Three New Species of Hagfishes, Genus *Eptatretus* (Cyclostomata, Myxinidae), from the Pacific Coast of North America, with New Data on *E. deani* and *E. stoutii*

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Abstract.—Three new species of the genus *Eptatretus*–*E. mcconnaugheyi*, from off Southern California and Northern Baja California, and an isolated population in the southern portion of the Gulf of California; *E. fritzi*, known only from the immediate vicinity of Guadalupe Island, Mexico; and *E. sinus*, confined to the midriff area of the Gulf of California—are described. New data are presented for *E. deani* and *E. stoutii*. A neotype is designated for *E. stoutii*.

Despite the extensive ranges of *E. deani* (southeastern Alaska to Guadalupe Island, Mexico) and *E. stoutii* (Vancouver Island, Canada, to Pt. San Pablo, about 80 miles southerly from Cedros Island, Mexico), no appreciable differences were found in counts and body proportions within each species. However, the disjunct populations of *E. mcconnaugheyi* display significant differences ($P>0.001$) in numbers of trunk and total slime pores; in all other characters the two populations are very similar.

Sex ratios for four of the species are notably uneven, ranging between 60% and 74% female, 26% and 40% male. The sex ratio for *E. stoutii* is essentially even, 49% female and 51% male.

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This study continues our efforts on the genus *Eptatretus*, a part of the unfinished work of Carl L. Hubbs (deceased 30 June 1979). Two previous studies (McMillan and Wisner 1984, Wisner and McMillan 1988) and this have resulted in descriptions of seven new species of *Eptatretus*, two from off Central Chile, one each from the Hawaiian and Philippine areas, and three herein. Also, we have described a new species, *Nemamyxine kreffti*, from off Rio de Plata, Argentina (McMillan and Wisner 1984). In addition, a study on the genus *Myxine* is progressing, involving at least six new species from off the Atlantic and Pacific coasts of North and South America.

The present effort includes the largest amount of study material, about 2300 specimens. Many specimens of *E. stoutii* and *E. deani* are not included in the lists of material examined due either to poor preservation, to questionable capture data, or to a surfeit of material from an area, particularly off southern California. All specimens from near the extremes of ranges are included, as are all specimens of the three new species.

Due to the availability for the first time of large numbers of specimens of *E. stoutii* and *E. deani*, each having extensive distributions, we attempted to delineate an annual and spatial period of deposition (extrusion) of eggs for each. Capture data for females containing eggs of at least 20 mm length showed that eggs of this size were present in both species throughout the year throughout all areas of their ranges. The maximum lengths of eggs were 28.6 mm for *E. stoutii* and 52.3 for *E. deani*. Although these lengths may not indicate the ultimate lengths of eggs at time of deposition, it is very probable that deposition by both species occurs throughout the year and in all areas of their distributions.

Except for two collected in November, all specimens of *E. fritzi* were taken in April; eggs to 33 mm were present. Similarly, specimens of *E. sinus* were taken within two short periods, 20–22 January and 28 February–2 March eggs to 32 mm were present.

The occurrence and arrangement of head grooves (lateral lines of authors) in all species treated here agree well with those described and figured by Ayers and Worthington (1907:332–333, figs. 5, 6) and by McMillan and Wisner (1984:255, fig. 4).

Methods and materials

Methods of counting and measuring are those recommended by McMillan and Wisner (1984) and Wisner and McMillan (1988). Features used in

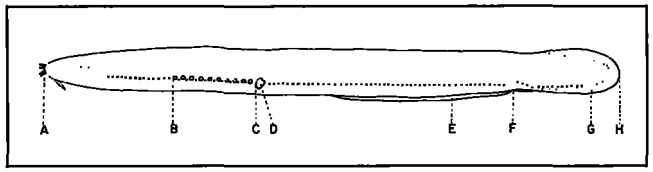


Figure 1

Outline of hagfish (*Eptatretus*) showing regions and features used in measuring and counting: A–H, total length (TL); A–B, prebranchial length; B–C, branchial length, including gill apertures (GA); D, external opening of pharyngocutaneous duct (PCD); E, ventral finfold; C–F, trunk length; F, origin of cloaca; F–H, tail length; G, caudal finfold. The linear series of dots represents the prebranchial, branchial, trunk, and cloacal-caudal (tail) slime pores.

counting and measuring are shown in Figure 1. Abbreviations used are given below and identified in Figure 4.

Abbreviations

ABA Afferent branchial artery; one of the small blood vessels that lead to each gill pouch from VA or its branches (Fig. 4).

DM Dental muscle; the firm elongate, cylindrical complex of muscles and cartilages that moves the dental plates and sets of cusps during feeding. Posterior portions of DM are shown in Figures 2–4, lying between rows of gill pouches.

GA Gill (branchial) aperture; external opening of the efferent duct leading from a gill pouch (Fig. 1).

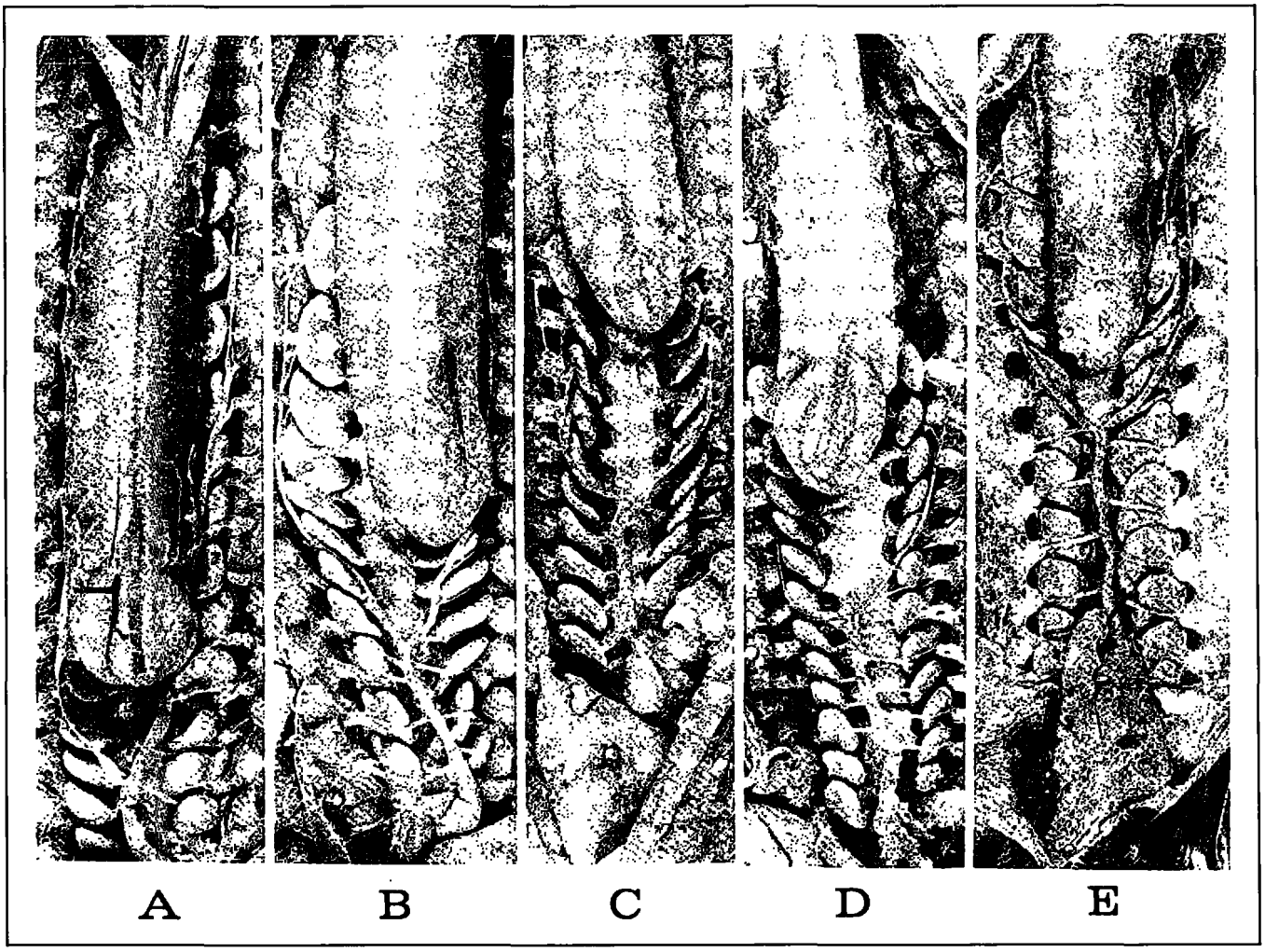
GP Gill pouch; rounded, serially arranged structures along and posterior to the dental muscle (Fig. 4).

PCD External opening of the pharyngocutaneous duct; always confluent with the posteriormost left gill aperture in most species of *Eptatretus*, and much larger than all other apertures (Fig. 1).

VA Ventral aorta; the portion between the heart (ventricle) and to where it branches to each side of DM (Fig. 4).

Figure 2

Branchial areas of holotypes of (A) *Eptatretus mcconnaugheyi*, (B) *E. fritzi*, and (C) *E. sinus*; (D) neotype of *E. stoutii*; (E) *E. deani*. The dental muscle (DM) is the cylindrical mass lying between the rows of gill pouches (GP).



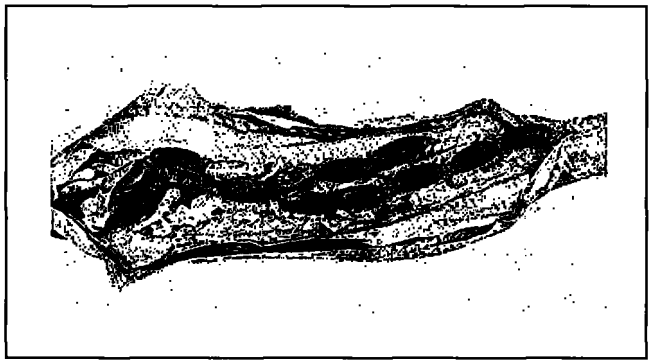


Figure 3
Mature eggs of holotype of *E. mcconnaugheyi* showing *in situ* arrangement and connections by anchor filaments (terminal hooks).

Other features used are:

Preocular length From center of left eyespot to center of rostrum.

Barbel length From crease at mesial base to tip of barbel.

Collection data and deposition of specimens are listed for each species. All specimens were taken on bottom, with a trap or trawl, except for two of *E. stoutii* taken by scuba divers near San Diego. Institutions which have provided study material, or in which type specimens are deposited, are SIO, CAS, LACM, MCZ, USNM, OSUO, BCPM, and UW. These symbolic institutional codes follow the usages in Leviton et al. 1985.

We introduce length of barbel as a systematic character. Barbels have not been used in the taxonomy of hagfishes except for the presence, absence, or degree of pigmentation between bases and tips. No tabular comparison of lengths has previously appeared in print, perhaps due to the small numbers of specimens available. However, in this study a total of 2613 measurements of length of first nasal barbel, left side, provided material for comparison. Data in Table 6, first barbel length for 25-mm increments of total length, show significant differences in lengths within the five species treated.

Key to species of *Eptatretus* of the Pacific coast of North America

1a Prebranchial length usually less than branchial length, very rarely equal to or even slightly greater. Tail length always less than branchial length..... ***E. mcconnaugheyi* n. sp.**

1b Prebranchial and tail lengths always greater than branchial length..... **2**

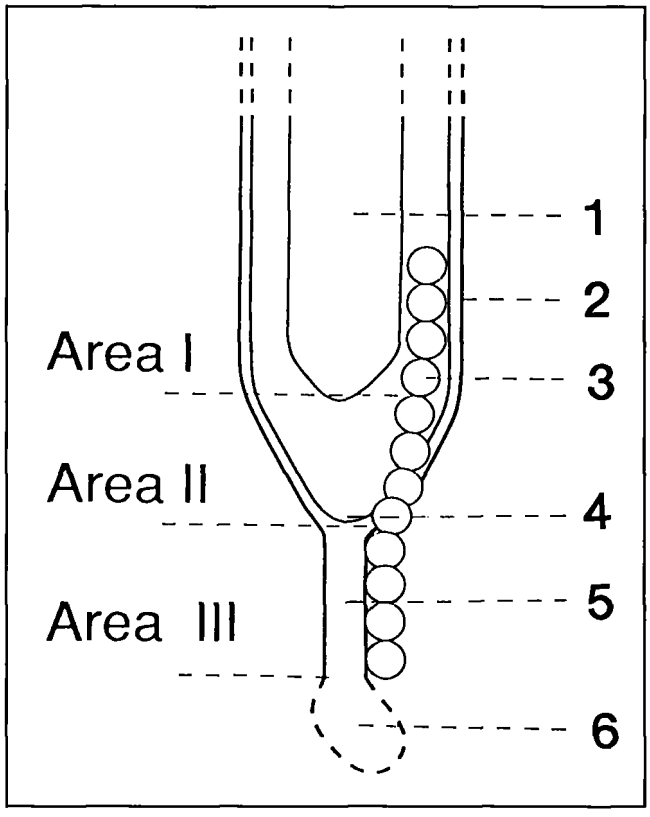


Figure 4
Sketch of branchial area, ventral view, of a hagfish (*Eptatretus*) delineating Areas I, II, and III, referred to in counts of gill pouches for each Area given in Table 8. (1) DM, posterior portion; (2) left branch of VA; (3) gill pouch; (4) point of branching of VA; (5) VA; (6) ventricle.

2a Prebranchial slime pores 7(4–10). Ventral finfold weakly developed, often vestigial or absent. Barbels small, not robust. Color dark purplish brown..... ***E. deani***

2b Prebranchial slime pores 12–17. Ventral finfold variably well developed to absent. Barbels variably large to small. Color purplish to light or dark reddish brown **3**

3a All barbels large, robust. Third barbel 49%(42–59%) of preocular length. Prebranchial slime pores 12–13(10–15). Branchial apertures 11(10–12). Ventral finfold very weakly developed, usually absent. Color dark purplish brown..... ***E. fritzi* n. sp.**

3b All barbels small, not robust. Third barbel 34%(31–37%) of preocular length. Prebranchial slime pores 13–17. Ventral finfold either prominent, vestigal or absent. Branchial apertures 10–14. Color dark brown to light reddish brown **4**

4a Branchial apertures 12(10–14). Ventral finfold prominent, with wide pale margin. Color light reddish gray or light brown. Extensive piebaldness common ..... ***E. stoutii***

4b Branchial apertures 10(9–12). Ventral finfold vestigial or absent. Color dark reddish brown, not piebald ..... ***E. sinus* n. sp.**

Systematics

Eptatretus mcconnaugheyi new species

It is not feasible to attempt a meaningful synonymy for this new species, as it and *E. stoutii* are very similar and occur sympatrically off southern California. *Eptatretus stoutii* has long been extensively used in biochemical and physiological research. However, none of this research material has been examined by us, and no identification credited to competent ichthyologists. As *E. mcconnaugheyi* is not previously known, it is very likely to have formed a part of this research material, particularly from southern California.

Holotype SIO69-231E, female, 482 mm TL, taken at 32°32′0″N, 117°21′07″W, in a trap on bottom at 148 m, 11–12 April 1969.

Paratypes SIO69-228B, 14(185–400 mm TL), taken at 32°05.9′N, 117°04.4′W, 177 m, 10–11 March 1969; SIO71-114, 7(360–440 mm TL), taken at 28°21.0′N, 115°43.0′W, 689 m, 25–26 May 1971; SIO69-231E, 7(200–448 mm TL), taken with the holotype; SIO68-126, 5(355–409 mm TL), taken at 25°49′N, 110°51′W, 351 m, 25–26 January 1968; CAS 63203, 7(210–400 mm TL), taken at 32°31.8′N, 117°21.6′W, 145 m, 29 September 1972; LACM 44409-1, 6(195–430 mm TL), taken at 32°31.8′N, 117°21.1′W, 145 m, 29 September 1972; USNM 29630, 7(245–380 mm TL), taken at 32°31.8′N, 117°21.1′W, 145 m, 29 September 1972.

Additional material SIO56-9, 1(340), 42 m; SIO68-109, 1(390), 415 m; SIO68-11, 1(230), 177 m; SIO68-124, 1(249), 205 m; SIO68-125, 19(239–347), 278 m; SIO68-126, 5(355–409), 351 m; SIO68-127, 3(315–440), 238 m; SIO69-179, 2(235–376), 109 m; SIO69-181, 2 (141–312), 183 m; SIO69-225C, 1(392), 371 m; SIO69-228B, 14(195–406), 99 m; SIO69-228C, 1(433), 166 m; SIO69-231C, 1(372), 139 m.

Distribution *Eptatretus mcconnaugheyi* appears to consist of two disjunct populations: one from Santa Monica Bay, California, to the Cedros and San Benito Islands, Mexico, and one apparently restricted to the lower portion of the Gulf of California. These two populations appear to differ significantly ($P>0.001$) in numbers of trunk and total slime pores, the higher counts occurring in the southern California population.

Depths of capture range between 42 and 384 m off southern California and between 177 and 415 m in the Gulf of California. Collecting efforts between the Cedros and San Benito Islands and the mouth of the Gulf have failed to take the species.

Diagnosis Prebranchial length usually less than branchial length, rarely equal to or very rarely even slightly longer. Body moderately robust, deepest at midbody, its width about half its depth, increasingly laterally compressed toward tail. Tail length 13–16% of TL, its depth about half its length. Ventral finfold usually prominent, often low, with pale margin. Caudal finfold prominent, wide, the margin thin and pale. Three fused cusps (multicusp) on anterior, two fused cusps on posterior, set of cusps.

Etymology We take great pleasure in dedicating this new species to Ronald R. McConnaughey, friend and superb marine technician, who was instrumental in the development of capture gear and party to the collecting of many of the thousands of specimens of species examined by us.

Description Counts (Tables 2–8) and body proportions (Table 1) are given and compared with similar data for the other four species treated here. Body moderately robust, deepest at midbody, the width about half the depth, increasingly laterally compressed toward tail. Tail spatulate, its length about twice its depth, its ventral margin sloping downward below level of body. A thin, deep caudal finfold, with a narrow pale margin, extends from cloaca around end to about over cloaca dorsally. Ventral finfold low, usually entirely unpigmented. Head at eyespots about as deep as wide, narrowing to rostrum. Width of rostrum about half the width of head at eyespots. Eyespots rather prominent, of moderate size, the margins well defined. Oral surface short, sloping posteriorly at about 45° angle from the vertical. Barbels small, the distal thirds unpigmented. First barbel only slightly shorter than second, often equal to or slightly longer, averaging 64%(52–79%) of length of third, the second barbel averaging 70%(51–84%) of length of third. Length of first nasal barbel, left side, is given in Table 6 and compared with that of other species treated.

Head grooves Grooves present before and behind eyespots on each side of dorsal midline. Three to six grooves, each side, before eyespots lie in longitudinal rows, and two to four ventrad in transverse rows. One to eight grooves may occur behind eyespots. Most lie transversely, with none to three longitudinally, at sides. As many as 24 grooves may occur on one specimen.

Color a dark, reddish brown in life without pale spots or areas. Barbels pale on distal thirds.

Length of DM 27% (21–39%) of TL. DM width 68% (57–90%) of its depth. VA variable in length, averaging 11% (5–22%) of DM length. DM to VA 14% (5–26%) of DM length, and 1.4% (0.5–9%) of VA length. Number of GP in positions relative to DM and VA, Areas I, II, III, are given in Table 7, defined in Figure 4, and compared with similar data for the other four species discussed herein. Afferent duct of last GP, left side, always confluent with PCD.

Higher numbers of GA, left vs. right sides, may differ between the two populations (Table 8). Off southern California, the higher count is about equal for both sides at 4 and 5 each. In the Gulf population, the higher count is always on the left side.

Eggs The holotype contains 18 mature eggs, the largest 25.2 × 9.0 mm. The largest egg found in any female is 26 × 8 mm. The smallest female with eggs, most in round or slightly ovoid stages, is 267 mm TL. It may be that females of the Gulf population mature at a smaller size than do those from southern California. One, 267 mm TL, has eggs to 15.8 mm; one, 352 mm TL, has eggs to 20.8 mm; and one, 32 mm TL, has eggs to 17.6 mm. These figures contrast sharply with those of the southern California population, in which eggs ranging between 15 and 29 mm occur only in females of 400–508 mm TL. Perhaps these differences are an artifact of sampling or of developmental stages relative to both time and size, or to the relatively small number of specimens available (97).

All mature eggs of the holotype have fully developed anchor filaments (terminal hooks) with most free of encapsulating membrane (Fig. 3), and apparently ready for extrusion. This condition was rarely observed among the nearly 2400 specimens of all species of *Eptatretus* examined by us in the course of our studies. The eggs are linked by filaments in rows in a fashion similar to that shown by Dean (1989) and Jensen (1966).

The sex ratio is unbalanced. Of a total of 58 specimens for which sex could be reliably determined, 64% were female and 36% male.

Differentiation All body proportions and most counts for the two disjunct populations are very similar. However, significant differences ($P>0.001$) occur in numbers of trunk and total slime pores (Tables 3, 4), despite considerable overlap in values of thousandths of total length.

Discussion This species and *E. stoutii* appear to be closely related and occur sympatrically off southern California. However, the two are readily separable in that the prebranchial length of *E. mcconnaugheyi* is less, rarely even slightly longer, than the branchial length, and always greater in *E. stoutii*. Also, the numbers of prebranchial slime pores differ notably, 8–9 (6–11) in *E. mcconnaugheyi* and 13 (10–16) in *E. stoutii* (Table 2).

Eptatretus fritzi new species

Holotype SIO66-26, male, 550 mm TL, taken at 28°51′N, 118°14′W, in a trap on bottom at 512 m, 3–4 April 1966.

Paratypes SIO66-26, 30(280–585 mm TL), taken with the holotype; CAS 63201, 15(325–540 mm TL), taken with holotype; LACM 44407-1, 15(375–495 mm TL), taken with the holotype; USNM 296318, 15(350–570 mm TL), taken with the holotype; SIO63-177, 20 (324–522 mm TL), taken at 28°52′N, 118°14′W, 2743 m, 24 April 1963; SIO66-22, 36(232–521 mm TL), taken at 29°06′N, 118°17′W, 402 m, 12 April 1966; SIO66-23, 195(286–556 mm TL), taken at 28°54′N, 118°13′W, 444 m, 2–3 April 1966; SIO66-36, 2(354–405 mm TL), taken at 29°30′N, 117°17′W, 512 m, 6–7 April 1966; SIO67-60, 120(281–498 mm TL), taken at 29°09′N, 118°16′W, 832 m, 26–27 April 1966; SIO68-664, 2 (425–535 mm TL), 183 m, 15–16 November 1968; SIO72-294, 4(207–541 mm TL), taken at 29°10′N, 118°16′W, 256 m, 12–13 April 1970.

Distribution Known only from the immediate vicinity of Guadalupe Island, Mexico. Depths of capture range between 182 and 2743 meters.

Diagnosis All barbels notably larger and more robust than on any other species of *Eptatretus* known to us (Table 6). Ventral finfold absent or vestigial, without pale margin. Prebranchial and tail lengths each greater than branchial length. Color a dark purplish-brown. Prebranchial slime pores 12 (10–15). Three fused cusps (multicusp) on anterior set of cusps, two fused cusps on posterior set.

Etymology We take great pleasure in dedicating this species to Frithjof (Fritz) Ohre, friend, willing, eager, and industrious volunteer on many of the expeditions on which all species treated here were taken, particularly those to Guadalupe Island.

Description Counts (Tables 2–8) and body proportions (Table 1) are given and compared with similar data for the other four species treated here. Body robust, deeper than wide, deepest at midbody, increasingly laterally compressed toward tail. Tail spatulate, its depth about half its length, its ventral outline not sloping downward from cloaca. Caudal finfold variably

thin to thick, beginning at cloaca and extending around tail to about over origin of cloaca, without pale margin. Ventral finfold usually absent, present in only 28 of 341 specimens (8.2%). When present it is intermittently and weakly developed along its length. It is thick, heavy, and without pale margin.

Head at eyespots about as deep as wide, narrowing to rostrum. Eyespots prominent, the margins irregular. Oral surface sloping posteriorly at about a 35° angle from the vertical. All barbels are notably longer and thicker in proportion to total length than on any other myxinid known to us (Table 6). First and second barbels about equal in length, the third averaging 49%(42–50%) of preocular length. First barbel as long or longer than width of nasal orifice when manually flattened (124%(100–203%)). First barbels average less than 50% of this width in all other species of *Eptatretus*.

Head grooves Grooves always present behind eyespots but occasionally absent before. Those behind average 5(3–10) in number and are arranged mostly in transverse rows with an occasional few grooves lying ventrad and longitudinally. Those before eyespots average 3(1–6) in number and lie longitudinally. Grooves behind eyespots originate very near the dorsal midline but do not cross. Those before eyespots are notably more distant from the midline.

Color Color a dark purple to black in most specimens, a chocolate brown in others, rarely showing pale spots. Notes by the senior author, party to the first and most subsequent captures, state, "a dark color." The chocolate color may be an artifact of preservation. GA, slime pore margins, and ventral finfold are without pale margins.

DM short, moderately robust, its length 27%(21–34%) of TL. DM width 13%(11–15%) of its length, its depth 73%(58–88%) of its width. VA length variable, 16%(8–42%) of DM length. DM to VA also variable, 15%(4–32%) of DM length and 90%(24–206%) of VA length. Numbers of GP in positions relative to DM and VA, Areas I, II, III, are given in Table 7, defined in Figure 4, and compared with similar data for the other four species treated here. Afferent duct of last GP, left side, always confluent with PCD.

Variation occurs in numbers of GA between left and right sides, the higher number always on the left side, 81 vs. 0 instances (Table 8).

Eggs The largest egg, 33.8 × 8.5 mm, occurred among 14 large eggs in a 386-mm TL female. No more than 16 and as few as 10 almost fully developed eggs were found in any female. No egg had free anchor filaments, but occasionally they were visible through the encapsulating membranes.

The sex ratio is unbalanced. Of a total of 358 specimens for which sex could be reliably determined, 60% are female and 40% male.

Discussion This species and *E. deani* occur sympatrically near Guadalupe Island, Mexico. Both were taken in the same trap on two occasions. They are similar in coloration, being very dark brown to purplish-black, but *E. fritzi* seems much less prone to piebaldness than *E. deani* as very few pale spots were noted. Primary differences are that the barbels of *E. fritzi* are much longer and more robust than those of *E. deani* (Table 6), and that it has more prebranchial pores, 12 (10–15) vs. 7(4–10). Also, *E. fritzi* usually has no ventral finfold (313 of 341 specimens, 91.8%), whereas in *E. deani* this finfold is usually present (863 of 892 specimens, 96.6%), although rather weakly developed.

Eptatretus sinus new species

Holotype SIO68-108, female 307 mm TL, taken at 25°49′N, 110°44′W, in a trap on bottom at 708 m, 22–23 January 1968.

Paratypes SIO68-108, 31(230–425 mm TL), taken with the holotype; SIO68-94, 29(129–346 mm TL), taken at 29°20′N, 113°10′W, 263 and 283 m, 20 January 1968; SIO68-100, 60(267–464 mm TL), taken at 29°00′N, 113°25′W, 467 m, 20–21 January 1968; CAS 63202, 15(270–400 mm TL), taken at 25°49′N, 110°44′W, 708 m, 22–23 January 1968; LACM 44408-1, 14 (270–400 mm TL), taken at 25°49′N, 110°44′W, 708 m, 22–23 January 1968; USNM 296319, 15(275–420 mm TL), taken at 25°49′N, 110°44′W, 708 m, 22–23 January 1968.

Additional material SIO68-97, 7(223–308), 881 m; SIO68-98, 17(276–338), 881 m; SIO68-99, 11(263–420), 668 m; SIO68-101, 16(264–355), 198 m; SIO69-201, 1 (190), 1454 m; SIO69-203, 11(381–630), 759 m; SIO69-206, 54(363–430), 768 m; SIO69-207, 57(259–404), 475 m.

Distribution Known only from the midriff area of the Gulf of California, Mexico, between about 28° and 30°N latitudes. Depths of capture range between 198 and 1330 meters.

Diagnosis Prebranchial length greater than branchial length. Tail length usually greater than branchial length, occasionally equal to or less. Ventral finfold low, unpigmented, occasionally absent. Barbels usually unpigmented, except rarely at bases. Three fused cusps (multicusp) on anterior, two fused cusps on posterior, sets of cusps.

Etymology From the Latin "sinus," meaning gulf, by reason of its apparent restriction to the midriff area of the Gulf of California, Mexico.

Description Counts (Tables 2–8) and body proportions (Table 1) are given and compared with similar data for the other four species treated here.

Body robust, deepest at midbody, deeper than wide, increasingly laterally compressed toward tail. Tail spatulate, its depth about half its length, its ventral outline not sloping downward from cloaca. Caudal finfold thickened ventrally, thinner around tail, ending dorsally over cloacal origin. Ventral finfold usually present, low, unpigmented. It is absent on 10% of 363 specimens.

Head at eyespots as deep as wide, the oral surface sloping posteriorly at about 35° from the vertical. Eyespots prominent, the margins well defined. Barbels short, unpigmented except rarely at bases. Second barbel usually longer than first but occasionally shorter or of equal length. First and second barbels respectively 60% and 64% of third barbel. Length of first nasal barbel is given in Table 6 and compared with that of other species treated.

Head grooves Grooves present before and behind eyespots, each side. One to five grooves occur behind eyespots, most lying transversely, but a few lying longitudinally at side of head. One to four grooves lie before eyespots in longitudinal rows. Occasionally no grooves occur before eyespots.

Color Color reddish-brown, without pale markings or spotting. GA, PCD, and an occasional slime pore have narrow pale margins.

Length of DM 24%(21–29%) of TL. DM width 14% (12–17%) of its length, its depth 65%(54–86%) of its width. DM to VA 16%(15–26%) of DM length. VA length 25%(17–39%) of DM length. VA length variable, averaging 66%(22–127%) of distance from DM to VA. Numbers of GP in position relative to DM and VA, Areas I, II, III, are given in Table 7, defined in Figure 4, and compared with similar data for the other four species treated here. Afferent duct of last GA, left side, always confluent with PCD.

Variation in numbers of GA occurs between left and right sides, with higher numbers predominating on the left, 65(15%) vs. 8(2%), *N* 444 (Table 8).

Eggs The holotype, 370 mm TL, contains many small eggs, to about 4 mm. The largest egg found (among 21 large ones) was 32 × 7.5 mm in a female of 371 mm TL. The most eggs found was 37 (18 × 5 mm) in a female of 420 mm TL. Eggs (28) to 21 mm were found in a female of 372 mm TL, and to 23 mm in one of 335 mm TL. Apparently, *E. sinus* matures at a short total length, as a male of 130 mm and a female of 142 mm were noted. These are surprisingly small sizes, for in other species, these total lengths are distinctly juvenile, and the sex determinable only under very high magnification, if at all. Encapsulated anchor filaments are visible on eggs of 20 mm length.

The sex ratio of *E. sinus* is unbalanced. Of a total 424 specimens for which sex was reliably determined, 65% are female, 35% male.

Eptatretus deani (Evermann and Goldsborough 1907)

Synonymy

Polistotrema deani Evermann and Goldsborough 1907: 221–222, 225–226, fig. 1 (original description; compared with *Polistotrema stoutii*; Albatross Station 4235, Spacious Bay, Cleveland Peninsula, 130–193 fathoms, and Albatross Station 4238, Nose Point, Behm Canal, southeastern Alaska, 229–231 fathoms); Wilimovsky 1954a: 3, and 1954b: 281 (SE Alaska to California), 1958: 18 (compared with *P. stoutii*; SE Alaska to California); Barham et al. 1967: 780, fig. 7 (shown associated with *Anoplopoma fimbria*, Trieste Dive 105; 1060 m in San Diego Trough) [presumptive].

Polistotrema curtiss-jamesi Townsend and Nichols, 1925: 4–5, 18, 20, fig. 1 (original description; compared with *P. stoutii*; south of Monterey to Santa Barbara I.: 440–585 fathoms; Albatross Stations 5695, 5696, 5697, 5698; type locality Station 5697, 585 fathoms).

Heptatretus deani Regan, 1912: 534–535 (comparisons; synonymy; references; diagnosis; Alaska).

Bdellostoma deani, Adam and Strahan 1963; 6 (11–12 gills; length to 620 mm; Alaska).

Eptatretus deani, Day and Pearcy 1968: 2668, 2771 (listed; about 1200 meters off Oregon); Bourne and McAllister 1969: 3246–3248, fig. 1 (first British Columbia records, 54°47′N, 130°58′30″W at 90–250 fathoms: 48°53′N, 126°40′W at 373 m: description); Kukowski 1972: 7, 24 (Monterey Bay; references); Miller and Lea 1972: 32 (Cedros and Guadalupe Is., Baja California to SE Alaska: length to 20 inches; depth 1560–3500 feet; common in deep water, uniform purplish black); Fitch 1973; 815 (off Eureka, California, 565–585 m); Hart 1973: 10, 16–18, fig. 1 (first description for Canada; comparisons in key; description; geographical and bathymetric distributions; references); Gates and Frey 1974: 60 (vernacular, California): Smith and Hessler 1974; 72–73 (14 miles off San Diego; depth 1230 m; respiration rate measured *in situ*; a dominant species in San Diego Trough); Jespersen 1975: 189–190, 195, 197,

fig. 15 (spermiogenesis; southern California off San Clemente I. at about 1280 m; off Los Coronados I. at about 1097 m; Theisen 1976: 167–173, figs. 2. 4. 7. 10 (microstructure of olfactory system; southern California; 1097 m.

Holotype USNM 57820, sex not determined, "21" inches (about 535 mm TL), taken near Yes Bay, Behm Canal, Cleveland Peninsula, southeastern Alaska, easterly of Ketchikan, about 55°55'N, 131°55'W, by dredge at 419–423 m (Albatross Station 4238), 8 July 1903.

Paratypes USNM 61162, two: one a female, in rotting condition, taken at Albatross Station 4229 and 4235, Behm Canal, southeastern Alaska, Nose Point, near the holotype, by dredge at 419–423 m, 16 July 1903. (The type specimens were examined by Carl L. Hubbs at USNM, 25 February 1972.)

Additional material SIO59-47, 6(359–458), 823 m; SIO60-540, 1(484), 1920 m; SIO63-177, 20(286–457), 2743 m; SIO63-868, 21(345–498), 107 m; SIO64-281, 1(451), 587 m; SIO64-496, 5(374–455), 475 m; SIO64-497, 26(335–445), 512 m; SIO64-498, 37(291–441), 616 m; SIO64-499, 38(294–473), 960 m; SIO65-499, 54 (321–521), 933 m; SIO65-465, 19(370–554), 1302 m; SIO66-27, 2(148–455), 1252 m; SIO66-36, 130(233–509), 512 m; SIO66-535, 21(377–453), 1013 m; SIO66-537, 1(417), 1244 m; SIO66-551, 2(390–401), 1156 m; SIO67-64, 20(380–510), 980 m; SIO67-109, 52(312–523), 1024 m; SIO67-110, 1(369), 1445 m; SIO67-118, 51(288–467), 732 m; SIO68-427, 5(396–470), 1840 m; SIO68-428, 6(320–481), 800 m; SIO69-225F, 38(342–429), 633 m; SIO69-227B, 26(288–495), 744 m; SIO69-288D, 56(182–423), 609 m; SIO71-103, 4(401–484), 1373 m; SIO71-7, 42(280–484), 1244 m.

The following collections, with incomplete data were taken between British Columbia and northern California: OSUO 3869, 3(267–450), OSUO 3870, 2(385–415), OSUO 3871, 2(404–447), BCPM 46-15, 1(366), BCPM 72-9, 4(402–475), BCPM 72-10, 1(460), CAS 10877, 1(390), CAS 26633, 2(318–365), CAS 20404, 1(395), Albatross Station 3126, 1(317), 378 m; UW 00379, 1(440), 155 m; UW 18148, 1(391), 595 m; UW 18149, 1(383), 1098 m; UW 18151, 1(405), 1190 m; UW 18152, 7(370–445), 1190 m; UW 18153, 2(402–466), 932 m; UW 18154, 1(354), 183 m; UW 18155, 6(376–433), 1190 m; UW 18157, 5(400–440), 732 m; UW 18158, 12(342–459), 824 m; UW 18159, 2(343–375), 732 m; UW 19095, 3(421–440), UW 19127, 2(414–444), UW 19206, 1(320), UW 19310, 6(382–479).

Distribution Southeastern Alaska to near Guadalupe Island, Mexico. Despite this extensive range of about 2600 miles, no significant variation in counts or measurements with latitude was demonstrated.

Diagnosis Prebranchial slime pores 7(4–10). Prebranchial length usually greater than branchial length, rarely equal to or less. Tail length variably equal to, or slightly less or greater than branchial length. Color a purplish-black, with occasional pale spots and areas. Anterior part of head often pale. Three fused cusps (multicusp) on anterior set of cusps, two fused cusps on posterior set.

Description Counts (Tables 2–8) and body proportions (Table 1) are given and compared with similar data for the other four species treated here.

Body robust, deeper than wide at midbody, progressively laterally compressed toward tail. Prebranchial slime pores 7(4–10). Branchial apertures 11(10–12). Prebranchial length usually greater than branchial length, rarely equal to or less. Tail length greater than branchial length in 45%, equal-to in 30%, and less-than in 26% of 441 specimens. Ventral finfold weakly developed, occasionally absent, without pale margin. Tail spatulate, its ventral surface sloping downward at a slight angle from the ventral body line. Head wider than deep. First barbels usually shorter than second, occasionally equal to or slightly longer; the first about 58% of length of third barbel, the third about 70% of preocular length. Eyespots prominent, variable in size, usually with irregular margins. Length of first nasal barbel is given in Table 6 and compared with that of other species treated.

Head grooves Of 104 specimens selected for mucus-free condition, 18 (17%) had no grooves. Of those having grooves before eyespots, 45% had them on both sides, about 6% had them on either the right or left side only. Grooves occur on both sides behind eyespots in 80%, on the left only in 8%, and on the right side only in 12% of the 104 specimens.

Color Color usually a purplish-black or very dark brown. Specimens with a brownish base color show variable amounts of pale spots and patches (piebaldness) that range from slight to considerable. An occasional specimen has a pale head from rostrum to first few prebranchial slime pores. Most heads are pale near tip of rostrum. On pale heads, the barbels usually are unpigmented. Ventral and caudal finfolds without pale margin except when spotted in piebald specimens. Gill apertures and slime pores with narrow pale margins. Cloacal margins with rather wide pale areas.

Variation occurs in numbers of GA between left and right sides with higher numbers predominating on the left, 125 (11%) vs. 21 (2%) on the right side in 1145 counts (Table 8).

DM length 24% (20–26%) of TL. Width of DM 15% (13–18%) of its length, its depth 64% (54–80%) of its width. DM to VA 9% (0–15%) of DM length. VA length 31% (23–36%) of DM length. Numbers of GP in positions relative to DM and VA, Areas I, II, III, are given in Table 7, defined in Figure 4, and compared with similar data for the other four species treated herein. Afferent duct of last GA, left side, always confluent with PCD.

Eggs Mature eggs large, usually distinctly curved. The largest egg found measured 52.3 × 10.5 mm and was among 14 large eggs in a 500-mm TL female. Apparently very few eggs mature at one time from the many hundreds of tiny, round to slightly ovoid eggs normally present. No more than 15 nor fewer than 8 large eggs (30 mm and longer) were present in any female. Anchor filaments were visible on all eggs of 35 mm length or more, but were still encapsulated.

The sex ratio of *E. deani* is notably unbalanced. Of a total of 480 specimens, 74% were female, 26% male. The smallest female noted was 249 mm TL, the smallest male 255 mm TL.

Eptatretus stoutii (Lockington 1878)

Synonymy The following synonymy includes only those references arbitrarily considered by us to have taxonomic, behavioral, or distributional value and not mere usage of the name. About 120 references using the name *stouti* or *stoutii* pertain only to biochemical and/or physiological studies that serve no apparent taxonomic purpose and are not included.

Bdellostoma stoutii Lockington, 1878:792–793 (original description; compared with *B. polytrema*; mouth of Eel River, Humboldt County, California); Jordan and Gilbert 1883:6 (brief description, after Lockington; coast of California; not rare).

Bdellostoma stouti, Dean 1899:223–276 (embryonic development of larvae and eggs).

Bdellostoma dombeyi, Jordan and Gilbert 1883:57 (in part; characters and feeding habits; California); Worthington 1905:625–663 (description, behavior in aquaria; habitat in Monterey Bay; counts of gill openings; feeding; eggs); Ayers and Worthington 1907: 327–336 (figures and description, lateral lines found only on head).

Homea stoutii, Dean 1903:295–298 (partial albinism in anterior portion), 1904: 6. 7. 16, 18, 20 (seasonal spawning; largest are females; California).

Heptatretus stouti, Regan 1912:534–535 (synonymy; comparisons; diagnosis; California).

Eptatretus stouti, Starks and Morris 1907:161 (common in deep water off San Diego; north to Cape Flattery; abundant in Monterey Bay); Strahan 1963:22 (behavior and attitudes in aquaria); Linthicum 1971: 17–22 (immunological study; tying itself in knots to remove slime; slime production, teeth); Kukowski 1972:24, 37, 43 (Monterey Bay and Elkhorn Slough; references), 1973:7, 19, 22–23 (Monterey Bay; occurrence data; recurrent groupings); Anonymous 1973: 68 (observed at camera station at 306 m, SW of White's Point, southern California); Allen 1976:95 (only species not taken in otter trawl or by setline in Santa Monica Bay, southern California; has been so collected elsewhere); Downing et al. 1981:326–328 (description and figures of mucus thread cells in slime glands); Fernholm 1985:113–122 (in part; no ciliated cells or innervation or electroreceptory capacity found in lateral lines).

Polistotrema stouti, Clemens and Wilby 1946:9 (characters; white margin on ventral finfold; reaches 25 inches; species attacked; attachment of eggs; W coast, Vancouver I.).

Polistotrema stoutii, Fowler 1908:461 (Pacific Grove on Monterey Bay, California; gill opening counts for 8 specimens); Clemens and Wilby 1961:18, 49–50 (description; history on British Columbia west coast; eggs; southern California to SE Alaska; in part); McInerney and Evans 1970:966–968 (habitat characteristics; Mayne Bay in Barkley Sound, Vancouver I.); Sasaki 1972:283 (Queen Charlotte Sound, Vancouver I.; rare).

Dodecatrema stoutii, Fowler 1947:3 (proposed new name to replace *Bdellostoma*).

Eptatretus stoutii, Jensen 1959:798 (albino and piebald variants; ratio to normal; habitat; abundance in southern California; submarine canyons tributary to San Diego Trough; 210 fathoms), 1966:82–90 (habits; description and figures of the four hearts; functions); Taylor 1967:181–187 (chromosome numbers; probably supernumeraries; Alaska to Baja California; habitat; 60–1800 feet); Day and Pearcy 1968:2668 (depth distribution off Oregon); Bourne and McAlister 1969:3248 (compared with *E. deani*); Miller and Lea 1972:32 (Pt. San Pablo, Baja California, to SE Alaska; length to 25 inches; depth range 30-2400 feet; description); Hart 1973:16, 18–19, 53 (comparisons in key; description; common; geographical and bathymetric distribution in and off Barkley Sound; probably quite generally distributed in British Columbia; Alaska records not confirmed in recent reviews; references; egg cases); Smith and Hessler 1974:72–73 (*in situ* respiration rate significantly greater than that of *E. deani*); Anonymous 1974:50 (observed only during day at baited camera off Palos Verdes, California); Fernholm 1975:201–203 (structure and deposition of eggs compared with that of *E. burgeri*; *Bdellostoma dombeyi* of Worthington referrable to *E. stoutii*); Jespersen 1975:189–198

(spermiogenesis; offshore in 45.7 and 53.0 m); Knaggs et al. 1975:56–57 (taken off central Baja California; southern range extended from Cedros I. to Pt. San Pablo); McMillan and Wisner 1984:255 (lateral line described and figured); Wisner and McMillan 1988:231 (the term "head grooves" suggested to replace that for lateral lines.

Neotype SIO68-426, male, 530 mm TL, taken about 2 miles southwest of the whistler buoy at entrance to Humboldt Bay, California, in a trap on bottom at 38–44 m, on 27 August 1963.

Additional material, northernmost collections SIO 68-426, 34(291–527), taken with the neotype. BCPM 60-1, 2(474–580), taken at about 49°33'N, 126°38'W, outside Nootka Bay, Vancouver I.; no other data; BCPM50-3, 2(192–420), taken off west coast of Vancouver I.; no other data; BCPM98-2, 1(506), taken off west coast of Vancouver I.; no other data; UW-15869, 4(144–400), taken at 48°51.8'N, 124°35.8'W, in Strait of Juan de Fuca, in a trawl; depth not recorded; 27 March 1956; UW-18161, 6(437–512), taken "8 mi out" from Depoe Bay, Oregon at 79 m; method of capture not recorded, 30 August 1964; CAS 19191, 1(403), taken at Holmes Harbor, Puget Sound; no other data; OSU-OTB-180, 1(435), taken at 44°43.5'N, 124°18.1' W, in a bottom trawl at 96 m, 24 July 1967.

Twelve collections in the California Academy of Sciences, comprising one or two specimens each, and with very incomplete or absent capture data, were taken between Cape Mendocino and San Diego, California (CAS 6832, 7353, 11115, 12751, 12881, 20290, 26491, "Acc. 1954:XI:23," IU 1006, 1069, 1086, 1613 (the IU collections are now at CAS). Similarly, three collections (MCZ 28802, 28803, and 32782), totaling five specimens, with very limited data, were taken in Monterey Bay, California.

Material was taken in 1963 by David Jensen, then of Scripps, in collaboration with the University of Washington Atomic Energy Program. Most specimens were sacrificed to that program. A total of six collections were made between Cape Disappointment, at mouth of Columbia River, off Depoe Bay, Oregon, off Humboldt Bay, and Fort Bragg, California. Numbers of specimens ranged between 6 and 152, and were taken at depths of 38–132 m in bottom traps.

More than 40 collections, comprising nearly 1500 specimens, taken in the southern California area (Pt. Conception to Islas Todos Santos, Baja California, Mexico) were used for certain counts but are not listed among the study material. In addition, hundreds of specimens in the Scripps Marine Vertebrate Collection taken off San Diego were examined for certain characters only and are not listed. However, all collections from outside the Southern California area are listed.

Southernmost collections SIO59-92, 1(345), 28°23' N, 115°21'W, 280 m; SIO62-91, 3(164–207), 28°11'N, 115°23'W; SIO64-951, 1(363), 31°08'N, 116°35'W, 137 m; SIO71-114, 30(300–465), 28°21'N, 115°43'W, 384 m; SIO71-121, 7(283–384), 28°18'N, 115°29'W, 311–330 m; SIO71-126, 83(195–460), 30°22'N, 116°07'W, 201 m; SIO73-373, 2(320–395), 28°50'N, 114°48'W, 92–95 m.

Distribution Nootka Bay, west side of Vancouver Island, British Columbia, Canada, to Pt. San Pablo, Baja California (about 27°14'N, 114°30'W). Although *E. stoutii* has been reported from southeastern Alaska, we have found no valid records of capture north of Nootka Bay (about 49°33'N, 126°38'W). Despite this extensive range of about 2200 miles, no significant variation in counts or measurements with latitude was demonstrated.

Carl L. Hubbs, at USNM, 28 June 1972 (personal notes), examined collections from southeastern Alaska, labeled as *E. stoutii*, and found them to be either misidentified or with the capture data indicating localities far from Alaska, as follows: USNM 53963, listed as from southeastern Alaska, but with coordinates indicating the vicinity of Monterey, California; USNM 53964, listed as from Alaska, but with coordinates given as 33°08'N, 118°40'W, the vicinity of Santa Barbara, California. Hubbs recorded this specimen as *E. deani* "without question;" USNM 73737, Albatross Station 3077, east of Sitka, Alaska, labeled as *E. stoutii* but referrable to *E. deani*, based on the skin being jet black and eggs to 38 mm length—a length much greater than found in *E. stoutii* (28 mm); in addition, a collection, UW 02738, four, 332–390 mm TL, was recorded simply as "S.E. Alaska; International Fish Commission, 1931."

Depths of capture range between 16 m off the San Onofre Nuclear Power Plant, near San Clemente, southern California, and 633 m at 31°47'N, 116°50'W, south of Ensenada, Baja California, Mexico.

Latitude may be of limited significance in depths of capture (habitat), as the farthest-north least depth is 44 m, off Humboldt Bay, and the farthest south the 16 m capture off the San Onofre Nuclear Power Plant. The species has been taken by scuba divers between 18 and 21 m near La Jolla, California.

Diagnosis Body slender, only slightly deeper than wide. Prebranchial length greater than branchial length. Branchial apertures 12(10–14). Ventral finfold prominent, the distal margin pale. Eyespots small, prominent, the margins well defined. Color a light brown with pale spotting and small blotches common.

Three fused cusps (multicusp) on upper and two fused cusps on lower sets of cusps.

Description Counts (Tables 2–8) and body proportions (Table 1) are given and compared with similar data for the other four species treated herein.

Body slender, only slightly deeper than wide, progressively laterally flattened toward tail. Tail spatulate, its ventral profile not slanting downward, but lying on a straight line with ventral profile of body, its depth 43% (30–56%) of its length. A thin, well developed, pale-margined finfold extends from cloaca around tip of tail, ending about over cloaca. Tail length usually greater than branchial length, but is equal-to in 12% and less-than in 8% of 421 specimens. Ventral finfold prominent, with pale distal margin. Head at eye spots about as deep as wide, narrowing toward rostrum. Eyespots small, with distinct margins. Barbels small, usually without pale tips. Second barbel usually longer than first, the first shorter than second in 41%, about equal to in 51%, and longer than second in 7% of 315 specimens. First barbel 51% (41–84%), the second 64% (49–98%) of third barbel. Length of first nasal barbel is given in Table 6 and compared with that of other species treated.

Variation occurs in numbers of GA, left and right sides, with higher numbers predominating on the left, 167 (11%) vs. 56 (4%), N-1554 (Table 8).

Head grooves Grooves present above and below eyespots. Two to four (rarely five) grooves lie above eyespots in lines nearly parallel to the longitudinal axis of the body. Grooves below eyespots are arranged in two groups; 2–5 grooves lie transversely, and from 0–3 lie alongside laterad to and nearly parallel with the longitudinal axis. No grooves cross the dorsal midline.

Color Color ranges between a light to purplish-gray to light brown, with occasional pinkish overtones. Pale spots and blotches (piebaldness) are common. Complete albinism and piebaldness was reported by Jensen (1959:798, figs. 1, 2). Dean (1903:295–296, fig. 1) descriped and figured a specimen with large pale areas on head and anterior ventral surface.

DM short, moderately robust, its length 25% (22–28%) of TL, its width 12% (11–13%) of DM length, its depth 74% (64–77%) of its width. Distance from tip of DM to branching of VA 14% (8–20%) of DM length, and that distance is 42% (25–72%) of VA length. VA length 32% (22–40%) of DM length. Numbers of GP in positions relative to DM and VA, Areas I, II, III, are given in Table 7, defined in Figure 4, and compared with similar data for the other four species treated here. Afferent duct of last GA, left side, always confluent with PCD.

Eggs The largest egg found measured 28.6 × 7.5 mm, in a female of 435 mm TL. Well developed eggs with anchor filaments are visible but encapsulated. The number of almost fully developed eggs (20 mm or longer) varies from 11 (23 × 7 mm) in a 330-mm TL female to 48 (20 × 6 mm) in one of 515 mm TL. Neither specimen had been opened prior to our examination.

Sex was determinable in a female of 179 mm TL (the eggs tiny) and in a male of 200 mm TL.

The sex ratio of the study material is essentially equal. Of a total of 870 specimens for which sex was reliably determined, 49% were female, 51% male. This ratio contrasts notably with other species described herein, in which females dominated by 60–74%. The maximum size of each sex appears to be equal, the largest male measuring 550 mm TL, the largest female 515 mm TL. Four large females ranged between 491 and 500 mm TL, the next largest 475 mm TL.

Discussion Lockington (1878:792–793) very briefly described *Bdellostoma stoutii* as, "Eleven gill openings on each side; ten teeth in the anterior and nine in the posterior series. 15½" long. Eel River, Humboldt County."

There is no doubt that the specimen represented a hagfish, but Lockington's subsequent statement indicates that perhaps he confused it with a species of lamprey, possibly *Lampetra tridentata*, as he stated, "It is rather singular that this fish, which is abundant in Eel River and is sold for food, and also occurs in this harbor, should have hitherto escaped notice. I believe it to be the only species of its genus hitherto found on the Pacific coast of North America; and it differs from *Bdellostoma polytrema*, a species which occurs along the coast of Chile, both in the number of its gill openings and that of the teeth, *B. polytrema* having fourteen of the former and twelve of the latter in each series."

There can be no serious question as to the pertinence of the name *stoutii* to this species, although the diagnosis is extremely short and Lockington ascribed the species primarily to Eel River, indicating it as abundant there. But he added, "also occurs in this harbor," meaning, presumably, San Francisco Bay, since there is no harbor at the mouth of Eel River, but only an estuarine embayment.

Perhaps the specimen was sent from near the mouth of Eel River, almost certainly from central or northern California. We maintain the name *stoutii* because it is the only other species of the genus from the area fitting the description. *Eptatretus deani* is a deep purplish-black in color, not light brown. It generally occurs at much greater depths, and it is unlikely that a fisherman would have taken *E. deani* in the 1870s because of this greater depth of habitat. Unfortunately, Lockington did not state the numbers of prebran-

chial pores, which, aside from color, is an important character separating the two species.

Lockington did not designate his specimen as a holotype or state that it was deposited anywhere. If deposited, the most likely place would have been the California Academy of Sciences. W.E. Eschmeyer (Calif. Acad. Sci., San Francisco, pers. commun.) has informed us that Lockington's specimen is not now at the Academy, and stated that it and any record of it may have been destroyed in the San Francisco earthquake and fire.

Therefore, in view of the possible confusion of *E. stoutii* with *E. mcconnaugheyi*, especially off southern California, we designate as neotype of *Eptatretus stoutii*, SIO68-426, a male, 530 mm TL, taken near the whistler buoy at entrance of Humboldt Bay, California. This locality is about 8 miles northerly from the mouth of Eel River, the type locality of Lockington's *Bdellostoma stoutii*.

Discussion

The relationship of the five species treated above superficially appear to be close. We are aware of the speculative and debatable nature of intraspecific variation, and that any proposed new species may be considered a variant of a similar-appearing, sympatric known species.

Thus, it may be argued that *E. deani* and *E. fritzi* are mere variants, due primarily to their very dark coloration, much darker than in any of the other species treated, and due perhaps to their sympatric occurrence in the presently restricted range of *E. fritzi* near Guadalupe Island, Mexico. However, the virtually non-overlapping numbers of prebranchial slime pores, 7(4–10) in *E. deani* vs. 12–13(10–15) in *E. fritzi* (Table 2), alone are adequate for specific separation. In addition, the very large barbels of *E. fritzi* do not occur in *E. deani* (Table 6) of sympatric occurrence or in any portion of the nearly 2600 miles of its total range.

The superficial similarity of *E. stoutii* and the sympatric *E. mcconnaughtyi* also invites speculation as to being mere variants. However, the notable and non-overlapping difference in respective prebranchial lengths alone distinguishes between the two species (Table 1). Also, the numbers of prebranchial slime pores differ significantly, with minor overlap (Table 2).

Similary, *E. stoutii* and *E. sinus* are alike in most counts and proportions, but the very prominent ventral finfold of *E. stoutii* does not occur in *E. sinus*, where it is absent or vestigial. Also, when fresh material of each is compared, the much darker reddish-brown of *E. sinus* contrasts sharply with the much lighter gray-reddish brown of *E. stoutii*.

All the above principal characters differentiating the five species are constant, often non-overlapping, and show little or no variation within species.

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Table 1

Averages and ranges (in thousandths of total length) of selected body proportions for five species of hagfishes (genus *Eptatretus*) from the Pacific coast of North America. Values for type specimens are given first and followed in parentheses by ranges in values for all material.

Species	Average (range of values)				
	E. mcconnaugheyi	*E. fritzi*	*E. sinus*	*E. deani*	*E. stoutii*
N (Size range in mm)	91 (147–470)	233 (207–592)	458 (129–481)	460 (130–523)	520 (179–468)
Preocular length	62 (45–74)	54 (48–82)	52 (41–82) *	61 (42–89)	53 (40–77)
Prebranchial length	153 (147–181)	198 (176–245)	226 (197–278)	175 (144–204)	240 (187–253)
Branchial length	200 (155–216)	140 (115–158)	113 (92–172)	155 (127–182)	138 (115–142)
Trunk length	532 (482–557)	499 (462–556)	501 (450–540)	517 (480–555)	509 (470–535)
Tail length	130 (122–161)	158 (132–181)	151 (102–174)	151 (126–192)	134 (104–178)
Tail depth	72 (60–88)	65 (58–92)	78 (48–90)	80 (52–103)	55 (45–83)
Body depth with finfold	91 (61–98)	No finfold	67 (49–104)*	78 (47–105)	62 (50–97)
Body depth without finfold	89 (55–90)	63 (53–102)	58 (46–101)*	72 (45–105)	51 (41–90)
Body depth at cloaca	53 (47–71)	56 (45–72)	61 (39–86) *	63 (38–85)	53 (38–79)

*330 specimens measured.

Table 2

Numbers of gill pouches, prebranchial, branchial, and tail slime pores for five species of hagfishes (genus *Eptatretus*) from the Pacific coast of North America. Values, left side, for type specimens are indicated by an asterisk.

	Gill pouches															
	9	10	11	12	13	14								*N*	$\bar{X}$	δ
E. mcconnaugheyi				28	67*	2								97	12.73	0.487
E. fritzi		31	261*	64										356	11.09	0.508
E. sinus	77	248*	103	7										435	10.09	0.685
E. deani		21	536	43										600	11.04	0.325
E. stoutii		2	173	691*	63	2								931	11.88	0.507
	Prebranchial slime pores															
	4	5	6	7	8	9	10	11	12	13	14	15	16	17	*N*	$\bar{X}$	δ
E. mcconnaugheyi			1	5	27	50*	11	2							96	8.74	0.845
E. fritzi							3	40*	123	118	31	3			318	12.45	0.898
E. sinus							3	27	85	142*	117	44	14	3	435	13.26	1.231
E. deani	1	7	90	275	197	23	7								600	7.26	0.854
E. stoutii							2	29	142	366	315*	59	7		920	13.27	0.946
	Branchial slime pores															
	8	9	10	11	12	13	14	15	16						*N*	$\bar{X}$	δ
E. mcconnaugheyi				15	52	16*	5	2	2						92	12.27	1.012
E. fritzi		14	233	105*	4										556	10.28	0.549
E. sinus	72	246*	107	10											435	9.13	0.698
E. deani		16	425	125	30	4									600	10.30	0.636
E. stoutii		3	151	587	80*	1	1								823	10.91	0.551
	Tail slime pores															
	7	8	9	10	11	12	13	14	15						*N*	$\bar{X}$	δ
E. mcconnaugheyi		2		21	44*	22	8								97	11.13	0.915
E. fritzi		2		19	87	149	80*	18	1						356	11.96	0.999
E. sinus	2	28	130	168	76*	22	7	2							435	9.90	1.088
E. deani			7	128	224	188	47	5	1						600	11.27	0.958
E. stoutii		4	64	239*	357	125	22	2							813	10.75	0.935

Table 3

Numbers of trunk slime pores for five species of hagfishes (genus *Eptatretus*) from the Pacific coast of North America. Values, left side, for type specimens are indicated by an asterisk.

	Trunk slime pores																		
	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	*N*	$\bar{X}$	*d*
E. mcconnaugheyi																			
Southern California								8	7	6	13	13*	8	3	2		60	46.03	1.871
Gulf of California				1	2	3	4	11	11	3	2						37	43.08	1.566
E. fritzi					2	3	15	38	85	112	67*	24	9	1			356	44.77	1.413
E. sinus	1	4	10	35	64	102	86*	65	40	12	7	7	1	1			435	41.67	1.943
E. deani				1	2	6	38	87	137	152	99	51	22	5			600	44.70	1.601
E. stoutii				1	8	38	96	154	196*	154	110	41	13	5	2	1	819	44.12	1.726

Table 4

Numbers of total slime pores for five species of hagfishes (genus *Eptatretus*) from the Pacific coast of North America. Values, left side, for type specimens are indicated by an asterisk.

Total slime pores	*E. mcconnaugheyi*				
	Southern California	Gulf of California	*E. fritzi*	*E. sinus*	*E. deani*	*E. stoutii*
66				1		
67		2		2	2	
68				9	5	
69				11	16	
70		1		16	26	
71		2		39	48	1
72	2	5		57	100	1
73	2	8		53	111	1
74	5	11	1	63	98	11
75	3	3	6	60*	78	26
76	2	1	14	59	63	61
77	11	1	38	21	34	107
78	12	2	50	16	16	142
79	9	1	87	12	2	141
80	6*		71	9	1	116*
81	2		46*	4		100
82	4		23	3		60
83	1		10			29
84	1		8			12
85			2			7
86						3
87						
88						1
N	60	37	356	435	600	819
$\bar{X}$	77.80	73.43	79.36	73.98	75.91	79.03
d	2.650	2.444	1.909	2.796	2.186	2.280

Table 5

Numbers of anterior and posterior unicusps, and total cusps, for five species of hagfishes (genus *Eptatretus*) from the Pacific coast of North America. Values, left side, for type specimens are indicated by an asterisk.

	Anterior unicusps															
	6	7	8	9	10									N	$\bar{X}$	s
E. mcconnaugheyi		25	151*	15										191	7.95	0.455
E. fritzi		73*	266	32	1									372	7.90	0.531
E. sinus	62	453*	336	21										872	7.36	0.649
E. deani	3	62	604	308	11									988	8.27	0.601
E. stoutii	16	524	390*	11	1									942	7.42	0.555
	Posterior unicusps															
	6	7	8	9										N	$\bar{X}$	s
E. mcconnaugheyi		40*	143	8										191	7.83	0.472
E. fritzi		37	270*	65										372	8.08	0.518
E. sinus	11	310*	491	60										872	7.69	0.614
E. deani		233	680	75										988	7.84	0.535
E. stoutii	4	347	570*	21										942	7.65	0.531
	Total cusps															
	34	35	36	37	38	39	40	41	42	43	44	45	46	N	$\bar{X}$	s
E. mcconnaugheyi					4	3	11*	14	48	9	4	2		95	41.60	1.364
E. fritzi					3	5	29*	22	75	25	17	7	3	186	41.92	1.527
E. sinus	1	3	18	13	83*	46	92	39	105	16	15	1	4	436	40.10	2.089
E. deani				1	5	12	55	59	160	68	25	14	3	402	41.86	1.433
E. stoutii			3	4	84	66	126	76	93*	13	5	1	1	471	40.16	1.583

Table 6

Numbers, averages, and ranges of lengths (in mm) of first nasal barbel, left side, for 25-mm increments of total length of five species of hagfishes, genus *Eptatretus*, from the Pacific coast of North America.

	Average N(Range)				
	E. mcconnaugheyi	*E. fritzi*	*E. sinus*	*E. deani*	*E. stoutii*
200–225	3.0 3(2.6–3.5)	6.5 1(—)	2.2 6(1.5–2.6)	3.3 16(2.4–4.5)	2.3 20(2.0–3.0)
226–250	3.3 5(2.9–3.8)	5.9 4(5.6–6.2)	2.6 7(2.0–3.9)	3.5 33(2.6–4.5)	2.8 16(1.9–3.2)
251–275	3.9 8(3.1–4.6)	6.1 3(5.7–6.4)	2.8 25(2.3–3.7)	3.6 31(2.5–4.5)	3.0 52(2.0–4.0)
276–300	4.1 12(3.2–4.9)	6.9 4(6.3–7.2)	2.9 50(2.2–4.3)	4.2 30(3.3–5.3)	3.3 70(2.2–4.5)
301–325	4.2 13(3.6–5.4)	6.3 8(5.0–6.9)	3.1 71(2.0–4.4)	3.8 39(3.2–5.2)	3.5 77(2.4–4.6)
326–350	4.5 10(3.8–5.0)	6.8 24(6.5–9.6)	3.4 80(2.1–4.4)	4.1 42(2.5–5.5)	3.7 110(2.5–5.2)
351–375	4.9 11(4.1–6.3)	7.4 40(5.6–9.1)	3.1 72(2.7–5.6)	4.4 103(2.8–6.0)	3.7 127(2.5–5.1)
376–400	4.9 8(3.9–5.6)	7.8 49(6.2–8.9)	4.0 35(3.0–5.2)	4.6 202(3.0–6.6)	4.1 148(2.6–6.0)
401–425	6.1 6(5.2–7.0)	7.7 71(6.5–10.2)	4.2 17(3.5–5.4)	5.0 235(3.1–6.9)	4.2 109(2.9–5.3)

Table 6 (continued)

	Average *N*(Range)				
	E. mcconnaugheyi	*E. fritzi*	*E. sinus*	*E. deani*	*E. stoutii*
426–450	6.0 6(5.0–7.1)	8.2 50(7.4–10.2)	3.9 8(2.9–5.8)	5.1 174(3.1–7.0)	4.3 65(2.8–6.1)
451–475	6.5 2(6.5–6.5)	9.8 42(7.6–10.8)	3.8 2(3.2–4.4)	5.3 68(3.8–6.6)	5.3 33(3.7–5.9)
476–500	6.8 1(—)	8.9 21(7.2–10.3)	4.1 6(3.8–4.4)	5.4 28(4.0–6.5)	4.7 11(3.9–6.0)
501–525	6.0 2(5.8–6.1)	10.4 9(9.1–11.3)		5.2 10(4.1–5.9)	5.0 13(3.8–6.9)
526–550		10.9 7(10.3–11.7)		4.7 1(—)	4.4 8(4.3–5.4)
551–575		10.4 2(9.7–11.3)		4.6 1(—)	6.1 1(—)
576–600		10.2 2(9.5–10.8)			6.8 1(—)
N	87	273	379	1013	861

Table 7

Gill pouches, both sides, in positions relative to Areas I, II, and III of the branchial regions of five species of hagfishes (genus *Eptatretus*) from the Pacific coast of North America. Areas are identified in Figure 4. Values, left side, for type specimens are indicated by an asterisk.

Gill pouches	0	1	2	3	4	5	6	7	8	9	10	*N*	$\bar{X}$	δ
Area I														
E. mcconnaugheyi						2	13	23	45*	34*	9	126	7.98	1.137
E. fritzi				9	49	34*	8					100	4.41	0.763
E. sinus	2	61*	136	103	23	11	5					341	2.40	1.067
E. deani				1	46	62	11					120	4.69	0.643
E. stoutii		7	61	75*	49	19	1					212	3.07	1.023
Area II														
E. mcconnaugheyi	5	13	42*	30*	23	13						126	2.73	1.275
E. fritzi	2	7	12	43*	31	5						100	3.09	1.040
E. sinus	7	20	85	151	65*	11	1					341	2.84	0.994
E. deani	30	44	43	3								120	1.16	0.827
E. stoutii	19	38	68	65*	13	9						212	2.20	1.197
Area III														
E. mcconnaugheyi	4	25*	80	16								126	1.86	0.663
E. fritzi			9	42*	35	13	1					100	3.55	0.865
E. sinus		7	11	13	65	125*	101	17	2			341	4.97	1.229
E. deani				3	16	71	28	2				120	5.08	0.726
E. stoutii				1	3	17*	71	87	32	1		212	6.60	0.933

Table 8

Numbers and percent of occurrence of higher numbers of branchial apertures on left and right sides of five species of hagfishes (genus *Eptatretus*) from the Pacific Coast of North America.

Species	*N*	Higher on left side	Higher on right side
E. mcconnaugheyi			
Southern California	61	4 (6%)	5 (8%)
Gulf of California	37	5 (19%)	0
E. fritzi	316	81 (26%)	0
E. sinus	446	63 (14%)	7 (2%)
E. deani	1145	125 (11%)	21 (2%)
E. stoutii	1554	167 (11%)	56 (4%)
Totals	3559	445 (12.5%)	89 (2.5%)