave & Malahoff, 1998; Chave & Mundy, 1994; Matsuura, 2015), as well as several other Pacific localities where R.V. *Okeanos Explorer* has observed them.

4.4 | Phylogenetic placement

Morphological studies have proposed that *Atrophacanthus* and a clade containing *Bathyphylax* + *Halimochirurgus* and another including *Tydemania* + *Macrorhamphosodes* were related lineages derived from a *Paratriacanthodes*-like clade (Tyler, 1968, 1980). Our molecular analysis supports three major clades among triacanthodids: (1) a clade composed of *Parahollardia*; (2) a clade including *Halimochirurgus*, *Tydemania*, *Paratriacanthodes* and *Bathyphylax*; and (3) a clade including *Triacanthodes*, *Atrophacanthus and Macrorhamphosodes* (Figure 5). The close relationship of *Atrophacanthus* and *Macrorhamphosodes* is contrary to the interpretation of Tyler (1968: pp. 164–166) and Tyler (1980: p. 70), in which *Tydemania* was thought to have the closest relationship to *Macrorhamphosodes*, but those studies were based only on osteological features. We do not attempt to resolve that issue herein because further taxonomic and genetic sampling are needed to obtain a better understanding of the relationships among triacanthodid genera. We note that the support evidenced in our molecular phylogeny clearly challenges the non-cladistic conclusions of Tyler (1968, 1980) concerning these genera of triacanthodids.

To date, neither a cladistically based morphological analysis nor a comprehensive molecular phylogenetic analysis has assessed the relationships within the Triacanthodidae. The deep habitats of Triacanthodidae (continental shelf, slope and mesopelagic for juveniles of *A. japonicus*), comparatively infrequent collection and relatively low number of specimens available for study have challenged such research. Our ML analysis provides strong support for the sister-group relationship of *Atrophacanthus* and *Macrorhamphosodes* (bootstrap support = 99%), but we still lack DNA sequence data for three genera considered to be among the earliest branching lineages (*Hollardia*, 3 species; *Mephisto*, 2 species; and the monotypic *Johnsonina*; Tyler, 1968, 1980).

Our molecular results imply two independent origins of elongated snouts within triacanthodids (*Halimochirurgus* and *Macrorhamphosodes*). It also implies that lepidophagy (scale feeding) has evolved twice, once in *Tydemania* (Mok, 1978) and also in *Macrorhamphosodes* (Nakae & Sasaki, 2002). Future studies addressing instances of morphological and ecological convergence among triacanthodids may provide insights into the evolutionary mechanisms responsible for convergence.

5 | OTHER MATERIAL EXAMINED

Each lot only has one specimen unless otherwise indicated.

Atrophacanthus japonicus: 105 specimens examined: ANSP 103654, 88.0 mm L_S, Tanzania; BMNH 1987.1.23.51–52, two specimens, est. 30 mm, est. 35 mm L_S, South Indonesia; BMNH 1987.1.23.54–56, three specimens, est. 32 mm, est. 20 mm, est. 23 mm L_S, South Indonesia; BMNH 1996.9.25.1, 60.5 mm L_S, Maldives; MNHN 2002–2990, 54.9 mm L_S, Philippines.

MNHN 2014–2112, 117.2 mm L_S, Madagascar; USNM 265190, 46.9 mm L_S, Sumatra, Indonesia; USNM 440413, 51 mm L_S, Guam; USNM 440414, 47 mm L_S, Guam; USNM 440415, 54 mm L_S, Guam; USNM 440416, 44 mm L_S, Guam; USNM 440417, 51 mm L_S, Guam; USNM 440418, 42 mm L_S, Guam; USNM 440419, 51 mm L_S, Guam; USNM 440420, 49 mm L_S SL, Guam; USNM 440421, 48 mm L_S, Guam; USNM 440422, 51 mm L_S, Guam; USNM 440423, 46 mm L_S, Guam; USNM 440424, 49 mm L_S, Guam; USNM 440425, 44 mm L_S, Guam; USNM 440426, 38 mm L_S, Guam; USNM 440427, 47 mm L_S, Guam; USNM 440428, 48 mm L_S, Guam; USNM 440429, 46 mm L_S, Guam; USNM 440430, 51 mm L_S, Guam; USNM 440431, 78 specimens, 37–50 mm L_S, Guam.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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