

Systematic Review of the Family Choristellidae (Archaeogastropoda: Lepetellacea) with Descriptions of New Species

by

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Abstract. The known species in the family Choristellidae Bouchet & Warén, 1979 (= Choristidae of authors) are revised. All occur in continental shelf to abyssal depths and live in spent egg cases of sharks and rays, upon which they feed. The family is assigned to the Lepetellacea by Haszprunar on anatomical characters (1988a, b, c, 1992). Two genera with divergent shell form are recognized: the naticiform *Choristella* Bush, 1897, and the discoidal *Bichoristes*, gen. nov. The radula is unique to the family; shell characters are also diagnostic—extremely thin shell, deep suture (except in *Bichoristes*), complete peristome, sharp umbilical carination, small size, smooth protoconch with bulbous tip, and compressed earliest teleoconch. Previously described species of *Choristella* are *C. tenera* (Verrill, 1882) and *C. leptalea* Bush, 1897, both from the northwestern Atlantic, and *C. vitrea* (Kuroda & Habe, 1971) from Japan. New species proposed here are *C. marshalli* from New Zealand, *C. nofronii* from the Mediterranean, *C. ponderi* from eastern Australia, and *C. hickmanae* from Oregon. The monotypic new genus *Bichoristes* is based on *B. wareni* from New Caledonia. *Bichoristes* is considered to be derived from *Choristella*.

Species previously but incorrectly assigned to *Choristes* Carpenter are discussed in the appendix. *Choristes elegans* Carpenter, 1872, has already been referred to Naticidae, but is here placed as a synonym of *Amauroopsis islandica* (Gmelin, 1791).

INTRODUCTION

The family Choristellidae Bouchet & Warén, 1979, comprises a poorly known group of small, thin-shelled, trochiform or naticiform species living offshore at continental shelf to abyssal depths. Living specimens have been collected only within the spent egg capsules of sharks and skates, upon which they feed. Shells are paper-thin and easily crushed.

The Choristellidae are better known in literature prior to 1979 as the Choristidae Verrill, 1882, the family name having been intended for a species for which some unusual details of the radula, jaw, and external anatomy were originally described. The type species of *Choristes*, however, is a fossil species that later proved to be a member of the Naticidae. BOUCHET & WARÉN (1979) restored the original concept of the Choristidae by substituting the family name Choristellidae, a name based on *Choristella* Bush, 1897, another genus proposed in the family.

Until recently, the systematic position of the family Choristellidae has been a matter of speculation. The radula provides few direct clues, as it is neither rhipidoglossate nor taenioglossate. VERRILL (1882) said nothing about the possible familial affinity of Choristidae, although BUSH (1897) reported that "Professor Verrill placed it among the Tectibranchiata." THIELE (1929), followed by WENZ (1938) and TAYLOR & SOHL (1962), placed Choristidae in the Rissoacea; KEEN (1971) placed it near Vitrinellidae; ABBOTT (1974:90) stated that "it may be a tectibranch." GOLIKOV & STAROBOGATOV (1975:212, 220) placed Choristidae in Naticacea (as order Aspidophora) "on the basis of shell characters and the shape of the radular teeth."

HICKMAN (1983) considered the choristellid radula to be close to that of the cocculiniform limpet *Cocculinella* Thiele, 1909. Further evidence in support of affinity between choristellids and cocculiniform limpets was provided by the anatomical investigations of HASZPRUNAR (1988a, b, c), who placed the family in Lepetellacea, noting that

two of the included families, the Addisoniidae and Choristellidae, "have a common ancestry, as revealed by their shared feeding biology (on empty egg-cases of skarks or skates), gill-type (with skeletal rods and mucous zones), and alimentary tract (complete loss of stomach)" (HASZPRUNAR, 1988a:19). Further details on choristellid anatomy and relationships are given by Haszprunar in the accompanying paper (HASZPRUNAR, 1992).

This review started as an effort to give a name to the new eastern Pacific species cited by HICKMAN (1983), but it soon became apparent that additional new choristellids have recently been collected and have been awaiting attention in other museum collections. Here I update the classification of the family and add one new genus and five new species. Taxa removed from the family are discussed further in the Appendix to this paper.

MATERIALS AND METHODS

This review is hampered by a shortage of well-preserved material in collections. No material of the first and second named members of the family has been collected in recent years, and none of the original material remains wet-preserved, making it difficult to verify the early descriptions of soft parts by examination of original material. It is only the newly collected material of the species described here that has made it possible for HASZPRUNAR (1988a, b, c, 1992) to report on the internal anatomy.

Radulae were extracted after dissolution of tissue in 10% NaOH at room temperature; dry specimens of *Choristella tenera* were first rehydrated in detergent prior to treatment in NaOH. The radular ribbons were washed in distilled water, dried from a drop of water placed on a stub having a thin smear of rubber cement, and coated with gold or gold/palladium for examination with SEM. Jaws were also extracted with room temperature NaOH and examined with SEM. Preserved specimens were critical point dried and examined with SEM.

All depths that were originally cited in fathoms have been changed to meters.

Abbreviations of institutions mentioned in the text: AMS, Australian Museum, Sydney; BMNH, Natural History Museum, London; LACM, Los Angeles County Museum of Natural History; MCZ, Museum of Comparative Zoology, Harvard University; MNHN, Museum National D'Histoire Naturelle, Paris; NMNZ, National Museum of New Zealand, Wellington; NZOI, New Zealand Oceanographic Institute, Wellington; USNM, National Museum of Natural History, Washington, D.C.

SYSTEMATICS

Order ARCHAEOGASTROPODA Thiele, 1925

Suborder COCCULINIFORMIA Haszprunar, 1987

Superfamily LEPETELLACEA Dall, 1892

Although a monofamilial superfamily has been proposed for the Choristellidae (Choristiacea Kuroda & Habe, 1971,

emended to Choristelliacea by HICKMAN, 1983), HASZPRUNAR (1988c) united the families Lepetellidae, Bathyphytophilidae, Pyropeltidae, Pseudococculinidae, Osteopeltidae, Cocculinellidae, Addisoniidae, and Choristellidae in the Lepetellacea, on the basis of sharing compact shell muscles, two kidneys, separated gonad with simple gonoducts, and statocysts with several statocones.

Except for the Choristellidae, the lepetellaceans are hermaphroditic limpets. The family Choristellidae is the only member having a coiled shell and the only member that is gonochoristic.

Family CHORISTELLIDAE

Bouchet & Warén, 1979

CHORISTIDAE of authors (see below): VERRILL, 1882:540; THIELE, 1929:179; CLARKE, 1961:359; KEEN, 1971:388; ABBOTT, 1974:90; BOSS, 1982:1010.

CHORISTELLIDAE BOUCHET & WARÉN, 1979:225; HICKMAN, 1983:86; HASZPRUNAR, 1988c:66.

Included genera: *Choristella* Bush, 1897, and *Bichoristes* McLean, gen. nov. *Choristella* species are defined by differences in shell proportions, opercular coiling, and external anatomy, although knowledge of external anatomy remains incomplete. *Bichoristes* is monotypic and based on a single specimen for which the shell, radula, operculum, and jaw are known. The description of external anatomy in the diagnosis that follows is based on that of *Choristella*.

Diagnosis: Shell small (maximum dimension not exceeding about 10 mm), extremely thin, periostracum thin; whorls 3 to 3.5, rounded or carinate (carinate only in *Bichoristes*); suture deeply channeled (except in *Bichoristes*); spire height low to moderate; peristome complete, area of contact minimal; final lip slightly flared; umbilicus narrow to wide; umbilical wall with sharp descending carina. Protoconch diameter 250–300 μ m, tip bulbous, surface smooth. Operculum of 3–10 whorls, multispiral to paucispiral.

Jaw of two prominent, dark brown, finely reticulate plates, fused dorsally, laterally bowed to produce oval mouth opening with jagged edge.

Radula. Rachidian tooth triangular, with short base and bluntly pointed overhanging cusp. First lateral tooth with quadrangular shaft, singly cusped in *Choristella*, bicuspid in *Bichoristes*. Second lateral tooth with long shaft, bicuspid in *Choristella*, unicuspid in *Bichoristes*. Third lateral tooth with long shaft and pointed cusp. Fourth lateral tooth similar, except reduced and fused to third in *Bichoristes*. Fifth lateral tooth vestigial.

Remarks: MARINCOVICH (1975, 1977) correctly placed *Choristes* Carpenter in Dawson, 1872, in the Naticidae (see further notes on *Choristes elegans* under excluded species), which left the living species of *Choristes*, of authors, in limbo. Without citing Marinovich, BOUCHET & WARÉN (1979) proposed Choristellidae in a brief note. They wrote: "We want to use this occasion to point out that the genus *Choristes* Carpenter MS, Dawson, 1872 is a naticid. An

examination of the types of *Choristella leptalea* Bush, 1897 (type species of *Choristella*) and *C. tenera* Bush, 1897 [evidently a lapsus for *C. brychia* Bush, 1897] has proved that they are synonyms of *Choristes elegans* var. *tenera* Verrill, 1882. Verrill's name therefore has to be used for the type species. Another consequence is that the name Choristidae has to be changed to Choristellidae."

BOSS (1982) missed the proposal of Choristellidae and followed MARINCOVICH (1977) in leaving all species described under *Choristes* within the Naticidae.

Diagnostic shell characters for Choristellidae are the extremely thin shell, smooth protoconch with a bulbous tip, maximum of 3.5 teleoconch whorls, the complete peristome, and the sharp carination that descends within the umbilicus. Additionally, *Choristella* has a deeply channeled suture. Surprisingly, the descending umbilical carination has not previously been noticed, although it provides a consistent shell character for the family.

The overall aspect of the radula is similar in the two genera, but differs in having the first lateral bicuspid in *Bichoristes* and the second lateral bicuspid in *Choristella*. Shared features are that the lateral teeth are robust and slope away from the rachidian, and that the shafts of the rachidian and first lateral are relatively short, whereas those of the second, third, and fourth laterals are longer and articulate together, and the fifth lateral is vestigial.

The choristellid radula cannot be confused with that of any other family. Despite a statement (HICKMAN, 1983: 86) about radular affinity with the Cocculinellidae ("same basic pattern"), the resemblance is superficial. The cocculinellid radula, as illustrated by MARSHALL (1983), has the rachidian flanked by a pair of small teeth, followed by a series of stout interlocking teeth of similar morphology with serrate outer edges. Marshall considered the latter to be marginal teeth and the lateral teeth to be represented by the small inner pair. The choristellid radula differs in having the rachidian flanked by massive teeth and none of the succeeding teeth in the row are similar. The bicuspid second lateral tooth of *Choristella* and the bicuspid first lateral tooth of *Bichoristes* are evidently fused from the primitive condition for the family, which is not represented in a living genus. The teeth of both families are probably homologous, but I am more inclined to regard the teeth of each family as lateral teeth than as marginals for two reasons: I know of no other examples of massive lateral teeth and the paired teeth of the choristellid radula could hardly be considered marginals because they have laterally extended shafts, as well as exhibiting partial fusion.

The choristellid protoconch has a bulbous tip, similar to that of the Cocculinidae (see MARSHALL, 1986:fig. 5D), but unlike the compressed and laterally pinched tip of the cocculinellid protoconch (MARSHALL, 1983:fig. 11) or the pseudococculinid protoconch (MARSHALL, 1986:fig. 9H). Close affinity with either family is therefore not supported on evidence from the protoconch. Unfortunately, the adisoniid protoconch remains unknown (MCLEAN, 1985) and it is not yet possible to confirm with protoconch evi-

dence the affinity of the two families as advocated by HASZPRUNAR (1992) on anatomical evidence.

Genus *Choristella* Bush, 1897

Choristes Carpenter, of VERRILL, 1882:540; DALL, 1908:328; THIELE, 1929:179; CLARKE, 1961:359; KEEN, 1971:388; ABBOTT, 1974:90. Not *Choristes* Carpenter in Dawson, 1872 [Naticidae].

Choristella BUSH, 1897:138; THIELE, 1929:179; BOUCHET & WARÉN, 1979:225; HICKMAN, 1983:86.

Type species (original designation): *Choristella leptalea* Bush, 1897.

Diagnosis: Shell small (maximum dimension about 10 mm), extremely thin (maximum thickness of broken edge 0.05 mm), easily damaged; periostracum thin; whorls 3 to 3.5, rounded; suture deeply channeled, spire height low to moderately high. Peristome complete, contact with previous whorl limited to narrow band; final lip flared but not thickened, reflected near base of columella. Umbilicus narrow to broad, umbilical wall with sharp descending carina that terminates on reflected region of lip at base of columella. Protoconch diameter 250 μ m, surface smooth; tip bulbous. Outer edge of first quarter turn of teleoconch compressed, not forming regular curve. Operculum thin, up to 5 whorls, multispiral or with final whorl enlarged to give paucispiral effect.

External anatomy. Snout prominent, eyes lacking, cephalic and epipodial tentacles lacking micropapillae. One to two suboptic tentacles short, posterior to right cephalic tentacle. Gill pectinibranch, leaflets numerous. Sexes separate; male using right cephalic tentacle as copulatory organ; open seminal groove on right tentacle.

Jaw. As described for family.

Radula. Rachidian tooth relatively small, with triangular shaft and small overhanging cusp; base of shaft broadly emerging from ribbon. First lateral tooth massive, shaft quadrangular, overhanging cusp large, triangular, with bluntly pointed tip; base of shaft articulating with tooth below, base of shaft buttressed on inner and outer edges; second lateral tooth separated from third by open channel. Second lateral tooth largest in row, with two large cusps, the innermost with triangular cusp matching that of second lateral, the outermost cusp having a more obtuse angle; position of both cusps descending away from rachidian; base with projecting ridge above excavation that accommodates tooth below. Third lateral tooth with long shaft and thick, rounded cusp that projects over the outer cusp of second lateral tooth; base buttressed on inner side by narrow ridge. Fourth lateral tooth with longest shaft and small, beaklike cusp, base buttressed on inner side by projecting ridge. Fifth lateral tooth vestigial, closely appressed to base of fourth lateral tooth.

Remarks: *Choristella* species may be recognized on shell characters alone (thin shell, channeled suture, complete peristome, compression of early teleoconch, and descending umbilical carination). The descending umbilical carination

may be shared with some skeneiform genera, including *Trenchia* Knudsen, 1964, as discussed here under rejected species. On shell characters, *Choristella* may be distinguished from such genera in having a much more deeply channeled suture and by the compression of the early teleoconch (for the latter see especially Figure 22).

The radulae of all species examined are closely similar. Some differences that may be apparent in the illustrations for each species can be attributed to wear, rather than interspecific differences. The most useful radular characters for interspecific discrimination are the morphology and relative size of the rachidian tooth.

The bulbous tip of the protoconch is treated under the family heading. In some species the protoconch remains unknown; in all the available specimens of such species it is replaced by a calcareous plug, representing an internal mold of the original protoconch (see Figure 11).

In proposing *Choristella*, BUSH (1897) emphasized a radular difference from *Choristes*. According to Bush, *Choristella leptalea* has 13 teeth in the row, as opposed to 11 teeth in *Choristes elegans* var. *tenera*. Both CLARKE (1961: 359) and BOUCHET & WARÉN (1979) discounted a radular distinction, and attributed the tooth count discrepancy to varying interpretations of the second lateral tooth either as a bicuspidate compound tooth or two separate teeth. I interpret the second tooth as a compound tooth derived by fusion of two separate teeth. BOUCHET & WARÉN (1979: fig. 12) provided a drawing of the radula of *Choristella tenera* that showed the rachidian and five lateral teeth, making a total of 11 teeth in the row. That interpretation of the radula is followed here. Although the radula of *Choristella leptalea* is not available for SEM study, a generic distinction based on radulae is evidently unfounded.

Despite the lack of evidence from the radula, the conclusion that the taxa proposed separately by Verrill and Bush are the same is not supported here. There are other, more important differences, one of which was well figured in the original accounts: the operculum of *Choristella tenera* is shown with three whorls and expands so rapidly that it looks to be paucispiral (see VERRILL, 1882:pl. 58), whereas the operculum of *C. leptalea* is shown as multispiral, with five whorls (BUSH, 1897:fig. 8). There are also differences in shell proportions between the two species: *C. leptalea* is clearly lower-spined than *C. tenera*, and is smaller. Both have the same number of whorls, which suggests that they are based on mature specimens. There are also differences in the external anatomy that can be detected from a careful reading of the original descriptions.

Bush recognized two species and intended to place them in separate genera. I accept that there are two species (contrary to BOUCHET & WARÉN, 1979, who recognized only one), but am unable to support a generic distinction. The other species treated here cannot be placed into two separate groups on characters now available. Unfortunately, the replacement of *Choristes* by *Choristella* changes the type species of the nominate genus to *Choristella leptalea*, a species that remains poorly known.

On the basis of shell proportions there are two groups of species in *Choristella*, a relatively high-spined group and a relatively low-spined group. Opercular characters do not support generic groupings based on shell proportions, however. High-spined species are *C. tenera* (Verrill, 1882), *C. vitrea* (Kuroda & Habe, 1971), *C. marshalli* sp. nov., and *C. nofronii* sp. nov. Low-spined species are *C. leptalea* Bush, 1897, *C. ponderi*, sp. nov., and *C. hickmanae*, sp. nov.

Choristella tenera (Verrill, 1882)

(Figures 1–7)

Choristes elegans var. *tenera* VERRILL, 1882:541, pl. 58, figs. 27 [shell with operculum], 27a [radula]; VERRILL, 1884: 256, pl. 29, figs. 9, 9a, 9b [shells of 3 juvenile specimens].

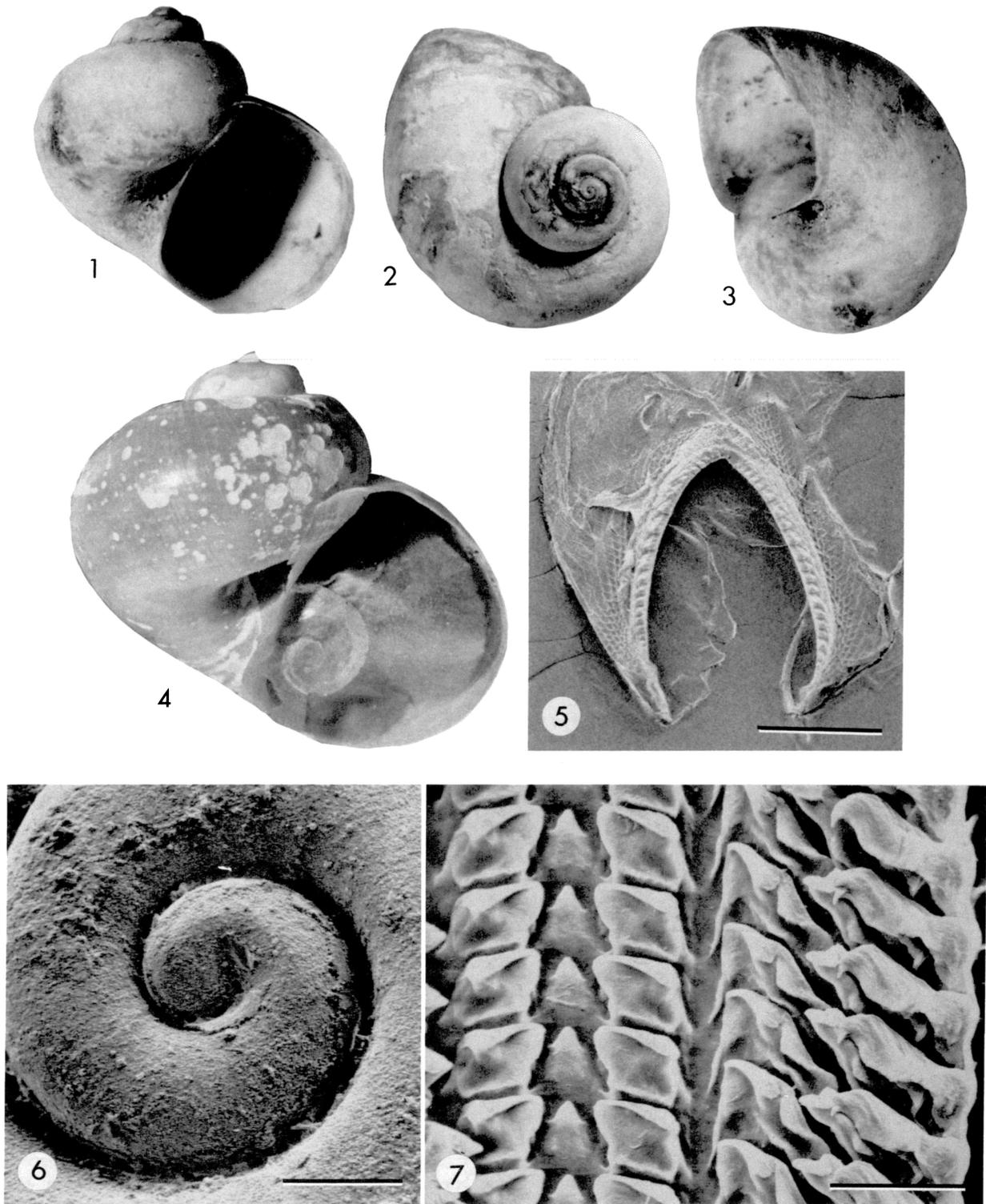
Choristes tenera: CLARKE, 1961:360; ABBOTT, 1974:90, fig. 865 [copy figs. of VERRILL, 1882].

Choristella tenera: BOUCHET & WARÉN, 1979:225, fig. 225 [new drawing of radula, based on paratype, USNM 45151].

Description: Shell (Figures 1–4) large for genus (maximum diameter 10.5 mm), spire height relatively high (height–width ratio of holotype 0.87). Shell wall extremely thin. Surface shiny, brown, periostracum thin, surface finely pitted. Protoconch usually eroded and filled with secondary plug, separated from first teleoconch whorl. Teleoconch whorls 3.5, rounded, smooth; suture deeply impressed. Umbilicus narrow, deep, not obstructed by reflection of inner lip. Spiral sculpture represented by fine striae strongest on base and by single narrow ridge deep within umbilicus; axial sculpture lacking except for fine growth increments. Peristome complete, area of contact with previous whorl minimal. Lip flared at base of columella where buttressed by umbilical ridge. Operculum (Figure 4) pale brown, nucleus slightly excentric, 3 whorls, inner edge growing under outer edge of previous whorl (which raises the outer edge of previous whorls), final whorl expanding to produce paucispiral pattern.

Dimensions. Height 5.4 mm, width 6.2 mm (holotype); height 9.0 mm, width 10.5 mm (largest specimen, USNM 78902).

External anatomy. Because freshly collected, preserved specimens are not available, VERRILL's (1882) original description of the animal is repeated here: "Head large, short, thick, rounded or truncate, with two short, flat, obtuse anterior tentacles, wide apart, but connected together by a transverse fold; posterior tentacles short, thick, conical, smooth; no eyes visible; proboscis [buccal mass] short, thick, retractile; jaws crescent-shaped, strong, black. Verge situated just below the right posterior [error for anterior?] tentacle, small, papilliform, swollen at base; below this and farther back, a larger and thicker papilla with basal swelling; on each side, between the mantle and foot, at about midlength of the foot, a small mammiform papilla; and two small flat cirri, behind and beneath the operculum. Foot broad, ovate, with two tentacle-like pro-



Explanation of Figures 1 to 7

Figures 1–7. *Choristella tenera* (Verrill, 1882). Figures 1–3. Holotype, USNM 45151, off Martha’s Vineyard Island, Massachusetts, USA. Height 5.4 mm. Apertural, oblique spire, and umbilical views. Figure 4. Largest specimen, showing operculum in place, USNM 78902, USFC Sta. 2730, off Cape Hatteras, North Carolina. Height 9.0 mm. Figure 5. SEM view of jaw, USNM 78902. Scale bar = 200 μ m. Figure 6. Protoconch, USNM 45253. Scale bar = 100 μ m. Figure 7. SEM view of radula, USNM 78902. Scale bar = 40 μ m.

cesses in front. Gill large, consisting of numerous thin lamellae, attached to the inner surface of the mantle, over the left side of the neck, and extending obliquely across and over the neck to the right side."

Jaw (Figure 5). Typical for family.

Radula (Figure 7). Characteristic for family. Rachidian tooth stout, relatively broad, tip apparently not overhung in present preparation.

Type locality: Off Martha's Vineyard Island, Massachusetts, USFC Sta. 1031, 466 m, "taken from the interior of an old egg-case of a skate (*Raia*, sp.)."

Type material: Holotype, USNM 45151, USFC Sta. 1031, collected in 1881, shell intact, body dried. Eight paratypes in similar condition, USNM 859486. USNM 508720, USFC Sta. 1031, 1 paratype same station as type lot. The shell surface of the type lot is dull from prior preservation in alcohol, although other specimens have a shiny surface.

Referred material: 7 USNM lots, all dry, most with dried bodies: USNM 45252, USFC Sta. 1096, 580 m off Martha's Vineyard, 4 broken shells, one loose body attached to operculum. USNM 45253, USFC Sta. 1124, off Martha's Vineyard, 2 large and numerous small shells. USNM 45254, USFC Sta. 1154, 353 m off Martha's Vineyard, 1 shell, operculum in place. USNM 45255, USFC Sta. 2234, off Martha's Vineyard, 1 shell, operculum in place. USNM 40309, USFC Sta. 2262, off Nantucket Shoals, 3 shells, opercula in place. USNM 78902, USFC Sta. 2730, off Cape Hatteras, North Carolina, 1 large and several small shells, all with opercula in place. USNM 78901, USFC Sta. 2731, off Cape Hatteras, North Carolina, 4 small shells, 2 with dried bodies.

Remarks: All specimens have the sharp, steeply descending umbilical carination, a diagnostic character that was missed by VERRILL (1882) in the original description and not subsequently noticed. Verrill reported that large specimens have 4 to 5 whorls, but this is clearly in error, as the largest specimens do not exceed 3.5 whorls. Verrill compared it to a small specimen of *Choristes elegans* Carpenter, which he had received from Dawson (VERRILL, 1882:542, pl. 58, fig. 28), considering it "a thin and delicate variety of the ancient type."

Verrill's description of the external anatomy noted a "verge" [penis] posterior to the right cephalic tentacle, but this is here regarded as a suboptic tentacle.

Choristella marshalli McLean, sp. nov.

(Figures 8–15)

Description: Shell (Figures 8–10) large for genus (maximum diameter 8.8 mm), spire height relatively high (height–width ratio of holotype 0.90). Shell wall extremely thin, maximum thickness of broken lip 0.05 mm. Surface shiny, light brown; periostracum thin, surface finely pitted. Protoconch usually etched away and filled with secondary

plug, separated from first teleoconch whorl. Teleoconch whorls 3.3, rounded, smooth; suture deeply impressed. Umbilicus narrow, deep, not obstructed by reflection of inner lip. Spiral sculpture represented by fine striae and by single narrow ridge deep within umbilicus; axial sculpture lacking except for fine growth increments. Peristome complete, area of contact with previous whorl minimal. Lip flared at base of columella where buttressed by umbilical ridge. Operculum (Figure 12) pale brown, nucleus slightly excentric, final 3 whorls evenly expanding.

Dimensions. Height 7.9 mm, width 8.8 mm (holotype).

External anatomy (Figure 14). Right cephalic tentacle of male with open groove.

Jaw (Figure 13). Typical for family.

Radula (Figure 15). The radula closely approximates that given for the familial description. The shaft of the rachidian is well marked and there is a small overhanging tip. The outermost tooth in the row is unusually well developed.

Type locality: SE of Banks Peninsula (44°55.4'S, 174°04.9'E), New Zealand, 1097–1116 m, in empty skate egg case.

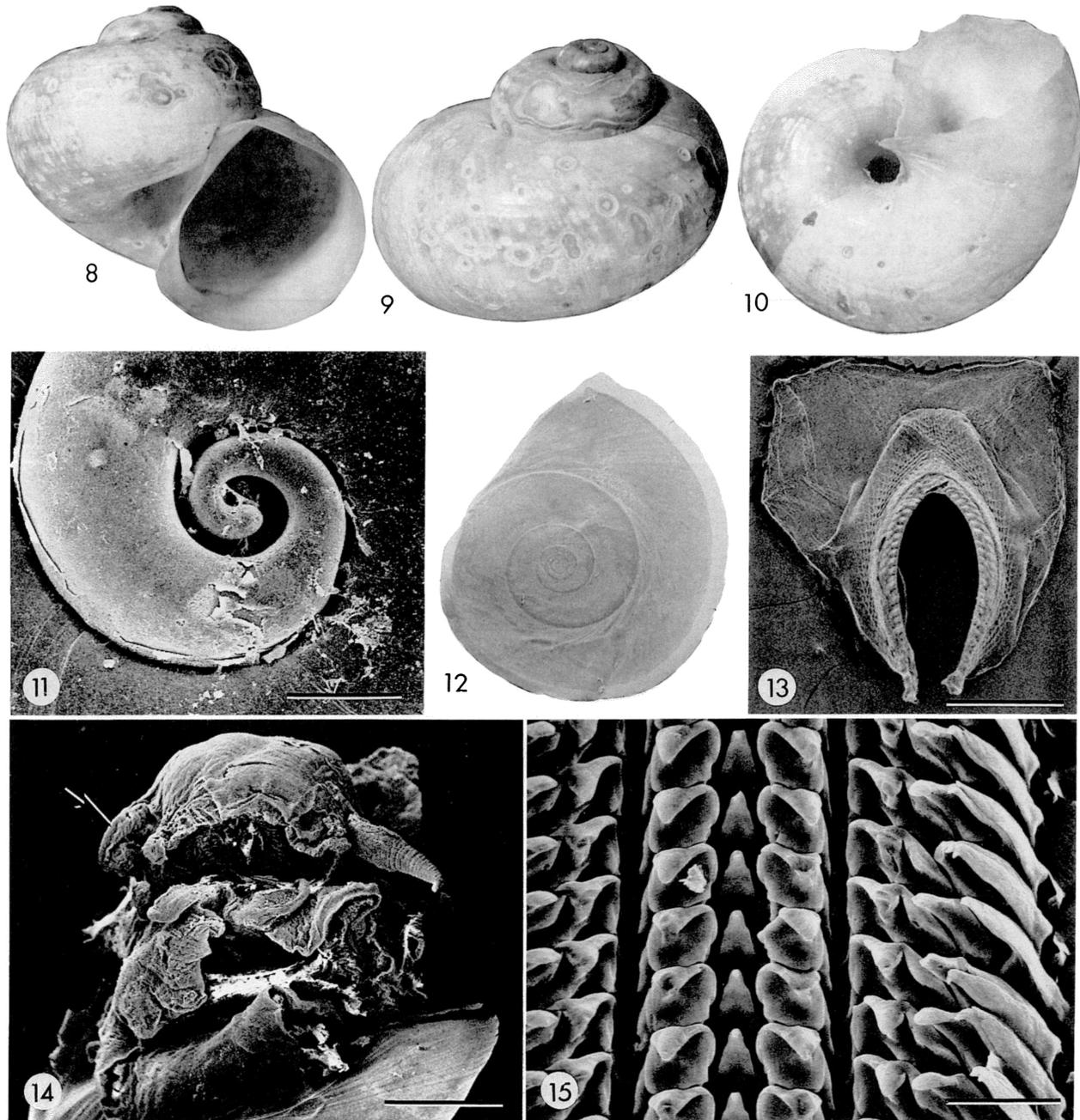
Type material: 26 specimens—11 intact shells, 15 specimens with broken shells and bodies preserved in alcohol—from type locality, R/V *James Cook*, Sta. J10/37/84, 15 June 1984. The visceral mass has disintegrated in the preserved specimens, which were initially preserved by freezing. Holotype NMNZ M.109053 and 23 paratypes NMNZ M.75210; 1 paratype LACM 2247; 1 paratype AMS.

Referred material: NZOI Sta. I32 off Cape Brett, New Zealand (35°11.7'S, 174°49.8'E), 376–450 m, R/V *Tangaroa*, 7 May 1975, 2 dried, damaged specimens and 1 small preserved body. NZOI Sta. P292, Tasman Basin (40°42.8'S, 167°56.0'E), 1029 m, 4 preserved specimens, shells broken. NMNZ M.89950, NE of Chatham Island, New Zealand (42°52.3'S, 175°37.3'E), 1032 m in elasmobranch egg case, F/V *Akagi Maru*, 9 June 1987, about 15 decalcified or broken-shelled juveniles in alcohol plus about 12 small specimens with dried bodies (SEM of early whorls, Figure 11).

Remarks: This species is characterized by its relatively large size and high spire. It resembles *Choristella tenera* in its size and proportions, but has a less prominent periostracum. As in *C. tenera*, the protoconch of most specimens is etched away, leaving only a plug that is well separated from the first teleoconch whorl (Figure 11). The operculum (Figure 12) is like that of *C. tenera*, although it has more numerous whorls and the final whorl is not so rapidly expanding.

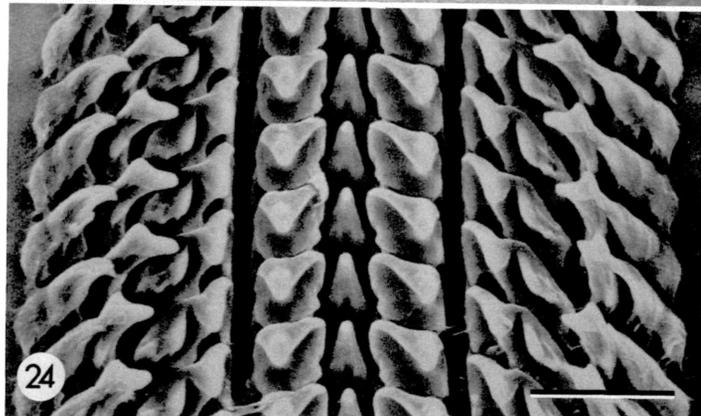
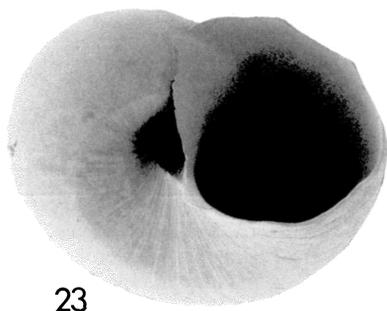
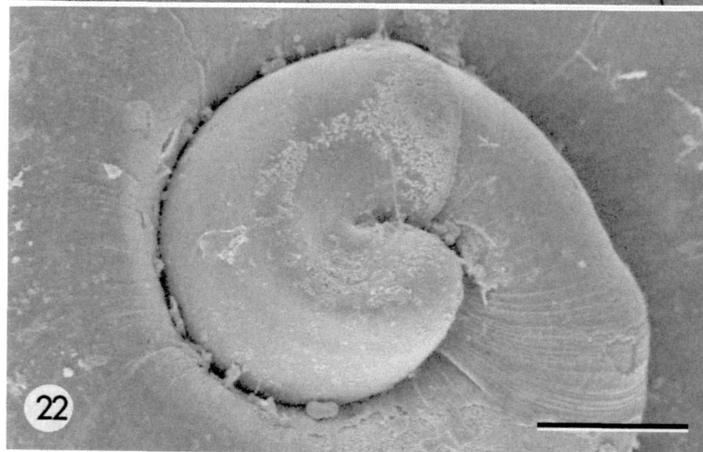
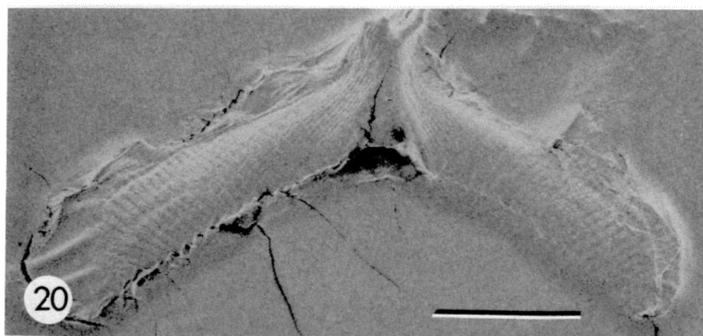
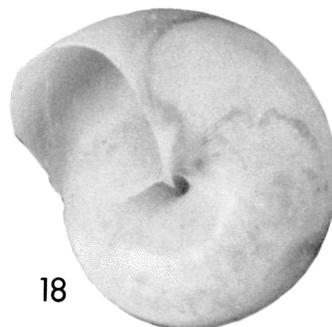
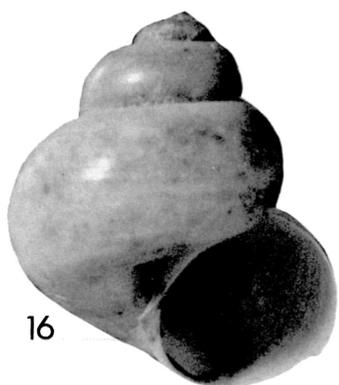
The open seminal groove on the right cephalic tentacle is visible in the critical point dried specimen examined with SEM (Figure 14).

HICKS (1986) reported that skate egg cases containing



Explanation of Figures 8 to 15

Figures 8–15. *Choristella marshalli* McLean, sp. nov. Figures 8–10. Holotype, NMNZ 75210, SE of Banks Peninsula, New Zealand. Height 7.9 mm. Apertural, oblique lateral, and umbilical views. Figure 11. Early Whorls, showing plug filling protoconch, NMNZ M.89950, NE of Chatham Islands, New Zealand. Scale bar = 200 μ m. Figure 12. SEM view of operculum, NMNZ 75210, paratype. Scale bar = 1 mm. Figure 13. SEM view of jaw, NMNZ 75210, paratype. Scale bar = 200 μ m. Figure 14. SEM view of critical point dried paratype, anterior view of body attached to operculum, showing groove on right cephalic tentacle (arrow), NMNZ 75210, paratype. Scale bar = 1 mm. Figure 15. SEM view of radula, NMNZ 75210, paratype. Scale bar = 40 μ m.



Choristella species (cited here as the type material of *C. marshalli*) also yielded type material of the harpacticoid copepod *Paramphiascopsis waihonu* Hicks, 1986. Harpacticoids have been noted to feed on microbiota associated with fecal pellets (HICKS, 1986).

Etymology: The name honors Bruce A. Marshall of the National Museum of New Zealand, Wellington.

Choristella vitrea (Kuroda & Habe, 1971)

Choristes vitreus Kuroda & Habe in KURODA, HABE & OYAMA, 1971:62, pl. 107, fig. 11.

Description (copied from Kuroda & Habe): "Shell rather small, thin, translucently white, turbinate in shape. Spire conical and with 5 whorls, rather rapidly increasing their width to the body whorl, well inflated and separated by the deeply impressed sutures. Surface smooth and polished and covered by a thin periostracum and sculptured by the very faint spiral threads and growth lines. Body whorl large and well rounded at the periphery and the base. Aperture wide and semicircular. Outer margin well rounded, thin and slightly expanded. Innermargin [sic] deposited the thin callus on the parietal wall and rather straight [sic]. Columellar margins reflexed and dilated over the widely and deeply perforated umbilicus. Operculum thin, corneous, pale yellowish brown and paucispiral."

Dimensions. Height 10.7 mm, diameter 9.5 mm (holotype); height 12.2 mm, diameter 9.4 mm (paratype).

Type locality: Sagami Bay, Japan, "parasitic on the egg capsules of shark," depth not indicated.

Type material: Holotype and paratype, presumably in Imperial Household Collection, Japan. No other specimens are known.

Remarks: Although the original material has not been examined and the radula has not been described, the description of this species is compatible with that of the high-spired species group of *Choristella*. The shell is comparable to *C. tenera* in size, thinness of shell, and opercular morphology, and to *C. nofronii* in having the height of the shell exceed the breadth. The operculum was said to be paucispiral. The height-width ratio of the holotype is 1.3, compared to 1.13 for *C. nofronii*.

Choristella nofronii McLean, sp. nov.

(Figures 16–24)

Cithna naticiformis Jeffreys, 1883, of GUBBIOLI & NOFRONI, 1986:204 [figures not numbered, size not indicated], non *Cithna naticiformis* Jeffreys, 1883

Description: Shell (Figures 16–18) medium size for genus (maximum height 6.1 mm), spire height relatively high (height-width ratio of holotype 1.13). Shell wall extremely thin, maximum thickness of broken lip 0.05 mm. Surface shiny, yellowish white, periostracum thin. Protoconch (Figures 21, 22) diameter 250 μ m, surface smooth. Teleoconch whorls 2.7 rounded, smooth; suture deeply impressed. Umbilicus narrow, deep, partially obstructed by reflection of inner lip. Spiral sculpture of faint striae and single narrow ridge deep within umbilicus, terminating at columellar flare. Base of mature shell rounded, that of immature shell with angulation. Axial sculpture of extremely fine growth increments, sharply raised on umbilical slope. Peristome nearly complete. Operculum (Figure 19) pale brown, nucleus slightly excentric, final whorl becoming paucispiral.

Dimensions. Height 6.1 mm, width 5.4 mm (holotype). **Jaw** (Figure 20). Typical for genus.

Radula (Figure 24). Typical for the family; the shaft of the rachidian is weakly projecting, the overhanging tip of the rachidian is small but clearly revealed.

Type locality: Alboran Sea, westernmost Mediterranean, west of Cabo de Gata, Spain (extending from 01°30'W and 35°30' to 36°30'N, according to P. Bouchet), 50–100 m.

Type material: Holotype (Figures 16–18) MNHN uncataloged, operculum and radula scanned. Four paratypes MNHN uncataloged (heights 5.2, 3.1, 1.7, 1.2 mm). Two paratypes LACM 2248 (height 3.0 mm, protoconch scanned; height 4.1 mm, lip broken). All specimens from the generalized type locality, obtained by I. Nofroni from local fishermen.

Referred material: AMS C.167316, Al Hoceima, Morocco (35°14'N, 03°56'W), 50–100 m, with *Raja* egg cases, August 1986, F. Gubbioli, 2 dry specimens.

GUBBIOLI & NOFRONI (1986) wrote: "All our findings, dozens of specimens, many live, come from eggs of *Raja*

←

Explanation of Figures 16 to 24

Figures 16–24. *Choristella nofronii* McLean, sp. nov. Figures 16–18. Holotype, MNHN, Alboran Sea, western Mediterranean. Height 6.1 mm. Apertural, spire, and umbilical views. Figure 19. SEM view of operculum of holotype. Scale bar = 1 mm. Figure 20. SEM view of jaw of holotype (elements separated). Scale bar = 200 μ m. Figure 21. SEM view of larval shell, topotypic material, courtesy A. Warén. The straight diagonal line is an artifact of scanning. Scale bar = 100 μ m. Figure 22. SEM view of protoconch and first teleoconch whorl of paratype, LACM 2248. Scale bar = 100 μ m. Figure 23. SEM, oblique umbilical view of juvenile shell showing basal ridge, topotypic specimen, courtesy A. Warén. Scale bar = 1 mm. Figure 24. SEM view of radula, paratype, LACM 2448. Scale bar = 40 μ m.

cf. *clavata* fished in the quadrilateral Marbella, S. Roque (Spain), Tetuan, Al Hoceima (Morocco) at depths between 50 and 100 m.”

Remarks: *Choristella nofronii* is characterized by its relatively small size and high profile. In addition, small shells have a weak mid-basal ridge, a feature not observed in any other species.

GUBBIOLI & NOFRONI (1986) found this species in 5% of 250 of the egg cases they examined and found that three times as many had specimens of the limpet *Addisonia lateralis* (Requien, 1848). Both species were noted in 3% of the examined egg cases.

The choristellid affinity was unknown by GUBBIOLI & NOFRONI (1986), who identified it as “*Cithna*” *naticiformis* Jeffries, 1883. The basal ridge that characterizes small shells (Figure 23) led them to associate the species with Jeffreys’ taxon from 1453 m (795 fm) off the Portuguese coast. However, the basal ridge of that species (syntypes, BMNH 85.11.5.1615–1617, Figures 60, 61) is much more pronounced, and there is a concave rather than convex surface between the umbilical and basal ridges. Jeffreys’ species is treated further in the Appendix.

GUBBIOLI & NOFRONI (1986) also suggested that “*Cyclostrema*” *valvatooides* Jeffreys, 1883, might also be referable to the present species. I have examined the holotype of that species (BMNH 85.11.5.1593). Choristellid affinity is ruled out because it does not have the umbilical ridge characteristic of the family.

Etymology: The name honors Italo Nofroni, one of the collectors of the original material.

Choristella leptalea Bush, 1897

(Figures 25–29)

Choristella leptalea BUSH, 1897:139, text fig. 8 [operculum], text fig. 9 [shell], pl. 23, figs. 16, 16a [radula].

Choristella brychia BUSH, 1897:139, text fig. 10 [spire view of shell].

Description: Shell (Figures 25–29) small for genus (maximum diameter 4.0 mm), spire height relatively low (height-width ratio of holotype 0.71). Shell wall extremely thin. Shell white, periostracum thin, light brown. Protoconch diameter about 300 μ m. Teleoconch whorls 3.4, rounded, smooth, suture deeply impressed. Umbilicus narrow, deep, not obstructed by reflection of inner lip, inner extent of umbilicus defined by narrow ridge. Spiral sculpture lacking; axial sculpture lacking, except for fine growth increments. Peristome complete, area of contact with previous whorl minimal; lip flared below, broadest at base of columella, where meeting umbilical ridge. Operculum of 4.5 whorls, nucleus slightly excentric, final 3 whorls evenly expanding in multispiral pattern.

Dimensions. Height 2.5 mm, width 3.5 mm (original measurements of holotype); height 3.1 mm, width 4.0 mm (new measurements of holotype of *Choristella brychia*).

External anatomy. BUSH’s (1897) description is copied

here: “The animal has a broad emarginate head with one pair of long slender tentacles; with a rather broad, short, tapered, ciliated verge just beneath the base of the right one. Eyes none. Gill attached to the left side lying across the top of the body just within the mantle edge.”

Radula. As noted in the remarks under the genus, the radular illustration and tooth count provided by Bush is incorrect; the radula is probably typical for the genus.

Type localities: For *Choristella leptalea*, off Martha’s Vineyard Island, Massachusetts (USFC Sta. 2547), 713 m, 1885. For *C. brychia*, off Martha’s Vineyard Island, Massachusetts (USFC Sta. 2234), 1481 m, 1884.

Type material: Holotype, *Choristella leptalea*, USNM 52504 (Figures 25, 26). Although collected alive, the specimen is now broken, the final whorl separated. The label reads “jaw-radula, operculum mounted,” but these preparations could not be located.

Holotype, *Choristella brychia*, USNM 77622 (Figures 27–29). The specimen is intact, although the lip is now broken at the base.

Remarks: *Choristella leptalea* is a relatively small-sized member of the family, having a maximum dimension of only 4.0 mm, compared to 10 mm reached by some species. The number of whorls is equal to that of other species, which suggests that it is based on mature specimens. It occurs sympatrically with *C. tenera*, from which it differs in its lower spire.

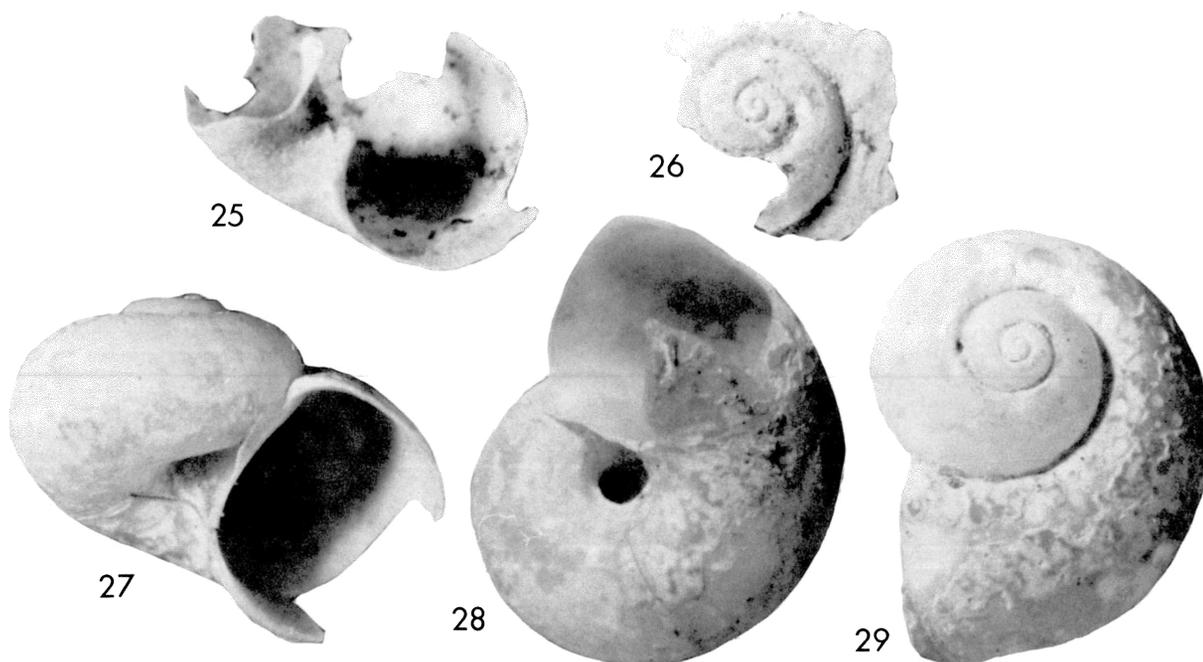
Choristella brychia Bush, 1897, was based on a single specimen. It was described briefly: “This is a larger species of firmer texture than the preceding [*C. leptalea*], although of the same number of whorls. Sculpture none. Color dirty white tinted with brown. Where not worn the surface is slightly lustrous. Interior of aperture very smooth and lustrous, showing a sutural band of delicate rose color.” The size difference of 0.5 mm is not sufficient grounds to recognize *C. brychia* as a species distinct from *C. leptalea*. The original figures of the shells are not helpful because an apertural view was used for *C. leptalea*, whereas a spire view was given for *C. brychia*.

Although Bush did not state that the operculum of *Choristella leptalea* is multispiral, her fig. 8 clearly shows 4.5 whorls in a multispiral pattern. The diagnosis above includes mention of periostracum, based on my examination of the holotype of *C. brychia*, although this was not mentioned by Bush. The remains of the holotype of *C. leptalea* show an extremely thin, pale periostracum, not as dark as that of *C. tenera*. The original description of *C. leptalea* does not include mention of the carination that descends within the umbilicus, which is clearly visible on the holotypes of both *C. leptalea* and *C. brychia*.

Choristella ponderi McLean, sp. nov.

(Figures 30–38)

Description: Shell (Figures 30–33) small for genus (maximum diameter 4.7 mm), spire height relatively low (height-



Explanation of Figures 25 to 29

Figures 25–29. *Choristella leptalea* Bush, 1897. Figures 25, 26. Holotype, USNM 52504, off Martha's Vineyard Island. Original height 2.5 mm (BUSH, 1897). Figure 25, broken remains of aperture. Figure 26, broken remains of spire. Figures 27–29. Holotype of *Choristella brychia* Bush, 1897, USNM 77622, off Martha's Vineyard Island. Height 3.1 mm. Apertural, basal, and oblique spire views.

width ratio of holotype 0.68). Shell wall extremely thin. Surface shiny, white, periostracum thin, colorless. Protoconch (Figure 36) tip bulbous, surface smooth. Teleoconch whorls 3, rounded, smooth, suture deeply impressed. Umbilicus narrow, deep, not obstructed by reflection of inner lip, inner extent of umbilicus defined by narrow ridge. Spiral sculpture represented only by umbilical ridge; axial sculpture lacking, except for fine growth increments. Peristome complete, area of contact with previous whorl minimal; lip flared below, broadest at base of columella, where buttressed by umbilical ridge. Operculum (Figure 34) pale brown, nucleus slightly excentric, final whorl rapidly expanding to produce paucispiral pattern.

Dimensions. Height 3.2 mm, width 4.7 mm (holotype); height 3.5 mm, diameter 4.7 mm (figured specimen, AMS C.155463).

External anatomy (Figure 37). The mouth is bordered laterally by projecting oral lappets. No groove on the right tentacle was detected, but the specimen may be female.

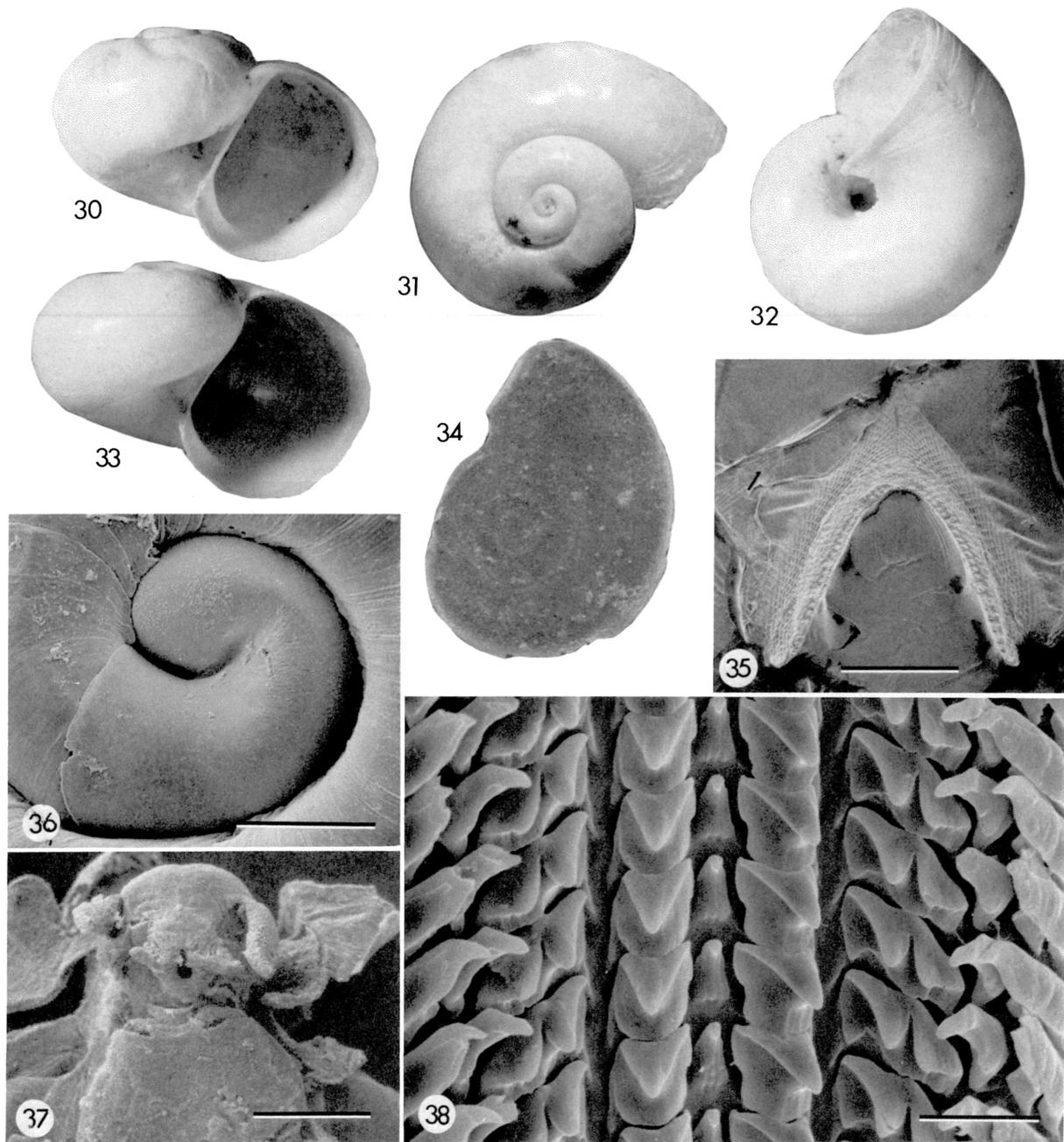
Jaw (Figure 35). As described for genus.

Radula (Figure 38). The radula agrees with that given for the family. The rachidian is unusual in the genus in seeming to have three projecting nubs at the base of the shaft.

Type locality: Off Sydney, New South Wales, Australia (33°47.5'S, 151°28.5'E), 124 m, in skate egg case.

Type material: 6 specimens from type locality, R/V *Kapala* Sta. K86/14/16, 2 July 1986. Holotype and paratypes AMS C.151524, bodies preserved separately. Ten additional paratypes, off Shoalhaven Heads, N.S.W. (34°56'S, 151°9.5'E), 494–585 m, in elasmobranch egg cases, R/V *Kapala* Sta. K86/23/04, 10 September 1986, small to medium-sized specimens with dried bodies, 3 specimens wet-preserved; distribution: 6 paratypes AMS C.167692; 1 paratype LACM 2630, 2 paratypes NMNZ, 1 paratype MNHN.

Referred material (arranged north to south): AMS C.155457, NE of North Reef, Queensland (23°08.4'S, 152°12.3'E), R/V *Kimbla* Sta. 20, 14 December 1977, 1 dead specimen. AMS C.155458, E of North West Island, Queensland (23°19.5'S, 152°35.4'E), 320 m, R/V *Kimbla* Sta. 23, 14 December 1977, 1 dead specimen. AMS C.155462, E of Lady Musgrave Island, Queensland (23°33.7'S, 152°37.0'E), 339 m, R/V *Kimbla* Sta. 3, 17 November 1977, 1 dead specimen. AMS C.155459, NE of Lady Musgrave Island, Queensland (23°38.8'S, 152°45.5'E), 365 m, R/V *Kimbla* Sta. 24, 14 December 1977, 4 small dead shells. AMS C.155461, E of Lady Musgrave Island, Queensland (23°44'S, 152°49'E), 357 m, R/V *Kimbla* Sta. 2, 17 November 1977, 1 dead specimen. AMS C.151990, E of Lady Musgrave Island, Queensland (23°52.2'S, 152°42.2'E), 296 m, R/V *Kimbla*



Explanation of Figures 30 to 38

Figures 30–38. *Choristella ponderi* McLean, sp. nov. Figures 30–32. Holotype, AMS C.151524, off Sydney, New South Wales, Australia. Height 3.2 mm. Apertural, spire, and umbilical views. Figure 33. AMS C.155463, off Fraser Island, Queensland, Australia. Height 3.5 mm. Figure 34. SEM view of operculum of paratype, AMS C.151524. Scale bar = 1 mm. Figure 35. SEM view of jaw of paratype, AMS C.151524. Scale bar = 200 μ m. Figure 36. SEM view of early whorls, showing protoconch and first teleoconch whorl. SEM photo by B. Marshall. AMS C.82431, off Caloundra, Queensland. Scale bar = 100 μ m. Figure 37. SEM view of critical point dried body, showing cephalic tentacles, oral lappets, and foot with pedal gland, paratype, AMS C.151524. Figure 38. SEM view of radula, paratype, AMS C.151524. Scale bar = 25 μ m.

Sta. 15, 7 July 1984, 3 dry specimens. AMS C.155460, off Frazer Island, Queensland (24°57.9'S, 153°37.3'E), 210 m, R/V *Kimbla* Sta. 27, 15 December 1977, 1 small dead specimen. AMS C.155463, S end Fraser Island Queensland (27°57'08"S, 153°51'03"E), 201 m, R/V *Kimbla* Sta. Q13, 10 November 1976, 1 dry specimen (Figure 33). AMS C.150125, N of Coolongatta, Queensland (28°07'S, 153°50'E), 146 m, R/V *Kapala* Sta. K78-17-14, 18 August 1978, 1 small specimen. AMS C.82431, E of Caloundra, Queensland, 91–110 m (50–60 fm), T. A. Garrard Coll., 1 specimen (Figure 37, protoconch). AMS C.150127, off Kiama, N.S.W. (34°46'S, 151°13'E), 387–552 m, in egg case, R/V *Kapala* Sta. K86-09-03, 15 April 1986, 2 small specimens, dry shells and wet bodies separate.

Remarks: This species is characterized by its small size, low spire, and relatively few whorls. There are a sufficient number of records to be certain that the specimens are mature. In its small size and low spire it is most similar to *Choristella leptalea* Bush, a species too poorly known to allow full comparison.

Choristella ponderi is broadly distributed on the east coast of Australia. Records are known from Queensland (23°08'S) to New South Wales (34°56'S).

Etymology: The name honors Winston Ponder, of the Australian Museum, Sydney.

Choristella hickmanae McLean, sp. nov.

(Figures 39–45)

Choristella n. sp.: HICKMAN, 1983:86, fig. 29 [radula].

Description: Shell (Figures 39–43) large for genus (maximum diameter 9 mm), spire height relatively low (height-width ratio of holotype 0.72). Shell wall extremely thin, maximum thickness of broken lip 0.1 mm. Surface dull, yellowish white, periostracum not evident, surface finely pitted. Protoconch and earliest teleoconch whorl missing. Remaining whorls 3.5, rounded, smooth; suture deeply impressed. Umbilicus broad, deep, not obstructed by reflection of inner lip. Spiral sculpture represented only by single narrow ridge deep within umbilicus; axial sculpture lacking, growth increments not apparent. Peristome complete, area of contact with previous whorl minimal. Operculum (Figure 39) pale brown, nucleus slightly excentric, final 3 whorls evenly expanding in multispiral pattern.

Dimensions. Height 6.5 mm, width 9.0 mm (estimated dimension of holotype prior to breakage); height 7 mm, diameter 10 mm (estimated dimension of sectioned paratype).

External anatomy. Figure 44 shows the left (umbilical view) side of a paratype specimen prior to sectioning. Four epipodial tentacles are shown adjacent to the operculum.

Radula (Figure 45). The radula agrees with the generic description in its overall morphology. The rachidian tooth

has a weakly projecting shaft, but a small, clearly distinct, overhanging cusp.

Type locality: Northern Cascadia Abyssal Plain, at base of continental slope, 95 nautical miles (172 km) west of Strait of Juan de Fuca, Washington (48°38.1'N, 126°58.0'W), 2176 m, gray silty clay. CAREY (1981) described the bottom conditions for the Cascadia Abyssal Plain.

Type material: 3 specimens from type locality, all with damaged shells, collected with beam trawl by A. Carey, Oregon State University (BMT-DWD Sta. 9), 11 September 1971. Holotype, LACM 2249 (Figures 42, 43) body used for light microscope preparation of radula. Two paratypes, LACM 2250, one sectioned, shell destroyed, photograph of shell and body prior to sectioning (Figures 39–41), one paratype specimen with badly damaged shell used for SEM preparation of radula by C. Hickman (Figure 45).

Remarks: *Choristella hickmanae* is a relatively low-spined species comparable to *C. leptalea* and *C. ponderi*, but is larger than either species (9 mm maximum dimension, compared to 4.0 mm for *C. leptalea* and 4.7 mm for *C. ponderi*). Each species has 3.5 whorls. The umbilicus of *C. hickmanae* is broader than that of *C. leptalea* and *C. ponderi*, in which the peristome is slightly reflected over the umbilicus.

The fine pitting on the surface of the shell is probably a result of etching due to the original preservation in formalin.

There is no record of association of the type lot with shark or skate egg cases, but the extremely thin shell and damaged condition of all specimens suggest that protection within an elasmobranch egg case would be essential to this species.

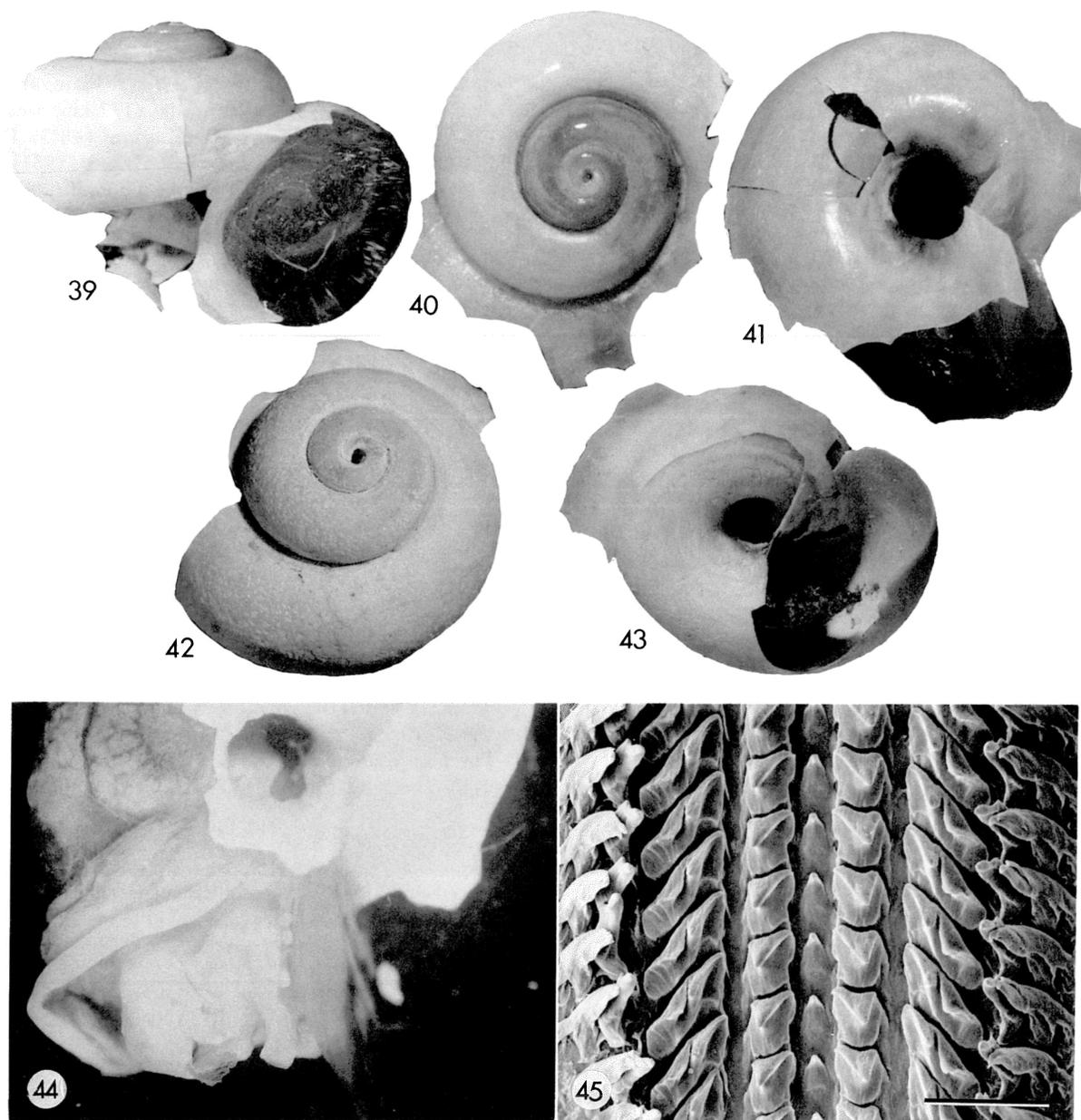
Etymology: This species is named after Carole S. Hickman, University of California, Berkeley.

Further Records of *Choristella* spp.

Four additional lots of *Choristella* species from the MNHNP collection were received on loan from P. Bouchet subsequent to the initial submission of this paper. All represent immature specimens and I refrain from describing further new taxa from this material because mature examples are unknown. These lots are listed here:

MNHN uncataloged, Mozambique Channel (11°44'S, 47°35'E), 3716 m. R/V *Suroit*, BENTHEDI Expedition, Sat. 87, 3 April 1977. Five specimens, maximum diameter 2.0 mm. Specimens of 1.0 mm in diameter show a basal carination.

MNHN uncataloged, Norfolk Ridge (23°03'S, 167°19'E), 503 m. R/V *N. O. Vauban*, SMIB 3 Expedition, Sta. DW22, 24 May 1987. Two specimens, maximum



Explanation of Figures 39 to 45

Figures 39–45. *Choristella hickmanae* McLean, sp. nov. Figures 39–41, 44. Paratype specimen prior to sectioning, Northern Cascadia Abyssal Plain off Washington, LACM 2250. Height 6.5 mm (estimate). Figures 42, 43. Holotype, same locality, LACM 2249. Diameter of broken shell 8.0 mm. Figure 45. SEM view of radula of paratype, LACM 2250. Scale bar = 50 μ m.

diameter 2.0 mm. Shell profile low, not showing basal carination. Radula and jaw examined with SEM, typical for *Choristella*.

MNHN uncataloged, Tanimbar Islands, Indonesia (08°42'S, 131°54'E), 356–368 m. R/V *Baruna Jaya 1*, KARUBAR expedition, Sta. CP69, 2 November 1991. Six specimens, maximum diameter 3.5 mm. Shell profile of

medium height; small specimens not showing basal carination. Radula and jaw examined with SEM, typical for *Choristella*.

MNHN uncataloged, Kai Islands, Indonesia (06°08'S, 132°45'E), 390–502 m, R/V *Baruna Jaya 1*, KARUBAR expedition, Sta. CP35, 27 October 1991. One specimen, maximum diameter 4.0 mm, similar to preceding lot.

Bichoristes McLean, gen. nov.

Type species: *Bichoristes wareni* McLean, sp. nov.

As the genus is monotypic, the generic diagnosis and remarks are combined in the species treatment below.

Bichoristes wareni McLean, sp. nov.

(Figures 46–53)

Description: Shell (Figures 46–48) minute (maximum diameter 3.2 mm), thin, periostracum unknown, whorls 3.2, quadrangular in section, growth form planispiral with two acutely angled, projecting carinations at outer edge, one above and the other below position of protoconch; upper carina projecting slightly more than lower carina. Suture at position of upper carination of previous whorl, not channeled; whorl extending above suture, forming rounded angulation, base defined at position of broadest possible umbilicus by sharp angulation. Spiral sculpture lacking except for these four carinations. Axial sculpture of exceedingly fine growth increments, prosocline on upper surface of whorl, greatest curvature close to suture, opisthocline on outer surface between the two keels, prosocline on base, greatest curvature close to umbilical keel. Aperture quadrangular, peristome complete; mature upper lip, outer lip, and lower lip slightly flared. Protoconch (Figure 49) diameter 200 μ m, tip bulbous, surface smooth, visible equally in spire and umbilical views, similarly recessed in both views. Operculum (Figure 50) thin, multispiral, about 10 whorls visible.

Dimensions. Height 1.4 mm, diameter 3.2 mm (holotype); height 1.2 mm, diameter 3.0 mm (paratype).

External anatomy. Unknown.

Jaw (Figure 51). Typical for family.

Radula. (Figures 52, 53). Rachidian tooth relatively large, with triangular shaft and prominent overhanging cusp; base of shaft with lateral nubs and one central nub. First lateral tooth massive, with two cusps, the innermost small and blunt like that of rachidian, the outermost acutely triangular and with long overhang; shaft base articulating with tooth below, inner edge of shaft articulating with rachidian. Second lateral tooth largest in row, with single large acutely pointed overhanging cusp, its upper profile descending away from rachidian, shaft long and deeply excavated for accommodation of outer lateral teeth. Third lateral tooth with long shaft and pointed cusp that projects over the deeply excavated shaft of second lateral tooth. Fourth lateral tooth small, fused with and emerging from shaft of third. Fifth lateral tooth vestigial, a small flap at the base of the shaft of the third lateral tooth.

Type locality: Norfolk Ridge, S of New Caledonia (24°55'S, 162°22'E), 505–515 m.

Type material: Holotype MNHN uncataloged, from type locality, R/V *Jean Charcot*, BIOCAL Expedition Sta. DW66, 3 September 1985. The body of the specimen was

extracted through a hole filed in the shell by A. Warén, who examined the operculum, radula, and jaw with SEM and provided the prints used here. One paratype, MNHN uncataloged, Norfolk Ridge (23°03'S, 167°19'E), 503 m, R/V *N. O. Vauban*, SMIB 3 Expedition Sta. DW22, 24 May 1987.

Remarks: The discovery of a planispirally coiled member of the Choristellidae was unanticipated. Although the shell morphology seems to be completely different from that of other choristellids, there are a number of shared characters: (1) shell is extremely thin; (2) protoconch surface is smooth; (3) teleoconch whorls do not exceed 3.5; (4) contact with the previous whorl is limited to the thin layer that makes the peristome complete where it fuses with the parietal wall, and (5) the umbilicus is as broad as is physically possible, the inner basal keel of *Bichoristes* corresponding to the sharp umbilical ridge of *Choristella*. *Bichoristes* adds the outer two keels; these delimit the area of contact for the next whorl, and the result is a planispiral growth form.

The radula has the basic choristellid plan, differing from that of *Choristella* in having the first rather than second lateral tooth the bicuspid tooth. Other distinctions are the nubs at the base of the shaft of the rachidian and the fusion of the fourth lateral tooth with the third.

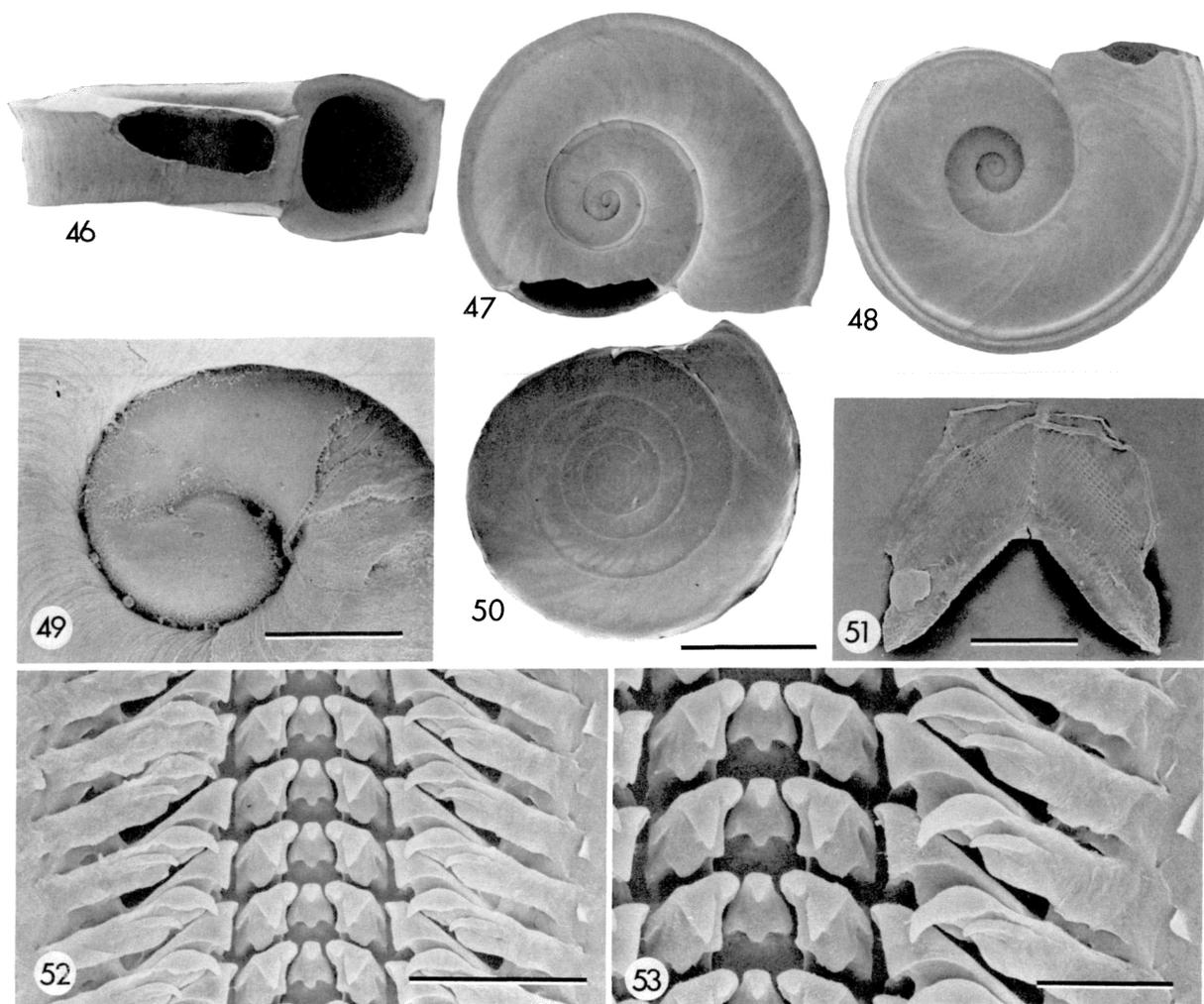
The sculptured shell of *Bichoristes* has to be interpreted as either derived or primitive in the family. I interpret *Bichoristes* as derived from the low-spired shell form typified by *Choristella ponderi* by the not so extreme modifications to the sculpture noted above. Its jaw and radula are so like those of other choristellids that it is difficult to conceive of a differing life mode. Functionally, its quadrangular shell morphology provides structural support. The narrow planispiral shell form would enable access to the deep crevices at both ends of the elasmobranch egg case, where a planispiral shell could be expected to penetrate further than the helically coiled shell form of *Choristella*.

Etymology: The name honors Anders Warén, of the Swedish Museum of Natural History, Stockholm, who recognized the familial affinity of the species among material in the MNHN collection.

DISCUSSION

Choristellidae and Addisoniidae share many characters of internal anatomy (HASZPRUNAR, 1988c, 1992) and a similar habitat and feeding specialization on the spent egg cases of elasmobranchs. Members of both families are thin-shelled, affording little protection from predators; instead, protection is provided by the thick walls of the egg cases within which they live.

The radula in the Choristellidae and Addisoniidae is relatively large and is provided with robust teeth that are capable of gouging into the walls of the egg cases to provide a direct source of food. Marshall (personal communication) reports that the inner wall of egg cases that contained



Explanation of Figures 46 to 53

Figures 46–53. *Bichoristes wareni* McLean, sp. nov. All are SEM views of holotype specimen, MNHN, Norfolk Ridge. Diameter 3.2 mm. Figures 46–48. Apertural, spire, and umbilical views. Figure 49. Protoconch. Scale bar = 100 μm . Figure 50. Operculum. Scale bar = 400 μm . Figure 51. Jaw. Scale bar = 100 μm . Figure 52. Radula. Scale bar = 20 μm . Figure 53. Radula. Scale bar = 10 μm .

Choristella marshalli were eaten by the limpets. McLEAN (1985) illustrated radular grazing marks made on the inner wall of an egg case by *Addisonia brophyi* McLean, 1985.

The radula in other cocculiniform families is relatively small with weakly developed teeth in the central field; most of these families also differ in having marginal teeth that are used for sweeping. MARSHALL (1986) has emphasized that the diet in these families is likely the bacteria that are associated with the decomposition of the biogenic substrates, rather than the direct food source provided by the substrate.

There is no indication that members of either the Choristellidae or Addisoniidae occur in the capsules of developing elasmobranchs. The thin-shelled mollusks would be exposed to predators during penetration of the egg case. Thus

it is incorrect to say that these mollusks are parasitic. Dispersal of these mollusks would necessarily be possible only during the larval stage, at which time the larvae would settle on and enter a spent capsule through the opening from which the young elasmobranch had emerged.

Sizes of the egg cases available in the benthos places limits on the maximum size attained by choristellid and addisoniid species. The maximum size of 10 mm in choristellids could only be exceeded if the elasmobranch capsule were unusually large.

The distribution of each species must depend upon the availability of egg cases of sharks and skates. As noted earlier (McLEAN, 1985), egg cases are produced by three elasmobranch families, the cat sharks (family Scyliorhinidae), with about 85 species in the world, the bullhead or

horn sharks (family Heterodontidae) and the skates (family Rajidae) (ESCHMEYER *et al.*, 1983). COX (1963) and ESCHMEYER *et al.* (1983) illustrated the egg cases of the species in these families known from California. If a worldwide study of capsule producing elasmobranchs were available, it would be possible to predict the likelihood of associated species of choristellids and addisoniids. Because too few records are currently known, it is unknown whether choristellid species are host specific.

WOURMS (1977) reviewed the literature on elasmobranch egg-case structure and formation. Egg cases are composed of layers of the structural protein collagen, which exhibits unique chemical and physical properties when deployed in the egg cases. Shark embryos develop within the egg cases for up to nine months, during which there is little evidence of deterioration of the egg cases. The duration of spent egg cases in the benthos is unknown, nor am I aware of their being used as food by other organisms, but the cases undoubtedly persist in the benthos for a number of years. The egg cases should therefore provide a persistent and reliable food source.

SUMMARY

Additions to knowledge of the Choristellidae that result from this study are:

(1) Family-level shell characters are minute to small size, extremely thin shell, complete peristome, deep suture (except *Bichoristes*), umbilical ridge, smooth bulbous protoconch, and maximum of 3.5 teleoconch whorls.

(2) The radula is unique to the family. Its resemblance to that of the Cocculinellidae is superficial.

(3) The bulbous protoconch tip is unlike the compressed, laterally pinched protoconch tip of Pseudococculinidae and Cocculinellidae. Protoconch characters may yet confirm the affinity to Addisoniidae suggested by anatomical characters (HASZPRUNAR, 1992), but have not helped because the protoconch of Addisoniidae is deciduous and remains unknown.

(4) Taxa based on shell characters can readily be excluded from the genus if they do not meet all these criteria. In the Appendix, 10 species-level taxa that have previously been assigned to the family are excluded. Skeneiform genera with a sharp umbilical ridge may be excluded by lacking the deep suture.

(5) Specific characters in *Choristella* are relative size, relative proportions of height to width, and whether the multispiral operculum looks multispiral or appears to be paucispiral as a result of having only three whorls. External anatomy is too poorly known to be useful at this time.

(6) The new genus *Bichoristes* has a uniquely bicarinate and planispiral shell, although the radula is close to that of *Choristella*. Most of the shell characters diagnostic for *Choristella*, including thin shell, 3.5 whorls, smooth protoconch, and umbilical ridge, are present.

(7) Although most species are allopatric, one sympatric pair is known: *Choristella tenera* and *C. leptalea*.

(8) No species is known to be free living and unassociated with the spent egg cases of elasmobranchs.

(9) Shell size is limited by the size of available egg capsules.

(10) The family is broadly distributed, having been found in the most extensively sampled regions of the world in temperate zones at continental shelf to abyssal depths.

ACKNOWLEDGMENTS

Treatment of new species included here would not have been possible had not Philippe Bouchet of the Museum d'Histoire Naturelle, Paris, Bruce Marshall of the National Museum of New Zealand, and Winston Ponder of the Australian Museum, Sydney, turned over to me the undescribed choristellid species they had recognized in their museum collections, as well as some scanning work that had been done. SEM micrographs of the radula of *Choristella hickmanae* were provided by Carole Hickman. All illustrations for *Bichoristes wareni* were provided by Anders Warén, who also provided two views used for *Choristella nofronii*. Bruce Marshall provided the radular illustrations for *Trenchia agulhasae* used in the Appendix. I thank staff members of the Natural History Museum, London, and the U.S. National Museum of Natural History for the loan of pertinent type specimens. I thank Philippe Bouchet, Gerhard Haszprunar, Bruce Marshall, and Anders Warén, and the anonymous reviewers for reading the manuscript and offering helpful suggestions.

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APPENDIX—TAXA EXCLUDED FROM CHORISTELLIDAE

A number of taxa have been incorrectly allocated to the family Choristellidae (originally assigned to the "Choristidae"). The following taxa have not been shown to have the choristellid radular plan and lack some or all of the diagnostic shell characters (small size, extremely thin shell, complete peristome, deep suture, and sharp carination descending into the umbilicus). Some of the misallocated taxa are naticids, but many are potential members of the family Skeneidae (superfamily Trochacea). Skeneidae and families of similar appearance have been poorly understood but have received recent attention from MARSHALL (1988), HICKMAN & MCLEAN (1990), and WARÉN (1991, 1992). It is beyond the scope of this paper to allocate the following taxa, although some suggestions are made.

1. *Choristes elegans* Carpenter, 1872 (Figure 54)

Choristes elegans Carpenter in DAWSON, 1872:392, pl. 7, figs. 13, 13a; VERRILL, 1882:542, p. 58, fig. 28 ["I have figured a young fossil specimen for convenient comparison"]; RICHARDS, 1962:79, pl. 17, fig. 15 ["Montreal, Pleistocene"]; CLARKE, 1961:360 [in list of species under *Choristes*]; MARINCOVICH, 1977:338 [as valid genus and species of Naticidae]; BOUCHET & WARÉN, 1979, fig. 47 [syntype]. Type locality: Pleistocene, St. Lawrence River Estuary, Montreal, Quebec. **Lectotype (here designated):** USNM 188948; 2 paralectotypes: USNM 56385.

Carpenter was uncertain as to the familial relationships of the Pleistocene fossil he described as *Choristes elegans*: "It is hard to pronounce satisfactorily on its relationships. In its thin, coated shell it resembles *Velutina*; the striae and loose whirls recall *Naticina*; the straight pillar lip reminds us of *Fossarus*; while the umbilicus and rounded base, with entire mouth, best accord with the *Natica* group."

Although MARINCOVICH (1977) used *Choristes* for eastern Pacific naticid species, he cited only the original illustration of the type species; it is not clear whether he examined specimens. He did not cite the illustration of RICHARDS (1962:79, pl. 17, fig. 15), who figured a specimen identified as *Choristes elegans* from the Montreal Pleistocene and placed it in Choristidae without comment. BOUCHET & WARÉN (1979) figured a syntype without citing a catalog number. There are three shells in the USNM collection labeled *Choristes elegans* Carpenter, "Postpliocene, Montreal, Dawson." A **lectotype** (USNM 188948, height 20.1 mm, Figure 54) and two **paralectotypes** (USNM 56385, heights 16.7 mm and 17.2 mm) are

here designated. The lectotype (Figure 54) shows irregular spiral sculpture and the inner lip detached from the parietal wall. Carpenter noted the "smooth epidermis lining the umbilical chambers, conspicuously preserved, even in these fossil specimens, between the closest part of the parietal region."

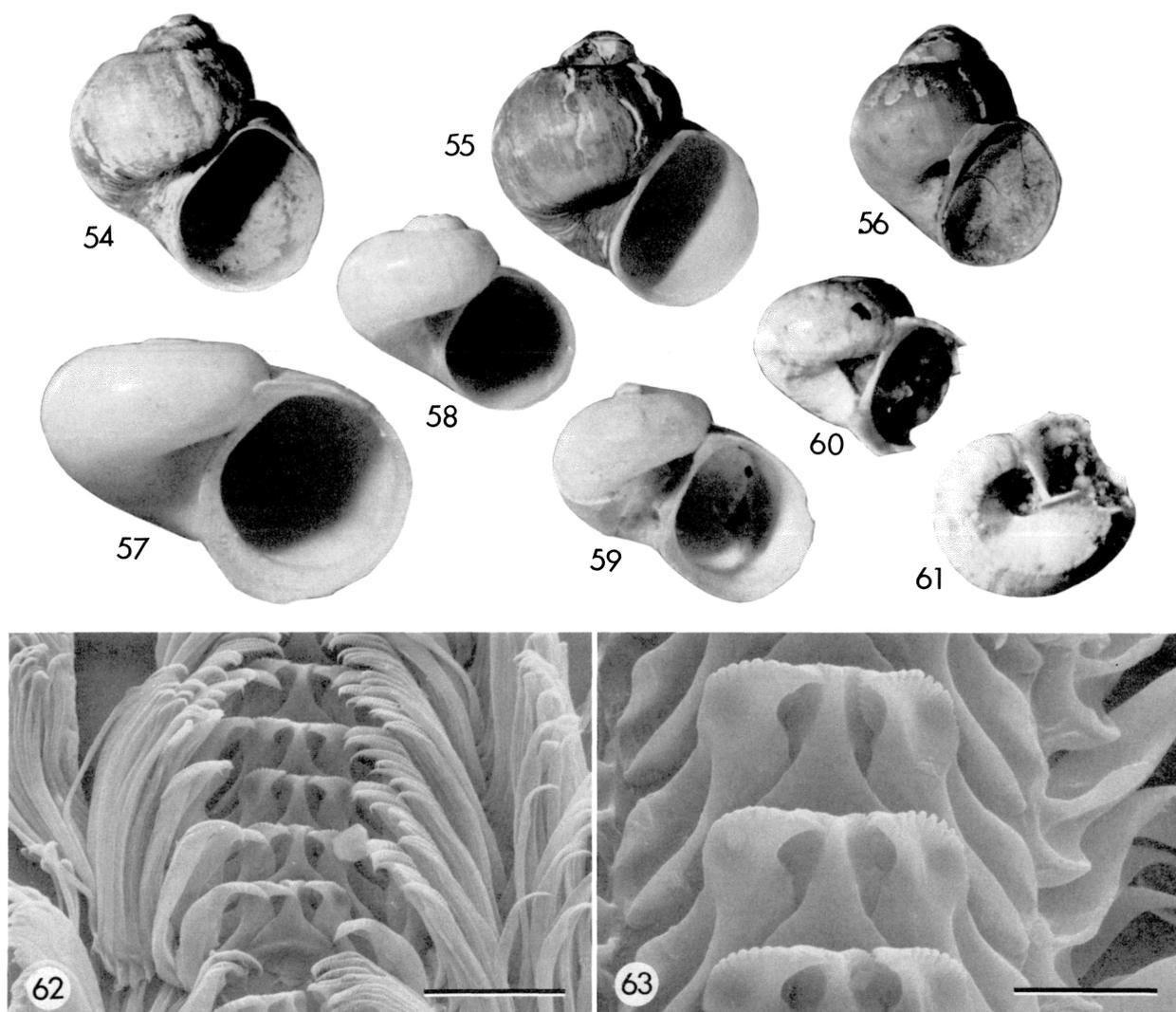
The type material of *Choristes elegans* is here identified as a variation of the naticid *Amauropsis islandica* (Gmelin, 1791), a morphologically variable species that is broadly distributed in shallow to moderate depths in the North Atlantic and Arctic Oceans. In his redescription of *A. islandica*, MARINCOVICH (1977:217, pl. 17, figs. 1-4, pl. 22, fig. 1) described the umbilicus as "open, extremely narrow and slitlike, usually concealed by periostracum of inner lip margin." This description of the periostracum agrees with that of Carpenter for *Choristes elegans*. The three specimens have broader umbilici than most specimens of *A. islandica*, but such a shell form may possibly correlate with the lowered salinity in the estuary of the St. Lawrence River.

MARINCOVICH (1977:338) was the first subsequent author to correctly assign *Choristes* to the Naticidae. GOLOKOV & STAROBOGATOV's (1975) assignment to the Naticidae on radular characters cannot be credited because it could only have been based on published illustrations of the radula of "*Choristes*" *tenera* (which is not a naticid). However, Marincovich did not note the fact that *Choristes elegans* would have to be considered extinct if recognized as a valid species; he did not compare it to *Amauropsis islandica* and he did not conclude that *Choristes tenera* Verrill should be assigned elsewhere, despite noting that the radular dentition of that species differed from that of two Recent naticids he assigned to *Choristes*. Instead, he stated that "another radular mount should be made to confirm the radular dentition reported by VERRILL (1882)."

KABAT (1989, 1991) was aware that Choristellidae Bouchet & Warén, 1979, solved the nomenclatural problem for the choristellids, but pointed out that Choristidae Verrill, 1882 (Naticacea) presented a problem of homonymy for the well-known insect family Choristidae Esben-Petersen, 1915 (nominotypical genus *Chorista* Klug, 1836). Kabat proposed that Choristidae Verrill be emended to Choristeidae Verrill, to conserve Choristidae Esben-Petersen and to retain Choristeidae in the event that it might prove to have utility in the Naticacea. Kabat (personal communication) now agrees with the synonymization of *Choristes* with *Amauropsis*.

2. *Choristes carpenteri* Dall, 1896 (Figures 55, 56)

Choristes carpenteri DALL, 1896:10; DALL, 1908:328, pl. 3, fig. 4; KEEN, 1971:388, fig. 424 [copy fig. of DALL, 1908]; CLARKE, 1961:360 [in list of *Choristes* species]; MARINCOVICH, 1977:340, pl. 31, figs. 8, 9, text fig. 11b [radula]. Type locality: Gulf of Panama, 2693 m. Holotype: USNM 123039.



Explanation of Figures 54 to 63

Figures 54–63. Type specimens of taxa incorrectly referred to Choristellidae. Name combinations as originally proposed. Figure 54. Lectotype, *Choristes elegans* Carpenter, 1862. USNM 56385. Pleistocene, St. Lawrence River Estuary, Montreal, Quebec. Height 20.1 mm. Figure 55. Holotype, *Choristes carpenteri* Dall, 1896. USNM 123039. Gulf of Panama, 2693 m. Height 21.0 mm. Figure 56. *Choristes carpenteri*, second reported specimen, USNM 123038. Gulf of Panama, 2690 m. Figure 57. Holotype, *Cyclostrema pompholyx* Dall, 1889. USNM 214279. Gulf of Mexico, 1472 m. Diameter 4.1 mm. Figure 58. Holotype, *Choristes agulhasae* Clarke, 1961. MCZ 224955. Cape Basin off South Africa, 4585 m. Height 2.0 mm. Figure 59. Holotype, *Choristes agulhasae argentinae* Clarke, 1961. Argentine Basin, 5130 m. MCZ 224956. Height 2.3 mm. Figures 60, 61. Syntype, *Cithna naticiformis* Jeffreys, 1883. BMNH 85.11.5.1615–1617. Porcupine Expedition of 1870, Sta. 17a, off Portugal, 1353 m. Height 1.8 mm. Specimen is still attached to cardboard mount. Figures 62, 63. SEM views of radula from holotype of *Choristes agulhasae* Clarke, 1961, courtesy B. Marshall. See text for generic assignment to *Trenchia* Knudsen, 1964. Scale bar of Figure 62 = 100 μ m, of Figure 63 = 40 μ m.

Despite the fact that *Choristes* was based on a shallow-water type species, MARINCOVICH (1977) retained the genus for two abyssal, eastern Pacific naticid species, *Choristes carpenteri* Dall, 1896, and *C. coani* Marinovich, 1975, invoking a unique radular definition (“moncuspsate rachidian, one moncuspsate lateral, and two moncuspsate

marginal teeth per half row”). Now that *Choristes* is relegated to the synonymy of *Amauropsis*, these two species are in need of generic reassignment in Naticidae. Affinity to *Amauropsis* is ruled out, as its type species has a tricuspsate rachidian tooth.

The holotype of *Choristes carpenteri* (USNM 123039,

from USFC Sta. 3382), is 21 mm in height, which is sufficiently large to remove it from consideration as a member of the Choristellidae. No mention of an operculum was made in the original account and the specimen appears not to have been collected alive. This specimen has the apical area worn. It is illustrated here for the first time (Figure 55).

In his subsequent account DALL (1908) mentioned a second specimen, from USFC Sta. 3361, 2690 m, Gulf of Panama. This must have been the specimen to which he referred in reporting that "the animal agrees in general appearance with that of *Choristes elegans* var. *tenera* Verrill, as described by Verrill." This specimen, USNM 123038, from USFC Sta. 3361 (Figure 56) is also marked "type"; it measures 15.0 mm in length. It exhibits a characteristic sculptural pattern of naticids in having collabral ridges on the upper part of the whorl near the suture. This specimen has the operculum and a dried body, but the body does not have the epipodial tentacles that may be seen on the dried bodies of *Choristella tenera*. Clearly and inexplicably Dall erred in reporting that the animal agreed with Verrill's species. Although MARINCOVICH purported to figure the holotype (1977:fig. 8), he actually figured this second specimen mentioned by Dall (USNM 123038), and incorrectly gave the length at 20.5 mm, rather than 15.0 mm.

3. *Choristes coani* Marincovich, 1975

Choristes coani MARINCOVICH, 1975:169, figs. 2, 6, 7; MARINCOVICH, 1977:341, pl. 31, figs. 10-12, text fig. 11c [radula]. Type locality: off Central Oregon, 2830 m. Holotype: USNM 741014.

This was described by Marincovich in the family Naticidae. Like the preceding species, it is in need of generic reassignment.

4. *Cyclostrema pompholyx* Dall, 1889 (Figure 57)

Cyclostrema pompholyx DALL, 1889:394, pl. 28, fig. 9; BUSH, 1897:139; TURNER, 1978:17, figs. 11, 12. Type locality: Gulf of Mexico, 1472 m. Holotype: USNM 214279.

Choristes pompholyx: CLARKE, 1961:360 [in list of *Choristes* species].

DALL (1889) originally stated: "I am in doubt as to the generic place of this species, so simple in its characters and without the soft parts. I had thought of putting it under *Choristes* or with *Vitrinella*, and finally in placing it here [*Cyclostrema*] feel by no means satisfied that the choice is a correct one." BUSH (1897) noted that Dall's species "may prove to be another species of *Choristes*," accounting for CLARKE (1961) having placed it in *Choristes*.

The shell is sturdy with a broadly inflated lip. It lacks the umbilical ridge of *Choristella*. There is no evidence to support the allocation of this species to the family Choristellidae.

5. *Choristes agulhasae* Clarke, 1961 (Figure 58)

Choristes agulhasae CLARKE, 1961:361, pl. 3, fig. 1. Type locality: Cape Basin (corrected from Agulhas Basin), SW of Cape Town, South Africa, 4585 m. Holotype: MCZ 224955.

No evidence was advanced to support the assignment of this species to the family, although there is an umbilical carination similar to that of *Choristella*. The radula (Figures 62, 63, SEM photos by Bruce Marshall) is rhipidoglossate, unlike that of Choristellidae. Marshall (personal communication) has identified it as that of *Trenchia* Knudsen, 1964 (family Skeneidae), characterized by the elongate and laterally excavated base of the first lateral tooth.

6. *Choristes agulhasae argentinae* Clarke, 1961 (Figure 59)

Choristes agulhasae argentinae CLARKE, 1961:361, pl. 3, figs. 2, 3. Type locality: Argentine Basin, ESE of Buenos Aires, Argentina, 5130 m. Holotype: MCZ 224956.

The holotype (Figure 59) is a single empty shell, larger than that of the preceding taxon. No evidence supports assignment to Choristellidae. It may be regarded as a possible member of *Trenchia*.

7. *Cithna naticiformis* Jeffreys, 1883 (Figures 60, 61)

Cithna naticiformis JEFFREYS, 1883:112, pl. 20, fig. 11; WARÉN, 1980:21; GUBBIOLI & NOFRONI, 1986:204, figs. Type locality: Porcupine Expedition of 1870, Sta. 17a, off Cape Mondego, Portugal, 1353 m. Syntypes: 3 shells, BMNH 85.11.5.1615-1617.

GUBBIOLI & NOFRONI (1986) incorrectly used this name for *Choristella nofronii* described here, as detailed in the remarks that follow the new species description. A syntype specimen is illustrated here (Figures 60, 61). Although radular material is not available, it is also a possible species of *Trenchia* on evidence from shell characters.

8. *Cyclostrema valvatooides* Jeffreys, 1883

Cyclostrema valvatooides JEFFREYS, 1883:92; WARÉN, 1980:19; GUBBIOLI & NOFRONI, 1986:205. Type locality: Porcupine Expedition, 1870, Sta. 17a, off Cape Mondego, Portugal, 1353 m. Holotype: BMNH 85.11.5.1593.

GUBBIOLI & NOFRONI (1986) also suggested that this name might apply to *Choristes nofronii* described here. I have examined the holotype, which is in bad condition due to chemical exfoliation; it lacks the umbilical carination of *Choristella*.

9. *Choristes mollis* Okutani, 1964

Choristes mollis OKUTANI, 1964:389. Type locality: off Miyake Island, Japan, 1230–1350 m.

No evidence supported the original placement in *Choristes*. The granular sculpture, and of most importance, the incomplete peristome as illustrated by Okutani are not characters of the family. The operculum is figured as multispiral with more whorls than in species of *Choristella*. Reassignment may be possible if the radula is intact in the holotype. Marshall (personal communication) suggests that it be compared to *Granigyra* Dall, 1889 (family Skeneidae).

10. *Choristes nipponica* Okutani, 1964

Choristes nipponica OKUTANI, 1964:388, pl. 6, fig. 2. Type locality; Sagami Bay, Japan, 1360–1385 m.

No evidence was given to support the assignment of this taxon to *Choristes*. The “shining shell,” sutural shelf rather than channeled suture, produced basal lip, and incomplete peristome are not characters of *Choristella*. The operculum is illustrated as multispiral. Assignment on radular characters may be possible.