An endemic radiation of *Trituba* (Mollusca, Gastropoda) on the North Atlantic seamounts

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Abstract: Ten species of the genus *Trituba* are recognized on the seamounts of the North Atlantic south of the Azores, and interpreted as the product of a single radiation in a taxon which has had a relict distribution since the Miocene. The species are *Trituba superstes* (Bouchet and Fechter, 1981) and *T. incredita* n. sp. from Meteor bank; *T. anelpistos* (Bouchet and Fechter, 1981) from Meteor, Hyères, and Irving banks; *Trituba recurvata* n. sp. from Hyères bank; *T. constricta* n. sp., *T. fallax* n. sp., and *T. additicia* n. sp. from Hyères and Irving banks; *T. lima* n. sp. from Irving bank; *T. elatissima* n. sp. from Plato and Atlantis banks; and *T. hirta* n. sp. from Atlantis bank. The level of bank-to-bank endemism is high, with four species endemic to a single bank. This indicates that the distances, in the order of magnitude of 100 to 200 km, between the banks are barriers for larvae and egg capsules of these species of *Trituba*, which are inferred to have an intracapsular larval development. There is very much difference in the success of the different species, as reflected by their relative abundances, ranging from the 64 specimens and over 500 shells collected of *T. constricta* to the 4 shells of *T. additicia*; some of the rarer species could be very prone to extinction or may even be extinct. The diversification into a set of species with different depth ranges and morphologies is interpreted as a factor that will enhance the probability of survivorship in the lineage. The common species suffer important predation pressure, presumably from a muricid gastropod, and one third to two thirds of the adult shells are drilled in the large populations of *T. constricta*.

Key Words: Triforidae, endemism, survivorship, seamount, dispersal

The seamounts of the Meteor group, situated approximately 600 km south of the Azores and 1100 km west of the Canaries, hold one of the most isolated benthic biota in the North Atlantic. To date, there is only very fragmented knowledge of this fauna. The only previous museum material was that collected by R/V Meteor cruise 9C in 1967. The Seamount 2 expedition visited the banks in January-February 1993 and yielded a large amount of material which is currently under study.

This paper deals with a group which has been known hitherto from the two species described by Bouchet and Fechter (1981) and from a fragmentary shell figured by Bouchet and Warén (1993). The Seamount 2 material contains a large number of specimens, many of which were live-collected. There are several closely related species, either sympatric or allopatric from bank-to-bank, making it possible to find one to four sympatric species within a particular sample, and up to five different species on a particular seamount.

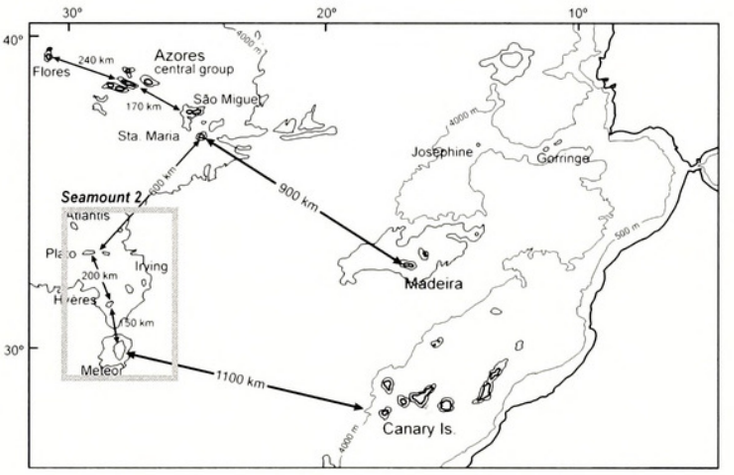

Fig. 1. Map showing the location of the Northeast Atlantic seamounts and their distances to the mainland.

MATERIAL AND METHODS

The Seamount expeditions were directed to general collecting of the benthic fauna with views to understand the colonization of remote sites by the benthos, at the initiative of Philippe Bouchet (of Muséum National d'Histoire Naturelle, Paris, hereafter MNHN). Seamount 2 (Fig. 1) was conducted in January/February 1993 by the author and visited the Great Meteor bank, Hyères, Irving (also named Cruiser), Plato, Atlantis, and Tyro seamounts (69 dredge hauls and 16 beam trawl operations shallower than 1000 m). The material was sorted to the species level and

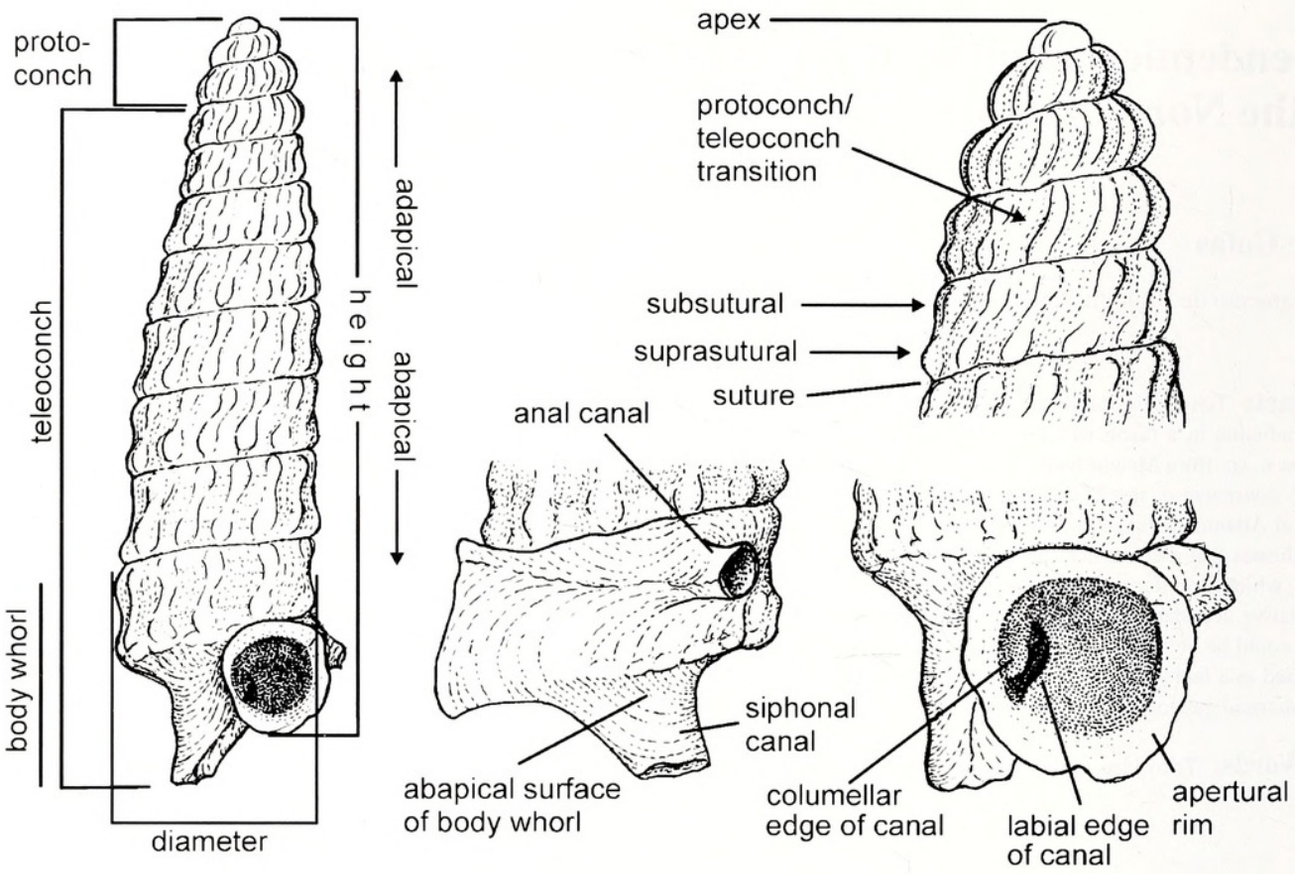

Fig. 2. The shell of a *Trituba* species, showing some descriptive terms used in this paper.

deposited in the malacological collection of MNHN.

Most of the collected material consisted of shells, and these were taken into account in the mollusc counts. The coarse fractions, usually above 10 mm, were mostly sorted on board to phyla, then sorted to species level in the lab. The finer fractions were preserved as whole on board, and later sieved on 5 mm, 2 mm, 1 mm, 0.5 mm, and 0.3 mm sieves, and sorted under a stereomicroscope. Drawings of living animals were prepared wherever possible, and include one entry for *Trituba*. The specimens and shells of *Trituba* were collected in dredge hauls containing large quantities of geodid and other sponges, on which these gastropods may feed. The coordinates and depths of the relevant hauls are indicated in Table 1.

Heights of shells of *Trituba* (Fig. 2) were measured from the apex to the lower edge of the lip. The maximum diameter was measured on the penultimate whorl so as to leave out the peristome features. Juvenile specimens had a flat abapical surface and lacked the adult apertural features, but were usually easy to assign to a particular species by assembling growth series and comparing protoconch characters and teleoconch sculpture.

Important and stable characters, well correlated with independent teleoconch characters, were found in the shape and sculpture of the protoconch. The number of whorls could not be determined with very much precision, because there was no physical limit and a very gradual transition to the teleoconch; the demarcation was indicated by the change in sculpture, where the ribbed pattern was replaced by a pattern of knobs, but this is not clear cut in species where the teleoconch was also ribbed. The profile of the protoconch also provided informative characters, including whether the apex was sunken in the next whorl or protruding, and if the later protoconch whorls were swollen so as to depart from the general profile of the spire or conformed to the high conical template.

On the teleoconch, characters were derived from the sculpture, the general profile, and the apertural features. The profile of the body whorl may be constricted, that is with a diameter smaller than would be expected from the geometrical continuation of the previous spire whorls. There were two canals in addition to the aperture, which were usually closed and tubular in the adults, one siphonal (anterior in life position) and another, anal, opposite to it. The length and curvature of the anal canal was an informative feature. The morphology inside the siphonal canal i.e. how the columellar edge of the canal related to the opposite edge, has been shown as important by Marshall (1977). Among the species studied herein, this character was used for discriminating the two Meteor bank species described by Bouchet and Fechter (1981), but was not very helpful elsewhere. The abbreviations used for the material

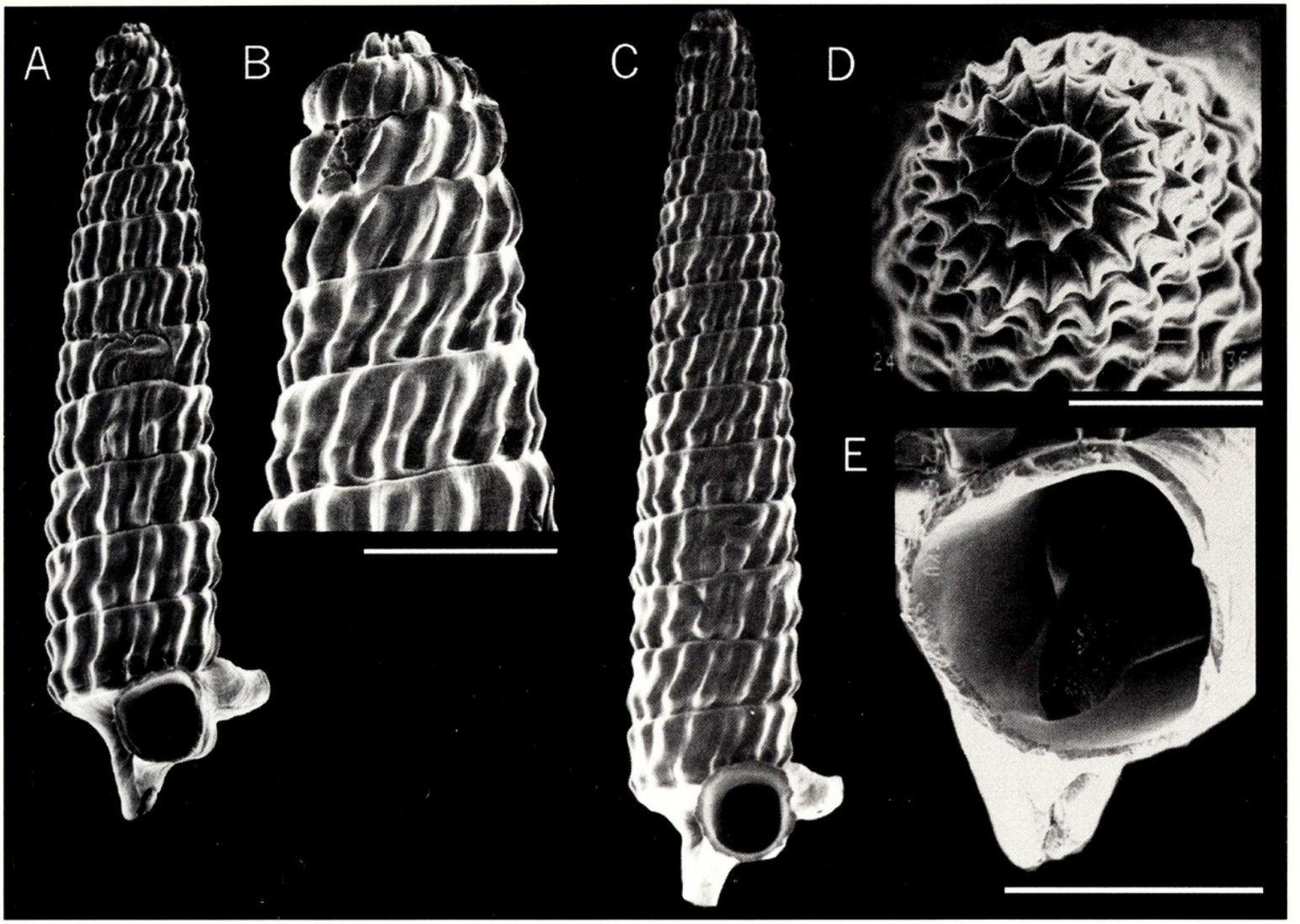

Fig. 3. *Trituba superstes* (Bouchet and Fechter, 1981) from Meteor bank, DW152. **A.** Shell (4.9 mm long). **B.** Protoconch, same specimen as A. **C.** Shell (6.7 mm long). **D.** Apical view of protoconch of another specimen. **E.** Oblique view of the aperture, to show the widely separated edges of siphonal canal, same specimen as A. Scale bars = 500 µm.

examined are: sh, shell(s); spm, live-collected specimen(s); sta, station number of research vessel.

SYSTEMATICS

Genus *Trituba* Jousseaume, 1884

Remarks

The genus considered in this paper has been hitherto known as "*Triforis* Deshayes, 1834." Bouchet and Marshall (in press) has requested ICZN to confirm *Triforis* "Deshayes, 1834" as an incorrect subsequent spelling of *Triphora* Blainville, 1828, so that the valid generic name for the species described herein should be *Trituba* Jousseaume, 1884 (Type species by original designation: *Triforis bitubulatus* Baudon, 1856, a fossil from the Eocene of France).

The genus was placed in the family Triforidae Jousseaume, 1884, and superfamily Cerithiopsoidea by Marshall (1980).

Trituba superstes (Bouchet and Fechter, 1981)
(Figs. 3, 4)

Type material

Holotype (sh., 4.9 x 1.4 mm) and 2 paratypes (sh.) in Zoologische Staatssammlung, München; 1 paratype (sh.) in MNHN; all from "Meteor" cruise 9c sta. 172.

Type locality

Meteor bank, 29°48'N - 28°23'W, 300-310 m.

Material examined

Meteor bank, DW143: 1 sh. (3.9 x 1.1 mm); DW152: 11 spm. (7 adult, 4.9 x 1.2 to 6.9 x 1.4 mm) and 31 sh. (18 adult).

Table 1. List of sampling stations of Seamount 2 cruise where *Trituba* spp. were collected.

Meteor bank			
DE 140	30°01.1'N	28°27.7'W	308 m
DW 143	30°09.9'N	28°28.1'W	330 m
DW 152	30°02.0'N	28°22.1'W	470 m
DW 166	29°36.0'N	28°22.8'W	575 m
DW 172	30°05.1'N	28°41.5'W	455 m
DW 179	30°00.6'N	28°42.3'W	730 m
Hyères bank			
DW 182	31°23.2'N	28°53.5'W	480 m
DW 184	31°24.4'N	28°52.3'W	705 m
DW 186	31°26.1'N	28°51.8'W	1520 m
DW 188	31°30.0'N	28°59.5'W	310 m
DW 190	31°29.0'N	29°00.0'W	750 m
DW 192	31°27.9'N	28°59.1'W	750 m
DW200	31°19.1'N	28°36.0'W	1060 m
DW202	31°16.5'N	28°43.1'W	640 m
DW203	31°09.5'N	28°43.5'W	845 m
Irving bank			
DW205	32°01.1'N	27°57.2'W	348 m
DW209	31°59.2'N	27°55.9'W	460 m
DW215	31°53.6'N	28°02.9'W	275 m
DW216	31°53.7'N	28°03.0'W	270 m
DW225	32°08.6'N	28°10.7'W	1035 m
DW231	32°01.5'N	27°54.5'W	745 m
DW237	32°15.9'N	27°31.8'W	670 m
DW238	32°17.3'N	27°32.3'W	890 m
Plato bank			
DW240	33°12.3'N	29°01.9'W	565 m
DW241	33°11.9'N	28°59.3'W	695 m
DW242	33°11.8'N	28°57.0'W	710 m
DW247	33°13.7'N	29°35.3'W	580 m
DW248	33°13.6'N	29°32.5'W	735 m
Atlantis bank			
DW255	34°04.9'N	30°15.3'W	340 m
DW258	33°59.8'N	30°12.1'W	420 m
DW263	34°25.9'N	30°32.5'W	610 m
DW274	34°05.1'N	30°13.6'W	280 m

Redescription

Shell up to 6.8 x 1.4 mm, turriculate, solid, white, with 12-15 whorls. Protoconch ca. 2.5-3 whorls, with maximum diameter 0.75 mm, the nucleus quite sunken in the following whorl, resulting in a very blunt apex; protoconch whorls strongly and evenly convex, sculptured with strong and elevated, sharp, widely spaced ribs starting on the very first whorl, slightly oblique on the first and second whorls, still more oblique on the third.

Teleoconch whorls sculptured with quite strong, slightly oblique ribs on which there is a subsutural and a suprasutural bulge, separated by a broad depression; the suprasutural bulges bordered adapically by a faint spiral line. Body whorl hardly narrowing; its abapical surface smooth and circled by a faint keel on which the ribs terminate.

Aperture with a continuous, moderately flaring peristome. Siphonal canal moderately long, narrowing towards outer opening, inside with columellar and labial edges set widely apart. Anal canal similar in size and shape to the siphonal, moderately curved, pointing sidewards.

Remarks

Trituba superstes was not found outside Meteor bank. Specimens from Hyères bank with this kind of teleoconch sculpture had a more protruding first protoconch whorl and thus lacked the very characteristic blunt apex of *T. superstes*; they are treated as a different species, *Trituba fallax*.

A living specimen of this species was observed from DW152 (Fig. 4). The head-foot was tiny in comparison to the shell, but nevertheless the animal managed to crawl around. The mantle edge remained concealed inside the aperture at the time of observation. The cephalic tentacles were tapered, with blunt ends, and set close together so as to form a V-shaped structure as in *Cerithiopsis*. The foot was truncated anteriorly, tapered posteriorly, and bore a longitudinal median groove on the sole, extending from the propodium to the metapodium. On the sides, there was also a shallow groove slightly above the edge of the sole. A pedal gland was visible by transparency in the posterior part of the foot, beneath the operculum. The head-foot was entirely white.

Trituba anelpistos (Bouchet and Fechter, 1981)
(Fig. 5)

Type material

Holotype (sh., 4.4 x 1.3 mm) in Zoologische Staatssammlung, München, from "Meteor" cruise 9c sta. 172.

Type locality

Meteor bank, 29°48'N - 28°23'W, 300-310 m.

Material examined

Meteor bank, DE140: 1 sh. (4.3 x 1.2 mm); DW143: 1 sh.; DW152: 21 spm. (17 adult, 3.1 x 1.0 to 5.4 x 1.3 mm) and 49 sh. (38 adult); Hyères bank, DW182: 15 sh. (adult, 3.1 x 0.9 to 4.8 x 1.4 mm), DW188: 1 spm. (4.3 x 1.1 mm) and 2 sh.; Irving bank, DW237: 3 spm. (adult, 3.7 x 1 to 5.1 x 1.3 mm) and 23 sh. (21 adult).

Redescription

Shell up to 5.4 x 1.3 mm, turriculate, solid, white, with 10-13 whorls. Protoconch ca. 2.5-3 whorls, with maximum diameter 0.6 mm, the nucleus quite protruding; protoconch whorls convex, sculptured with strong, thick ribs, almost axial on the first and second whorl, more oblique on the third whorl.

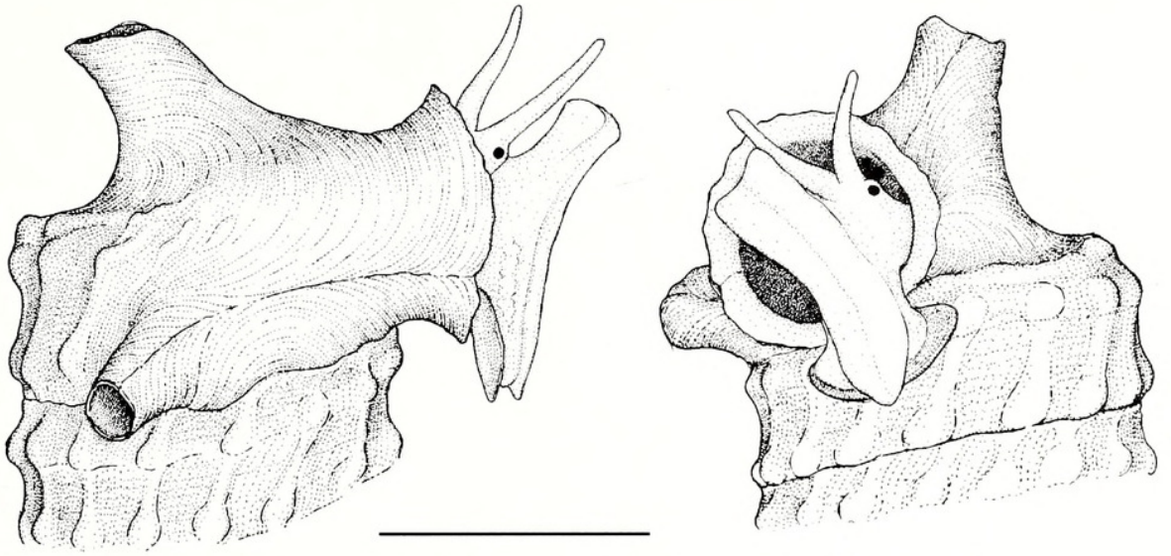

Fig. 4. *Trituba superstes*, drawing of a living animal from Meteor bank, DW152. Scale bar = 500 µm.

Teleoconch whorls sculptured with quite strong, blunt, slightly oblique ribs, very slightly swollen towards their subsutural and suprasutural parts, and depressed in between; the suprasutural swells are more distinct and bordered adapically by a very faint spiral line. Body whorl slightly narrowing, with ribs attenuated or absent; its abapical surface smooth and circled by a strong keel on which the ribs, if any, terminate.

Aperture with a continuous, moderately flaring peristome. Siphonal canal moderately long, narrowing towards outer opening, inside with columellar and labial edges coming very close together. Anal canal similar in size and shape to the siphonal, moderately curved, pointing sidewards.

Remarks

Specimens referable to *Tributa anelpistos* were found on Meteor, Hyères, and Irving banks. Specimens from Irving were smoother and had a very sharp keel on the body whorl, and also had a thicker (maximum diameter 0.75 mm) protoconch with less convex whorls. They also occurred deeper (670 m, see Fig. 14). Although some differentiation did occur, I did not find useful to formally name a subspecies.

Trituba fallax n. sp. from Hyères bank resembled *T. anelpistos* in having a heavily ribbed protoconch and a predominantly axial teleoconch sculpture, but was larger, had a non-constricted body whorl, a distinct spiral line bordering the suprasutural knobs on the ribs, and had smaller canals.

Trituba incredita Gofas, new species

(Fig. 6)

Type material

Holotype (spm., 6.2 x 1.4 mm) and paratypes, 1 spm. (adult) and 33 sh. (17 adult, largest 8.2 x 1.9 mm) from Seamount 2 sta. DW152.

Type locality

Meteor bank, 30°02.0'N - 28°22.1'W, 470 m.

Other material examined

Meteor bank, DW166, 1 sh. (8.8 x 2.0 mm without protoconch); DW172, 1 sh. (8.7 x 1.9 mm); DW179, 3 sh. (1 adult, 10.0 x 2.2 mm).

Description

Shell up to 10 x 2.2 mm, turriculate, solid, white, with 12-18 whorls. Protoconch ca. 3 whorls, the nucleus moderately protruding, with a pupoid profile, inflated so as to depart slightly from the general spire profile; protoconch whorls moderately convex, less so along the subsutural portion, sculptured with numerous, delicate, evenly spaced, oblique and flexuous ribs.

Teleoconch whorls sculptured with strong subsutural and suprasutural knobs, arranged in two spiral rows which are offset from each other so as to form oblique axial ribs; the suprasutural knobs stronger on the first teleoconch whorl and bordered adapically by a definite spiral line. Body whorl hardly narrowing; its abapical surface smooth and circled by a quite strong keel on which the ribs terminate.

Aperture with a continuous, flaring peristome. Siphonal canal moderately long, parallel sided, inside with columellar and labial edges coming moderately close together. Anal canal smaller than the siphonal, moderately curved, pointing sidewards.

Etymology

The name alludes to the shipboard party's scepticism, at the beginning of the expedition, about finding more than one species of this genus.

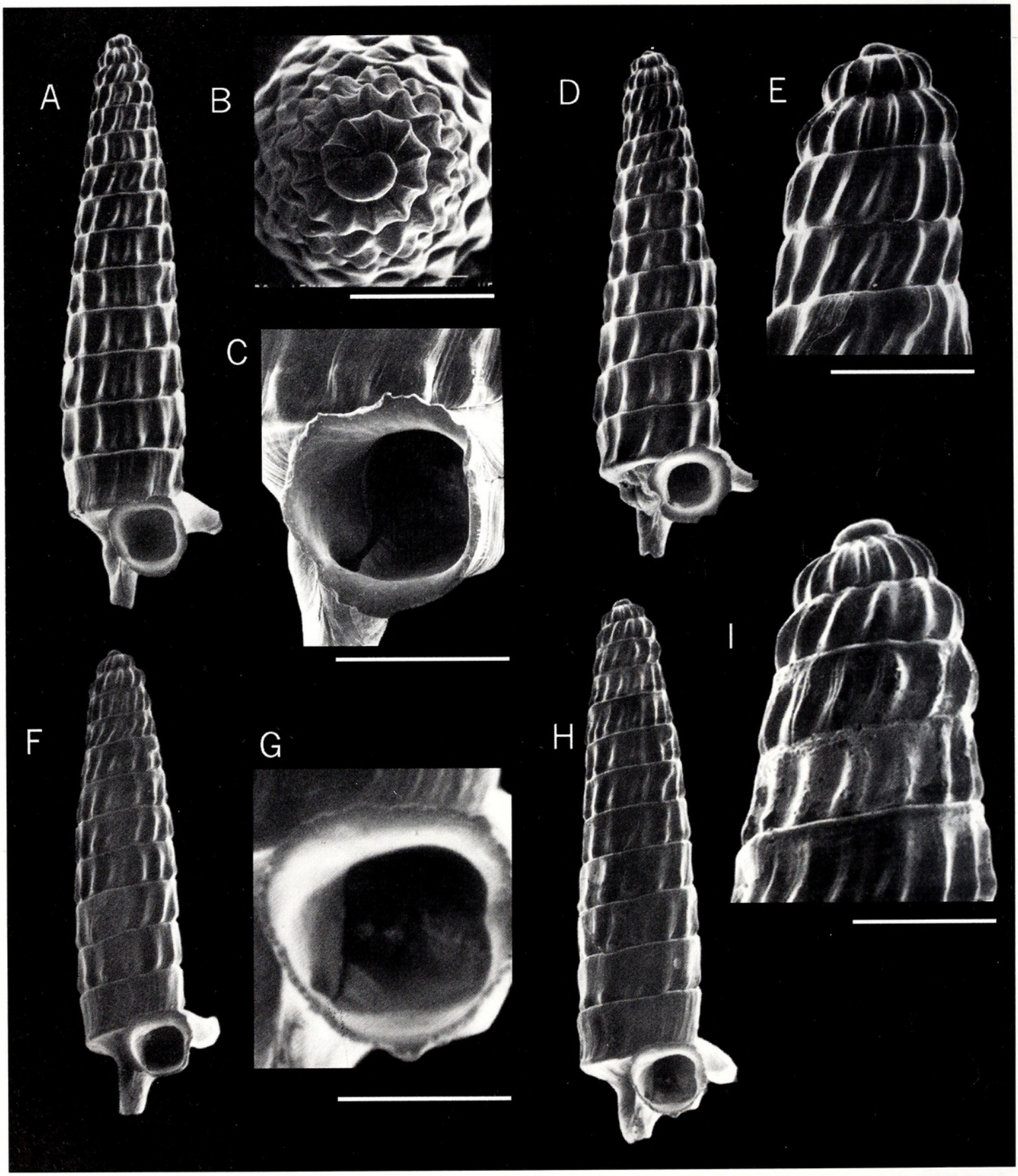

Fig. 5. *Trituba anelpistos* (Bouchet and Fechter, 1981). **A.** Shell from Meteor bank, DW152 (5.4 mm long). **B.** Apical view of protoconch. **C.** Aperture, to show the closely set edges of siphonal canal, same specimen as A. **D.** Shell from Hyères bank, DW188 (4.3 mm long). **E.** Protoconch, same specimen as D. **F, H.** Specimens from Irving bank, DW237 (4.2 and 5.1 mm long respectively). **G.** Aperture, same specimen as H. **I.** Protoconch, same specimen as H. Scale bars = 500 μm.

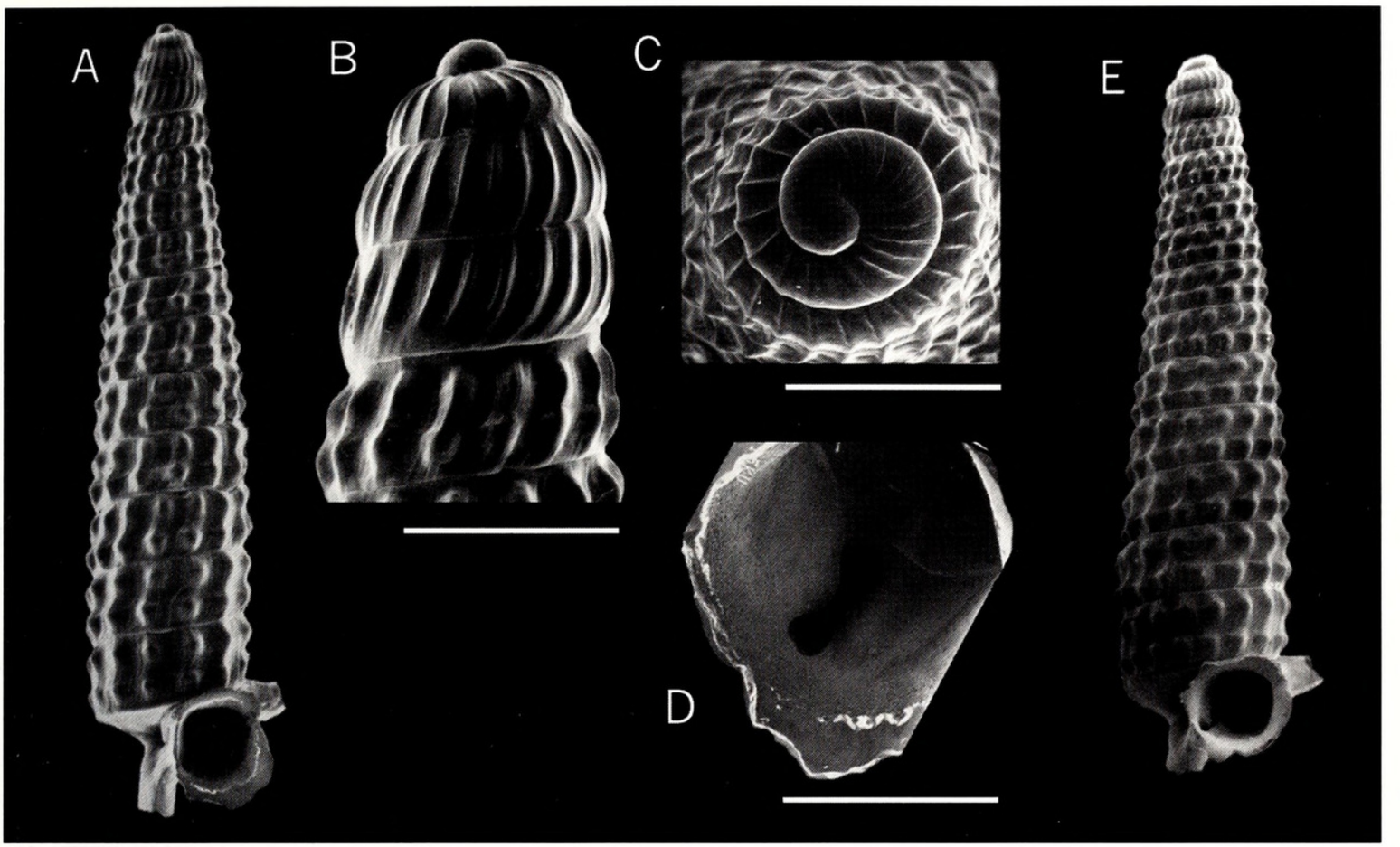

Fig. 6. *Trituba incredita* n. sp. **A.** Holotype from Meteor bank, DW152 (6.2 mm long). **B.** Protoconch of the holotype. **C.** Apical view of protoconch of another specimen. **D.** Oblique view of the aperture of the holotype, to show the inside of siphonal canal. **E.** Paratype from Meteor bank, DW 152 (5.6 mm long). Scale bars = 500 µm.

Remarks

This species differed from the two other Meteor bank species by the delicately sculptured, oblong protoconch and more cylindrical canal. The type of protoconch sculpture was shared with two species of Hyères bank and may indicate that they are related. *Trituba recurvata* was similar in most respects but differed in having a very long and curved anal canal. The morphs of *T. constricta* with the more accentuated sculpture looked quite similar as well, but the knobs from the two adjacent spiral rows tended to unite axially so as to form axial ribs; *T. constricta* also reached a larger size, and had a distinctly narrowing body whorl.

Trituba constricta Gofas, new species

(Fig. 7)

Type material

Holotype (spm., 9.4 x 2.1 mm) and paratypes, 10 spm. (9 adult) and 14 sh. (11 adult, 9.4 x 2.0 to 15.0 x 2.7 mm) from Seamount 2 sta. DW188.

Type locality

Hyères bank, 31°30.0'N - 28°59.5'W, 310 m.

Other material examined

Hyères bank, DW182: 3 spm. (juvenile) and 56 sh. (16 adult); DW184: 3 spm. (2 adult, 14.5 x 2.6 mm, 14.5 x 3.1 mm) and 30 sh. (28 adult, 13.0 x 2.7 to 19.0 x 3.2 mm, of which 20 drilled by gastropod predator); DW186: 5 sh. (broken, very smooth); DW188: 43 spm. (33 adult, 8.5 x 1.9 to 15.1 x 2.8 mm) and 336 sh. (248 adult, 9.0 x 1.9 to 15.5 x 2.8 mm, of which 80 drilled by gastropod predator); DW190: 3 spm. (adult, 11.7 x 2.5 to 13.9 x 2.8 mm) and 1 sh. (8.9 x 2.1 mm); DW192: 4 spm. (3 adult, 8.9 x 2.0 to 10.2 x 2.1 mm) and 11 sh. (9 adult, 8.9 x 2.0 to 10.7 x 2.4 mm); DW202: 5 sh. (adult, 14.0 x 2.6 to 18.3 x 3.0 mm); DW203: 8 spm. (6 adult, 12.5 x 2.5 to 14.0 x 2.9 mm) and 78 sh. (52 adult, 10.0 x 2.5 to 16.9 x 3.0 mm) Irving bank, DW205: 1 sh. (8.0 x 1.9 mm); DW209: 1 spm. (6.9 x 1.8 mm) and 13 sh. (12 adult, 8.0 x 1.9 to 10.8 x 2.5 mm).

Description

Shell up to 19 x 3.2 mm, turriculate, solid, white, with 20-22 whorls. Protoconch ca. 3-3.5 whorls, with maximum diameter 0.7 mm, the nucleus quite protruding; first protoconch whorl with maximum convexity along suprasutural zone; the second whorl convex, with the suprasutural

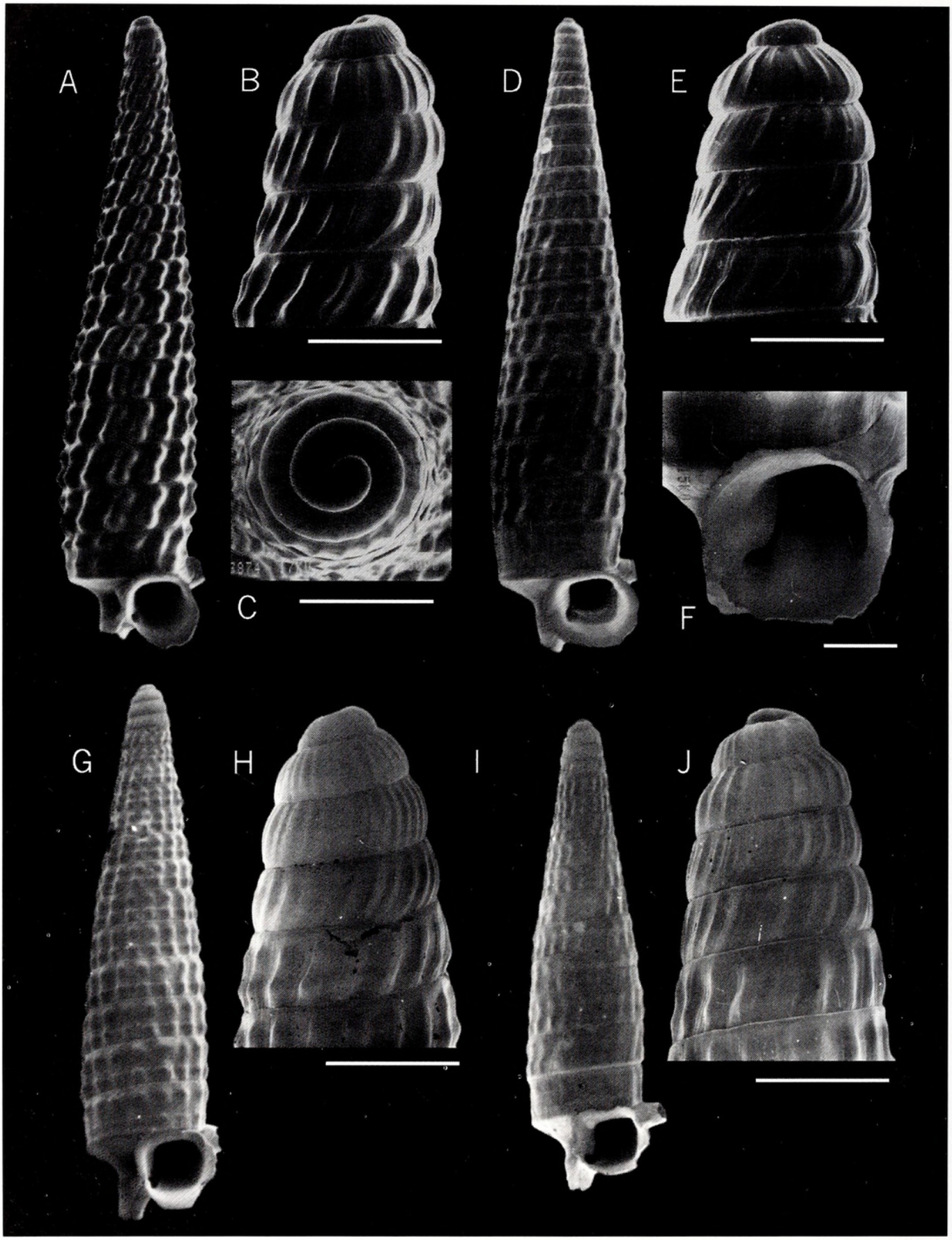

Fig. 7. *Trituba constricta* n. sp. **A.** Holotype from Hyères bank, DW188 (9.4 mm long). **B.** Protoconch of the holotype. **C.** Apical view of protoconch of another specimen. **D.** Specimen from Hyères bank, DW 203, with attenuated sculpture (12.5 mm long). **E.** Protoconch, same specimen as D. **F.** Aperture or a paratype from DW188. **G.** Specimen from Irving bank, DW209 (7.9 mm long). **H.** Protoconch, same specimen as G. **I.** Another specimen from Irving bank, DW209, with very attenuated sculpture (6.9 mm long). **J.** Protoconch, same specimen as I. Scale bars = 500 µm.

portion slightly overhanging the following whorl; first protoconch whorl nearly smooth, the following sculptured with weak folds, nearly axial on the first whorl, more oblique on the second and third whorls.

Teleoconch whorls with a glossy surface, sculptured with slightly oblique ribs on which there are two variably developed bulges separated by a depression; the suprasutural bulges bordered adapically by a faint spiral line. Body whorl definitely constricted, with axial sculpture gradually becoming attenuated or disappearing; its abapical surface smooth and circled by a strong keel on which the ribs, if any, terminate. On some specimens, the abapical row of bulges continued on the body whorl as a faint additional keel.

Aperture with a continuous, flaring peristome. Siphonal canal very short, narrowing towards outer opening, inside with columellar and labial edges coming moderately close. Anal canal small and short, pointing sidewards.

Etymology

The name recalls the narrowing profile of the body whorl.

Remarks

This species was present in large numbers in samples from the broad depression on the NW upper slope of Hyères bank, where sponges were thriving. Specimens referable to this species were also collected on Irving bank. Its large size, very short canals, attenuated sculpture and narrowing body whorl made it unmistakable among the NE Atlantic seamount radiation. The protoconch morphology with delicate sculpture was shared with several species: *Trituba incredita*, of Meteor bank, was smaller, had more distinct beads on the teleoconch and did not narrow the body whorl so much; the sympatric *Trituba recurvata* differed in the same characters and in having a very long, reflected anal tube; *Trituba lima*, from Irving bank, was similar in size and profile and also had very short canals, but differed in having a rough teleoconch sculpture and one more protoconch whorl.

There is a distinct variation with depth on Hyères bank, where specimens from the shallower samples (300-600 m) were smaller (8.5 to 15.5 mm) and had more distinct bulges, which could almost be termed knobs, on the ribs, whereas those from the deeper samples were larger (up to 19 mm) and tended to have attenuated sculpture. However, every transition could be seen in the large samples examined, and there was no other character correlated with this variation which could indicate that more than one species was involved.

The few specimens collected from Irving bank (Fig. 7, G-J) differed in being somewhat more stout and in that the knobs on spire teleoconch whorls were aligned more or less parallel to the main axis, rather than oblique. However, the other characters, including the protoconch sculpture and the constriction of the body whorl, were similar, so that they were tentatively considered as conspecific. There was also a variation in the intensity of sculpture, the most extreme specimens being quite smooth.

Trituba fallax Gofas, new species

(Fig. 8)

Type material

Holotype (spm., 8.8 x 1.8 mm) and paratypes, 7 spm. (5 adult, 5.8 x 1.5 to 8.8 x 1.8 mm) and 10 sh. (adult, 6.5 x 1.6 to 9.9 x 1.9 mm) from Seamount 2 sta. DW188.

Type locality

Hyères bank, 31°30.0'N - 28°59.5'W, 310 m.

Other material examined

Hyères bank, DW182: 65 sh. (15 adult, 6.6 x 1.7 to 11.8 x 2.5 mm); DW188: 38 sh. (36 adult, 6.8 x 1.6 to 10.4 x 2.2 mm); DW192: 16 sh. (10 adult, 6.6 x 1.6 to 12.2 x 2.4 mm); Irving bank, DW205: 2 spm. (1 adult, 15.2 x 2.6 mm) and 1 sh.; DW209: 1 spm. (10.5 x 2.1 mm) and 2 sh. (broken); DW215: 1 sh. (9.4 x 2.0 mm, broken apex); DW216: 1 sh. (8.8 x 1.9 mm); DW231: 1 fragment.

Description

Shell up to 12.2 x 2.4 mm, turriculate, solid, white, with 14-20 whorls. Protoconch ca. 2.5-3 whorls, with maximum diameter 0.7 mm; the nucleus quite protruding and the whorls regularly increasing in diameter; protoconch whorls convex, sculptured with strong, thick ribs, almost axial on the first whorl, then more oblique.

Teleoconch whorls with a glossy surface, sculptured with quite strong, oblique ribs, swollen towards their subsutural and suprasutural parts, and depressed in between; the subsutural end with definite knobs in the early whorls, less so in the later ones; the suprasutural knobs distinct throughout and bordered adapically by a definite spiral line. Body whorl not narrowing; its abapical surface smooth and circled by a strong keel on which the ribs terminate.

Aperture with a continuous, moderately flaring peristome. Siphonal canal short, hardly narrowing towards outer opening, inside with columellar and labial edges coming very close together. Anal canal short, pointing sidewards.

Etymology

The name alludes to the misleading similarities with a large *Trituba anelpistos*.

Remarks

Trituba fallax resembled *Trituba anelpistos* in the general pattern of sculpture of the protoconch and

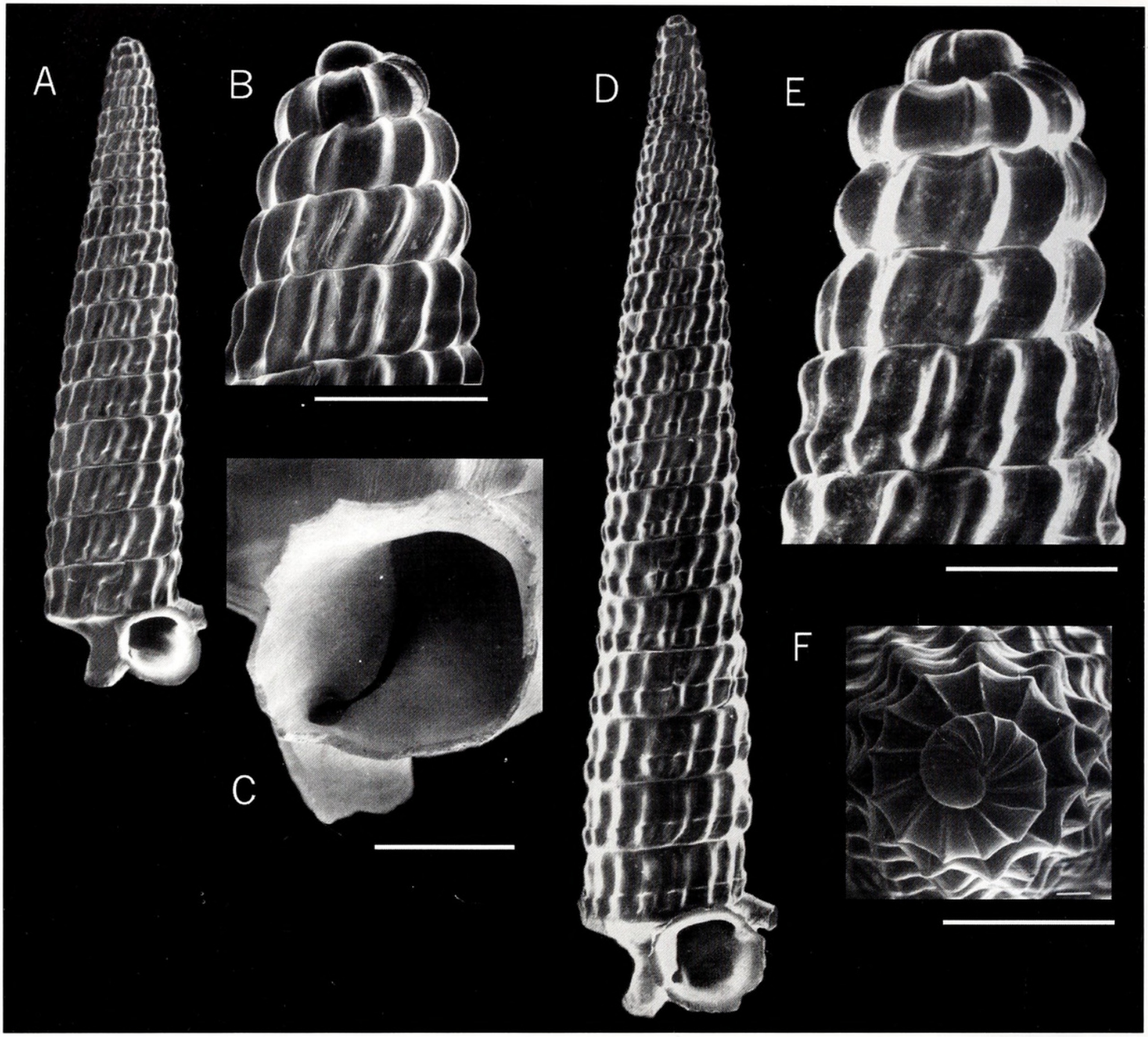

Fig. 8. *Trituba fallax* n. sp. **A.** Holotype from Hyères bank, DW 188 (8.8 mm long). **B.** Protoconch of the holotype. **C.** Oblique view of the aperture of the holotype, to show the closely set edges of siphonal canal. **D.** Specimen from Irving bank, DW205 (15.2 mm long). **E.** Protoconch, same specimen as D. **F.** Apical view of protoconch of another specimen from Irving. Scale bars = 500 µm.

teleoconch. However, it grew much larger (maximum length usually over 10 mm) and had more whorls than *T. anelpistos*. The protoconch was accordingly broader and had more widely spaced ribs, particularly on the first whorl. The siphonal and the anal canals were much shorter, even in the small specimens, and the ribs on the teleoconch formed more distinct bulges. *Trituba constricta* was commonly of similar size but the protoconch had a delicate sculpture, the body whorl was constricted, and the axial ribs, if well developed, had more distinct bulges.

The description above is based on specimens from Hyères, but there were specimens collected on Irving bank tentatively assigned to *Trituba fallax*. The largest one (Fig. 8, D-E) had 23 whorls and resembled *Trituba elatissima* from Plato bank. However, the protoconch sculpture is stronger and the shell surface is glossy (even fresh shells of *T. elatissima* are dull). In addition, the teleoconch sculpture forms ribs similar to those of the pyramidellid genus *Turbonilla* Risso, 1826 in *T. fallax*, whereas in *T. elatissima* the nodose pattern is prevalent.

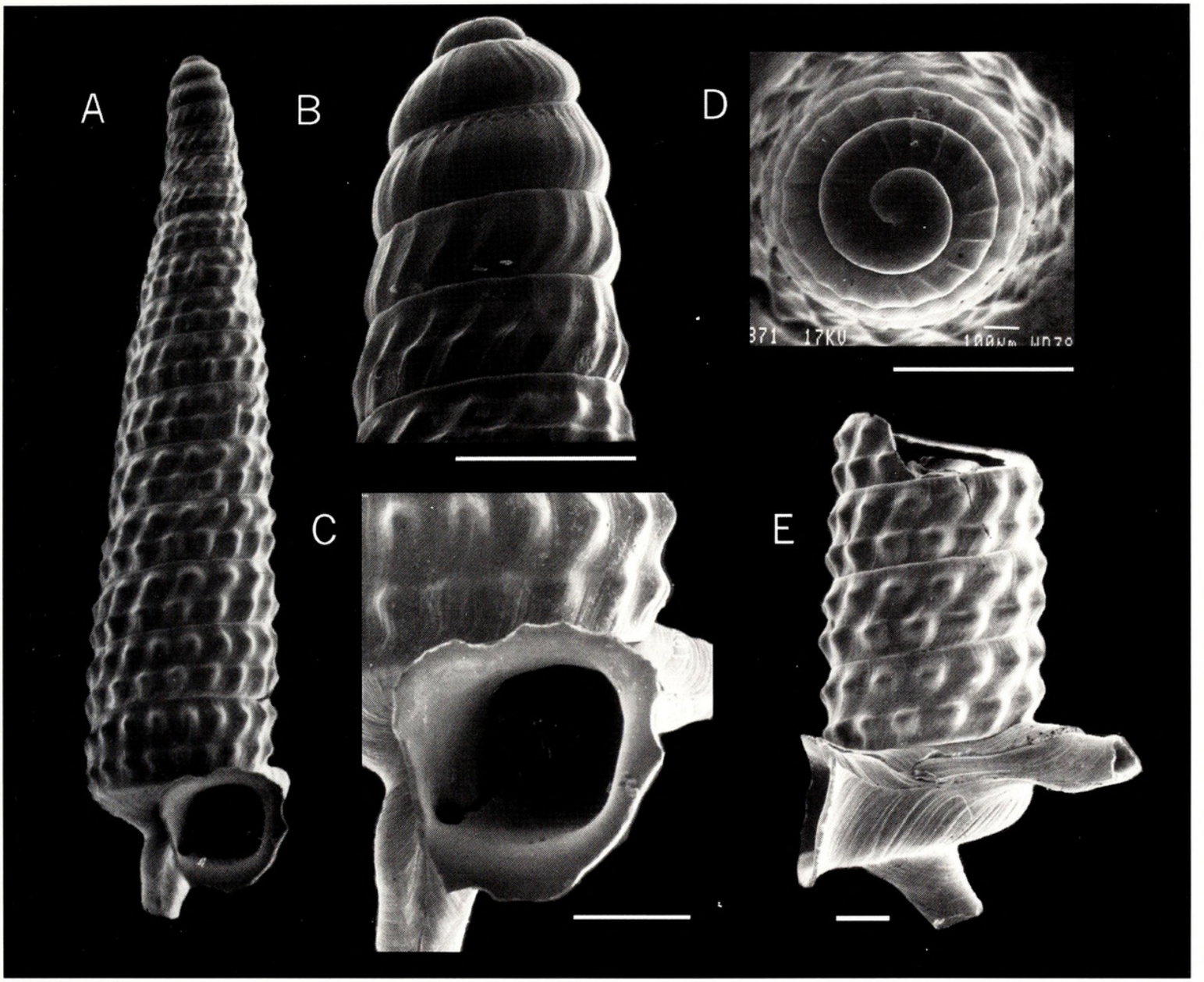

Fig. 9. *Trituba recurvata* n. sp. **A.** Holotype from Hyères bank, DW 203 (8.5 mm long). **B.** Protoconch of the holotype. **C.** Oblique view of the aperture of the holotype, to show the inside of siphonal canal (external tubes are incompletely shown). **D.** Apical view of the protoconch of another specimen. **E.** Lateral view of another specimen, to show the long, curved anal canal. Scale bars = 500 µm.

Trituba recurvata Gofas, new species

(Fig. 9)

Type material

Holotype: (spm., 8.5 x 1.9 mm) and paratypes, 3 spm (adult, 12.3 x 2.3 mm, other 2 with broken apex) and 15 sh. (10 adult, 7.3 x 1.8 to 13.2 x 2.5 mm) from Seamount 2 sta. DW203.

Type locality

Hyères bank, 31°09.5'N - 28°43.5'W, 845m.

Other material examined

Hyères bank, DW184: 3 sh. (9.6 x 2.3 mm, others broken); DW200: 2 spm. (1 adult, 10.8 x 2.0 mm) and 22 sh. (7 adult, 5.5 x 1.5 to 11.5 x 2.3 mm); DW202: 1 sh. (8.1 x 1.9 mm).

Description

Shell up to 13.2 x 2.5 mm, turriculate, solid, white, with 15-20 whorls. Protoconch ca. 3-31/2 whorls, the nucleus moderately protruding, with a somewhat pupoid profile, inflated so as to depart slightly from the general spire profile; protoconch whorls moderately convex, less so along the subsutural portion, sculptured with delicate, irregular, oblique, and flexuous ribs.

Teleoconch whorls sculptured with strong subsutural and suprasutural knobs, arranged in two spiral rows

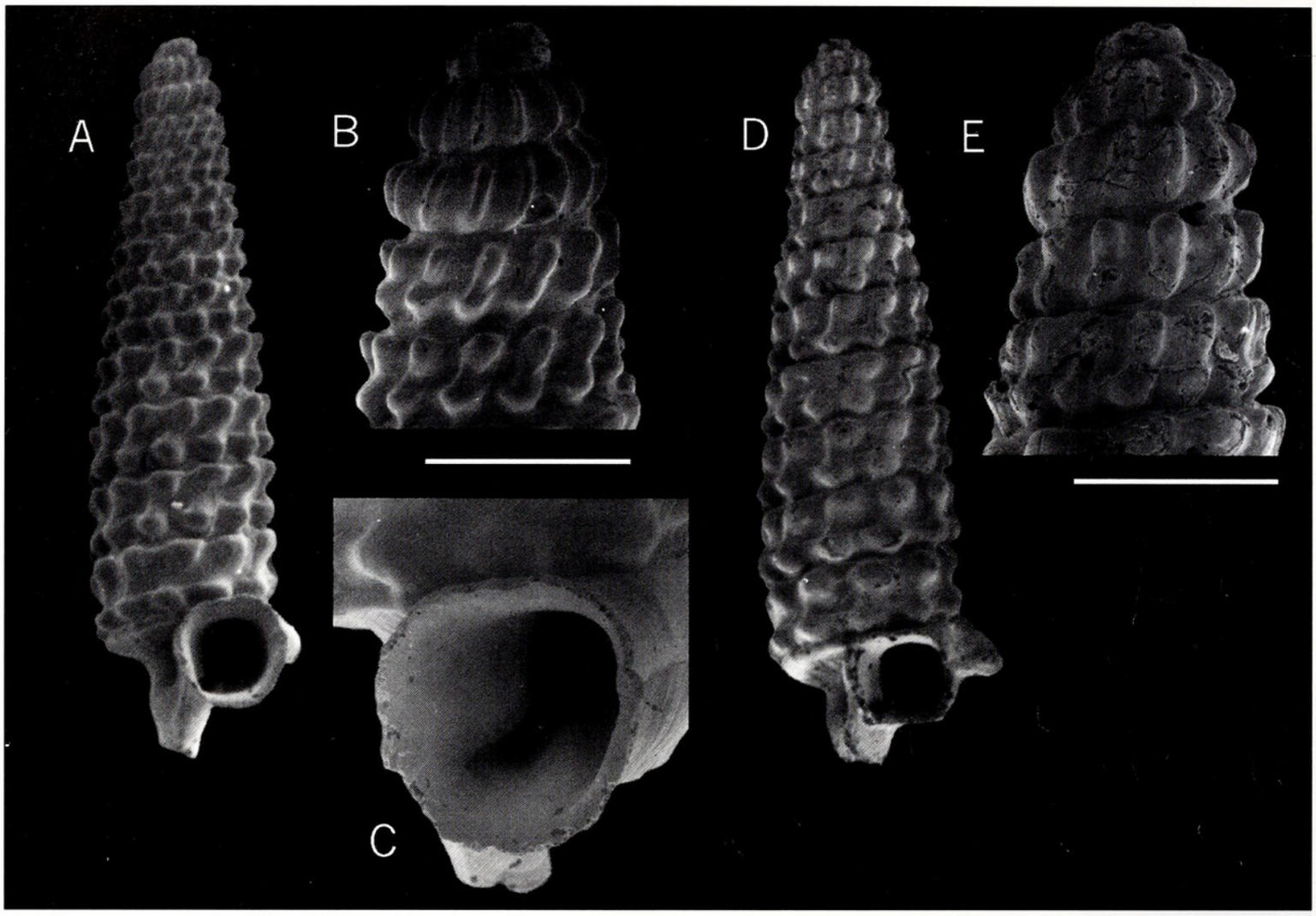

Fig. 10. *Trituba additicia* n. sp. **A.** Holotype from Hyères bank, DW 188 (4.0 mm long). **B.** Protoconch of the holotype. **C.** Oblique view of the aperture of the holotype, to show the widely separated edges of siphonal canal. **D.** Specimen from Irving bank, DW215 (4.2 mm long). **E.** Protoconch, same specimen as D. Scale bars = 500 µm.

which are offset from each other so as to form loosely defined, oblique axial ribs; the suprasutural knobs starting earlier on the first teleoconch whorl and bordered adapically by a definite spiral line. Body whorl hardly narrowing; with the spiral rows of knobs becoming gradually fused and then disappearing; abapical surface smooth and circled by a faint keel.

Aperture with a continuous, flaring peristome. Siphonal canal moderately long, slightly narrowing towards its opening, inside with columellar and labial edges quite close together. Anal canal very long and curved backwards, making a wide angle with apertural plane.

Etymology

The name alludes to the long, curved anal canal.

Remarks

The most similar species was *Trituba incredita* from Meteor bank which differed essentially in having a rather short anal canal. The delicate protoconch sculpture was also found in the sympatric *T. constricta* n. sp., which differed in its larger size, smoother teleoconch sculpture and more predominantly axial, narrowing body whorl and very short canals.

This species was found rather deeper (640-845 m) than the other species on Hyères.

Trituba additicia Gofas, new species

(Fig. 10)

Type material

Holotype (sh., 4.0 x 1.1 mm) from Seamount 2 sta. DW188; Paratypes, 2 sh. (3.6 x 1 mm, 3.2 x 0.95 mm) from Seamount 2 sta. DW182.

Type locality

Hyères bank, 31°30.0'N - 28°59.5'W, 310 m.

Other material examined

Irving bank, DW215: 1 sh. (4.2 x 1.15 mm).

Description

Shell up to 4 x 1.1 mm, turriculate, solid, white, with 10-13 whorls. Protoconch of nearly 3 whorls, with the nucleus quite protruding and the whorls regularly increasing in diameter; protoconch whorls very convex, sculptured with strong, thick ribs, almost axial on the first and second whorl, more oblique on the third whorl (maximum diameter of protoconch 0.6 mm).

Teleoconch whorls sculptured with strong subsutural and suprasutural knobs, arranged in two spiral rows which are offset from each other and connected by faint oblique ridges; both series of knobs starting simultaneously on the first teleoconch whorl, the subsutural one prominent so as to form a channelled suture. Body whorl hardly narrowing; with the abapical surface smooth and circled by a sharp, slightly undulated keel; the subsutural row of knobs abutting against the anal canal, the other one running next to the abapical keel.

Aperture with a continuous, strongly flaring peristome. Siphonal canal moderately long, narrowing towards outer opening, inside with columellar and labial edges quite far apart. Anal canal similar in size and shape to the siphonal, moderately curved backwards.

Etymology

The names means additional, as this species appeared in later sorting of the Seamount 2 material.

Remarks

The sculpture in this species was very strong and resembled that of *Trituba aspera* from Atlantis bank, but the canals were much longer and the protoconch had one more whorl.

Trituba lima Gofas, new species

(Fig. 11)

Type material

Holotype (spm., 9.6 x 2.5 mm, apex broken) and paratypes,

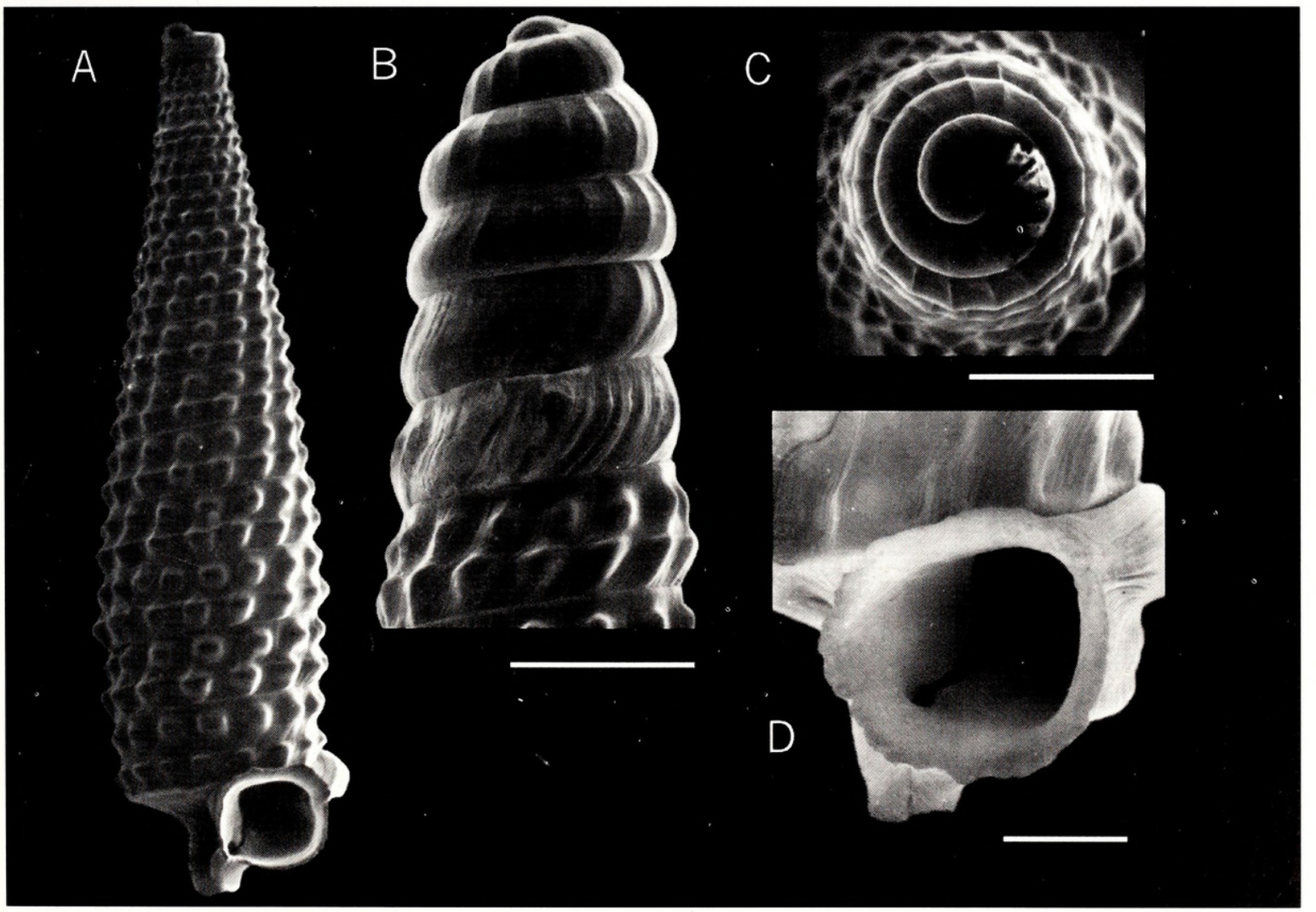

Fig. 11. *Trituba lima* n. sp. **A.** Holotype from Irving bank, DW 237 (9.6 mm long). **B.** Protoconch of another specimen from DW237. **C.** Apical view of the protoconch of another specimen. **D.** Oblique view of the aperture of the holotype, to show the closely set edges of siphonal canal. Scale bars = 500 μm.

7 sh. (3 adult, 8.6 x 2.4 mm, 9.4 x 2.6 mm, 12.5 x 2.9 mm) from Seamount 2 sta. DW237.

Type locality

Irving bank, 32°15.9'N - 27°31.8'W, 670m.

Other material examined

Irving bank, DW225, 4 sh. (3 adult, largest 16.0 x 3.2, broken apex), DW237, 37 sh. (3 adults, broken); DW238: 1 spm. (juvenile) and 11 sh. (3 adult, 9.8 x 2.4 to 13.0 x 3.1, broken apex).

Description

Shell up to 16 x 3.2 mm, fusiform, solid, white, with 19-22 whorls. Protoconch ca. 4-4.5 whorls, with the nucleus quite protruding and a somewhat pupoid profile; protoconch whorls quite convex, the second and third with the suprasutural portion slightly overhanging the following whorl; sculptured with weak ribs, almost axial on the first whorl, more oblique on the following whorls.

Teleoconch whorls sculptured with strong subsutural and suprasutural knobs, arranged so as to form two spiral rows and loosely defined, oblique axial ribs; the suprasutural knobs starting earlier on the first teleoconch whorl and bordered adapically by a definite spiral line, nearly as conspicuous as the suture. Body whorl quite narrowing, its abapical surface smooth and circled by a faint keel.

Aperture with a continuous, hardly flaring peristome. Siphonal canal very short, narrowing towards outer opening, inside with columellar and labial edges coming very close together. Anal canal small and short, pointing sidewards.

Etymology

Alludes to the rough sculpture, like that of a file.

Remarks

This species shared many character states such as size and shape of canals and the general profile, with *Trituba constricta*, and had the teleoconch sculpture as in *Trituba recurvata*. The protoconch had one more whorl than in *T. constricta*, and was broken on most of the adult specimens collected.

Trituba elatissima Gofas, new species

(Fig. 12)

Type material

Holotype (spm. 17.7 x 2.7 mm) and paratypes, 1 spm. (19.8 x 2.7 mm) and 10 sh. (7 adult, 9.5 x 1.7 to 21.2 x 3.3 mm) from Seamount 2 sta. DW248.

Type locality

Plato bank, 33°13.6'N - 29°32.5'W, 735 m.

Other material examined

Plato bank, DW240: 3 sh. (1 adult, 9.0 x 1.8 mm); DW241: 3 sh. (2 adult, broken); DW242: 35 sh. (4 adult, 6.0 x 1.5 to 12.1 x 2.3 mm); DW247: 2 sh. (broken); DW248: 1 spm. and 28 sh. (broken); Atlantis bank, DW255: 2 sh. (juveniles); DW263: 40 sh. (7 adult, 7.6 x 1.5 to 20.8 x 3.0 mm, the latter with apex and lip broken)

Description

Shell up to 21 x 3 mm, turriculate, solid, white, with 13-25 whorls. Protoconch ca. 4-5 whorls, the nucleus moderately protruding; protoconch whorls quite convex, sculptured with strong, sharp, oblique, and curved ribs.

Teleoconch whorls sculptured with strong subsutural and suprasutural knobs, arranged so as to form two spiral rows and loosely defined, oblique axial ribs; the suprasutural knobs starting earlier on the first teleoconch whorl. Body whorl not narrowing; its abapical surface smooth and circled by a keel.

Aperture with a continuous, flaring peristome. Siphonal canal moderately long, cylindrical, inside with columellar and labial edges not very close. Anal canal small and short, pointing sidewards.

Etymology

The name means extremely slender.

Remarks

This species was the only one collected on Plato bank. Large specimens were among the largest of all the seamount *Trituba*, but the smallest specimen (from DW242) was a mere 9 mm high. All, even the small ones, nevertheless had a protoconch with 4 whorls or more. The few specimens collected on Atlantis bank were not in very good condition, but were tentatively assigned to this species. Small specimens resembled the sympatric *Trituba hirta*, although the tubercles on the teleoconch were not so sharp. The main differences lay in the protoconch, which had at least one more whorl and less sharp ribs, and in the aperture, which was more projected.

Trituba hirta Gofas, new species

(Fig. 13)

Type material

Holotype, (sh., 6.3 x 1.7 mm) from Seamount 2 sta. DW274. Paratypes, 3 sh. (adults, 4.9 x 1.4 mm, 6.1 x 1.6 mm, 6.7 x 1.6 mm) from Seamount 2 sta. DW263.

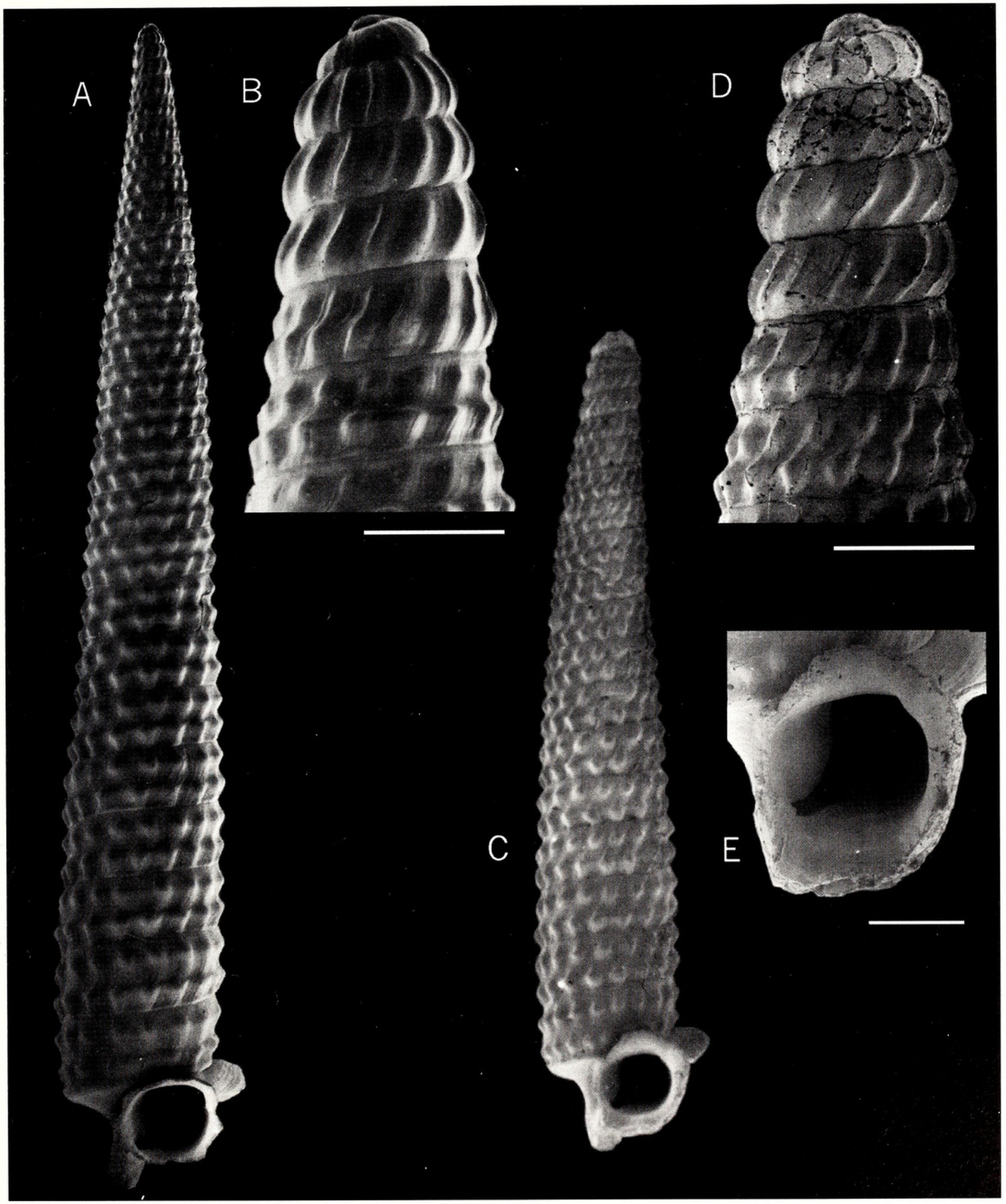

Fig. 12. *Trituba elatissima* n. sp. **A.** Holotype from Plato bank, DW248 (17.7 mm long). **B.** Protoconch of the holotype. **C.** Specimen from Atlantis bank, DW263 (11.7 mm long). **D.** Protoconch, same specimen as C. **E.** Oblique view of the aperture, same specimen as C. Scale bars = 500 µm.

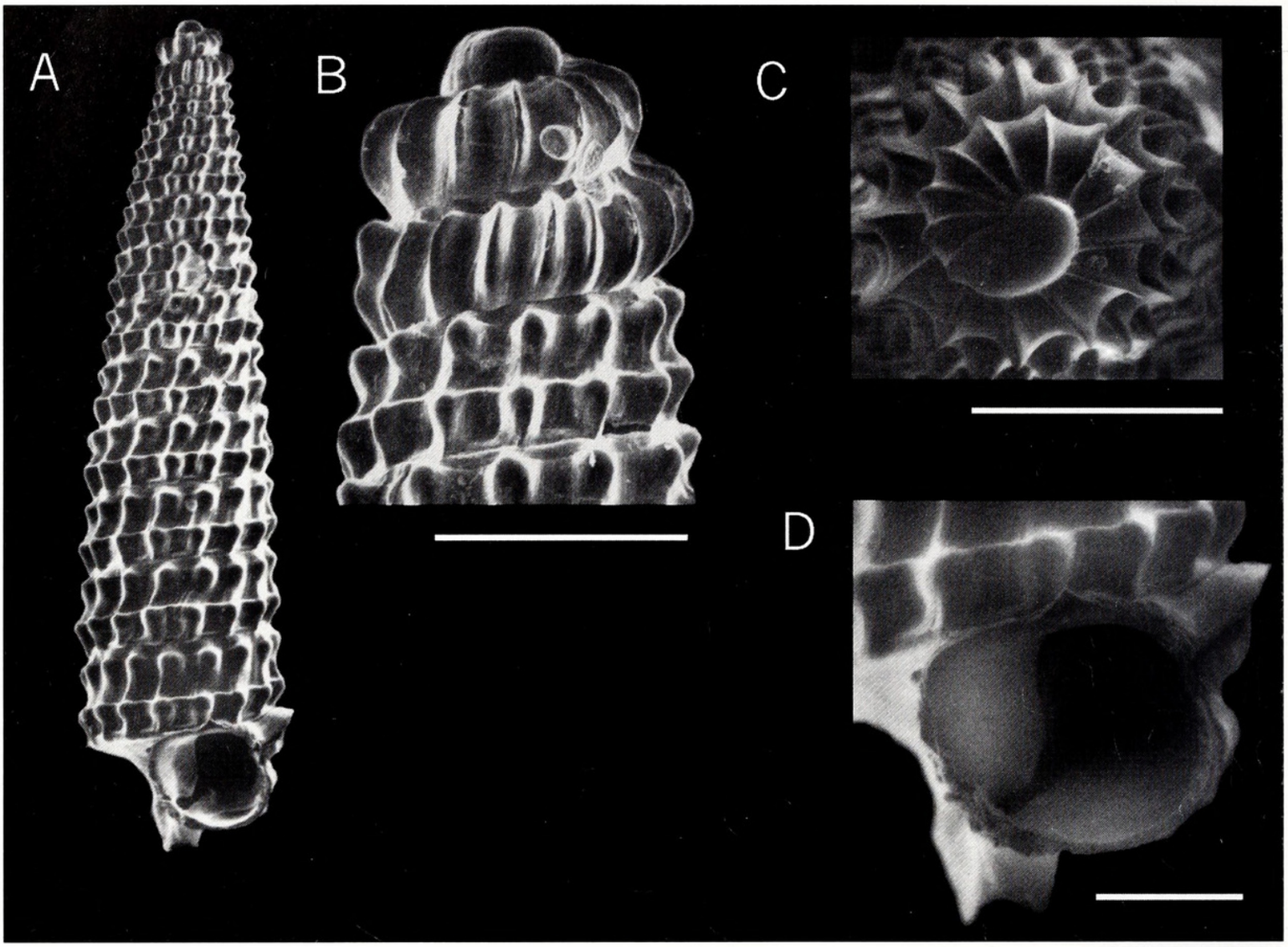

Fig. 13. *Trituba hirta* n. sp. **A.** Holotype from Atlantis bank, DW 274 (6.3 mm long). **B.** Protoconch of the holotype. **C.** Apical view of the protoconch of another specimen from Atlantis bank, DW 255. **D.** Oblique view of the aperture of the holotype. Scale bars = 500 µm.

Type locality

Atlantis bank, 34°05.1'N - 30°13.6'W, 280 m.

Other material examined

Atlantis bank, DW255: 17 sh. (1 adult, 7.2 x 1.7 mm, broken lip); DW258: 5 sh. (1 adult, 7.1 x 1.8 mm).

Description

Shell up to 7.2 x 1.8 mm, turriculate, solid, white, with 14-16 whorls. Protoconch ca. 2-3 whorls, the nucleus moderately protruding; protoconch whorls very convex, sculptured with very strong, sharp, slightly oblique ribs.

Teleoconch whorls sculptured with strong and sharp subsutural and suprasutural knobs, arranged so as to form two spiral rows and loosely defined, oblique axial ribs; both series of knobs starting simultaneously on the first teleoconch whorl, the suprasutural knobs bordered adapically by a definite spiral line. Body whorl not narrowing; its abapical surface smooth and circled by a faint keel on which the axial sculpture abuts.

Aperture with a hardly flaring peristome. Siphonal canal short, slightly narrowing towards its opening, inside with columellar and labial edges moderately close together. Anal canal very short, pointing laterally.

Etymology

The name means hirsute, alluding to the rough protoconch and teleoconch sculpture.

Remarks

Specimens of *Trituba hirta* were rare on Atlantis bank, despite a sampling and sorting effort which was similar to those on Meteor, Hyères, and Irving banks. This species differed from all others described here by its short, very strongly sculptured protoconch and by the rough sculpture of the teleoconch. All specimens examined could

be somewhat immature, and it was not clear if both canals would be closed on adult specimens. The fragment of a specimen from the Azores, illustrated by Bouchet and Warén (1993, fig. 1360) was similar for sculpture of both protoconch and teleoconch, but showed one more protoconch whorl and might not be conspecific.

The fossil species *Trituba tertia* (Lozouet, 1999), from the Oligocene of SW France, resembles *Trituba hirta*. It can be distinguished by a smaller protoconch with a more inflated first whorl and a narrow second whorl (see Lozouet, 1999: 58) contrasting with the stout, compact protoconch of the Recent species. However, despite this resemblance, the 25 million year time interval separating these two forms makes it most likely that the resemblance results from convergence in the very few morphological characters involved.

DISCUSSION

Trituba species are now very isolated on the North Atlantic seamounts and the Azores. The only known Recent congeneric species in the Atlantic is *Trituba barbadensis* (Coomans and Faber, 1984), found at 90-100 m depth off Barbados, and morphologically quite different. This Caribbean species has a coarsely ribbed protoconch resembling *Trituba fallax* or *Trituba addititia*, but has a genuine teleoconch sculpture with widely separated suprasutural knobs, which are not found in any of the species treated herein. Additional species are found in the 100-1000 m depth interval of the Indo-Pacific (Marshall, 1977).

The genus is believed to be extinct on the European continental margins, and is not recorded as a fossil in sediments younger than the Miocene. The Late Oligocene fossil representative *Trituba raulini* (Cossmann and Peyrot, 1822) resembles the Recent Atlantic species and may be viewed as a possible ancestor, but is unambiguously distinct at the species level. Material examined from the type locality (Pereyre, Landes, France, collected by P. Lozouet) has a high-conical, multispiral protoconch that is ornamented with delicate ribs and is clearly demarcated from the first teleoconch whorl. This protoconch morphology indicates planktotrophic development and, although equally multispiral, is distinct from the cyrtoconoid profile and gradual protoconch-teleoconch transition seen in the Meteor group species. The same Oligocene locality also yielded *Trituba tertia*, a species believed to have direct development, which has a coarsely ribbed protoconch and is astonishingly similar to the Recent *Trituba hirta* n. sp. I nevertheless have considered it more parsimonious to interpret it as having a convergent morphology, rather than to hypothesize that it has survived 25 million years and colonized the Atlantis bank separately from the other species.

Trituba dujardini (Mayer, 1862) from the Miocene of the shallow epicontinental Touraine basin, France, is quite distinct from both *Trituba raulini* and from the Recent species from the Meteor area in having large, closely set, pearl-like tubercles on the teleoconch, very much in the manner of many littoral Cerithiopsidae. The taxa *Trituba tauroturrita* and *T. tauroturrita* var. *spiraliornata*, described by Sacco (1895) from the Miocene of Northern Italy, also have a coarse sculpture but are based on quite poor material on which not much more can be said.

The ten species recognized here from the Meteor group seamounts show various combinations of a small array of character states, and are best interpreted as the product of a single radiation. However, because all of these shell characters are liable to reversal, the data do not provide evidence for a detailed phylogeny of the species. The occurrence of several discrete and sympatric forms in most sites (3 on Meteor, 5 on Hyères and Irving, 2 on Atlantis; Table 2) supports the view that the morphological differences reflect species-level separation.

The level of bank-to-bank endemism is high. Only

Table 2. Summary of the occurence of *Trituba* species on the Meteor group seamounts. Upper block: species with coarse protoconch sculpture, lower block: species with delicate protoconch sculpture.

Meteor	Hyères	Irving	Plato	Atlantis
superstes				
	additicia	*additicia*		
anelpistos	*anelpistos*	*anelpistos*		
	fallax	*fallax*		
				hirta

incredita				
	recurvata			
	constricta	*cf. constricta*		
		lima		
			elatissima	*cf. elatissima*

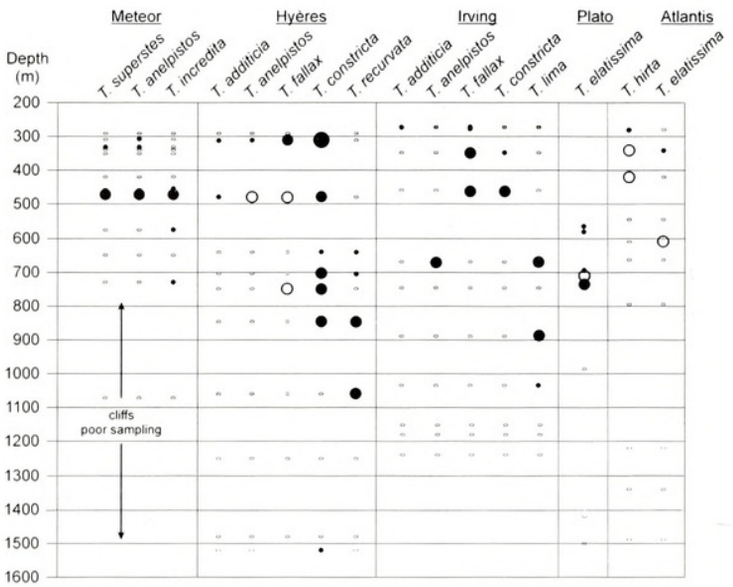

Fig. 14. Plot of the occurrence of *Trituba* species versus bathymetry in the material from Seamount 2 cruise. Dashes: samples without occurrence of *Trituba*; dots: 1-4 shells present; open circles: more than 4 shells, no living specimens; solid circles: living specimens present. Samples below 1600 m did not yield *Trituba* and are not shown.

Trituba anelpistos is found on three banks; four species are found on Hyères and Irving, one is shared between Plato and Atlantis, and the remaining four species are endemic to one bank. With the exception of *Trituba lima*, single-bank endemic species are found on the most external banks, viz. Meteor and Atlantis. Between Hyères and Irving, conversely, four out of five species are shared.

This pattern indicates that the distances between the banks, in the order of 100 to 200 km, are a barrier for larvae and egg capsules of *Trituba*, and that this could account for the speciation events in this species group. The reproductive biology is not known from direct evidence, and there were no egg capsules recorded among the material, despite sorting down to the 0.5 mm fraction. Although there is a multispiral protoconch, the larval development in the Recent North Atlantic species is inferred to be intracapsular from similarity of the larval whorls with those of *Cerithiella* (see Bouchet and Warén, 1993).

The barrier, however, is not absolute. Intracapsular larval development does not preclude dispersal into a broad geographic range (e.g. *Cerithiella metula* [Lovén, 1846]), and the endemic pattern of *Trituba* contrasts with that of most of the other direct developers of the seamounts that are found on more than one bank (e.g. the fasciolarid *Fusinus meteoris* Gofas, 2000; the muricid *Poirieria actinophora* [Dall, 1889], see Houart, 1996). In the case of *Trituba*, there must be an additional cause which would preclude rafting. Brooding can be ruled out because the morphology of the shell does not allow space for it, and a possible scheme would be some kind of nesting or embedding the egg capsules in the sponges on which the animal lives. Another possible explanation would be interspecific competition, which could impede successful colonization by one species where another one is well established.

From the above considerations, there is no straightforward conclusion regarding whether *Trituba* has colonized the seamounts as a planktotrophic species similar to *Trituba raulini*, which later lost planktotrophy in local populations, or whether it arrived as a non-planktotrophic species resembling *Trituba tertia*. In any case, the original colonization must predate the extinction on the European margin in the Miocene. The seamounts are older, 50-76 million years for the Irving-Cruiser plateau (Tucholke and Smoot, 1990), and were close to the sea surface at the time of *Trituba raulini* (see Fermont and Troelstra, 1983).

There appears to be great differences in the success of the different species, as reflected by their relative abundances, ranging from the 64 specimens and over 500 shells collected of *Trituba constricta* to the mere 4 shells of *Trituba additicia*. Some of the rarer species (e.g. *Trituba additicia, Trituba hirta, Trituba constricta*) could be very prone to extinction or may even be extinct. The rate of species turnover generated by successive back and forth colonization compensating extinctions is not known, but the global balance is such that it has allowed the persistence of the genus on the banks despite its extinction along the European mainland. Moreover, the diversification into a set of separate species with distinct bathymetric ranges (Fig. 14) and with different sizes and shapes could result in unequal susceptibility to predators and other extinction risk factors, and thus is likely to greatly enhance the probability of survivorship of the lineage as a whole. *Trituba recurvata* on Hyères and *Trituba lima* in Irving have a deeper bathymetric range (650-1100 m approximately) than the bulk of the species, which are found on the upper portions of the seamounts.

The common species suffer high predation pressure, as evidenced from the incidence of gastropod drillings on the large populations of *Trituba constricta* (one third to two thirds of the adult shells drilled in the large lots). The elongated shape, which allows the animal to withdraw deep into its shell, and the complicated aperture appear to provide good protection against crab predation (only seen with high impact on Atlantis bank). The heavier sculpture should be a protection against drilling but does not seem effective. The species responsible for drilling is probably the muricid *Poirieria actinophora*. There are no clues to how much time the drilling gastropods have been around, but they may be a relatively new element of the fauna since there is no detectable morphological difference between seamount and Caribbean specimens (which also rely on unpredictable rafting for dispersal). Thus, it is not certain that the current morphology in *Trituba* represents the best adaptive response to this predator.

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