Deep-Sea Research, Vol. 37, No. 2, pp. 267–283, 1990.
Printed in Great Britain.

0198–0149/90 $3.00 + 0.00
Pergamon Press plc

Biology and description of a bythitid fish from deep-sea thermal vents in the tropical eastern Pacific

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(*Received* 1 *March* 1989; *in revised form* 1 *August* 1989; *accepted* 11 *September* 1989)

Abstract—A new fish species of the world-wide genus *Bythites* (Bythitidae, Ophidiiformes) is based on a gravid female captured in a thermal vent in the Galapagos Rift Zone. No apparent morphological features of adults or larvae account for life in the vent environment. Gill arch structure does not indicate filter feeding. The few fish species living in vents are not representative of ancient groups and are probably recent arrivals. The species is intermediate between the nominal genera *Bythites* and *Abythites*; hence, the latter is considered a junior synonym. The new species differs from its four congeners in its high dorsal, anal, and pectoral fin ray counts and its broad interorbital space. Free sperm and spermozeugmata are present throughout the ovarian tissue. Intra-ovarian larvae have a well-developed yolk sac, large oil globule, and pigmented eyes. Brood size is about 10,000.

INTRODUCTION

THE earliest observers (CORLISS *et al.*, 1979) of the remarkable biota of deep-sea thermal vent systems in the tropical eastern Pacific remarked on the presence of fishes living in and around the vents. Of the approximately 20 species comprising the ichthyofauna of the general area of the Galapagos rise thermal vents (COHEN and HAEDRICH, 1983), only two have been observed living in warm water and only one is possibly an obligatory vent inhabitant (HESSLER and SMITHEY, 1984). This latter fish was identified from photographs and observations from the submersible *Alvin* as belonging to the live-bearing ophidiiform family Bythitidae and tentatively (and incorrectly) assigned to the genus *Diplacanthopoma* (COHEN and HAEDRICH, 1983; COHEN *et al.*, 1985). Similar fishes have been observed from *Alvin* and *Cyana* at vents near 11°N and 13°N (ROSENBLATT and COHEN, 1986; GEISTDOERFER, 1988).

A gravid female bythitid has now been captured from one of the Galapagos rise vents. The purpose of this paper is to discuss the classification of the species, to describe and name it, to describe what can be surmised of its reproductive biology, and to summarize what is known of the species' natural history.

SYSTEMATICS

Genus Bythites

Diagnosis. Bythitine fishes (COHEN and NIELSEN, 1978) are defined by the following combination of characters. Anal fin originating on posterior half of body, tail not greatly

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attenuate; ventral fins present, one ray in each, originating well posterior to the symphysis of the cleithra; caudal fin rays 10–13; pectoral fin rays 22–37, fin not on an elongate peduncle, pectoral radials not greatly elongate; imbricate scales present on body; no series of large circumorbital pores or prominent median interorbital pore; no prominent skin flap above opercle; opercular spine present; branchiostegal rays seven or eight; developed rakers on first gill arch 0–3; palatine teeth present; vomerine teeth not nearly or completely divided into two patches; precaudal vertebrae 13–20; male with a stalked intromittent organ.

Discussion. Although *Bythites* was first named in 1835, fishes of the genus are rare in collections. In a review published in 1973, Nielsen and Cohen recognized three North Atlantic species, *B. fuscus* Reinhardt, still known only from the holotype, and *B. islandicus* and *B. gerdae* which they described based on four and two specimens, respectively. In the same paper they proposed the genus *Abythites* for the western Pacific *B. lepidogenys* Smith and Radcliffe (with *B. matsubarai* Arai as a junior synonym).

The nominal genera *Bythites* and *Abythites* were separated by six characters (NIELSEN and COHEN, 1973). The fish described below as *Bythites hollisi* agrees with *Bythites* in three characters, with *Abythites* in two, and is intermediate in one (Table 1). Several alternate courses of action to resolve the issue of appropriate generic placement for *B. hollisi* are possible. These include the assignment of *B. hollisi* to a monotypic genus, inclusion of *B. hollisi* as a fourth species of *Bythites* or a second species of *Abythites*, or the placement of *B. hollisi* in an expanded genus *Bythites* with *Abythites* as a synonym.

B. hollisi is readily distinguishable from any of the three species of *Bythites* and the single species of *Abythites* (Table 2) in having more fin rays and vertebrae and a relatively broader inter-orbital and smaller eye (the two proportional characters are due perhaps to allometric growth, as the type of *B. hollisi* is more than twice as long as the next largest specimen of *Bythites*, the type of *B. fuscus*). There seem to be no other unique character states, however, distinguishing *B. hollisi.* Considering how little is known of the characters listed in Table 1, it is difficult to justify assigning *B. hollisi* to one or the other genus or to erect yet another monotypic genus.

Recognizing an expanded *Bythites* including *fuscus*, *islandicus*, *gerdae*, *lepidogenys* and *hollisi* creates a taxon that can be diagnosed only on the basis of a combination of character states (presented above as the diagnosis), many of which are probably plesiomorphic; there are no known synapomorphies for the five species combined. However, the alternative of erecting five monotypic genera would not clarify relationships and would burden the literature with still more names. Pending a more thorough study of bythitid genera and assessment of characters, the most practical, if not particularly satisfying, course of action is to recognize a possible paraphyletic *Bythites* containing five species.

Table 1. *Character states in the nominal Genera* Bythites, Abythites *and in* B. hollisi

	Bythites	*Abythites*	*B. hollisi*
Scales on head	Absent	Present	Absent
Tooth shape	Needle-like	Granular	Needle-like
Pseudobranch filaments	0	2	1
Developed gill rakers on anterior gill arch	0–1	3	3
Shape of precaudal neural spines nos 5–9	Pointed	Blunt	Pointed
Ribs on precaudal centra nos 1 and 2	Yes	No	No

Table 2. Comparison of characters in five species of Bythites. *Data from* Arai *(1969) and* Nielsen *and* Cohen *(1973)*

	B. hollisi	*B. fuscus*	*B. islandicus*	*B. gerdae*	*B. lepidogenys*
N	1	1	4	2	2
Standard length (SL)	304	146	72–88	59–63	72–99
Anal fin rays	88	70	46–50	51–56	49–56
Dorsal fin rays	122	88	76–79	87–94	75–81
Pectoral fin rays	37	29–30	25–26	24–27	22–24
Developed rakers on anterior gill arch	3	0	0	1	3
Form of small gill rakers	Separate knobs	Separate knobs	Separate knobs	Plate-like and coalesced	Separate knobs
Anterior anal fin ray below dorsal fin ray no.	41	27	29–32	43–44	24–29
Total vertebrae	76	53	40–50	46–47	44–45
Fleshy interorbital as % of SL	10.7	8.9	8.0–9.0	6.7	7.0–8.3
Diameter of eye as % of SL	3.0	4.8	5.5–6.0	4.8–5.0	3.9–4.9
Pairs of large pores on lower jaw	2	2	2	5	5
Branchiostegal rays	8	7	7	8	8

Table 3. Areal and depth distribution of five species of Bythites. *Data from* ARAI (1969) *and* NIELSEN *and* COHEN (1973)

	Area	Depth (m)
B. fuscus	West Greenland	"From great depths"
B. gerdae	Straits of Florida	786–832
B. hollisi	Galapagos thermal vent area on east Pacific rise	2500
B. islandicus	Southeast Iceland	229–283
B. lepidogenys	Philippines	296–400
	Tosa and Suruga Bays, Japan	100–400

Relationships. Among the dozen or more presently recognized genera (many of which are poorly defined) of the subfamily Bythitinae, *Bythites* is perhaps most similar to *Saccogaster*, which is characterized by having reduced body squamation and elongate pectoral radials. The former character is reductional and the latter needs closer investigation in *Bythites* than is possible with available material.

Species and distribution. The species are diagnosed in Table 2 and their known distributions are summarized in Table 3.

Bythites hollisi n. sp.

Brotulid fish; CORLISS and BALLARD (1977; color illustration).

Ophidioid fish; CORLISS *et al.* (1979).

"Vent fish" (a bythitid); LUTZ and HESSLER (1983) (color illustration from Corliss and Ballard).

?*Diplacanthopoma* (vent fish); COHEN and HAEDRICH (1983).

?*Diplacanthopoma*; HESSLER and SMITHEY (1984) (Fig. 5, color, Fig. 7).

(Un-named fish); JANNASCH (1984) (Fig. 1, color).

?*Diplacanthopoma* sp. (vent fish); COHEN *et al.* (1985).

Possibly *Diplacanthopoma*; GRASSLE (1985).

Diplacanthopoma; ROSENBLATT and COHEN (1986).

Diplacanthopoma (?); GEISTDOERFER (1988).

Bythites; HESSLER *et al.* (1988).

Diagnosis. See Table 2.

Holotype. SIO 88–97, a gravid ♀ 304 mm SL. Hydrothermal vent (Mussel Bed) on the Galapagos Rift Zone, 0°47.894′N, 86°9.210′W, 2500 m, D.S.R.V. *Alvin* dive 2026, 28 April 1988, R. Hollis, R. Hessler and J. O'Brien. Taken in a net held by the manipulator arm.

Etymology. Named for expert *Alvin* pilot Ralph Hollis, who finally captured this elusive fish.

Counts. Dorsal fin rays 122, anal fin rays 88, pectoral fin rays 37, ventral fin ray 1, caudal fin rays 12, branchiostegal rays 8, developed gill rakers on first arch 3, vertebrae (not counting ural centra) 20 + 56 = 76, first dorsal fin ray above approximately centrum 11, 1st anal fin ray below approximately centrum 29, first anal fin ray below approximately dorsal ray 41.

Measurements. (Some data imprecise due to partial mutilation of the specimen when tissue was dissected for physiological and biochemical analyses.) mm followed by percent SL in parentheses: SL 304; head length 92 (30.3); snout length 20.6 (6.8); upper jaw length 43.6 (14.3); horizontal eye diameter 9.2 (3.0); fleshy interorbital width 32.5 (10.7);

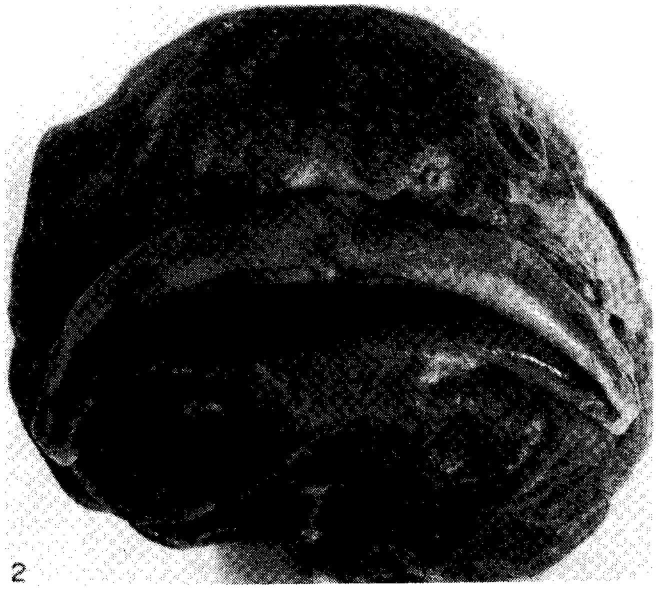

Fig. 1. *Bythites hollisi*, holotype, SIO 88–97, SL 304 mm.

Fig. 2. *Bythites hollisi*, holotype, SIO 88–97, SL 304 mm, anterior view.

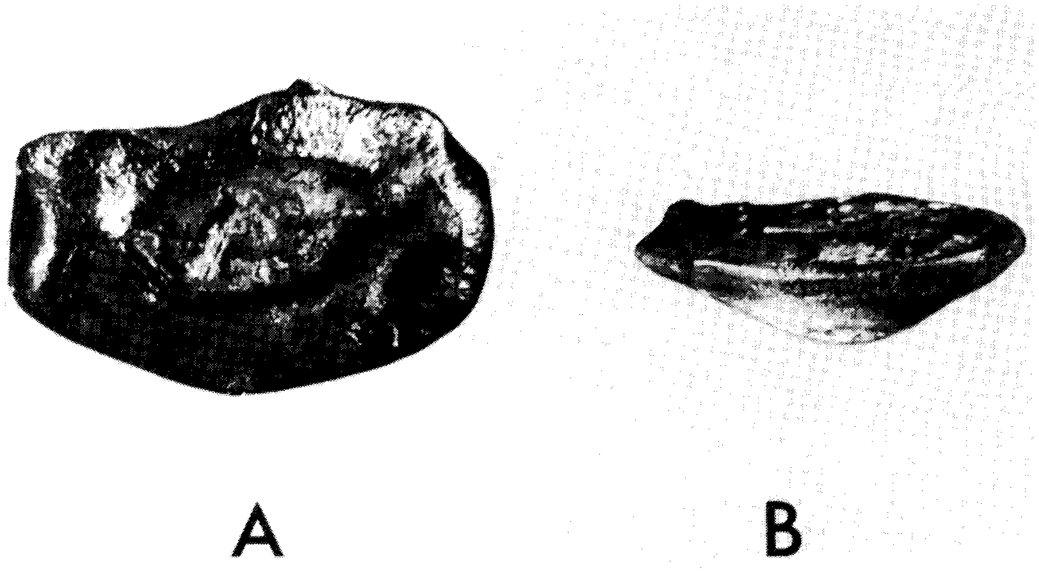

Fig. 4. *Bythites hollisi*, holotype, SIO 88–97, left sagitta, length 7.8 mm. (A) Medial view; (B) ventral oblique view.

body depth at vent 41.5 (13.7); preanal length 168 (55.3); predorsal length (measured from an X-ray photograph) 115 (37.8); least depth pectoral fin base 23.1 (7.6); pectoral fin length 36.2/41.4 (11.9/13.6); ventral fin length 20.5 (6.7).

Description. Body compressed, depth at vent about 7.3 in SL; tail not greatly attenuate (Fig. 1).

Head (Fig. 2) 3.3 in SL, depressed, slightly broader than deep; snout blunt, slightly rounded in lateral view, broadly rounded from the dorsal aspect. Anterior nostril a small pore with a slightly raised rim, located above the upper lip slightly medial to the level of the dorsal margin of the eye; posterior nostril a small, rimless pore located anterior to the midlevel of the orbit about mid-way between the anterior nostril and the anterior margin of the eye. Eye small, 2.2 times in snout length, 10 times in head length; in preserved holotype covered with a translucent spectacle. Jaws subequal; thick and fleshy; upper jaw oblique, extending posteriorly more than an eye diameter beyond the level of the posterior margin of the eye; maxillary probably sheathed posteriorly when the mouth is closed; rear margin with a slight concavity, neither rounded nor greatly expanded; no posterior-ventral spine or point. A single short, strong and blunt spine on the opercle, buried but visible inside the gill chamber.

The dorsal fin originates above the mid-length of the pectoral fin; the anal fin originates posterior to the mid-length of the fish. The pectoral fin is a broadly rounded paddle on a peduncle that is more than twice as deep as it is long; fin membrane frayed distally, rays unbranched, their tips free and filamentous. The ventral fins are closely adjacent at their bases, and insert well posterior to the symphysis of the cleithra (about 25 mm, although measurement is imprecise due to mutilation of the specimen). The caudal fin is confluent with dorsal and anal fins, posteriorly rounded, its rays not exserted. The dorsal-most caudal ray is apparently supported by an epural, 10 rays insert on posterior hypurals, and the ventral-most caudal ray is supported by a process (? parhypural or hypural) on PU1 or PU1 + U1.

The skin is thick and tough. Color in alcohol a dingy dark gray, paler posteriorly; lips pale; series of small papillae on the head are indicated by small, oval to elongate pale areas which are most densely distributed on the snout (see below). The broadest parts of the head (which is the broadest part of the fish) has many randomly arrayed pale narrow streaks which may represent scars. Tiny imbricate scales cover the entire body and extend far anteriorly on the occiput; the fins and the head are naked. Minute, dark papillae, embedded in congealed mucus in most areas, are evenly distributed on the head. Larger white papillae are arrayed in generally linear series on the post-orbital region of the head and are more densely distributed in an apparently random pattern on the snout and chin. A series of about 60 similar surface (although mostly embedded in mucus) white papillae marks the course of the lateral line along the body, originating anteriorly at the upper angle of the gill opening, descending gradually to the mid-line at about the level of the vent, and then coursing posteriorly and becoming obscure at nearly the end of the body; the anterior lateral line papillae arise from the surface of the skin; more posteriorly they arise from the anterior margin of small, anteriorly directed pits.

Mandibular pores 2; the most anterior is directed forward at the tip of the lower jaw; the other is immediately posterior in the gular fold and faces posteriorly. Preopercular series with a single pore posterior to the distal end of the premaxillary and about one-half the distance from that point to the level of the rear margin of the head. Supraorbital series with a single pore medial to the anterior nostril. Infra-orbital series with two pores in the skin fold over the upper lip ventral to the space between the two nostrils. No lateral or supratemporal pores.

Premaxillary teeth tiny, conical, sharply pointed, in a narrow band that is about 4–5 teeth wide slightly posterior to the symphysis and narrows to a single tooth row posteriorly. Dentary teeth slightly larger and stouter than upper jaw teeth and in a narrower band. Vomer and palatines bear teeth that are similar to those on the dentary, in a broadly V-shaped band on the vomer and a straight, narrow band on the palatine. No median basibranchial tooth patch. Tongue broad.

The branchial arches were excised without care before we received the specimen and only those from the right side are available; the first three were dissected out, number 4 remains in place. The first arch (Fig. 3) bears three small tubercles on the upper arm, a developed raker at the angle, two developed rakers on the lower arm, with a tubercle in each interspace, and a series of at least 14 tubercles on the lateral face of the ceratobranchial following the most anterior developed raker. A series of at least 14 larger tubercles on the medial face of the lower arm interlock neatly with a series of tubercles on the lateral face of the lower arm of the second arch. A similar arrangement of interlocking tubercles is present on subsequent gill arches. The gills are well developed, with filaments reaching a length of 11 mm on the lower arm of the first arch. Arches 2 and 3 also bear well-developed filaments. (Gills have been removed from the fourth arch.) A pseudobranch consisting of a single filament is present on the left side; the corresponding area on the right side has been mutilated.

The fish has been gutted, and most of the lining of the peritoneum removed; however, it is apparently dusky; the branchial chamber is mostly pale. The tongue and floor of the mouth are pale; the roof of the mouth is light gray.

The external urogenital area consists of a prominent fleshy mound covered with fleshy papillae and compressed, leaf-like structures.

The fish is well ossified. The first neural spine is shorter than following ones; all neural spines have sharp points. Ribs are lacking on centra 1 and 2; vertebrae 3–6 bear ribs

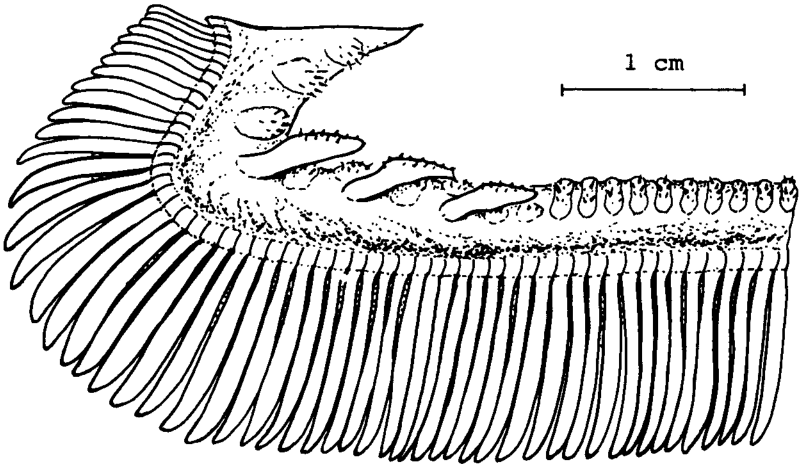

Fig. 3. *Bythites hollisi*, holotype, SIO 88–97, lateral view of first gill arch.

directly on the centra; 7–15 have ribs at the ends of progressively longer parapophyses; ribs on vertebrae 7–14 bear slender epipleurals.

The sacculith (sagitta) is 7.8 mm long, 5.0 mm in the dorso-ventral dimension, and 2.9 mm wide. The anterior margin is broadly rounded; the dorsal margin is slightly convex anteriorly and straight posteriorly; the posterior margin is truncate; the ventral margin is a smooth curve. The medial face of the otolith is nearly flat; however, it bears the outline of a nearly oval sulcus that is 4.3 mm long and 2.1 mm deep and is closer to the dorsal margin than to the ventral one, is not divided into ostium and cauda, and has no connection with an excisura. The lateral face is a prominent dome, broadest slightly posterior to the mid-length of the sacculith. Although the form of this otolith fits well NOLF's (1980) characterization of Bythitidae and in general resembles his figures of *Abythites lepidogenys*, *Bythites fuscus* and *B. gerdae* (plate 12, Figs 1–3), it differs from all of them in its markedly truncate posterior margin.

REPRODUCTIVE BIOLOGY

The specimen is a pregnant female that extruded larvae in the transport container on the way to the surface. The ovaries were removed in the shipboard laboratory and preserved in a solution of glutaraldehyde and 10% formalin. The ovaries are paired; each consists of an elongate mass of tissue surrounded by a thin-walled ovisac. The ovisacs converge posteriorly to form a short oviduct. The left ovary is 42.9 mm long × 17.1 mm wide; the right ovary measured 46.1 × 24.2 mm. Together their blotted wet weight was 16.6 g. Each ovary has a vascular trunk along its dorsal surface with branches of the ovarian artery and vein extending into the ovigerous tissue and the ovisac (Fig. 5). The left ovary had apparently extruded most of its brood, and the right ovary appears intact.

The ovarian tissue is arranged in irregular transverse folds that protrude into the lumen formed by the ovisac (Fig. 5C). The surface of the folds consists of thin-walled vascularized sacs or bulbs of varying sizes up to about 4.0 mm in length and 2.2 mm in diameter (Fig. 5D). A mode of yolked ova about 0.2 mm in diameter (up to 0.28 mm) is visible macroscopically. The larvae lie freely in the lumen and in the crevices formed by the folds.

Histological examination of the ovarian tissue showed the highly vascularized nature of the epithelial sacs which branch from the deeper-lying ovigerous tissue (Fig. 6). This tissue contains nests of oogonia surrounded by oocytes with diameters ranging up to those mentioned above (Fig. 6B). Also scattered throughout the ovarian tissue are structures that appear to be postovulatory follicles, each with well-developed epithelial walls and nuclei concentrated towards the lumen (Fig. 6C). Atretic oocytes are encountered infrequently in the sections (Fig. 6D). The inner surface of the ovisac is covered completely with a capillary bed (Fig. 6A). Sperm are present throughout the ovarian tissue, on epithelial surfaces and interstitially. Clumps of sperm in the form of spermozeugmata appear throughout the sections, usually in crevices at the bases of the epithelial bulbs. Frequently, the clumps have penetrated the connective tissue and lie next to the largest oocytes (Fig. 6D).

The larvae are hatched, have well-developed yolk sacs containing segmented yolk, a large anteriorly placed oil globule, and lack absorptive structures such as trophotaeniae (Fig. 7). The mouth is rudimentary. Small pectoral fin buds are the only fins represented; a well-developed median finfold about half as deep as the tail extends along the entire dorsum and ventrally as far forward as the anus. The heart is differentiated enough to be functional. The eyes are formed and pigmented.

The entire brood from the right ovary was counted giving a total of 4900 larvae (exact count). The appearance of this lobe suggests that few if any larvae were lost during transit to the surface. In contrast, few larvae were present in the left lobe. Since the lobes are symmetrical, and probably contained about equal numbers of larvae, the estimated total brood size is 10,000.

Body lengths for a sample of 25 larvae ranged from 4.8 to 5.6 mm (mean = 5.1 mm ± 1.93 S.D.). A sample of 10 larvae were measured. Mean values in mm with standard deviations for seven body parts are as follows: yolk sac length, 1.1 ± 0.09; yolk sac depth, 0.72 ± 0.02; oil globule diameter, 0.56 ± 0.04; head length, 0.71 ± 0.05, body depth at pectoral fin base (not including yolk sac), 0.35 ± 0.03; snout to anus length, 2.6 ± 0.09; eye diameter, 0.28 ± 0.02. The larvae are relatively heavily pigmented with small melanophores of about equal size. These are scattered above the hindbrain and continue posteriad along the entire dorsum as two continuous rows. A single midlateral row is present on each side. A line of melanophores is present on each side above the gut and yolk sac; these extend anteriorly below the hindbrain and posteriorly as a single line along the midventral margin of the tail.

The large numbers of young, the developmental coherence of the brood and the appearance and state of development of the larvae are similar to what we know of other bythitids with pelagic young (e.g. *Brosmophycis marginata*, MOSER, unpublished observations). The question of larval recruitment is an intriguing one. If they are benthic, or benthopelagic, how do they disperse to distant vents through food-poor or otherwise unsuitable areas? If they ascend to relatively food-rich surface waters, how do they locate the specialized adult habitat?

The profusely vascularized epithelial bulbs provide a highly developed mechanism for brood maintenance as proposed by SAUREZ (1975) for similar structures found in *Ogilbia cayorum*. These are undoubtedly efficient in gas exchange, in removal of metabolic wastes, and may perform a trophic function. Other apparently ovoviviparous fishes have been shown to provide maternal nutrition (e.g. BOEHLERT and YOKLAVICH, 1983; BOEHLERT *et al.*, 1987) and it may be that no teleosts are truly "ovoviviparous." The presence of a mode of small initially yolked oocytes suggests sequential brood production. This is further supported by the abundance of sperm and spermozeugmata interspersed in the ovigerous tissue and concentrated near the larger oocytes. The presence of a mode of well-formed postovulatory follicles in an ovary containing relatively advanced young is paradoxical since these structures are typically transitory. Perhaps some development had taken place within the follicles before the young were "ovulated" into the lumen (see review of this phenomenon in bythitids by WOURMS, 1981). Alternatively these postovulatory follicles may be specialized to perform some gestational function, such as the secretion of hormones or trophic compounds.

NATURAL HISTORY

The family Bythitidae, to which *B. hollisi* is assigned, includes most of the live-bearing fishes that were formerly classified in the nominal family Brotulidae. Seventy-two species of living bythitids are listed by COHEN and NIELSEN (1978); however, there are probably a hundred or more un-named ones.

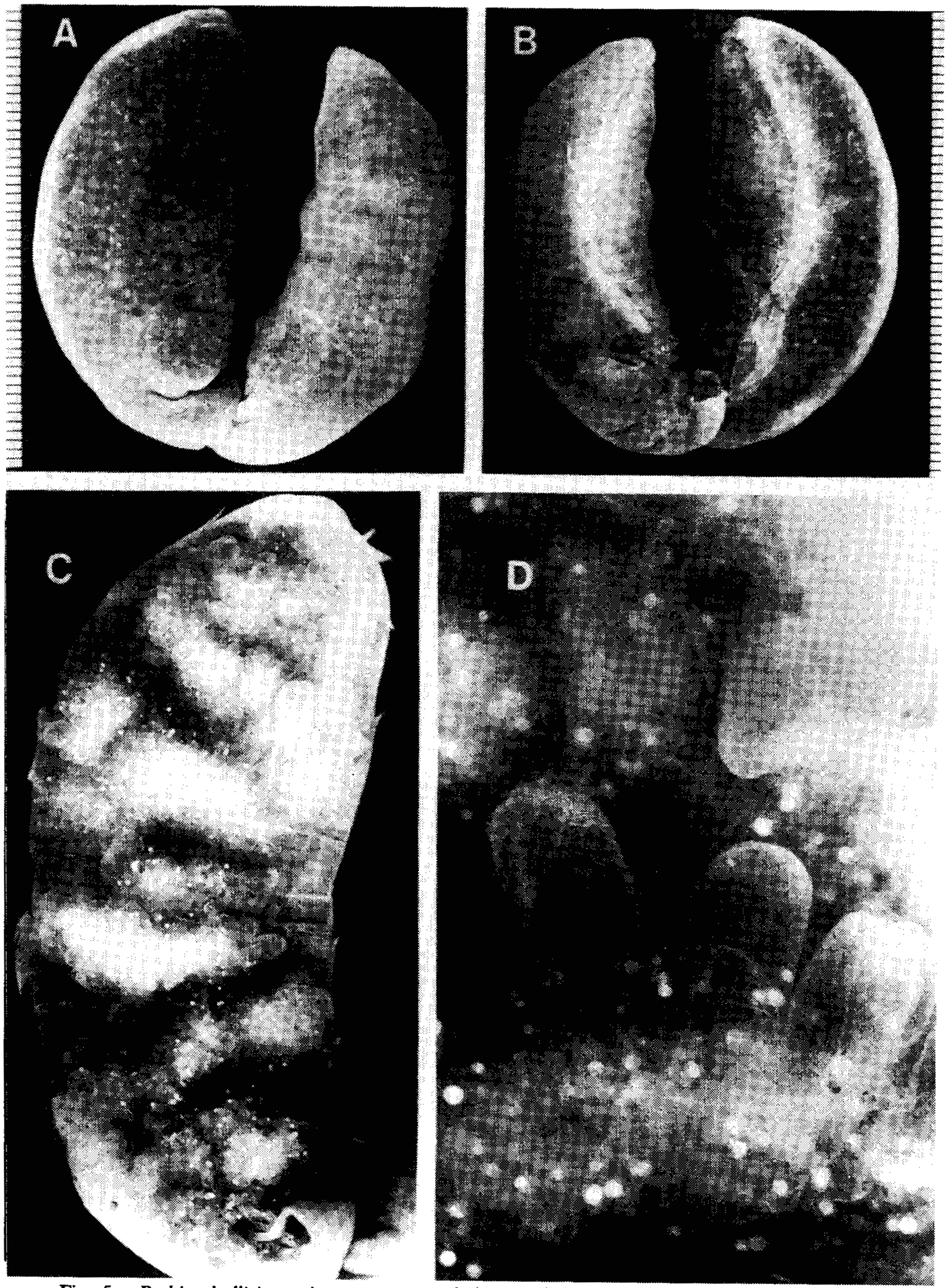

Fig. 5. *Bythites hollisi*, ovarian structure, scale in mm. (A) Ventral view of paired ovaries; (B) dorsal view showing vascular trunks and mesenteries; (C) ventral view of right ovary with ovisac and brood removed to show ovigerous tissue and epithelial bulbs; (D) enlarged view of epithelial bulbs showing their vascular networks. Note mode of small oocytes.

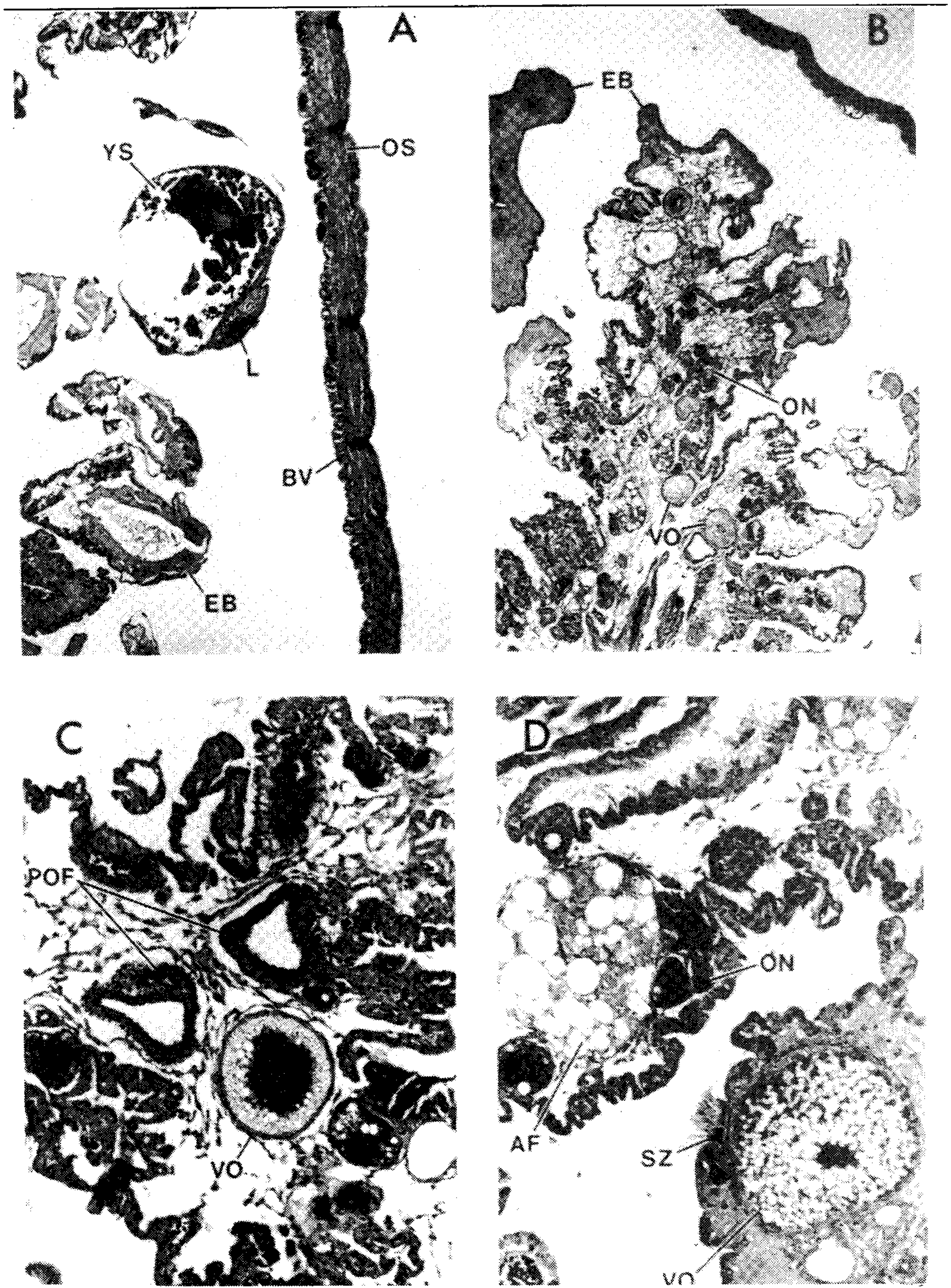

Fig. 6. *Bythites hollisi*, histological structure of the ovary. (A) Region near ovisac (OS) showing larva (L) with large yolk sac (YS), note epithelial bulbs (EB) and layer of blood vessels (BV) on inner surface of ovisac. ×25. (B) Ovigerous tissue containing oogonial nests (ON) and vitellogenic oocytes (VO), with portions of epithelial bulbs at margin. ×25. (C) Vitellogenic oocyte and two postovulatory follicles (POF). ×100. (D) Enlarged view of ovigerous tissue showing vitellogenic oocyte, oogonial nest, and atretic follicle (AF), note spermozeugmata (SZ) in contact with oocyte. ×250.

Fig. 7. *Bythites hollisi*, larvae. (A) Brood lying within ovarian lumen; (B) enlargement of portion of A; (C) drawing of yolk-sac larva, length 5.6 mm.

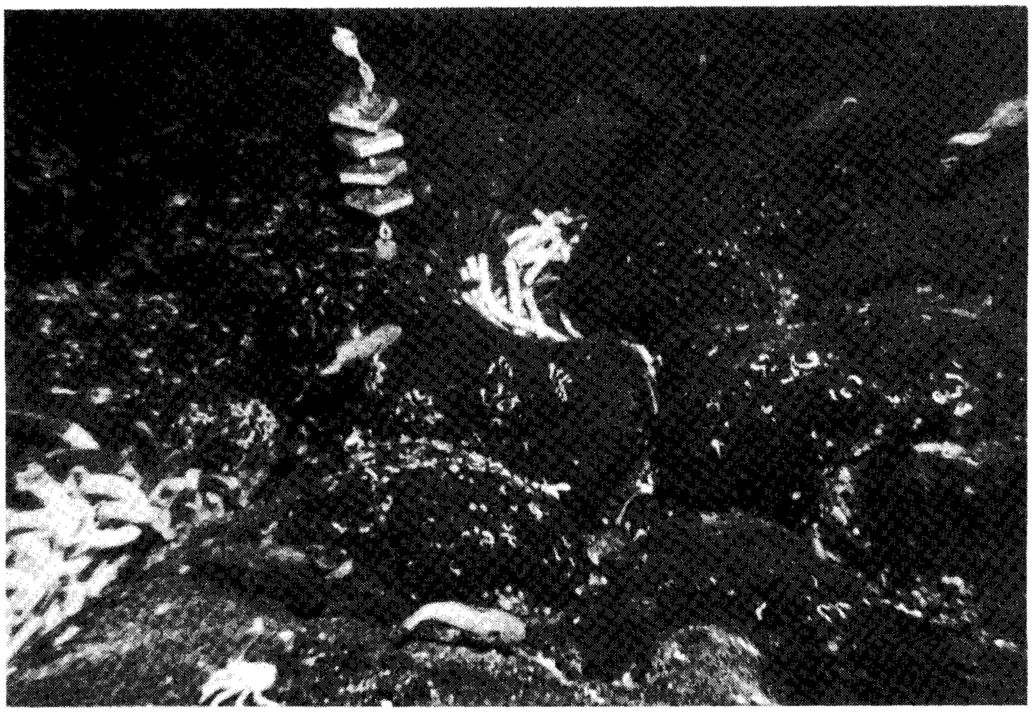

Fig. 8. *Bythites hollisi* at Garden of Eden thermal vent area. *Alvin* dive 993, 10 December 1979.

Bythitids vary widely in habitat and mode of life. The greatest diversity, comprised chiefly of undescribed species, consists of cryptic tropical reef dwellers; fewer species are found in temperate shallow waters; and very few species are known to live in fresh to brackish water caves and sinkholes in the Bahamas, Cuba, Yucatan and the Galapagos Islands. The second most diverse region is on the outer shelf and mid to upper slope, where four species of *Bythites* have been taken (Table 3) and most bythitids probably are benthopelagic. Finally, at least two species are mesopelagic.

Bythitids vary also in size, ranging from species of the Indo-Pacific reef dwelling genus *Microbrotula*, which mature at less than 40 mm, to the deep-sea species *Cataetyx laticeps* which reaches 665 mm.

Living *B. hollisi* have a pink to light tan body; the head and fins are pale blue-gray; in some photographs the lips are pink; the eyes are clear and dark.

General comments on behavior based on observations from *Alvin*, still photographs, and video are given by COHEN and HAEDRICH (1983, p. 376, quoted by COHEN *et al.*, 1985) and HESSLER and SMITHEY (1984). Although *B. hollisi* has almost always been seen above or on the substrate (Fig. 8), narrow pale streaks on the postorbital part of the head (which has the greatest circumference of any part of the fish) suggest that it may at least occasionally enter narrow passages with sharp edges.

Whether the small eyes are image forming or otherwise functional is not known. Densely distributed surface papillae on the head and along the lateral line are characteristic of many species of small-eyed fishes. The demonstrated agility of *B. hollisi* individuals (although not the holotype) indicates well-developed sensory perception of some kind.

Although *B. hollisi* has not been observed to feed, the possibility that the fish ingests bacterial masses was suggested by BALLARD and GRASSLE (1979), that it lives on microorganisms in the thermal fluid by GRASSLE (1985), and chemautotrophy has been suggested by HESSLER and SMITHEY (1984). The excised intestinal tract of our specimen is empty. The structure of the branchial arches, with few widely spaced gill rakers (Fig. 3), does not indicate filter feeding. The dentition is similar to that of other bythitids in general and three of the other known *Bythites* species in particular.

Virtually all fossil records of bythitids are from Cenozoic otoliths (NOLF, 1980). The only non-otolith fossil is *Propteridium*, a genus not far different from the nominal *Abythites*, from the Oligocene of Iran (COHEN and NIELSEN, 1978). Thus the family is apparently not of great antiquity. *B. hollisi* is not very different morphologically from other bythitids. Following the reasoning of NEWMAN (1985), the species (or its immediate forebears) is probably recently arrived at the vent habitat.

The relationships of the invertebrate fauna of the eastern Pacific vent systems have been reviewed by NEWMAN (1985 and personal communication). Although some 85 invertebrate species have been described, only three fish species, *Bythites hollisi*, *Thermarces cerberus*, and *T. andersoni* (ROSENBLATT and COHEN, 1986) are apparent vent endemics. Other fish species have been observed, but never in close association with the vents (COHEN and HAEDRICH, 1983; COHEN *et al.*, 1985). Even more striking is the disparity in endemism at higher taxonomic levels. Fully 60% of the genera and 45% of the invertebrate families are endemic.

Vents are an old feature of the ocean bottom (MALAHOFF, 1985), worm tube fossils have been reported from a Cretaceous hydrothermal vent deposit (HAYMON and KOSKI, 1985), and NEWMAN (1985) has argued persuasively for the antiquity of the extant invertebrate fauna of the vents. The fishes present a contrasting picture. *Thermarces* is a member of the advanced perciform suborder Blennioidei (ROSENBLATT, 1983) and *Bythites* is an ophidiiform. Bythitids and blennioids are known from the Eocene (60 my BP, NOLF, 1985). If the fishes were to resemble the invertebrates in relative phylogenetic position, one would have expected to find paleoniscoids (Paleozoic) or at least holosteans (Mesozoic). Instead we find two families of advanced teleosts and but three species.

Considering the near-ubiquity of fishes in marine environments, including the deep sea, and their dominant position as predators, their virtual absence from vent systems is at first glance puzzling. It may be argued that pre-teleost fishes never invaded the deep sea, but teleosts, members of a group that arose in the Triassic and radiated extensively in the Cretaceous, seemingly have had ample time to discover and exploit the rich food source represented by the vent ecosystem. It does not seem likely that elevated temperature was a factor. Although water coming from the very active vents known as smokers may be as hot as 350°C, it rapidly mixes with ambient seawater of 1–2°C (BAROSS and DEMING, 1955) and there is no reason to believe that the fishes need be living at more than a few degrees above normal deep-sea temperatures. However, in addition to its elevated temperature, vent water is characterized by a high concentration of sulfides, including hydrogen sulfide. Hydrogen sulfide is a potent poison that directly affects the nervous system as well as poisoning oxidative metabolism by binding to hemoglobin and inhibiting respiratory enzymes (NATIONAL RESEARCH COUNCIL, 1979). Some vent invertebrates have been shown to be resistant to elevated concentrations of H_2S, using a variety of methods to detoxify it (VETTER *et al.*, 1987). Invertebrates in general seem to be more resistant to H_2S (and anoxia) than vertebrates, perhaps because of less complex nervous systems and lower metabolic oxygen demands. It is interesting in this connection that another group of active predators, the Cephalopoda, is thus far unknown from the vent ecosystem. With no information available on the metabolism and biochemistry of vent fish, and so little known about effects of H_2S on marine fishes in general (NATIONAL RESEARCH COUNCIL, 1979), further speculation here does not seem profitable. Some estuarine and fresh water fishes do encounter low oxygen water and sulfide-rich sediments (ABEL, 1984), and investigation of their abilities to tolerate sulfide may, in conjunction with knowledge of the biochemistry of the fishes of the vents, provide an answer as to why there are so few kinds of vent fishes.

Acknowledgements—We thank R. Hessler for the specimen and related information, R. Vetter for UG tract dissections, H. J. Walker for assistance with X-rays, B. Macewicz for histological sections, H. Cheney, D. Meyer, H. Orr and T. Ross for illustrations, R. Lavenberg, W. Newman, D. Nolf and J. Webb for comments and B. Collette, R. Lavenberg and J. Nielsen for reading the entire manuscript.

REFERENCES

ABEL D. C. (1984) Terrestriality in the cyprinodontid fish *Rivulus marmoratus*: potential utility in H_2S and other bioassays. *Bulletin of Environmental Contamination and Toxicology*, **33**, 33–39.

ARAI R. (1969) *Bythites matsubarai*, a new brotulid fish from Japan. *Japanese Journal of Ichthyology*, **16**, 74–77.

BALLARD R. D. and J. F. GRASSLE (1979) Return to oases of the deep. *The National Geographic Magazine*, **156**, 689–703.

BAROSS J. A. and J. W. DEMING (1985) The role of bacteria in the ecology of black smoker environments. In: *The hydrothermal vents of the eastern Pacific: an overview*, M. L. JONES, editor, *Bulletin of the Biological Society of Washington*, **6**, 355–371.

BOEHLERT G. W. and M. M. YOKLAVICH (1983) Effects of temperature, ration, and fish size on growth of juvenile black rockfish, *Sebastes melanops*. *Environmental Biology of Fishes*, **8**, 17–28.

BOEHLERT G. W., M. KUSAKARI and J. YAMADA (1987) Reproductive mode and energy costs of reproduction in the genus *Sebastes*. In: *Proceedings of the international rockfish symposium, Anchorage, Alaska, USA, October* 20–22, 1986, University of Alaska, Alaska Sea Grant Report 87-2, pp. 143–152.

COHEN D. M. and J. NIELSEN (1978) *Guide to the identification of genera of the fish order Ophidiiformes with a tentative classification of the order*. National Oceanic and Atmospheric Administration Technical Report, National Marine Fisheries Service Circular no. 417, 72 pp.

COHEN D. M. and R. L. HAEDRICH (1983) The fish fauna of the Galapagos thermal vent region. *Deep-Sea Research*, **30**, 371–379.

COHEN D. M., R. H. ROSENBLATT and R. L. HAEDRICH (1985) Identity of thermal vent fishes in the eastern Pacific: an interim report. In: *The hydothermal vents of the eastern Pacific: an overview*, M. L. JONES, editor, *Bulletin of the Biological Society of Washington*, **6**, 229–230.

CORLISS J. B. and R. D. BALLARD (1977) Oases of life in the cold abyss. *The National Geographic Magazine*, **152**, 440–453.

CORLISS J. B., J. DYMOND, L. I. GORDON, J. M. EDMOND, R. P. VON HERZEN, R. D. BALLARD, K. GREEN, D. WILLIAMS, A. BAINBRIDGE, K. CRANE and T. H. VAN ANDEL (1979) Submarine thermal springs on the Galapagos Rift. *Science*, **203**, 1073–1083.

GEISTDOERFER P. (1988) Les peuplements ichthyologiques lies aux sites hydrothermaux et vivant a leur peripherie. *Oceanologica Acta*, **8**, 125–129.

GRASSLE J. F. (1985) Hydrothermal vent animals: distribution and biology. *Science*, **229**, 713–717.

HAYMON R. M. and R. A. KOSKI (1985) Evidence of an ancient hydrothermal vent community: fossil worm tubes in Cretaceous sulfide deposits of the Samail ophiolite, Oman. In: *The hydrothermal vents of the eastern Pacific: an overview*, M. L. JONES, editor, *Bulletin of the Biological Society of Washington*, **6**, 57–65.

HESSLER R. R. and W. M. SMITHEY (1984) The distribution and community structure of megafauna at the Galapagos Rift hydrothermal vents: In: *Hydrothermal processes at seafloor spreading centers*, P. A. RONA, K. BOSTROM, L. LAUBIER and K. SMITH, editors, NATO Conference Series IV, Vol. 12, Plenum Publishing Corporation, New York, pp. 735–770.

HESSLER R. R., W. M. SMITHEY, M. A. BOUDRIAS, C. H. KELLER, P. A. LUTZ and J. J. CHILDRESS (1988) Temporal change in megafauna at the Rose Garden hydrothermal vent (Galapagos Rift: eastern tropical Pacific). *Deep-Sea Research*, **35**, 1681–1709.

JANNASCH H. (1984) Microbial processes at deep-sea hydrothermal vents. In: *Hydrothermal processes at seafloor spreading centers*, P. A. RONA *et al.*, editors, NATO Conference Series IV, Vol. 12, Plenum, New York, pp. 677–709.

LUTZ R. A. and R. A. HESSLER (1983) Life without sunlight. *The Science Teacher*, **50**, 22–29.

MALAHOFF A. (1985) Hydrothermal vents and polymetallic sulfides of the Galapagos and Gorda/Juan de Fuca ridge systems and of submarine volcanoes. In: *The hydrothermal vents of the eastern Pacific: an overview*, M. L. JONES, editor, *Bulletin of the Biological Society of Washington*, **6**, 19–41.

NATIONAL RESEARCH COUNCIL, SUBCOMMITTEE ON HYDROGEN SULFIDE, DIVISION OF MEDICAL SCIENCES (1979) *Hydrogen sulfide*. University Park Press, Baltimore, 183 pp.

NEWMAN W. A. (1985) The abyssal hydrothermal vent invertebrate fauna: a glimpse of antiquity? In: *The hydrothermal vents of the eastern Pacific: an overview*, M. L. JONES, editor, *Bulletin of the Biological Society of Washington*, **6**, 231–242.

NIELSEN J. G. and D. M. COHEN (1973) A review of the viviparous ophidioid fishes of the genera *Bythites* Reinhardt and *Abythites* new (Pisces, Ophidioidei). *Steenstrupia*, **3**, 71–88.

NOLF D. (1980) Etude monographique des otolites des ophidiiformes actuels et revision des especes fossiles (Pisces, Teleostei). *Mededelingen van de Werkgroep voor Tertiare en Kwartaire Geologie, Contributions to Tertiary and Quaternary Geology*, **17**, 7–195.

NOLF D. (1985) Otolithi piscium. In: *Handbook of Paleoichthyology*, H. P. SCHULTZE, editor, Vol. 10, Gustav Fischer Verlag, Stuttgart, 145 pp.

ROSENBLATT R. H. (1983) Blennioidei: introduction. In: *Ontogeny and systematics of fishes*, H. G. MOSER, editor, *Special Publication of the American Society of Ichthyologists and Herpetologists*, **1**, pp. 551–552.

ROSENBLATT R. H. and D. M. COHEN (1986) Fishes living in deep sea thermal vents in the tropical eastern Pacific, with descriptions of a new genus and two new species of eelpouts (Zoarcidae). *Transactions of the San Diego Society of Natural History*, **21**, 71–79.

SUAREZ S. S. (1975) The reproductive biology of *Ogilbia cayorum*, a viviparous brotulid fish. *Bulletin of Marine Science*, **25**, 143–173.

VETTER R. D., M. E. WELLS, A. L. KURTSMAN and G. N. SOMERO (1987) Sulfide detoxification by the hydrothermal vent crab *Bytheograea thermydron* and other decapod crustaceans. *Physiological Zoology*, **60**, 121–137.

WOURMS J. P. (1981) Viviparity: the maternal–fetal relationship. *American Zoologist*, **21**, 473–515.