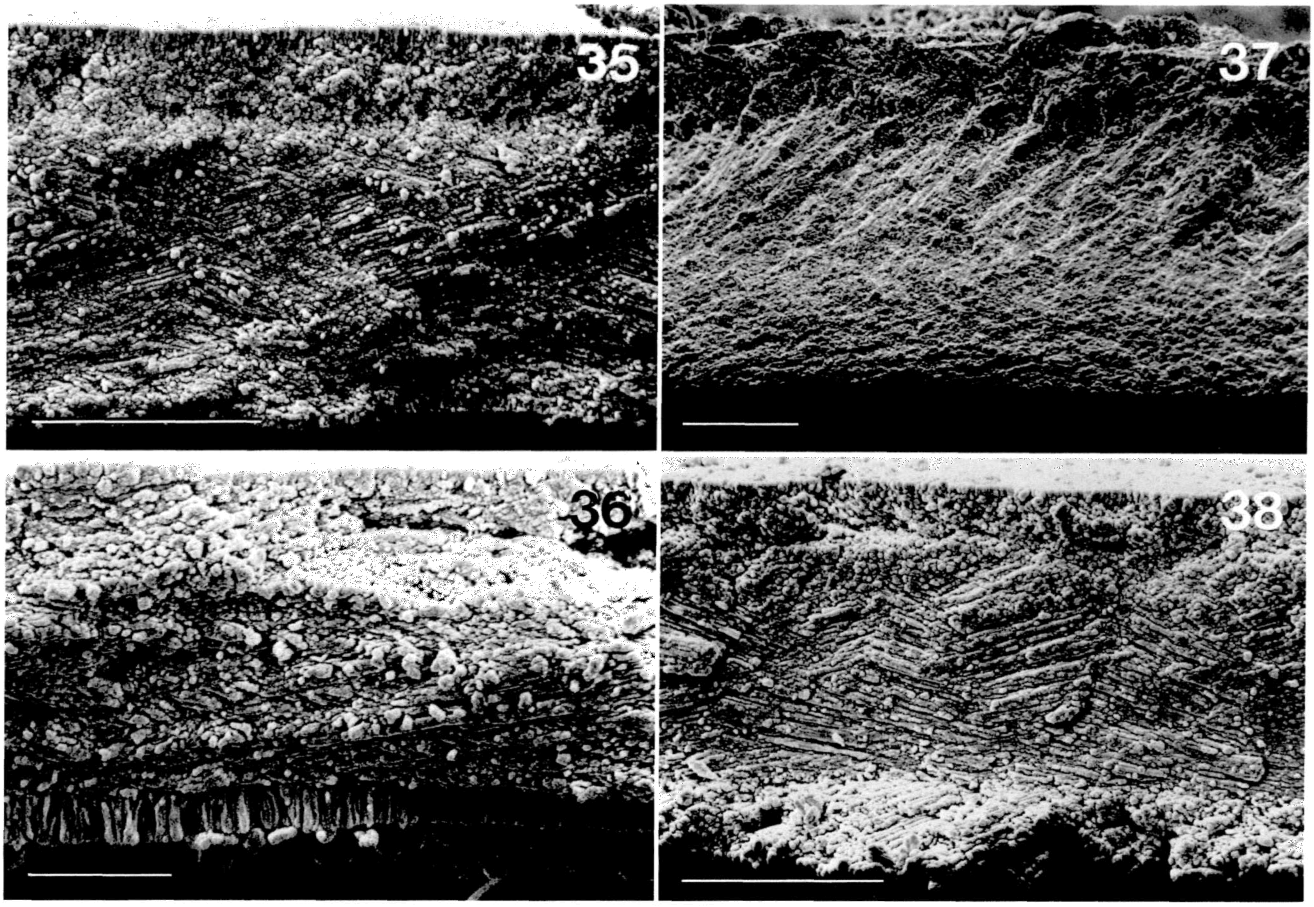

Figures 35–38. Comparison of shell ultrastructure. Exterior surface at top. SEM views taken on central slope of valves. **35.** *Vasconiella jeffreysiana*, SMNH uncataloged, scale bar = 20 μm. **36.** *Divariscintilla maoria*, NMNZ M.21965, scale bar = 10 μm. **37.** *Tryphomyax mexicanus*, LACM 69-22.3, scale bar = 20 μm. **38.** *Bellascintilla parmaleeana* new species, LACM 72-54 (from same lot as holotype), scale bar = 20 μm.

109°48′W) to Isla Salango, Manabi Province, Ecuador (01°35.5′S, 80°53.4′W).

Remarks: Known only from dead valves. This species is the smallest of the ventrally notched galeommatids. Information concerning the anatomy, reproduction, behavior and commensal association, if any, of this bivalve is not available.

Etymology: Named in honor of Dr. Paul W. Parmalee, Director of the Frank H. McClung Museum and Professor of Zooarchaeology, Emeritus, University of Tennessee, Knoxville, Tennessee, who first inspired my interest in bivalve mollusks.

DISCUSSION

The family Vasconiellidae was erected by Scarlato and Starobogatov (1979) to accommodate the ventrally notched genus *Vasconiella* Dall, 1899. Until the anatomy of more of the Galeommatidae has been studied and their relationships better understood, it seems premature to divide the Galeommatidae into subfamilies, much less additional families.

Tryphomyax shares with *Vasconiella* and *Divariscintilla* the tuberculiform cardinal teeth. However, the shell ultrastructures of these three genera exhibit major differences. Although the shell ultrastructure of *Galeomma* Turton, 1825, is unknown, the shell of *Tryphomyax* has a basic morphology suggesting affinity with *Galeomma*.

The presence of a ventral notch in the shell margin is the single shell character that genera *Vasconiella*, *Divariscintilla*, *Tryphomyax*, and *Bellascintilla* share in common. What is the purpose of the ventral notch, and does it serve the same function in all four genera? Powell (1932) believed the ventral notch to be "a true ventral byssus-sinus"; however, recent workers have demonstrated no correlation between the ventral notch and the byssus. Cornet (1982) showed that the outer and middle mantle of the right side, adjacent to the ventrally notched right valve of *Vasconiella*, formed a deep indentation whereas the inner mantle fold was straight. In *Divariscintilla* however, Judd (1971) reported that the mantle beneath the "slit" (ventral notch) was not "incised." As the structure of the mantle beneath the notch differs in these two genera, a functional similarity is regarded as unlikely. Judd (1971) demonstrated that the placement of the byssus on the foot of *Divariscintilla* was not anatomically correlated with the location of the ventral notch. He further reported that the ventral notch was completely absent from juveniles less than 2–3 mm in length, and did not develop until the shell was 3.5–4.5 mm. Cox (1969) stated that the byssus of early postlarval stages of many bivalves serves as an anchor and prevents larvae from suffocating by suspending the juveniles above the level of sediment deposition. Most bivalves lack a byssus, or it is vestigial, in the adult stage. The development of the ventral notch in *Divariscintilla* late in its life cycle may be taken as indirect evidence against the ventral notch functioning to accommodate the byssus. Other galeommatids that lack the ventral notch possess either a byssus or a byssal gland in the foot such as reported in *Phlyctaenachlamys* by Popham (1939). The function of the ventral notch in the four genera treated here remains unresolved.

Tryphomyax has the thickest shell (maximum thickness observed 59 μm), and is composed of only a single layer, which is structurally different from that of the other three ventrally notched galeommatids. *Bellascintilla* has a thinner shell (maximum thickness observed 37 μm), composed of four layers. The shell ultrastructure of *Vasconiella* is remarkably similar to that of *Bellascintilla*, but is thinner (maximum thickness observed 34 μm), and has an additional structural layer. Thus, *Vasconiella* has the most complex shell ultrastructure of the ventrally notched galeommatids studied to date. *Divariscintilla* has the thinnest shell of this group of galeommatids (maximum observed thickness 25 μm), composed of three layers that are unlike the ultrastructures of the other ventrally notched galeommatid genera. None of these genera conform to the shell ultrastructure reported by Taylor, Kennedy, and Hall (1973) for two species of *Scintilla* in terms of numbers of shell layers, or their composition. In contrast, they report finding two layers, an outer layer composed of crossed lamellar structure and an inner layer of complex crossed lamellar structure in *S. oweni* Deshayes and *S. rosea* Deshayes (Taylor *et al.*, 1973). Further investigation into the comparative shell ultrastructure of galeommataceans is warranted, both to provide characters for phylogenetic analysis as well as to examine possible variation within and between populations and environments.

In addition to a strong similarity in shell ultrastructure, *Vasconiella* and *Bellascintilla* show similarity in the formation of the mid-valve ridge, which in both genera exhibits two radiating ribs fused together with a suture between them. Prior to this study, *Vasconiella*, *Divariscintilla* and *Tryphomyax* were reported to have a single mid-valve radiating sulcus (Fischer, 1873; Olsson, 1961; Powell, 1932). Based on shell ultrastructure and the formation of the fused mid-valve ridges, *Bellascintilla* appears to be more closely related to *Vasconiella* than to either *Tryphomyax* or *Divariscintilla*, despite the differences of shell shape, hinge teeth, and zoogeography.

The hinge of *Bellascintilla* has some features in common with the family Leptonidae Gray, 1847 (*e.g.*, cuneiform cardinal teeth), and could conceivably be a primitive member of either family. It is therefore with some misgivings that I place *Bellascintilla* in the Galeommatidae. A clearer understanding of systematic relationships within the Galeommatacea will result when more information concerning the anatomy and shell ultrastructure of many of the genera becomes available. Because the definitions of the families in the Galeommatacea are not yet clarified (Ponder, 1971; Bernard, 1975), and in part because the anatomy and biology of *Bellascintilla* and *Tryphomyax* are unknown, the relationships of these four genera are subject to change as additional data becomes available.

I recognize a single species of *Divariscintilla*, the type species *D. maoria*. The two species described as *Divariscintilla yoyo* and *D. troglodytes* by Mikkelsen and Bieler (1989) are reassigned here to the genus *Phlyctaenachlamys* Popham, 1939. They share with *P. lysiosquillina* Popham, 1939, the type species of *Phlyctaenachlamys*, major conchological characters, including the unnotched ventral shell margin, hinge teeth and ligament morphology, shell ultrastructure, and anatomical characters including an internal shell, mantle morphology, and ctenidial morphology (see Mikkelsen & Bieler, 1989; Popham, 1939). As in *Phlyctaenachlamys lysiosquillina*, *P. yoyo* and *P. troglodytes* have shells that are equivalve, inequilateral, oval, flattened, and roundly elongate anteriorly. The hinge teeth and ligament are remarkably similar between the three species of *Phlyctaenachlamys*, but are quite different than those of *Divariscintilla maoria* Powell and *Bellascintilla parmaleeana*. The shell ultrastructure of *Phlyctaenachlamys lysiosquillina* is unknown. Mikkelsen and Bieler (1989) illustrate and describe the shell ultrastructure of *P. yoyo* and *P. troglodytes* as "cross-lamellar, with thin homogeneous layer on either side". This is somewhat similar to the ultrastructural arrangement of *Vasconiella* and of *Bellascintilla*, but is very different from the ultrastructural arrangement of *Divariscintilla*, and even more so from that of *Tryphomyax*. The shell of *Phlyctaenachlamys lysiosquillina* is internal (Popham, 1939), as it is in *P. yoyo* and *P. troglodytes* (Mikkelsen and Bieler, 1989). Only the anterior and posterio-dorsal margins of *Divariscintilla maoria* are covered by the mantle (Judd, 1971). The number and placement of mantle tentacles and defensive appendages is strongly similar between *P. lysiosquillina* and those of *P. yoyo* and *P. troglodytes* (see Mikkelsen & Bieler, 1989; Popham, 1939). There are two primary anterior tentacles in *P. lysiosquillina*, *P. yoyo* and *P. troglodytes* as illustrated by Popham (1939) and by Mikkelsen and Bieler (1989), although *P. troglodytes* has a second set of short anterior tentacles. *Divariscintilla maoria* has 6 to 8 large defensive appendages (Mikkelsen & Bieler, 1989) or posterior appendages (Popham, 1939), which are absent from *P. lysiosquillina*, *P. yoyo* and *P. troglodytes*. The ctenidia, usually an important source of phylogenetic information, are smooth in *Divariscintilla maoria*, but pleated in *P. lysiosquillina* (Popham, 1939) and in *P. yoyo* and *P.*

troglodytes (Mikkelsen & Bieler, 1989). The unusual "flower-like" organ of *Divariscintilla maoria* and those discovered in *P. yoyo* and *P. troglodytes* by Mikkelsen and Bieler (1989), were not reported by Popham (1939). Whether these "flower-like" organs were overlooked in *P. lysiosquillina*, or simply do not exist in this species, is unknown.

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LITERATURE CITED

Aartsen, J. J. van. 1975. Nogmaals *Vasconiella jeffreysiana* (P. Fischer) (uit Bretagne, Algeciras en Algerije). Correspondentie Blad Nederlandse Malacologische Vereniging 167:466–467.

Aartsen, J. J. van. 1982. European marine Mollusca: notes on less well-known species IV. *Vasconiella jeffreysiana* (P. Fischer, 1873). Basteria 46:125–126.

Bernard, F. R. 1975. *Rhamphidonta* gen. n. from Northeastern Pacific (Bivalvia, Leptonacea). Journal de Conchyliologie 112:105–115.

Bernard, F. R. 1983. Catalogue of the living Bivalvia of the Eastern Pacific Ocean: Bering Strait to Cape Horn. Canadian Special Publication of Fisheries and Aquatic Sciences 61:1–102.

Berry, S. S. 1959. Notices of New Eastern Pacific Mollusca—III. Leaflets in Malacology 1(18):107–114.

Bouchet, P., F. Danrigal, and C. Huyghens. 1978. Coquillages des Cotes atlantiques et de la Manche. Editons du Pacifique, Paris, 144 p.

Bruggeman-Nannenga, M. A. 1975. A northern extension of the known distribution of the bivalve *Vasconiella jeffresiana* (P. Fischer, 1873) (Galeomatidae) [sic]. Basteria 39: 14.

Carter, J. G. and G. R. Clark. 1985. Classification and phylogenetic significance of molluscan shell microstructure. *In:* Bottjer, D. J., C. S. Hickman, and P. D. Ward (eds.). Mollusks: notes for a short course. University of Tennessee, Studies in Geology 13, p. 50–71.

Chavan, A. 1969. Superfamily Leptonacea Gray, 1847. *In:* Moore, R. C. (ed.). Treatise on invertebrate paleontology. Part N. Mollusca 6. Bivalvia 2. Geological Society of America (Boulder, Colorado) & University of Kansas (Lawrence), p. 518–537.

Cornet, M. 1982. Anatomical description of *Vasconiella jeffreysiana* (P. Fischer, 1873) (Mollusca, Bivalvia, Leptonacea). Journal of Molluscan Studies 48:36–43.

Cox, L. R. 1969. General features of Bivalvia. *In:* Moore, R. C. (ed.) Treatise on invertebrate paleontology. Part N. Mollusca 6. Bivalvia 1. Geological Society of America (Boulder, Colorado) & University of Kansas (Lawrence), p. 2–129.

Dall, W. H. 1899. Synopsis of the Recent and Tertiary Leptonacea of North America and the West Indies. Proceedings of the United States National Museum 21:873–897, 2 pls.

Dekker, N. 1975. Nogmaals *Vasconiella jeffreysiana* (P. Fischer). Correspondentie Blad Nederlandse Malacologische Verniging 167:466.

Fischer, P. 1873. *In:* de Folin, L. Exploration de la fosse de Cap-Breton en 1872. Les Fonds de la Mer 2:65–84.

Fischer, P. 1874. Faune conchyliologique marine du departement de la Gironde et de cotes du Sud-Ouest de la France. Deuxieme supplement. Actes de la Societe Linneenne de Bordeaux 29:193–255.

Fischer, P. 1878. Essai sur la distribution geographique des Brachiopodes et des Mollusques du littoral oceanique de la France. Actes de la Societe Linneenne de Bordeaux 32: 171–215.

Fischer, P. 1887. Manuel de Conchyliologie et de Paleontologie conchyliologique. F. Savy, Paris, 1369 p., 23 pls.

de Folin, L. and L. Perier. 1878. Notice sur Les Fonds de la Mer. Memoires de la Societe des Sciences Physiques et Naturelles de Bordeaux 2:323–357.

Franc, A. 1960. Classe des Bivalves. *In:* Grasse, P. P. (ed.). Traite de Zoologie 5:1845–2133.

Hertz, C. M. 1984. Illustration of the types named by S. Stillman Berry in his "Leaflets in Malacology". The Festivus 15, Supplement:1–42.

Hildalgo, J. G. 1917. Fauna malacologica de Espana, Portugal y las Baleares. Moluscos testaceos marinos. Madrid, Trabajos del Museo National de Ciencias Naturales Serie Zoologica 30:1–752.

Judd, W. 1971. The structure and habits of *Divariscintilla maoria* Powell (Bivalvia: Galeommatidae). Proceedings of the Malacological Society of London 39:343–354.

Keen, A. M. 1971. Sea Shells of Tropical West America. (Second Ed.) Stanford University Press, Stanford, CA xiv + 1064 p.

Kisch, B. S. 1958. *Vasconiella jeffreysiana* (P. Fischer). Proceedings of the Malacological Society of London 33(1):21–24.

Mienis, H. K. 1975. *Vasconiella jeffreysiana* (P. Fischer) in de Golf van Biskaje. Correspondentie Blad Nederlandse Malacologische Vereniging 166:441.

Mienis, H.K. 1976. *Vasconiella jeffreysiana* (P. Fischer) ook van Quiberon. Correspondentie Blad Nederlandse Malacologische Vereniging 169:522.

Mikkelsen, P. M. and R. Bieler. 1989. Biology and comparative anatomy of *Divariscintilla yoyo* and *D. troglodytes*, two new species of Galeommatidae (Bivalvia) from stomatopod burrows in eastern Florida. Malacologia 31(1): 175–195.

Montero Aguera, I. 1971. Moluscos bivalvos espanoles. Publicaciones de la Universidad de Sevilla 5:1–358.

Morton, B. 1975. Dymantic display in Galeomma polita Deshayes (Bivalvia: Leptonacea). Journal of Conchology 28: 365–369.

Morton, B. 1976. Secondary brooding of temporary dwarf males in *Ephippodonta* (*Ephippodontina*) *oedipus* sp. nov. (Bivalvia: Leptonacea). Journal of Conchology 29:31–39.

Nordsieck, F. 1969. Die europaischen Meeresmuscheln (Bivalvia). Vom Eismeer bis Kapverden, Mittelmeer und Schwarzes Meer, Stuttgart.

Olsson, A. A. 1961. Mollusks of the tropical eastern Pacific, particularly from the southern half of the Panamic-Pacific faunal province (Panama to Peru): Panamic-Pacific Pelecypoda. Paleontological Research Institution, Ithaca, NY, 574 p., 86 pls.

Pasteur-Humbert, C. 1962. Les Mollusques marins testaces du Maroc. II Les Lamellibranches et les Scaphopodes. Travaux de l'Institut Scientifique Cherifien, Serie Zoologie 28: 1–184.

Ponder, W. F. 1971. Some New Zealand and Subantarctic bivalves of the Cyamiacea and Leptonacea with description of new taxa. Records of the Dominion Museum 7: 119–141.

Popham, M. L. 1939. On *Phlyctaenachlamys lysiosquillina* gen. and sp. nov., a lamellibranch commensal in the burrows of *Lysiosquilla maculata*. British Museum (Natural History), Great Barrier Reef Expedition 1928–29, Scientific Reports 6(2):61–84.

Powell, A. B. W. 1932. On some New Zealand pelecypods. Proceedings of the Malacological Society of London 20: 65–72, pl. 6.

Powell, A. B. W. 1962. Shells of New Zealand: an illustrated handbook, 4th ed. Whitcombe and Tombs Ltd., Christchurch, 203 p., 35 pls.

Powell, A. B. W. 1976. Shells of New Zealand: an illustrated handbook, 5th ed. Whitcoulls Publishers, Christchurch, 154 p., 45 pls.

Scarlato, O. A. and Y. I. Starobogatov. 1979. General evolutionary patterns and the system of the class Bivalvia. Proceedings of the Zoological Institute of the Academy of Sciences of the USSR 80:5–38.

Taylor, J. D., W. J. Kennedy, and A. Hall. 1973. The shell structure and mineralogy of the Bivalvia: II. Lucinacea—Clavagellacea conclusions. Bulletin of the British Museum (Natural History) 22(9):253–294, 15 pls.

Verduin, A. 1975. *Vasconiella jeffreysiana* (P. Fischer) ook van Agadir. Correspondentie Blad Nederlandse Malacologische Vereniging 166:422.

Warén, A. 1980. Marine Mollusca described by John Gwyn Jeffreys, with the location of the type material. Conchological Society of Great Britain and Ireland, Special Publication 1:1–60.