

Eptatretus strickrotti n. sp. (Myxinidae): First Hagfish Captured From a Hydrothermal Vent

PETER R. MØLLER^{1,*} AND W. JOE JONES²

¹Zoological Museum, Natural History Museum, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen East, Denmark; and ²Monterey Bay Aquarium Research Institute (MBARI), Moss Landing, California 95039-9644

Abstract. A single hagfish (Myxinidae, *Eptatretus*) specimen was recently captured at a hydrothermal vent site on the East Pacific Rise (38°S). This is the first capture of a member of the jawless fishes (agnathans) from a hydrothermal vent site. The specimen differs from all congeners by the very slender body (depth 2.9% of total length), the paired and median ventral nasal sinus papillae, and the presence of 10 afferent branchial arteries on the medial ventral aorta. It is further unique because of a combination of the following features: slime pore counts; paired dorsal nasal sinus papillae; 12 gill pouches and gill apertures; posterior left side of body widely separated from pharyngocutaneous duct; 3/2 multicuspid configuration; ventral aorta bifurcated anteriorly between 2nd and 3rd gill pouches (counted from the snout toward the heart); and pink coloration. The specimen is here described as a new species named *Eptatretus strickrotti*. Molecular 16S rRNA data places this new species as the basal-most species of *Eptatretus*, providing important new insight to the evolution of hagfishes as a whole.

Introduction

The number of recognized genera in the subfamily Eptatretinae is still controversial, with various specialists recognizing only *Eptatretus* Cloquet, 1819 (e.g., Strahan, 1975; Fernholm, 1998; Chen *et al.*, 2005), *Eptatretus* and *Paramyxine* Dean, 1904 (e.g., Mok, 2001), *Eptatretus* and *Quadratus* Wisner, 1999 (e.g., Froese and Pauly, 2005), or *Eptatretus*, *Paramyxine*, and *Quadratus* (e.g., Wisner, 1999;

McMillan and Wisner, 2004; Mok and McMillan, 2004). This lack of a consensus seems to be caused by the paucity of phylogenetic studies, which are surprisingly few (Jansson *et al.*, 1995; Kuo *et al.*, 2003; Chen *et al.*, 2005) given the importance of jawless fishes in vertebrate evolution, medical research, and fisheries (see, e.g., Nelson, 2006; Ota and Kuratani, 2006). The subfamily Eptatretinae has been extensively revised within the last 25 years (e.g., Fernholm and Hubbs, 1981; Kuo *et al.*, 1994; McMillan and Wisner, 2004)—almost tripling the number of known species from about 16 in 1980 to 46 currently (including the one herein described). The reasons for this increase are many, but a significant number of new species have been discovered after capture from submersibles in remote rocky habitats where traditional fishing methods are less successful (Minicarone and McCosker, 2004). So far, however, submarine investigations of hydrothermal vents have not captured any myxinids from these unique environments (Biscoito *et al.*, 2002; Wolf, 2005; Desbruyères *et al.*, 2006), and only a single unconfirmed record exists in the literature (*E. okino-seanus* from Okinawa Trough [Ohta and Kim, 2001]).

During the *Easter Microplate* expedition, 12 March–6 April 2005, with R/V *Atlantis* and DSV *Alvin*, a single myxinid specimen was caught by the *Alvin* slurp gun at the East Pacific Rise vent site known as 38°S (a video clip of the capture is available upon request from the authors). The specimen does not match any known species of hagfish and is here described as a new species of *Eptatretus*. Its phylogenetic position was determined using Bayesian analysis of molecular 16S rRNA data.

Materials and Methods

Methods of counting and anatomical terminology follow Fernholm and Hubbs (1981) and McMillan and Wisner

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* To whom correspondence should be addressed. E-mail: pdmoller@snm.ku.dk

Abbreviations: BPP, Bayesian posterior probabilities; E, *Eptatretus*; GA, gill aperture; GP, gill pouche; P, *Paramyxine*; PCD, pharyngocutaneous duct; Q, *Quadratus*; TL, total length; VA, ventral aorta.

(1984, 2004). Body width is measured at the pharyngocutaneous duct (PCD) following McMillan and Wisner (2004), and not McMillan and Wisner (1984) in which body width is the maximum width between the rostrum and PCD. Body depth is measured at the PCD and therefore does not follow McMillan and Wisner (2004), in which depth is maximum body depth. The reason for this choice is to maintain consistency in the measurement of body depth; however, for the present species, depth at the PCD and maximum depth are similar. Terminology of nasal sinus papillae follows Mok (2001), except for the lateral structures in the nasal sinus floor, which are here referred to simply as papillae, not longitudinal folds. Since only one specimen is available for examination, no attempt was made to dissect the nasal sinus as suggested by Mok (2001); we made only direct observations through the nasal opening.

Author names of species are provided in the Appendix. "Subgenera" abbreviations *Eptatretus E.*, *Eptatretus P.*, and *Eptatretus Q.* are used to illustrate that some authors recognize the genera *Paramyxine* and *Quadratus* and to facilitate comparison with earlier literature that uses these genera. Comparative material includes *Eptatretus E. deani*, KU 28249 (Southern California, 34°47'N, 120°85'W); *E. E. longipinnis*, SAMA F4042 Holotype, SAMA F7540 (South Australia, Port MacDonnell, ca. 38°S, 141°E), SAMA F5676, SAMA F3611; *E. E. cirrhatus*, ZMUC P02221-228 (Milford Sound, New Zealand). Institutional abbreviations: CAS = California Academy of Sciences; KU = University of Kansas; SAMA = South Australian Museum; ZMUC = Zoological Museum, University of Copenhagen.

Molecular sequencing

Phylogenetic analyses were conducted with a combination of published and original DNA sequences. We list the origin of specimens (geographical coordinates) used to obtain original sequences in Table 1 along with their voucher (museum) and GenBank accession numbers. To obtain the original sequences, we extracted genomic DNA from ethanol-preserved muscle tissue (50 mg) that was treated with the Qiagen Dneasy isolation kit, according to manufacturer's instructions (Qiagen Inc., Valencia, CA). Polymerase chain reaction (PCR) conditions for amplification of 16S rRNA contained 30–100 ng of template DNA, 5 µl of 10× buffer (supplied by manufacturer), 5 µl of MgCl₂ (2.5 µmol l⁻¹), 2 µl of each primer (10 µm final conc.), 2.5 units of *Taq* polymerase (Promega Inc., WI), 5 µl of a 2 mmol l⁻¹ stock solution of dNTPs, and sterile H₂O to a final volume of 25 µl. PCR was performed with a Cetus 9600 DNA thermocycler (Perkin-Elmer Corporation, Connecticut) using the conditions of Kuo *et al.* (2003).

PCR products were purified using a Qiagen PCR purification kit (Qiagen Inc., Valencia, CA) or Montage columns (Millipore, Billerica, MA). The purified template DNA was sequenced using a Big Dye Terminator cycle sequencing reaction kit (PE Biosystems, Foster City, CA) and ABI Prism 3100 DNA sequencers (Applied Biosystems Inc., Foster, CA). PCR products were sequenced bidirectionally from each individual sample, using the same forward and reverse primers as used in PCR. DNA sequence alignments were initially constructed using Sequencher (Gene Codes Corp. Inc., Ann Arbor, MI). Secondary structure of rRNA

Table 1

Summary of information for the specimens used for sequencing of 16S rRNA or phylogenetic analyses

Species	Voucher No.	Locality	GenBank No.
<i>Eptatretus E. burgeri</i>	—	Taiwan	AF364617, AY619579, AF364616
<i>Eptatretus P. cheni</i>	—	Taiwan	AF364620-1
<i>Eptatretus E. chinensis</i>	—	Taiwan	AY619580
<i>Eptatretus E. cirrhatus</i>	—	New Zealand	AF364619
<i>Eptatretus E. deani</i>	KU 28249	California, USA	EF014477
<i>Eptatretus E. longipinnis</i>	SAMA F07540	South Australia	EF014476
<i>Eptatretus Q. nelsoni</i>	—	Taiwan	AF364608
<i>Eptatretus P. sheni</i>	—	Taiwan	AF364610
<i>Eptatretus E. stoutii</i>	—	Oregon, USA	AF364618
<i>Eptatretus E. strickrotti</i> n. sp.	CAS 223480	East Pacific Rise	EF014478
<i>Eptatretus E. taiwanae</i>	—	Taiwan	AF364611
<i>Eptatretus Q. yangi</i>	—	Taiwan	AF364612-5
<i>Myxine circifrons</i>	—	Unknown	AF364628-9
<i>Myxine formosana</i>	—	Taiwan	AF364625
<i>Myxine</i> sp. 1	—	Taiwan	AF364622-4
<i>Myxine</i> sp. 2	—	Taiwan	AF364626
<i>Myxine</i> sp. 3	—	Taiwan	AF364627
<i>Petromyzon marinus</i>	—	Unknown	U11880

Dashes (—) indicate that data were not available from Kuo *et al.* (2003).

(i.e., stems and loops) was inferred using the program GeneBee (Brodsky *et al.*, 1992). The 16S rRNA alignment analyzed in this study is available in GenBank PopSet (accession numbers in Table 1).

Phylogenetic analyses

Bayesian phylogenetic trees were estimated for 16S rRNA using MrBayes version 3.0b4 (Huelsenbeck and Ronquist, 2001), partitioning by structure (stem *vs.* loop). Representatives of *Myxine* (Table 1) and *Petromyzon marinus* were chosen as outgroup taxa based on Kuo *et al.* (2003). Parameters are available upon request (WJJ). The Monte Carlo Markov chain (MCMC) length was 1.1×10^6 generations with 6 markov chains, and we sampled the chain every 100 generations to minimize autocorrelation. MCMC convergence was assessed by visually inspecting the sample paths of model parameters (to determine an appropriate burn-in period) and by repeating the analysis multiple times (at least 3) with random initial parameter values (to assess the dependence of posterior distributions on initial conditions).

Parameter estimates were graphically analyzed to assess

stability. Log-likelihood values and associated parameters for sampled trees stabilized after approximately $5-6 \times 10^5$ generations. Therefore, we conservatively used the last 5000 sampled trees to estimate Bayesian posterior probabilities (BPP). If $\geq 95\%$ of the sampled trees contained a given clade, we considered it to be significantly supported by our data (*sensu* Wilcox *et al.*, 2002).

Eptatretus strickrotti new species

Figures 1–4

Holotype

CAS 223480, 314 mm total length (TL), sex unknown, East Pacific Rise, $37^{\circ}47.363'S$, $110^{\circ}54.905'W$, 2211 m, 21:24 GMT, R/V *Atlantis*, DSV *Alvin* dive 4089 ($38^{\circ}S$), 23 March 2005, Starboard observer: Daniel Layton-Matthews, Port observer: William Jones, Pilot: Bruce Strickrott. Specimen caught, using the slurp gun/suction sampler on the *Alvin*, while swimming about 1 m above the bottom of lobate basalt flow along a fissure near Sebastian's Steamer hydrothermal vent (Fig. 1A).

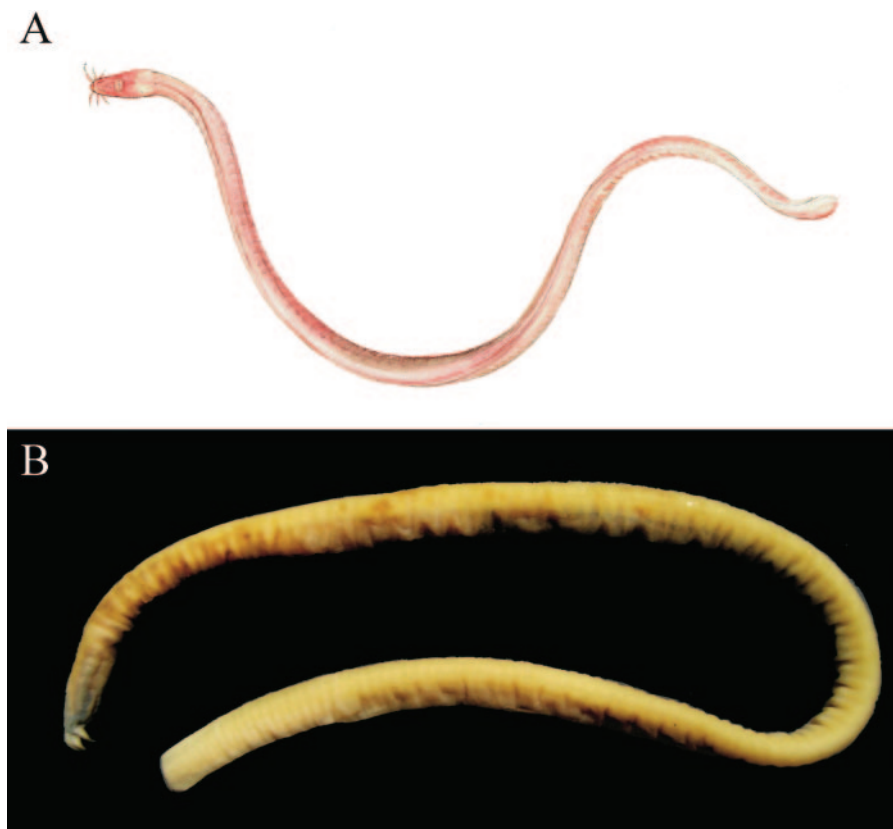


Figure 1. *Eptatretus strickrotti* n. sp. Holotype, CAS 223480. (A) Dorsal view, just after capture, still alive. Note that the dark stripe along the back is pigmentation, not a finfold. Drawing by Karen Jacobsen (In Situ Scientific Illustration); used with permission. (B) Same specimen, 7 months after preservation.

Diagnosis

Distinguished from all congeners by the slender body, depth at PCD 2.9% TL, paired and median ventral nasal sinus papillae, and presence of 10 afferent branchial arteries on the medial ventral aorta. It is further characterized by the combination of the following characters: slime pores—prebranchial 18, branchial 12, trunk 70, caudal 19, total 119; gill pouches (GP) and gill apertures (GA) 12, PCD widely separated from the opening of posterior left GAs; multicusps in anterior row 3 and multicusps in posterior row 2, total cusps 46; paired dorsal nasal sinus papillae; eyespot absent; body coloration pink.

Description

Body very slender, laterally compressed, and oval in cross section. Width/depth ratio at PCD 0.6. Rostrum rather long, rounded (Fig. 2A, B). Two bilaterally symmetrical, bi-tipped, crescent-shaped papillae present in the dorsal surface of the nasal tube (nasal sinus). In the floor of the nasal tube, a large, median, pillow-shaped papilla is present in addition to two bilaterally symmetrical, single-tipped papillae (Fig. 3). Eyespots and head grooves absent. Ventral finfold vestigial, maximum depth about 0.8 mm, beginning approximately at the middle of the body and extending posteriorly to the cloaca. Caudal finfold thin and low (missing about the last 3 mm), extending around the tail to dorsal surface, ending nearly above the cloaca. Tentacles relatively large, the first and third almost equal in length (1.4% and 1.5% TL, respectively), the second a bit shorter (1.1% TL) (Fig. 2A, B).

Dental muscle pale and short: length 17.8% TL, width 1.5% TL, only slightly overlapping with anteriormost gill pouch, resulting in the two rows of GPs lying closely together (Fig. 2E).

Twelve GPs and GAs, the posterior left GA widely separated from the opening of the PCD. The distance (1.4 mm) is about the same as that between the last two GAs (Fig. 2D). All efferent branchial ducts of about similar length. Ventral aorta (VA) bifurcating at an anterior position between 2nd and 3rd GP (counted from the snout toward the heart). Ten afferent branchial arteries on each side of the VA posterior to bifurcation. Each separated ventral aorta (SVA) has one afferent branchial artery and ends in the anteriormost (1st) GP.

Palatine cusp short (length 0.94 mm, width at base 0.44 mm). First 3 cusps in anterior row and first 2 cusps in posterior row fused at their bases (= multicusp configuration 3/2), followed by 9 unicusps in both rows. Total cusps 46. Longest cusp in anterior row is first unicusps next to multicusps, 1.7 mm long, 0.7 mm at base; longest cusp in posterior row is first unicusps next to multicusps, 1.5 mm long, 0.4 mm at base.

Slime pores very small and difficult to count, especially

in trunk region. Prebranchial slime pores 18, branchial slime pores 12, trunk slime pores 74, caudal slime pores 19 (2 of which are above the cloaca).

Coloration. Live specimen bright pink, with a narrow, darker red stripe along the dorsal surface (Fig. 1A). Preserved color pale, light yellow, with some internal dark pigmentation seen through skin, in the head and along mid-body (Fig. 1B). Specimens seen from submersible pale, whitish, probably due to the light source of the submersible.

Comparisons. Selected characters are provided for eptatretines in the Appendix. *Eptatretus E. strickrotti* is a very distinct species of hagfish, differing from all congeners by the very slender body (depth at PCD = max. depth 2.9% vs. 4.0%–15.3% TL) and numerous afferent branchial arteries from medial part of the VA (10 vs. 0–6) (Mok and McMillan, 2004).

It differs from the species often assigned to *Paramyxine* (8 species) and *Quadratus* (4 species) by having a high number of GPs and GAs (12 vs. 5–6 and 5–6), in a straight line (vs. fairly straight and nonlinear, crowded), corresponding long branchial region (9.3% vs. 1.3%–5.6% and 1.1%–2.8% TL), and in the number of caudal slime pores (19 vs. 5–14 and 7–12) (Appendix).

Eptatretus E. strickrotti resembles eight East Pacific congeners (*E. E. bischoffli*, *E. E. deani*, *E. E. fritzi*, *E. E. mcconnaugheyi*, *E. E. nanii*, *E. E. polytrema*, *E. E. sinus*, and *E. E. stoutii*) (see Appendix) by having a high (12 and 9–14) number of GPs and GAs and a long branchial region (9.3% and 9.2%–22.0% TL), but it differs from all these by the number of slime pores (e.g., caudal 19 vs. 7–17 and total 119 vs. 66–88), presence of dorsal (and ventral) nasal sinus papillae (vs. absent), lack of visible eye spot (vs. present), length of dental muscle (18% vs. 20%–39% TL), and anteriorly bifurcated VA (at GP 2–3 vs. 4–13) (Appendix). It is further separated from *E. E. bischoffli*, *E. E. nanii*, and *E. E. polytrema* from off Chile by the number of multicusps in the posterior row (2 vs. 3) and several body proportions (e.g., trunk length 59% vs. 45%–54% TL). Five Northeast American species (*E. E. deani*, *E. E. fritzi*, *E. E. mcconnaugheyi*, *E. E. sinus*, and *E. E. stoutii*) have 3/2 multicusps like *E. E. strickrotti*. In addition to the above-mentioned characters, however, *E. E. strickrotti* differs from these five in the body color (pink vs. gray, brown, or black, except for a few specimens of *E. E. stoutii* with pinkish overtones [Wisner and McMillan, 1990] and a single pink *E. E. deani* [McMillan, 1999]).

Eptatretus E. strickrotti resembles 11 of the remaining 24 species of *Eptatretus* by the 3/2 multicusp configuration, but it differs from all these by the more numerous gill pouches (12 vs. 5–8) and in total number of slime pores (119 vs. 72–110 or 128–130) (Appendix). Most similar slime-pore counts are seen in three Pacific deep-water species: *E. E.*

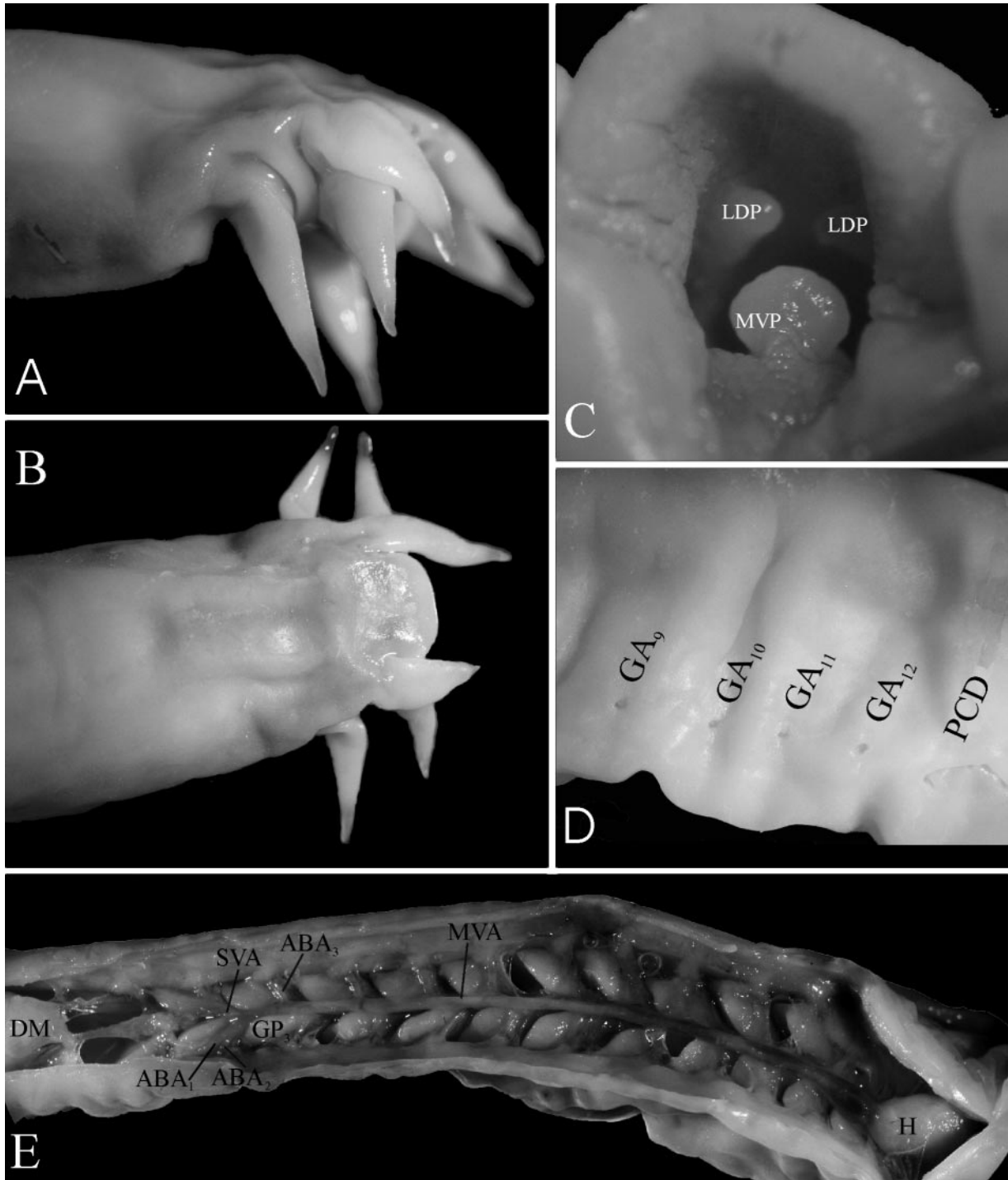


Figure 2. *Eptatretus strickrotti* n. sp. HT, CAS 223480, after 7 months of preservation. (A) Head lateral view. (B) Head dorsal view. (C) Anteriormost part of latero-dorsal nasal sinus papillae (LDP) and median ventral nasal sinus papilla (MVP), posterior tips of latero-dorsal nasal sinus papillae and lateral ventral nasal sinus papillae not seen. (D) Gill apertures (GA) and pharyngocutaneous duct (PCD); note that branchial slime pores below each GA are not seen due to mucus coverage. (E) Gill region dissected, gill pouches (GP), median ventral aorta (MVA), separated ventral aorta (SVA), afferent branchial arteries (ABA), dental muscle (DM), and heart (H). Note that left GP 1 and 12 are not clearly seen.

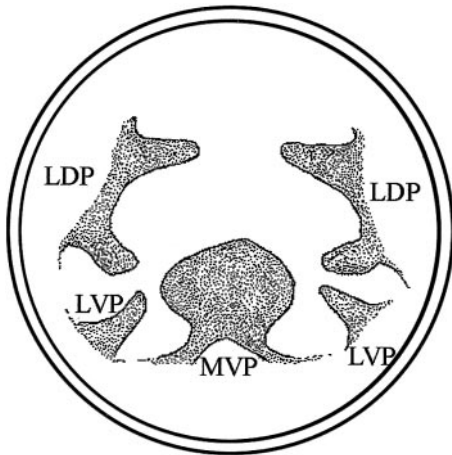


Figure 3. *Eptatretus strickrotti* n. sp. HT, CAS 223480. Sketch of nasal sinus papillae: latero-dorsal nasal sinus papillae (LDP), median ventral nasal sinus papillae (MVP), lateral ventral nasal sinus papillae (LVP).

carlhubbsi from off Hawaii, Guam and Wake Islands; *E. E. laurahubbsae* from off Chile; and *E. E. eos* Fernholm, 1991, from the Tasman Sea (e.g., trunk slime pores 70, 60–70, 60–67, and 70–75, respectively). *Eptatretus E. strickrotti* further resembles *E. E. carlhubbsi* and *E. E. laurahubbsae* in the paired dorsal sinus papillae, but differs in multicusp configuration (3/2 vs. 2/3 and 2/2) and by a much lower number of unicusps (46 vs. 64–71 and 61–68). *Eptatretus E. strickrotti* also resembles *E. E. eos* in the pink color, but differs in the number of slime pores (e.g., caudal pores 19 vs. 26–27), in addition to the aforementioned characters.

Etymology. Named in honor of DSV *Alvin* pilot Mr. Bruce Strickrott, in recognition of his expertise with *Alvin* and slurp-gun capture of the holotype specimen and other mobile hydrothermal vent animals.

Distribution. Known from the holotype only, caught at the East Pacific Rise, vent site (38°S), at 2211-m depth. This is the first member of the jawless fishes to be captured from a hydrothermal vent site, confirming that they do occur in this type of habitat. Hagfishes are often difficult to identify from photographs and are easily confused with synbranchid eels and even wormlike invertebrates. Ohta and Kim (2001) reported observations of specimens of *Eptatretus E. okinoseanus* from a vent on Iheya Ridge, Okinawa Trough, but neither illustrations nor text justifying the identification were provided. *Eptatretus E. strickrotti* is the fourth species of *Eptatretus* recorded from depths below 2000 m: *E. E. deani* (2743 m), *E. E. fritzi* (2743 m), and *E. E. laurahubbsae* (2400 m) (Fernholm, 1998).

During the French *Biospedo* expedition (Jollivet *et al.*, 2004) to the East Pacific Rise in 2004, at least seven specimens of myxinids were observed and filmed on the

vent sites *Grommit* (21°33.664'S, 114°17.982'W, 2838 m), *Oasis* (17°25.38'S, 113°12.29'W, 2586 m), and *Yaquina* (07°29.96'S, 107°53.95'W, 2700 m), thus extending the range for East Pacific Rise myxinids 30° to the north of the holotype catch site. Those observations also extended the depth range by about 800 m. Since none of these specimens were collected, we cannot be sure if they belong to the species here described. They have a similar slender body and appear pale to white on the video recordings, which is not in conflict with the light pink color of the collected specimen. Two myxinids were seen swimming toward the current like the captured specimen, and two were drifting with the current together with unidentified ophidiiform species.

In general, the obligate vent fish fauna of the East Pacific Rise is very poorly known, with only about 30 specimens of *Thermaces* spp. collected (Geistdoerfer and Seuront, 1995) and two specimens each of *Thermichthys hollisi* (Nielsen and Cohen, 2005) and *Ventichthys biospedoi* (Nielsen *et al.*, 2006).

Phylogenetic analysis

The complete aligned dataset consisted of 571 base pairs: 315 positions were designated as stems and 256 as loops. Three new 16S rDNA sequences were obtained in the present study: 267 sites were variable, including 123 that were parsimony informative.

The Bayesian analysis generated a topology in the monophyletic *Eptatretus* clade that was in accordance with the parsimony and neighbor-joining trees presented by Kuo *et al.* (2003) and Chen *et al.* (2005) (Fig. 4). The 16S rRNA phylogeny supports placement of *Eptatretus* in a reciprocally monophyletic clade relative to *Myxine* (Fig. 4). Resolution within *Eptatretus* was generally poor, as observed in Kuo *et al.* (2003) and Chen *et al.* (2005). *Eptatretus P. cheni* was resolved as a basal node but not highly supported (BPP = 0.63). Placement of *E. E. strickrotti* n: sp. as the most basal member of the *Eptatretus* clade was supported, but not strongly. Additional new 16S rRNA sequences collected in the present study include *E. E. deani*, which is strongly supported as the sister species to *E. E. stoutii*. Finally, *E. E. longipinnis* is placed with *E. Q. yangi* and *E. P. sheni*, though the support for these respective nodes are weak (Fig. 4).

Discussion

The gill pouch-gill aperture relationship has been extensively studied and has been used to establish genera and even subfamilies (Wisner, 1999). The present results with *Eptatretus E. strickrotti* in the most basal position add support to the view that a simple condition with the anterior gill aperture almost beside the anterior gill pouch is the plesiomorphic state, whereas a posterior origin of the gill apertures represents the

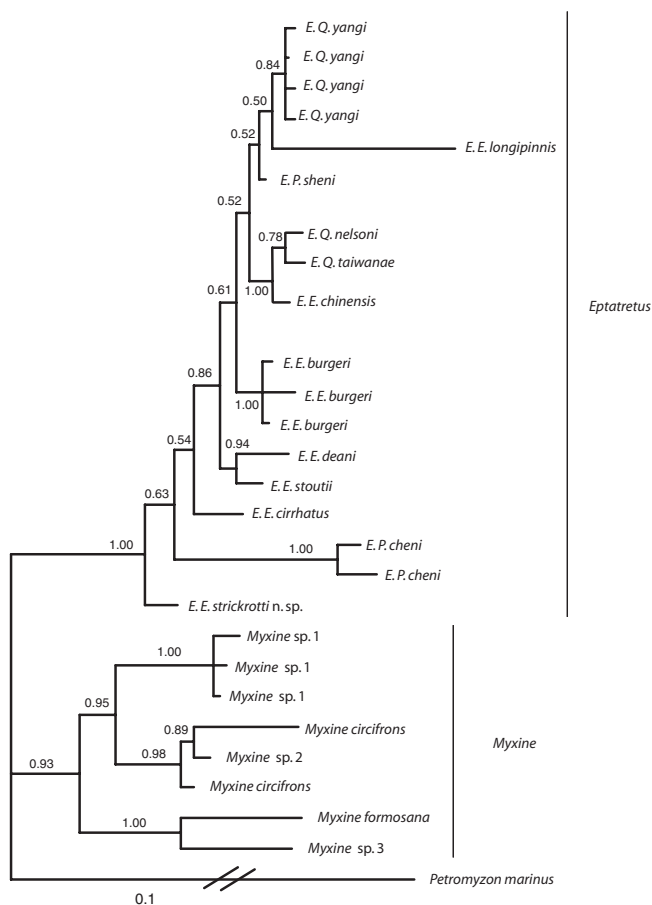


Figure 4. Bayesian trees of the 16S rRNA dataset. Scale bar indicates percent sequence divergence. All resolved nodes were recovered with a minimum of 0.50 Bayesian posterior probabilities (BPP; upper number).

apomorphic state. Other basal taxa with the simple condition are *E. E. cirrhatus*, *E. E. stoutii*, and *E. E. deani*, whereas the basal *E. cheni* contradicts this pattern by having a posterior origin of the first gill aperture, typical for the terminal taxa sometimes referred to as *Paramyxine* or *Quadratus*. In the present analysis, none of these form monophyletic groups, and we therefore support the synonymization of these genera in *Eptatretus*, as suggested by Fernholm (1998), Kuo *et al.* (2003), and Chen *et al.* (2005).

In a few myxinids, the PCD is not confluent with the last gill aperture. The present results with *E. E. strickrotti* and *E. P. cheni* in basal positions suggest that a separate PCD and last gill aperture is likely to be plesiomorphic in eptatretines, as it is expected to have been in the common ancestor of all hagfishes. More material is needed to show whether the condition is stable as in *Notomyxine tridentiger* (Garman, 1899), *E. E. bischoffli*, *E. P. cheni*, and *E. P. fernholmi* or variable as in several other species (*e.g.*, *E. E. burgeri*, *E. E. nanii*, and *E. E. polytrema*) (Wisner and McMillan, 1988; McMillan and Wisner, 2004).

Branching of the ventral aorta (VA) is considered synapo-

morphic for Eptatretinae (Mok and McMillan, 2004), in contrast to the plesiomorphic unbranched condition in Myxiniinae. Chen *et al.* (2005) argued that the transformation series suggested by Mok and McMillan (2004) (*i.e.*, bifurcation from a site midway between the heart and the 1st gill pouch [*e.g.*, *E. E. burgeri*] toward a site close to the heart [*e.g.*, *E. E. chinensis*, *E. E. cirrhatus*, *E. P. sheni*]) was not in conflict with their molecular data regarding *E. E. chinensis* and *E. P. sheni*. However, they did not comment on the fact that *E. E. cirrhatus*, which has a bifurcation very close to the heart, was placed in a basal position in their phylogeny. In the present analysis, the basal *E. E. strickrotti* with VA bifurcation close to the anterior gill pouches indicates that this is the plesiomorphic condition for eptatretines. We propose that to express this character by the GP number where the VA bifurcates gives a poor polarization of the character because of the large variation in the total number of GPs. We therefore suggest that it be expressed as the number of the GP at which bifurcation occurs divided by the total number of GPs (Appendix).

The dorsal nasal sinus papillae have proved to be specific and useful for resolving taxonomic problems in Myxiniidae (Mok, 2001; Møller *et al.*, 2005). The present phylogenetic reconstruction confirms that presence of paired dorsal papillae is the plesiomorphic state in Eptatretinae. They are present in *E. E. strickrotti*, *E. P. cheni*, and *E. E. cirrhatus*, and absent in the other, more terminal *Eptatretus* species surveyed. This is in agreement with Mok (2001), who suggested that the common ancestor of hagfishes could have had these papillae. With only one specimen available, it was not possible for us to check whether the papillae in *E. E. strickrotti* have the plesiomorphic supporting cartilage as in Myxiniinae and *E. P. cheni*.

Acknowledgments

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Appendix
Appendix Table 1. Selected characters of Epiplatretus spp.

Species	Gill pouches	Fused cusps	Total cusps	Total slime pores	Dorsal NSP	GP end of DM	ABA at MVA	VA bifurcates at GP	VA bifurcates at GP/total GP's	GA configuration	Last GA and PCD	Eyespots	Color	Max TL
<i>E. Q. ancon</i> Mok, Saavedra-Diaz & Acero-P, 2001	6	3/2	60	80	—	—	3	4–5	0.7–0.8	crowded	separate	present	light brown	220
<i>E. P. atami</i> (Dean, 1904)	6	3/3	47–52	71–78	absent	1–2	2	5–6	0.8–1.0	fairly straight	fused	faint or absent	purplish-brown-grey	610
<i>E. E. burgeri</i> (Girard, 1855)	5–6	3/2	35–42	81–92	absent	1–2	3	3–4	0.6–0.7	linear	fused (90%)	present	brownish	690
<i>E. P. cheni</i> (Shen and Tao, 1975)	5	3/3	50–53	75–81	paired	1–2	3	3	0.6	fairly straight	separate	absent	greyish brown	386
<i>E. E. bischoffii</i> (Schneider, 1880)	10–11	3/3	44–52	74–83	absent	6–11	0	10–11	1.00	linear	separate	present	black-brown	550
<i>E. E. caribbeaus</i> Fernholm, 1982	7	3/3	54–58	79–85	absent	—	0	—	—	linear	—	—	light tan	385
<i>E. E. carlhubst</i> McMillan and Wisner, 1984	7	2/3	64–71	93–110	paired	2–4	2	7	1.0	linear	fused	present	dark brown	1160
<i>E. E. chinensis</i> Kuo and Mok, 1994	6	3/3	46–52	72–83	absent	2–3	0–1	5–6	0.8–1.0	linear	fused	present	grey brownish	540
<i>E. E. cirrhatus</i> (Forster, 1801)	7	3/3	43–51	79–90	paired	4–7	0	7	1.0	linear	fused (exceptions)	present	dark brown, white marks	830
<i>E. E. deani</i> (Evermann and Goldsborough, 1907)	10–12	3/2	37–46	67–80	absent	5	5	6	0.5–0.6	linear	fused	present	black (rarely pinkish)	523
<i>E. E. eos</i> Fernholm, 1991	5	3/2–3	34	128–130	—	—	—	—	—	linear	fused	absent	pink	665
<i>E. E. fernholmi</i> McMillan and Wisner, 2004	8	3/2	51	81	—	—	—	—	—	linear	fused	absent	brownish	373
<i>E. P. fernholmi</i> (Kuo, Hang and Mok, 1994)	6	3/2	38–44	64–71	absent	1–3	3	3–4	0.5–0.7	fairly straight	separate	absent	greyish brown	359
<i>E. E. fritzi</i> Wisner and McMillan, 1990	10–12	3/2	38–46	74–85	absent	5	3	9	0.8–0.9	linear	fused	present	purplish black	592
<i>E. E. goliath</i> Mincarone and Stewart, 2006	7	3/3	54	92	paired	4	0	7	1.0	linear	fused	present	dark brown	1275
<i>E. E. grouseri</i> McMillan, 1999	5–6	3/2	44–48	71–79	—	1–2	—	5	0.8–1.0	linear	fused	prominent	ivory to brownish-black	420
<i>E. E. hexatrema</i> (Müller, 1836)	5–6	3/2	40–48	90–105	paired	—	3	—	—	linear	fused	—	light-blackish brown	720
<i>E. E. indrambarayi</i> Wongratana, 1983	8	3/2	45–48	77–82	—	2–3	0	8	1.0	linear	fused	present	purplish-brown	437
<i>E. E. lakeside</i> Mincarone and McCosker, 2004	5	3/3	36	88	paired	0	3	2	0.4	linear	fused	weak	pink-orange	275
<i>E. E. laurahubbsae</i> McMillan and Wisner, 1984	7	2–3/2	61–68	97–105	paired	2–5	3	5–7	0.7–1.0	linear	fused	weak	—	375
<i>E. E. longipinnis</i> Strahan, 1975	6	3/2	30	104–108	absent	2–3	2–3	4	0.7	linear	fused	absent	brownish	550
<i>E. E. mccoonaughteyi</i> Wisner and McMillan, 1990	12–14	3/2	42	67–84	absent	9	1–3	11	0.8	linear	fused	present	brownish	470

Appendix Table 1 (Continued)

Species	Gill pouches	Fused cusps	Total cusps	Total slime pores	Dorsal NSP	GP at end of DM	ABA at MVA	VA bifurcates		GA configuration	Last GA and PCD	Eyespots	Color	Max TL
								VA at GP	VA at bifurcates at GP/total GP's					
<i>E. mccooskeri</i> McMillan, 1999	8	3/3	48–51	72–74	—	4–6	2	6–7	0.8–0.9	linear	fused	weak	brownish-black	320
<i>E. E. mendozai</i> Hensley, 1985	6	3/3	56–61	77–82	paired	2–4	0	5–6	0.8–1.0	linear	fused	present	bluish-grey	450
<i>E. E. menezesi</i> Mincarone, 2000	7	3/3	52–60	86–94	—	2–5	2	5–6	0.7–0.9	linear	—	present	light brown	737
<i>E. E. minor</i> Fernholm and Hubbs, 1981	5–6	3/3	46–54	74–82	paired	3–4	0–1	5–6	0.8–1.0	linear	fused	—	—	395
<i>E. P. moki</i> (McMillan and Wisner, 2004)	6	3/2	38–42	75–82	—	1–2	—	3–4	0.5–0.7	fairly straight	fused	faint or absent	dark brown	470
<i>E. E. multitidens</i> Fernholm and Hubbs, 1981	6	3/3	52–57	87–91	paired	2–3	0	6	1.0	linear	fused	present	dark	815
<i>E. E. nanii</i> Wisner and McMillan, 1988	12–13	3/3	49–55	72–82	absent	4–7	6	4–9	0.3–0.7	linear	separate (61%)	present	black-brown	664
<i>E. Q. nelsoni</i> (Kuo, Huang and Mok, 1994)	3–5	3/2	32–40	57–67	absent	1–2	2	3–4	0.6–0.8	crowded	fused	absent	brownish-grey	234
<i>E. E. octatrema</i> (Barnard, 1923)	8	3/2	40	102–103	—	—	—	—	—	linear	fused	—	brownish	300
<i>E. E. okinosanus</i> (Dean, 1904)	8	3/2	40–49	87–97	absent	1–3	2	7–8	0.9–1.0	linear	fused	present	brownish	800
<i>E. E. polytrema</i> (Cirard, 1855)	13–14	3/3	45–51	72–79	absent	5–10	1	9–13	0.7–0.9	linear	fused (91%)	present	piebald-dark	460
<i>E. E. profundus</i> (Barnard, 1923)	5	3/2	42	82–83	absent	—	—	2–3	0.4–0.6	linear	—	—	dark brown	620
<i>E. P. sheni</i> (Kuo, Huang and Mok, 1994)	6	3/3	48–53	62–74	absent	3–4	0–1	4–5	0.7–0.8	fairly straight	fused	prominent	dark brown	436
<i>E. E. sinus</i> Wisner and McMillan, 1990	9–12	3/2	34–46	66–82	absent	2	6	5–6	0.5–0.6	linear	fused	present	reddish brown	481
<i>E. P. springeri</i> (Bigelow and Schroeder, 1952)	6	3/2	48–52	84–92	—	1–3	1	4–5	0.7–0.8	fairly straight	—	—	greyish brown	590
<i>E. E. stoutii</i> (Lockington, 1878)	10–14	3/2	36–46	71–88	absent	3	4	7	0.5–0.7	linear	fused	present	brownish (rarely pinkish)	468
<i>E. E. strahani</i> McMillan and Wisner, 1984	7	3/3	47–52	76–80	paired	3–5	0	7	1.0	linear	fused	absent	brownish	520
<i>E. E. strickrotti</i> n. sp.	12	3/2	46	119	paired	1	10	2–3	0.2–0.23	linear	separate	absent	pink	314
<i>E. Q. taiwanae</i> (Shen and Tao, 1975)	6	3/2	32–40	60–68	absent	1–2	3	4–5	0.7–0.8	crowded	fused	faint or absent	brownish-grey	334
<i>E. P. walkerii</i> (McMillan and Wisner, 2004)	5–6	3/2	38–44	69–79	—	1–2	—	3–4	0.5–0.7	fairly straight	fused	faint or absent	brownish	518
<i>E. E. wayuu</i> Mok, Saavedra-Diaz and Acero, 2001	5	3/2	41–43	73–75	—	0	3–5	1–2	0.2–0.4	linear	fused	present	pink	216
<i>E. E. wisneri</i> McMillan, 1999	8	3/2	44	76	—	3	—	5	0.6	linear	fused	distinct	brownish-black	356
<i>E. P. wisneri</i> (Kuo, Hang and Mok, 1994)	6	3/2	36–44	63–72	absent	2–4	3	3–4	0.5–0.7	fairly straight	fused	present	light brown	388
<i>E. Q. yangi</i> (Teng, 1958)	5	3/2	32–40	68–79	absent	1–2	2–3	4–5	0.8–1.0	crowded	fused	absent	brownish-grey	296

Species in bold included in the molecular phylogeny.

Abbreviations: *E.* = *Eptatretus*; *Q.* = *Quadratrus*; *P.* = *Paramyxine*; NSP = nasal sinus papillae; GP = gill pouches; DM = dental muscle; ABA = afferent branchial arteries; MVA = median ventral aorta; VA = ventral aorta; PCD = pharyngocutaneous duct; GA = gill apertures; VFF = ventral fin fold. Blanks as (—) where an extensive literature search failed to provide data.

Appendix Table 2. Body measurements of Eptatretus spp. in % of total length (TL)

Species	Prebr. length	Branchial length	Trunk length	Tail length	Depth w/o VFF	Depth at cloaca	Tail depth	Locality	Depth m	Major sources of information
<i>E. Q. ancon</i> Mok, Saavedra-Diaz & Acero-P, 2001	37	1.95	48	12.0	6.8	—	7.0	Caribbean Sea	470–488	Mok <i>et al.</i> , 2001
<i>E. P. atami</i> (Dean, 1904)	27–30	1.3–4.2	54–56	11.1–14.2	7.9–8.0	6.3–6.8	7.4–8.8	off Japan	300–536	McMillan and Wisner, 2004
<i>E. E. burgeri</i> (Girard, 1855)	25–30	6.2–7.8	48–55	13–17	4.0–8.3	4.5–5.8	5.1–8.5	off Japan, Korea, China & Taiwan	10–270	McMillan and Wisner, 2004
<i>E. P. cheni</i> (Shen and Tao, 1975)	33–36	2.2–3.4	46–51	13.2–16.7	7.7–9.9	7.8–9.9	7.6–10.2	off SW Taiwan	180–268	McMillan and Wisner, 2004
<i>E. E. bischoffii</i> (Schneider, 1880)	17.6–22.4	11.4–16.1	45–54	14.0–21.8	7.1–11.2	5.6–8.7	5.6–8.3	off Chile	8–50	Wisner and McMillan, 1988
<i>E. E. caribbeus</i> Fernholm, 1982	21–24	5.8–7.8	50–56	16.5–19.6	7.4–10.6	9.6–9.2	7.5–10.9	Caribbean Sea	365–500	Fernholm, 1982; Mincarone, 2000
<i>E. E. carlhubbsi</i> McMillan and Wisner, 1984	17–20	5.5–7.7	58–62	14.5–17.6	7.8–10.6	6.5–8.5	8.9–10.5	off Hawaii, Wake Isl., Guam	481–1574	McMillan and Wisner, 1984
<i>E. E. chinensis</i> Kuo and Mok, 1994	25–35	4.4–6.4	46–53	13.9–18.6	—	—	7.1–10.2	South China Sea	500–600	Chen <i>et al.</i> , 2005; McMillan and Wisner, 2004
<i>E. E. cirrhatus</i> (Forster, 1801)	21–24	6.9–8.9	53–56	13.5–16.8	8.1–10.2	5.7–7.4	7.7–9.1	off New Zealand, S & E Australia	30–700	McMillan and Wisner, 1984, present study
<i>E. E. deani</i> (Evermann and Goldsborough, 1907)	14–20	12.7–18.2	48–56	12.6–19.2	4.5–10.5	3.8–8.5	5.2–10.3	NE Pacific, off N. America	107–2743	Wisner and McMillan, 1990
<i>E. E. eos</i> Fernholm, 1991	23.5	4.7	54	18.0	—	—	—	Tasman Sea	991–1013	Fernholm, 1991; Mok <i>et al.</i> , 2001
<i>E. E. fernholmi</i> McMillan and Wisner, 2004	21	8.0	56	14.9	8.0	6.0	8.6	off Philippines	560	McMillan and Wisner, 2004
<i>E. P. fernholmi</i> (Kuo, Hang and Mok, 1994)	30–33	2.0–2.9	50–52	13.4–16.3	5.6–8.0	5.2–6.3	7.0–10.5	off Taiwan	300–412	McMillan and Wisner, 2004
<i>E. E. fritzi</i> Wisner and McMillan, 1990	18–25	11.5–15.8	46–56	13.2–18.1	5.3–10.2	4.5–7.2	5.8–9.2	off Guadeloupe Isl., Mexico	18–2743	Wisner and McMillan, 1990
<i>E. E. goliath</i> Mincarone and Stewart, 2006	18.8	6.7	58.8	15.7	9.5	8.2	11.4	off N New Zealand	811	Mincarone and Stewart, 2006
<i>E. E. grouseri</i> McMillan, 1999	20–24	6.3–8.1	54–57	14.6–17.5	4.2–8.8	5.7–6.5	6.3–7.9	off Galapagos	722	McMillan, 1999; Mincarone and McCosker, 2004
<i>E. E. hexatrema</i> (Müller, 1836)	27–32	5–6	—	—	6–7	—	—	off South Africa	10–400	Fernholm, 1986; Strahan, 1975
<i>E. E. indrambaryai</i> Wongratana, 1983	21–23	8.6–10.6	52–57	15.8–18.4	8.5–10.3	6.0–8.9	7.6–9.9	Andaman Sea	267–400	Wongratana, 1983
<i>E. E. lakeside</i> Mincarone and McCosker, 2004	25	6.2	51	18.2	6.4	5.4	6.0	off Galapagos	762	Mincarone and McCosker, 2004
<i>E. E. laurahubbsae</i> McMillan and Wisner, 1984	18–20	5.2–5.9	55–59	18.1–21.3	7.3–9.1	6.1–8.0	8.2–8.9	SE Pacific, off Chile	2400	McMillan and Wisner, 1984
<i>E. E. longipinnis</i> Strahan, 1975	29	4.0	59	8.3	4.0	3.5	4.2	off South Australia	40	Strahan, 1975; present study
<i>E. E. mccoonaugheyi</i> Wisner and McMillan, 1990	15–18	16–22	48–56	12.2–16.1	5.5–9.0	4.7–7.1	6.0–8.8	Gulf of California	42–415	Wisner and McMillan, 1990
<i>E. E. mccooskeri</i> McMillan, 1999	24–26	9.3–10.1	49–50	15.6–17.7	9.4–10.6	7.3	8.7–10.2	off Galapagos	215	McMillan, 1999
<i>E. E. mendozai</i> Hensley, 1985	22–25	4.7–6.6	51–55	16.2–19.3	8.0–10.9	6.5–8.2	8.0–9.4	Caribbean Sea	720–1100	Hensley, 1985; Mok <i>et al.</i> , 2001

Appendix Table 2 (Continued)

Species	Prebr. length	Branchial length	Trunk length	Tail length	Depth w/o VFF	Depth at cloaca	Tail depth	Locality	Depth m	Major sources of information
<i>E. E. menezesi</i> Mincarone, 2000	19-27	5.0-8.3	51-65	14.6-22.0	7.1-10.6	6.6-9.1	6.6-10.6	SW Atlantic, off Brazil	250-530	Mincarone, 2000
<i>E. E. minor</i> Fernholm and Hubbs, 1981	20-26	5.1-7.2	51-56	13.9-18.3	7.1-10.8	5.2-7.9	5.3-11.6	Gulf of Mexico	300-400	Fernholm and Hubbs, 1981
<i>E. P. moki</i> (McMillan and Wisner, 2004)	27-31	1.4-3.0	49-55	15.4-19.5	5.2-8.2	5.8-8.2	7.7-9.7	off Japan	100	McMillan and Wisner, 2004
<i>E. E. multidentis</i> Fernholm and Hubbs, 1981	19-21	6.1-6.9	55-57	16.9-18.8	7.8-11.3	6.0-8.1	6.6-8.6	Caribbean Sea and NE Brazil	239-770	Fernholm and Hubbs, 1981; Mincarone and Sampaio, 2004
<i>E. E. nani</i> Wisner and McMillan, 1988	12.8-15.6	17.5-22.0	48-53	15.2-17.3	7.3-9.9	4.2-7.6	6.2-9.2	off Chile	274	Wisner and McMillan, 1988
<i>E. Q. nelsoni</i> (Kuo, Huang and Mok, 1994)	31-33	1.1-2.8	50-53	15.0-18.0	14.7-15.3	—	8.9-10.1	off SW Taiwan	50-858	McMillan and Wisner, 2004
<i>E. E. octatrema</i> (Barnard, 1923)	25	—	—	—	4.0	—	—	off South Africa	45-75	Barnard, 1923; Fernholm, 1986
<i>E. E. okinoseanus</i> (Dean, 1904)	19-23	6.2-9.2	50-59	12.7-15.5	5.5-7.9	6.0	6.2-9.0	off Japan, Taiwan	300-1020	McMillan and Wisner, 2004
<i>E. E. polytrema</i> (Girard, 1855)	13.9-16.9	16.8-20.1	48-53	12.7-17.9	6.8-10.9	4.9-8.0	5.7-8.6	off Chile	10-350	Wisner and McMillan, 1988; Wisner, 1999
<i>E. E. profundus</i> (Barnard, 1923)	20	6.0	55	—	8.3	—	—	off South Africa	732	Barnard, 1923; Strahan, 1975; Mincarone and McCosker, 2004
<i>E. P. sheni</i> (Kuo, Huang and Mok, 1994)	25-31	2.4-4.2	53-56	14.4-16.7	6.9-9.2	—	8.3-10.0	off SW Taiwan	200-619	McMillan and Wisner, 2004
<i>E. E. sinus</i> Wisner and McMillan, 1990	20-28	9.2-17.2	45-54	10.2-17.4	4.6-10.1	3.9-8.6	4.8-9.0	Gulf of California	198-1330	Wisner and McMillan, 1990
<i>E. P. springeri</i> (Bigelow and Schroeder, 1952)	22-27	2.5-5.6	53-61	13.4-16.8	6.2-9.7	—	6.4-9.3	Gulf of Mexico	400-730	Mok <i>et al.</i> , 2001
<i>E. E. stoutii</i> (Lockington, 1878)	19-25	11.5-14.2	47-54	10.4-17.8	4.1-9.0	3.8-7.9	4.5-8.3	NE Pacific, off N. America	16-633	Wisner and McMillan, 1990
<i>E. E. strahani</i> McMillan and Wisner, 1984	21-23	5.2-8.7	48-56	17.4-20.2	10.1-12.5	—	10.9-12.5	South China Sea, Philippines	189	McMillan and Wisner, 2004
<i>E. E. strictrotti</i> n. sp.	19.7	9.3	58.9	12.1	2.9	2.6	2.4	East Pacific Rise	2211	Present study
<i>E. Q. taiwanae</i> (Shen and Tao, 1975)	28-35	1.3-2.7	52-56	12.1-14.6	6.3-10.6	—	8.1-11.8	off NE Taiwan	20-427	McMillan and Wisner, 2004; Mok <i>et al.</i> , 2001
<i>E. P. walkerii</i> (McMillan and Wisner, 2004)	27-32	2.0-3.1	53-58	13.0-15.6	6.2-8.2	5.6-6.8	7.1-8.3	off Japan	75-120	McMillan and Wisner, 2004
<i>E. E. wayum</i> Mok, Saavedra-Diaz and Acero, 2001	31-33	3.0-3.5	48-50	10.9-14.9	7.0-7.7	—	11.0-10.1	Caribbean Sea	300-306	Mok <i>et al.</i> , 2001
<i>E. E. wisneri</i> McMillan, 1999	19-23	10.0-11.1	50-53	16.7-17.1	8.5-8.9	6.5	7.6-7.8	off Galapagos	563	McMillan, 1999
<i>E. P. wisneri</i> (Kuo, Hang and Mok, 1994)	28-31	4.6	49.4	13.6	9.3	8.1	10.5	off SE Taiwan	200	McMillan and Wisner, 2004
<i>E. Q. yangi</i> (Teng, 1958)	29-32	1.1-1.7	53-55	12.2-15.6	6.3-9.6	6.3-8.8	6.5-10.0	off NE and SW Taiwan	20-225	McMillan and Wisner, 2004; Mok <i>et al.</i> , 2001

Species in bold included in the molecular phylogeny.

Abbreviations: E = *Eptatretus*; Q = *Quadratus*; P = *Paramyxine*.