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Fossil Cenozoic crassatelline bivalves from Peru: New species and generic insights

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Discoveries of new fossil Cenozoic crassatellines in Peru provide a new phylogenetic perspective on "large" Neogene genera, in which four lineages are considered to have arisen independently from different Paleogene *Crassatella* ancestors. Latest Oligocene and early Miocene species of the new genus *Tilicrassatella* gen. nov.—*T. ponderosa*, *T. torrens* sp. nov., and *T. sanmartini* sp. nov. from the East Pisco Basin—probably evolved from the late Eocene species, *Crassatella rafaeli* sp. nov., which itself differed in significant respects from slightly older species of the East Pisco Basin, *C. neorhynchus* and *C. pedroi* sp. nov. The paciphilic genus, *Hybolophus*, is raised to full generic status. Added to its ranks are the East Pisco Miocene species *H. maleficae* sp. nov., *H. terrestris* sp. nov., and the oldest species of the genus, the late Eocene or Oligocene *H. disenum* sp. nov. from the Talara Basin of northern Peru. *Kalolophus* gen. nov., encompassing circum-Caribbean fossil species, the extant species, *K. speciosus*, and the trans-isthmus species, *K. antillarum*, appears to have evolved from the early Oligocene Floridian species, *Crassatella portelli* sp. nov. The genus *Marvacrassatella* is a western Atlantic Miocene lineage most likely descended from *Kalolophus*. The genus *Eucrassatella* is restricted to Australian and New Zealand taxa. The Eocene New Zealand species, *Spissatella media*, is transferred to *Eucrassatella* and deemed a candidate for the most recent common ancestor of younger *Eucrassatella* and all *Spissatella* species. In the southern Pacific Ocean, the circum-Caribbean region, and tropical western America, crassatelline lineages developed one or more of the following characters: large resilifers, smooth ventral margins, and an extended left anterior cardinal tooth. Some of these late Paleogene convergent character changes might have countered increased shear forces exerted on the crassatelline valves while burrowing into finer-grained and more cohesive sediments in deeper or quieter water.

Key words: Bivalvia, Crassatellidae, evolution, Florida, New Zealand, Peru.

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Introduction

The bivalve subfamily Crassatellinae Férussac, 1822, is represented on the west coast of South America by two living species, *Eucrassatella gibbosa* (Sowerby, 1832) and *E. antillarum* (Reeve, 1842), and up until now, one Eocene species (Olsson 1931); Miocene, Pliocene, and Pleistocene species in northern Peru and Ecuador (Spieker 1922; Olsson 1932; Marks 1951; DeVries 1986); and one early Miocene species in Chile (Philippi 1887). Discoveries of new fossil species in Peru provide an opportunity to re-examine systematic relationships among American crassatellines and between American and Australian/New Zealand crassatellines.

Institutional abbreviations.—INGEMMET, Instituto Geológico, Minero y Metalúrgico, Lima, Peru; MUSM INV, invertebrate collection, Departamento de Paleontología de Vertebrados, Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima, Peru; OSU, Orton Museum of Natural History, Ohio State University, Columbus, USA; PRI, Paleontological Research Institution, Ithaca, USA; SBMNH, Santa Barbara Museum of Natural History, Santa Barbara, USA; SGO.PI., Philippi collection, Museo de Historia Natural, Santiago, Chile; UF, Florida Museum of Natural History, Gainesville, USA; USGS, United States Geological Survey, Reston, USA; USNM, Smithsonian National Museum of Natural History, Washington D.C., USA; UWBM, Burke Museum of Natural History and Culture, Seattle, USA.

Other abbreviations.—H, height (measured at right angles to the length); L, length (measured parallel to a line passing through the midpoints of the two adductor muscles); T, thickness (single valve: measured from the plane of commissure to the point of maximum inflation); vmHP, ventral margin of the hinge plate.

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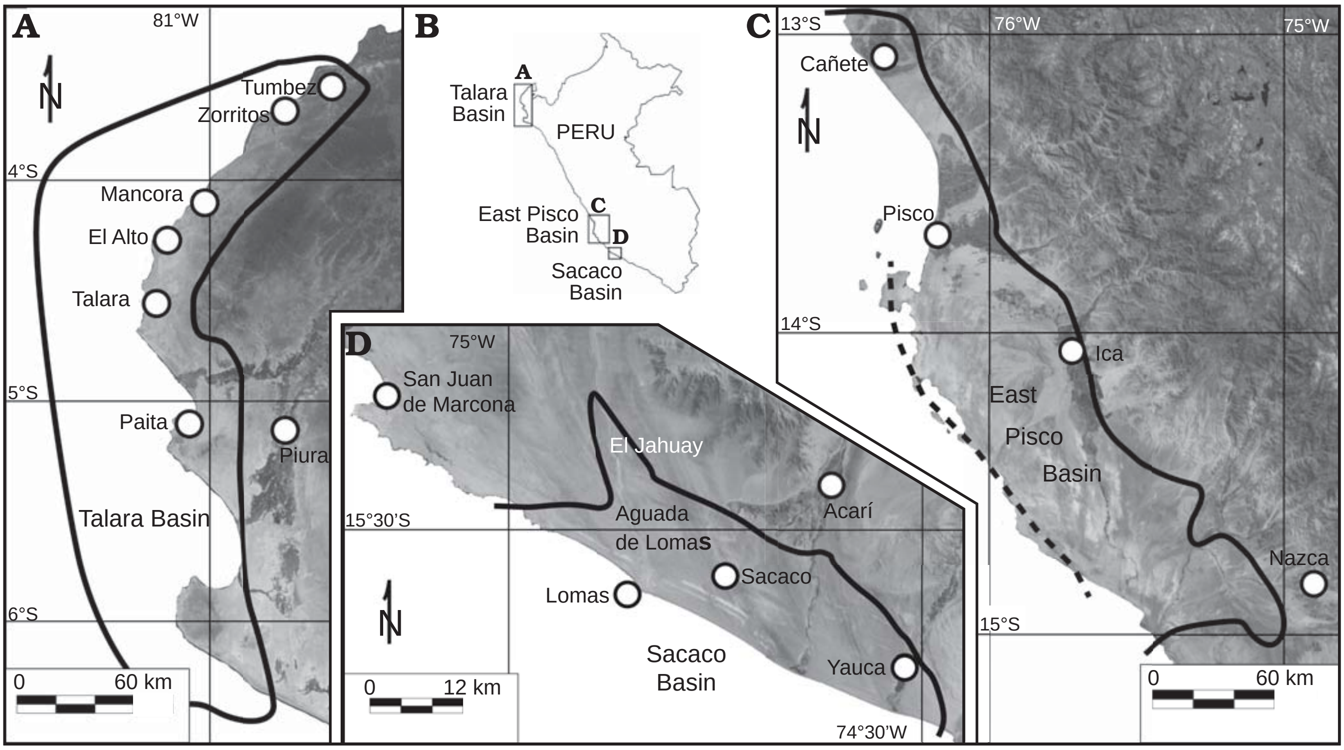

Fig. 1. Forearc basins in Peru with crassatelline-bearing Cenozoic deposits. **A**. Talara Basin of northern Peru. **B**. Location of three crassatelline-bearing Peruvian forearc basins. **C**. East Pisco Basin of south-central Peru. Dashed black line marks the inferred boundary between the East and West Pisco basins. **D**. The much smaller Sacaco Basin of southern Peru.

Geological setting

The East Pisco Basin, source of most of the new crassatelline material, stretches 350 km along the desert coast of south-central Peru (Fig. 1B, C). Nearshore and outer shelf sands were deposited in this forearc basin from the middle Eocene through the Pliocene (DeVries 1998). The fossil record of the East Pisco Basin is notable for its cetaceans and penguins, but mollusks are also present (Lisson 1925; Rivera 1957). Forty km south lies the Sacaco Basin, extending 50 km from El Jahuay to Yauca (Fig. 1B, D), where upper Miocene and Pliocene nearshore marine strata contain a diverse assemblage of marine vertebrates and mollusks (Muizon and DeVries 1985), including one crassatelline species.

The Talara Basin of northern Peru (Fig. 1A, B), source of additional crassatelline material, is best known for its fossil mollusks (Olsson 1931, 1932). Many thousands of meters of turbiditic, neritic, deltaic, and fluvial sediments accumulated from the Paleocene through the Pliocene (Higley 2004). Lower and middle Pleistocene marine terrace deposits now cover much of the older outcrop (DeVries 1988).

The Cenozoic stratigraphy for the East Pisco Basin has been described by DeVries (1998) and for the Sacaco Basin by Muizon and DeVries (1985). Ages are based on the occurrence of diatoms and radiolarians and K-Ar and ^{40}Ar-^{39}Ar radiometric dates from volcanic ash beds. Stratigraphic correlations across the basin are based on the author's fieldwork. Ages and stratigraphy for the Talara Basin are based on Higley (2004) and Martinez et al. (2005) and, for the Pliocene and Pleistocene, DeVries (1986, 1988). Period and stage boundaries are taken from the ICS International Chronostratigraphic Chart, version 2015/01. Stages are cited when absolute ages can be estimated. Depositional sequence names for the East Pisco Basin (Paracas, Lutetian to Bartonian; Otuma, Priabonian; Chilcatay, Chattian to Langhian; Pisco, Serravallian to Zanclean; see DeVries 1998) are used instead of the eponymous formation names.

Material and methods

Most of the new fossil crassatellines from Peru were found by the author. Comparative material was made available by the USNM, USGS, UF, PRI, UWBM, SBMNH, Museo de Historia Natural (Santiago, Chile), GNS Science (Lower Hutt, New Zealand), Department of Earth Sciences, University of California (Riverside, USA), and International Fossil Shell Museum (Utrecht, The Netherlands). Most figured specimens were coated with ammonium chloride before being photographed. Types and figured specimens of crassatellines are deposited in the UWBM and the Departamento de Paleontología de Vertebrados, Museo de Historia Natural, Lima, Peru.

Dimensional measurements (in mm) enclosed within parentheses apply to broken specimens. Locality-sample numbers of the author begin with "DV" (e.g., "DV 509-1").

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Most locality-samples also carry a locality number for the UWBM (e.g., "B8315"). Full locality-sample descriptions are listed in Appendix 1.

Hinge characters have been used to distinguish crassatellines at the generic level since Lamy (1917). A lack of agreement about such basic metrics as the number of cardinal teeth and presence or absence of lateral teeth has been an impediment to understanding crassatelline taxonomy. The scheme for naming hinge characters employed here is strictly descriptive and keyed to images (Fig. 2).

Terminology for lateral hinge structures has often been contradictory (Darragh 1965; Chavan 1969; Coan 1984; Wingard 1993). The left valve exhibits a thickening of the lunule margin distal to the beak and a thickening of the posterior ventral margin of the hinge plate (vmHP). The right valve exhibits a thickening of both the anterior vmHP and the distal end of the escutcheon margin. These "lateral ridges" (Wingard 1993) are variably developed and not used here for classification.

The left valve of crassatellines has two cardinal teeth. The posterior margin of the ligamental pit is sometimes thickened beyond the edge of the escutcheon in the left valve, creating a third ridge that has been termed the posterior cardinal tooth by Collins (2013). Most often, the ridge is entirely coalescent with the margin of the escutcheon or obsolete. The right valve has one cardinal tooth, but does have an anterior ridge on the hinge plate that can (i) join the dorsal ends of the cardinal tooth and lunule margin (Fig. $2C_2$), (ii) diverge anterioventrally from the lunule margin, or (iii) extend parallel to and even coalesce with the lunule margin (Fig. 2B, D_2). The right valve also has a lamellar posterior ridge that can diverge posterioventrally from the midpoint of the cardinal tooth at (i) a large angle, passing the resilifer ventrally to create a trigonal socket next to the vmHP (Fig. 2B), (ii) a small angle, passing the resilifer anteriorly to create a small elongate socket (Fig. $2C_2$), or (iii) emerge from beneath the beak and diverge posterioventrally from the cardinal tooth (Fig. $2D_2$). Both ridges, which often lack corresponding sockets, are termed pseudocardinal teeth (Wingard 1993). The inclination of hinge teeth is measured from the beak with respect to the dorsoventral axis.

Following Wingard (1993), the exterior angulation extending from the beak to the posterior margin is termed the posterior ridge; one or two can exist (Fig. $2D_3$). Small teeth along the inner ventral margin are termed crenulations (Fig. 2A, B).

Results

The genus *Crassatella* Lamarck, 1799, has a tortuous nomenclatural history that commenced with a misidentified type species (Stewart 1930; Vokes 1973; Wingard 1993). *Crassatella* is accepted here, as it was by Coan (1984), in the expectation of an overdue and successful formal petition to the International Commission on Zoological Nomenclature to validate the name. The type species is *Crassatella tumida* Lamarck, 1805 for reasons enumerated by Wingard (1993). The genus *Crassatellites* Krüger, 1823 is an unavailable homonym created for fossil crassatellids (Iredale 1921; Stewart 1930; Vokes 1973).

Diagnoses of *Crassatella* typically reference two characters: (i) a resilifer that in large specimens extends only about half way from the beak to the vmHP (Fig. 2A, B), and (ii) a crenulate inner ventral margin (Fig. 2A, B; Stewart 1930; Chavan 1969; Wingard 1993). The short resilifer appears in Cretaceous and Paleogene species and incongruously in modern crassatellines from South Africa, Japan, and Brazil (e.g., the genera *Indocrassatella* Chavan, 1952, *Nipponocrassatella* Kuroda and Habe, 1971, and *Riosatella* Vokes, 1973). In some late Paleogene specimens and species of *Crassatella*, however, the resilifer extends nearly to the vmHP (Wingard 1993; this paper). The full-length resilifer is typically associated with a distinctive Cenozoic genus, *Bathytormus* Stewart, 1930, and with Neogene crassatelline genera.

The crenulate inner ventral margin is more reliable for diagnosing *Crassatella*, although crenulations appear only on the largest specimens of some species (Wingard 1993; this paper). Rarely, *Crassatella*-style ventral crenulations incongruously occur together with a full-length resilifer, e.g., an Eocene species from New Zealand (Collins 2013) and an early Miocene species from Chile (Philippi 1887). (Note: a third example, the Californian Pleistocene species, *Eucrassatella lomitensis* [Oldroyd, 1924], is incorrectly described. The species in fact lacks ventral crenulations, both on the holotype [Coan 1984; Nigel Hughes, personal communication 2015] and on specimens examined by the author; see Fig. 2E).

The genus *Eucrassatella* was proposed by Iredale (1924) to replace Lamarck's (1799) *Mactra*-based *Crassatella* and Krüger's (1823) fossil genus, *Crassatellites*. The Recent Australian species, *Crassatella kingicola* Lamarck, 1805 (Fig. 2C), was designated the type species. Having incorrectly inferred that Iredale (1924) restricted *Eucrassatella* only to large living Australian species, Stewart (1930) proposed that the genus should also encompass tropical American taxa and set forth two diagnostic characters for the genus: a resilifer extending to or nearly to the vmHP and a smooth inner ventral margin.

Complicating the assignation of *Eucrassatella* to American taxa is a diagnostic character overlooked by all except Vokes (1973): the dorsal truncation of the left anterior cardinal tooth by the lunule. For most species of Cretaceous and Paleogene *Crassatella* and fossil and modern *Eucrassatella* from Australia and New Zealand (and some species of the genus *Spissatella* Finlay, 1926), the dorsal end of the lunule separates the left anterior cardinal tooth from the beak. In contrast, for most American species assigned to *Eucrassatella* (as well as a few species of southwestern Pacific *Spissatella*), the left anterior cardinal tooth extends from the vmHP to the beak with little or no separation by the lunule (compare Fig. $2C_1$ and $2D_1$).

Stewart (1930) noted the flattened umbo of American crassatelline species, contrasting it with the rounded umbo on a

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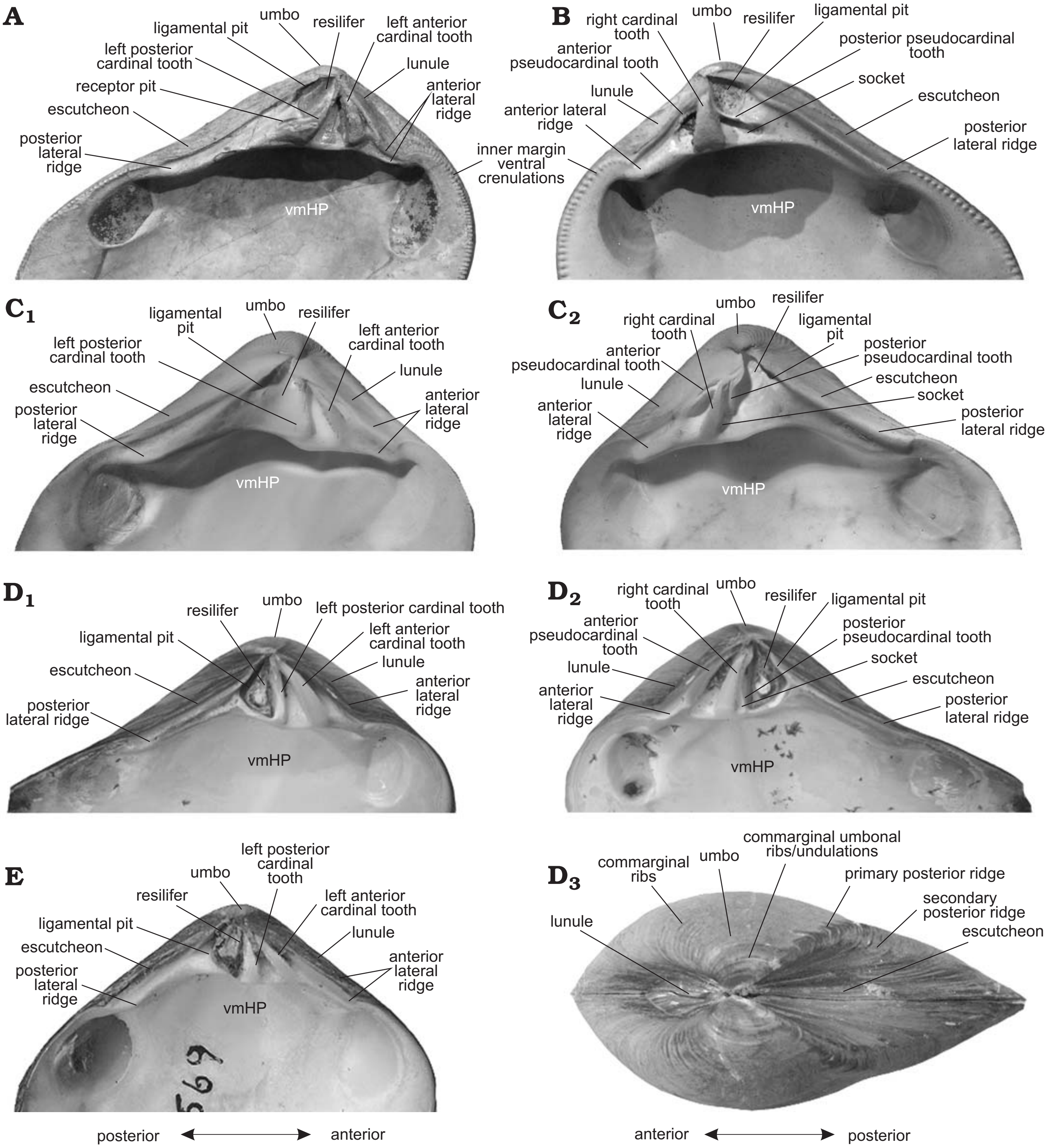

Fig. 2. Hinge characters and other features of crassatellines. **A**, **B**. *Crassatella vadosa* Morton, 1834, Cretaceous. **A**. USNM 450460, Mississippi, USA. **B**. USNM 451089, Alabama, USA. **C**. *Eucrassatella kingicola* (Lamarck, 1805), UWBM 101886, Recent, Victoria, Australia. **D**. *Hybolophus gibbosus* (Sowerby, 1832), SBMNH 213002, Recent, Gulf of California, Mexico. **E**. *Hybolophus fluctuatus* (Carpenter, 1864), SBMNH 137784, Recent, Santa Catalina Island, California. Left valves (A, C_1, D_1, E), right valves (B, C_2, D_2), valve in dorsal view (D_3). Abbreviation: vmHP, ventral margin of the hinge plate.

preponderance of Australian and New Zealand species (compare Fig. 2C and 2D). Rarely, specimens of the Australian *Eucrassatella kingicola* have a flattened umbo, but contrary to Stewart's (1930) inference based on a single specimen, most do not. A flattened umbo is therefore more diagnostic of American crassatellines than credited by Stewart (1930).

Having rejected the diagnostic value of a flattened umbo, Stewart (1930) turned to the tilt of the umbo (prosogyrate,

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orthogyrate, opisthogyrate). Assertions about the flattened umbo's tilt are often confused with assertions about the direction that the beaks point (Stewart 1930; Darragh 1965; Coan 1984). The two orientations need not be the same. *Eucrassatella* species from Australia and New Zealand, for example, have orthogyrate umbones but the beaks may be prosogyrate (*E. kingicola*) or orthogyrate (*E. pulchra* [Reeve, 1842]).

Stewart (1930) called attention to the strongly opisthogyrate flattened umbo of the modern American species, *Eucrassatella gibbosa* (Sowerby, 1832) (Fig. 2D), and designated it the type species of a new subgenus, *Hybolophus*, to which he also assigned the species *E. antillarum* (Reeve, 1842) (Fig. 3A, B), with a less opisthogyrate umbo, and a rumored Peruvian Miocene species, likely Spieker's (1922) account of *E. nelsoni* (Grzybowski, 1899). Oddly, Stewart (1930) also implied that fossil American *Eucrassatella* lacked opisthogyrate umbones, a claim belied by the existence of the Miocene species *E. berryi* (Spieker, 1922) and *E. elassa* Woodring, 1982 (Fig. 3C, D).

Olsson (1932) proposed that *Eucrassatella* (*Hybolophus*) include Miocene species of *Eucrassatella* similar to *E. gibbosa*. Darragh (1965) added to *E.* (*Hybolophus*) any American Neogene species with an orthogyrate umbo, e.g., *E. antillarum* and allied species. Woodring (1982) divided *E.* (*Hybolophus*) into an "elongate" group, represented by *E. gibbosa* with its strongly opisthogyrate umbo, and a "high" group, represented by *E. antillarum* with its weakly opisthogyrate or orthogyrate umbo. Species of the "gibbosa" group are strongly inflated ventral to the umbo with the inflation diminishing rapidly anteriorly and steadily posteriorly. Species of the "antillarum" group are only modestly inflated ventral to the umbo and hardly less so posteriorly as far as the posterior ridge.

Eucrassatella mediamericana (Brown and Pilsbry, 1913), an early Miocene (Kirby et al. 2008) species from the La Boca Formation of Panama, was retained by Woodring (1982) in *Eucrassatella* sensu stricto. Inspection of Woodring's (1982) specimens of *E. mediamericana* (Fig. 3E), as well as specimens of early Miocene (Bryant et al. 1992) *E. chipolana* (Dall, 1903) from the Chipola Formation of Florida, middle Miocene (Huddlestun 1984) *E. densa* (Dall, 1900) from the Shoal River Formation of Florida, a late Miocene unnamed crassatelline from the Gatun Formation of Panama (Woodring 1982) (Fig. 3F), Pliocene (Donovan 1998) *E. jamaicensis* (Dall, 1903) from the Bowden Formation of Jamaica (Fig. 3G), and examination of high-resolution photographs of the early Pleistocene (McGregor 2011) *E. mansfieldi* MacNeil, 1936 from the Waccamaw Formation of South and North Carolina shows that all share external and internal characters with the modern species, *E. speciosa* (Adams, 1854) (Fig. 3H). Specimens of *E. speciosa* differ from those of *E. antillarum* principally in this regard: the external sculpture of the latter consists of irregular commarginal growth lines, whereas the former exhibits regularly spaced commarginal ribs over much of the shell (compare Fig. $3A_1$ and $3H_1$).

A discovery in the collections of the Florida Museum of Natural History of undescribed crassatellines from the lower Oligocene (Bryan 1991) Suwannee Limestone of Florida, herein named *Crassatella portelli* sp. nov., casts new light on the classification of North American crassatellines. Suwannee specimens have the crenulate inner ventral margin and the widely divergent posterior pseudocardinal ridge typical of *Crassatella* and resilifers that extend either half-way or nearly to the vmHP but, typical of the American taxa *Eucrassatella* and *E.* (*Hybolophus*), a flattened umbo and left anterior cardinal tooth that extends nearly or entirely to the beak (Fig. 4A–D). The external characters of *C. portelli*—commarginal ribs covering most of the surface, a widely diverging and prominent posterior ridge, and a broadly truncated posterior margin—are all features of the modern *E. speciosa*.

Specimens of the younger *Eucrassatella chipolana* (Fig. 4E–H) have external features similar to those of *Crassatella portelli* and *E. speciosa*. Internally, specimens of *E. chipolana* lack a crenulate inner ventral margin; the resilifer typically extends from the beak nearly to the vmHP; and the left anterior cardinal tooth extends from the vmHP to the beak. Specimens of older ribbed crassatellines from the upper Eocene (Portell and Hulbert 2011) Ocala limestone of Alachua County, Florida (UF 18403, UF 18427, UF 18458, UF 18586), probably referable to the species *C. ocordia* Harris, 1951, have a rounded umbo, crenulate ventral margin, truncated left anterior cardinal tooth, and in most cases, a resilifer extending less than entirely to the vmHP—i.e., a typical *Crassatella* in nearly every respect.

The Ocala, Suwannee, Chipola, Gatun, and Bowden crassatellines and Recent *Eucrassatella speciosa* constitute a graded morphological series ranging from typical Paleogene *Crassatella* to the New World Neogene crassatellines of Woodring's (1982) "high" group. They stand apart morphologically from the strongly inflated "elongate" group of Woodring (1982). In accord with MacNeil's (1936: 528) prescient suggestion and Ward and Blackwelder's (1987: 151) implicit recommendation, a new genus, herein named *Kalolophus* gen. nov., is proposed for the "high" group, with *Crassatellites chipolanus* Dall, 1903 designated the type species. The paciphilic genus *Hybolophus*, comprising American species of Woodring's (1982) "elongate" group, which ranges from at least the early Oligocene (*H. disenum* sp. nov.) to the Recent (*H. gibbosus*), is elevated to full generic rank. Per Darragh's (1965) emphatic declaration, the name *Eucrassatella* is applied only to Australian and New Zealand species.

Diagnostic characters for the above-mentioned crassatelline taxa (Table 1) are the basis for generic assignments used in this paper. It should be understood that one or more specimens of a species, particularly species that are transitional between genera, can exhibit a character state contrary to that which otherwise would establish its generic placement.

Exceptions to this generic arrangement are large thick-shelled crassatellines from the lower to middle Miocene Navidad Formation of central Chile (Tavera 1979) and

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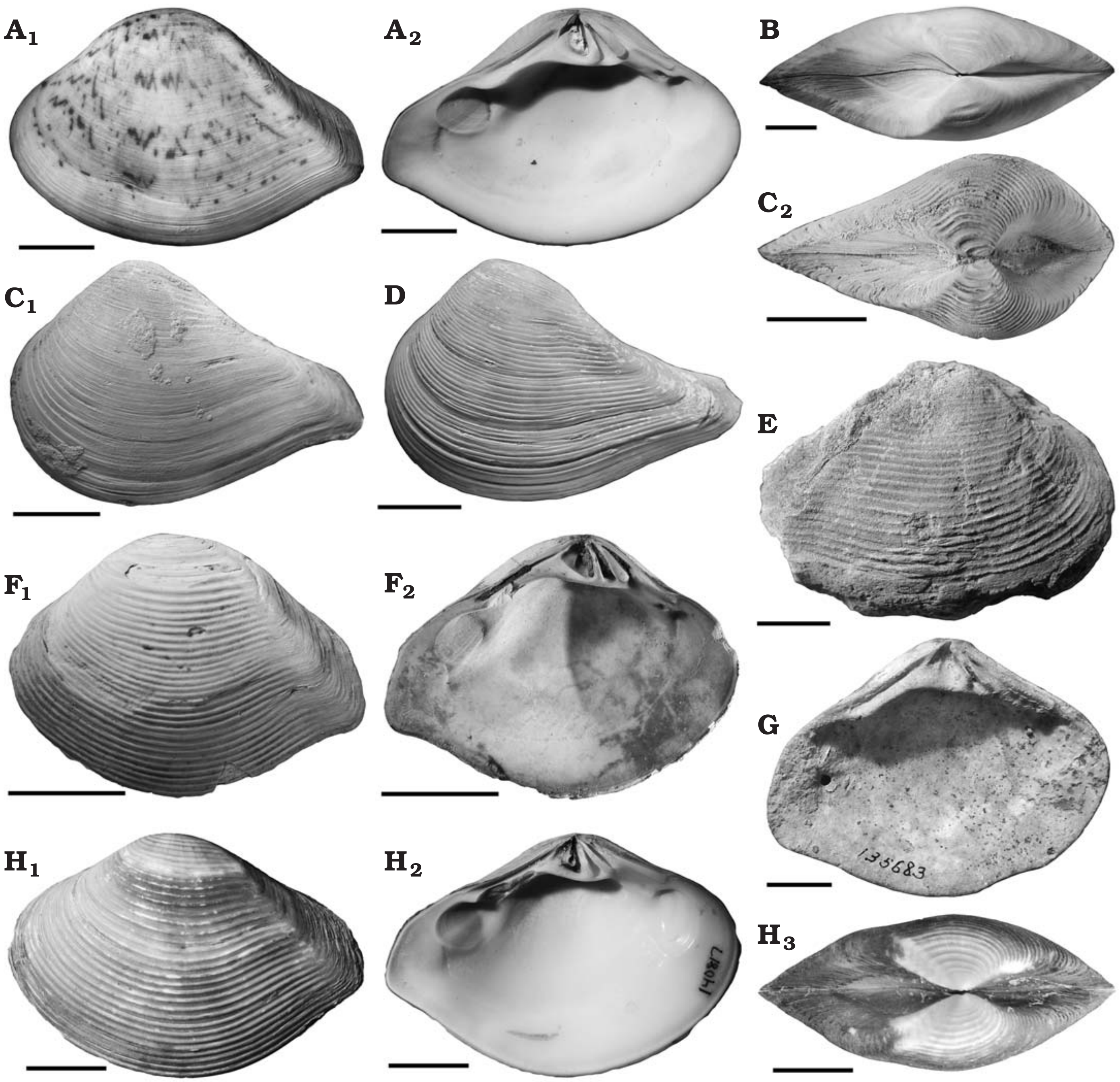

Fig. 3. Crassatelline bivalves from Central and South America. **A**, **B**. *Kalolophus antillarum* (Reeve, 1842). **A**. UWBM 101885, Recent, Pacific coast of Panama; exterior (A$_1$) and interior (A$_2$) of left valve. **B**. UWBM 101884, Recent, Venezuela; dorsal view of paired valves, anterior at right. **C**. *Hybolophus berryi* (Spieker, 1922), USNM 562399, early Miocene, lower Zorritos Formation, Zorritos, Peru; exterior of left valve (C$_1$), dorsal view of paired valves (C$_2$), anterior at right. **D**. *Hybolophus elassa* Woodring, 1982, USNM 647424, late Miocene, Gatun Formation, Panama; exterior of left valve. **E**. *Kalolophus mediamaricanus* (Brown and Pilsbry, 1913), USNM 647421, early Miocene, La Boca Formation, Panama; exterior of right valve. **F**. *Kalolophus* sp., USNM 647423, late Miocene, middle Gatun Formation, Panama; exterior (F$_1$) and interior (F$_2$) of left valve. **G**. *Kalolophus jamaicensis* (Dall, 1903), USNM 135683, Pliocene, Bowden Formation, Jamaica; interior of left valve. **H**. *Kalolophus speciosus* (Adams, 1854), SBMNH 140817, Recent, Panama City, Florida; exterior (H$_1$) and interior (H$_2$) of left valve; dorsal view of paired valves (H$_3$), anterior at right. Scale bars 10 mm.

Chattian to Langhian material from southern Peru. These specimens have a rounded and orthogyrate umbo, a resilifer that extends to the vmHP, a crenulate inner ventral margin on larger specimens, and a left anterior cardinal tooth separated from the beak by the lunule. This set of character states fits neither *Crassatella*, *Eucrassatella*, *Hybolophus*, nor *Kalolophus*. By reason of this character suite (Table 1) and associated characters described in the systematics section, a new genus is proposed for Philippi's (1887) species and two new species from southern Peru: *Tilicrassatella* gen. nov., with the type species designated as *Crassatella ponderosa* Philippi, 1887.

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Table 1. Generic characteristics of large crassatellines from Australia, New Zealand, and North and South America.

Genus and geographic distribution	Umbo	Resilifer's extent from beak across hinge plate	Inner ventral margin	Left anterior cardinal tooth to beak	Posterior inflation forward of posterior ridge
Crassatella worldwide	rounded, ortho- to prosogyrate	about half way to ventral margin	crenulate	separated by lunule	steadily diminishes
Eucrassatella Australia, New Zealand	rounded, ortho- to prosogyrate	nearly or entirely to ventral margin	not crenulate	separated by lunule	steadily diminishes
Hybolophus America	flattened, opisthogyrate	nearly or entirely to ventral margin	not crenulate	not separated by lunule	steadily diminishes
Kalolophus America	flattened, ortho- to opisthogryrate	nearly or entirely to ventral margin	not crenulate	not separated by lunule	does not steadily diminish
Tilicrassatella Peru, Chile	rounded, orthogyrate	nearly or entirely to ventral margin	variably crenulate	separated by lunule	steadily diminishes
Spissatella Australia, New Zealand	rounded, orthogyrate	nearly or entirely to ventral margin	not crenulate	may be separated or not by lunule	does not steadily diminish
Triplicitella New Zealand	rounded, orthogyrate	nearly or entirely to ventral margin	variably crenulate	separated by lunule	steadily diminishes
Marvacrassatella eastern North America	flattened, ortho- to opisthogyrate	nearly or entirely to ventral margin	not crenulate	not separated or barely so by lunule	very gently diminishes

A few American Neogene taxa, assigned tentatively to *Hybolophus*, do not fit the definitions of these five genera. The Quaternary Californian species, *H. fluctuatus*, has a widely divergent posterior ridge, a foreshortened posterior, and dorsally truncated left anterior cardinal tooth (Fig. 2E), one or more characters of which are shared with Pacific specimens of the late Eocene or early Oligocene northern Peruvian *H. disenum*, the early Miocene (Marks 1951) or early middle Miocene (Deniaud et al. 1999) Ecuadorian species, *H. carrizalensis* (Marks, 1951), the late Miocene (Landau et al. 2012) Ecuadorian species *H. picaderus* (Olsson, 1964) (Fig. 5A, B), and Caribbean specimens of the late Miocene (Bold 1966) Colombian species, *H. tuberus* (Olsson, 1964) (Fig. 5C). The phylogenetic position of these veneriform morphological outliers is addressed in the systematics and discussion sections.

Systematic palaeontology

Class Bivalvia Linnaeus, 1758

Family Crassatellidae Férussac, 1822

Subfamily Crassatellinae Férussac, 1822

Genus *Crassatella* Lamarck, 1799

Type species: *Crassatella tumida* Lamarck, 1805 (= *Venus ponderosa* Gmelin, 1791; see Wingard 1993); France, Eocene.

Crassatella portelli sp. nov.

Fig. 4A–D.

Etymology: Named in recognition of help provided by Roger W. Portell (Florida Museum of Natural History).

Type material: Holotype, complete adult left valve with hinge exposed: UF 26990A, L 38.9, H 28.5, T 9.1. Paratypes: UF 26990B, H 30.7, T 10.2; UF 27019, L 34.0, H 24.7, T 8.3; UF 32046B, L 35.9, H 27.4, T 8.3; UF 198567A, L 32.8, H 24.9, T 7.2; UF 241619, L 29.6, T 7.4; UF 243868A, L 36.3, H 27.3, T 8.3; from the type locality.

Type locality: Terramar pit 01, Socrum Quadrangle, Polk County, Florida, USA.

Type horizon: Suwannee Limestone, mining spoils, lower Oligocene.

Material.—UF 32046, additional 4 specimens; UF 198567, additional 3 specimens; UF 243868, additional 2 specimens. All specimens are from the type locality.

Diagnosis.—Shell trapezoidal, not inflated. Resilifer extending half the distance or more to vmHP. Umbo flattened. Left anterior cardinal tooth extending to or nearly to beak. Exterior with commarginal ribs. Inner ventral margin crenulate.

Description.—Shell to 40 mm long, trapezoidal, not inflated, L:H ratio 1.3, T:H ratio 0.2, maximum inflation ventral to beak. Anteriodorsal and posteriodorsal margins slightly concave; anterior margin broadly rounded, posterior margin weakly produced, broadly truncate; ventral margin evenly rounded. Strongly angular posterior ridge diverging 20–25°, secondary posterior ridge 5° from posteriodorsal margin. Lunule and escutcheon elongate, equally wide, both about 40% length of respective dorsal margins. Beak prosogyrate. Umbo flattened, slightly prosogyrate to slightly opisthogyrate, with widely spaced and pronounced commarginal ribs; remainder of exterior with closely spaced commarginal ribs; ribs weak or absent posterior to primary posterior ridge. Resilifer extending about half to full distance from beak to vmHP. Left anterior cardinal tooth narrow, wedge-shaped, inclined anteriorly 30–40°, extending to beak or nearly so. Left posterior cardinal tooth wedge-shaped, orthocline, extending to beak or nearly so. Receptor pit obsolete. Right anterior pseudocardinal tooth coalescent with lunule margin. Right cardinal tooth thick, wedge-shaped, inclined anteriorly 15–20°. Right posterior pseudocardinal tooth lamellar, diverging 30–60° from midpoint of cardinal tooth, passing resilifer ventrally. Inner ventral margin crenulate.

Remarks.—Specimens of *Crassatella portelli* exhibit characters of *Crassatella* (widely diverging right posterior

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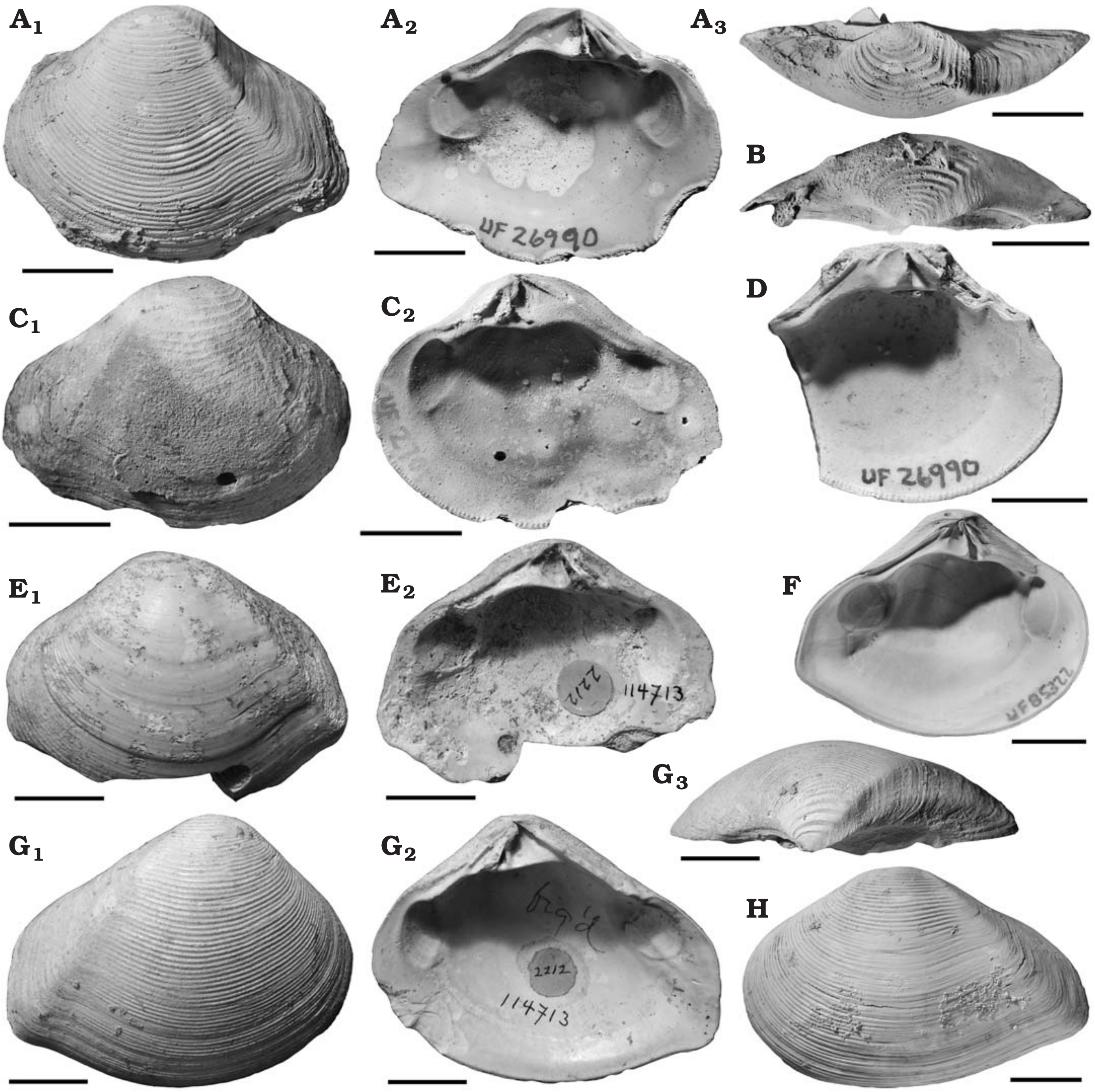

Fig. 4. Crassatelline bivalves from Florida. **A–D**. *Crassatella portelli* sp. nov., early Oligocene, Suwannee limestone. **A**. UF 26990a, holotype, exterior (A_1) and interior (A_2), and dorsal margin (A_3) of left valve. **B**. UF 32046b, paratype, dorsal margin of right valve. **C**. UF 27019, paratype, exterior (C_1) and interior (C_2) of right valve. **D**. UF 26990b, paratype, interior of left valve. **E–H**. *Kalolophus chipolanus* (Dall, 1903), early Miocene, Chipola Formation. **E**. USNM 114713c, exterior of left valve (E_1), interior (E_2). **F**. UF 85322l, interior of left valve. **G**. USNM 114713a, holotype, exterior (G_1), interior (G_2), and dorsal margin (G_3) of right valve. **H**. UF 85322f, exterior of left valve. Scale bars 10 mm.

pseudocardinal ridge, resilifer in some specimens not extending close to the vmHP, crenulate inner ventral margin) and *Kalolophus* and *Hybolophus* (flattened umbo, resilifer in some specimens reaching nearly to vmHP, left anterior cardinal tooth extending nearly to beak).

Stratigraphic and geographic range.—Lower Oligocene, Suwannee limestone, Florida.

Crassatella neorhynchus (Olsson, 1931)

Fig. 6A–F, H.

1931 *Crassatellites neorhynchus* sp. nov.; Olsson 1931: 44, pl. 7: 8, 10.

Type material: Holotype, articulated paired adult valves: PRI 1997. Paratype: PRI 1995 from upper Eocene, Chira, Peru.

Type locality: Mancora, Peru.

Type horizon: Mancora Formation, lower Oligocene.

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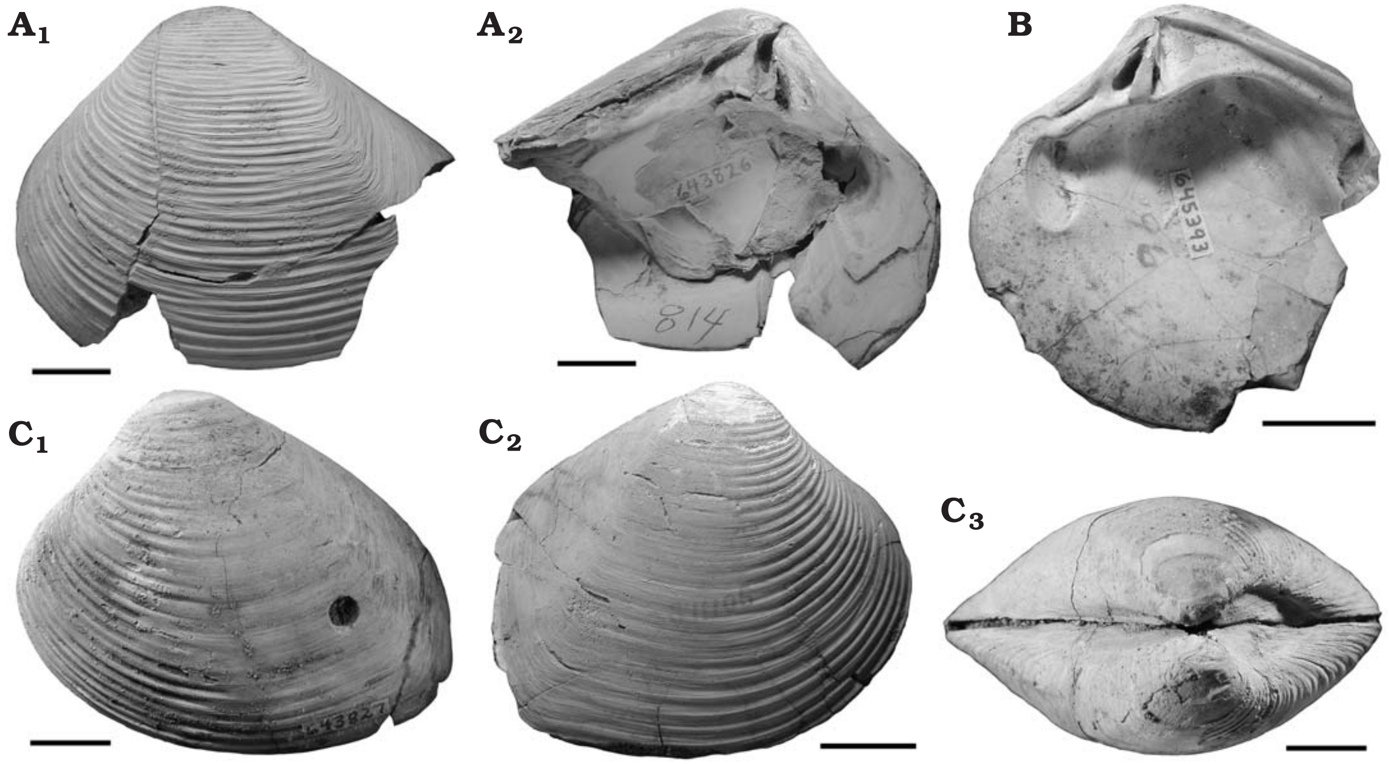

Fig. 5. Crassatellid veneriform bivalves *Hybolophus* species from the late Miocene of Ecuador and Colombia. **A**, **B**. *Hybolophus picaderus* (Olsson, 1964), Ecuador. **A**. USNM 643826, holotype, Picaderos Formation, Picaderos; exterior (A_1) and interior (A_2) of left valve. **B**. USNM 645393, paratype, Mompiche-Portete; interior of right valve. **C**. *Hybolophus tuberus* (Olsson, 1964), USNM 643827, holotype, Tubera Formation, Tubera-Puerto Caiman, Colombia; exterior of left (C_1) and right (C_2) valves, dorsal margin of paired valves (C_3), anterior at right. Scale bars 10 mm.

Material.—UWBM 101822, B8318, L (39.0), H 40.0, T 13.4; UWBM 101823, B8318, L (29.8), H 33.9, T 11.0; UWBM 101824, B8318, L 50.9, H 43.6, T 13.1; UWBM 101825, B8318, L (48.1), H (41.4), T 16.8; UWBM 101826, B8318, L 59.6, H 43.6; UWBM 101827, B8318, L 20.4, H 18.0, T 5.1; UWBM 101828, B8340, L 39.4, H 30.8, T 9.8; UWBM 101829, B8322, L 32.8, H 24.6, T 8.3; UWBM 101830, B8348, L (40.5); UWBM 101831, B8336, L 13.5, H 11.6, T 2.2; UWBM 101832, B8336, L 22.6, H 17.4, T 5.4; MUSM INV 203, B8318, L (38.0); MUSM INV 204, B8318, L (43.0), H (36.7), T 15.5; MUSM INV 205, B8318, L (48.6), H 40.0, T 13.2; MUSM INV 206, B8340, L 35.9, H 29.0, T 9.6; MUSM INV 207, B8348, L 44.9, H 35.0, T 13.2; MUSM INV 208, B8348, L 29.7, H 24.3, T 7.2; MUSM INV 209, B8336, L 13.8, H 10.8, T 2.2. Other specimens from B8327, B8331, B8339, B8346, B8347. All specimens from the East Pisco Basin, Peru.

Emended diagnosis.—Shell trapezoidal, inflated. Umbo rounded, with pronounced and well spaced commarginal ribs.

Description.—Shell to 60 mm long, trapezoidal, inflated, L:H ratio 1.3, T:H ratio 0.3−0.4, maximum inflation posterior to beak. Anteriodorsal and posteriodorsal profiles nearly straight, anterior margin sharply rounded, posterior margin broadly truncate, slightly produced in largest specimens; ventral margin evenly rounded or slightly angular. Weakly angular primary posterior ridge diverging 20−25° from posteriodorsal margin. Secondary posterior ridge obsolete. Lunule cordate, twice as wide as escutcheon; both longer than half the length of respective margins. Beak prosogyrate. Umbo rounded, prosogyrate, with pronounced commarginal ribs; ribs absent posterior to primary posterior ridge. Remainder of exterior with irregular commarginal growth lines. Resilifer extending about half way to vmHP. Left anterior cardinal tooth thick, wedge-shaped, inclined anteriorly 30°, separated from beak by lunule. Left posterior cardinal tooth wedge-shaped, inclined posteriorly 10°, extending from vmHP to beak. Receptor pit absent. Right anterior pseudocardinal tooth nearly coincident with margin of lunule. Right cardinal tooth thick, wedge-shaped, orthocline. Right posterior pseudocardinal tooth lamellar, diverging 35° from cardinal tooth, passing resilifer ventrally. Inner ventral margin crenulate on largest specimens.

Remarks.—External characters of East Pisco Basin specimens match those of the Talara Basin specimens; internal features of the latter are not visible. Large specimens are more elongate than inferred by Olsson (1931) (Fig. 6A).

The stratigraphic placement of *Crassatella neorhynchus* in Chira valley is unambiguous, although the accepted age of the Chira shales has changed from early Oligocene (Olsson 1931) to late Eocene (Higley 2004). The stratigraphic placement of *C. neorhynchus* near Mancora is less certain. The lower Oligocene Mancora Formation, cited by Olsson (1931)

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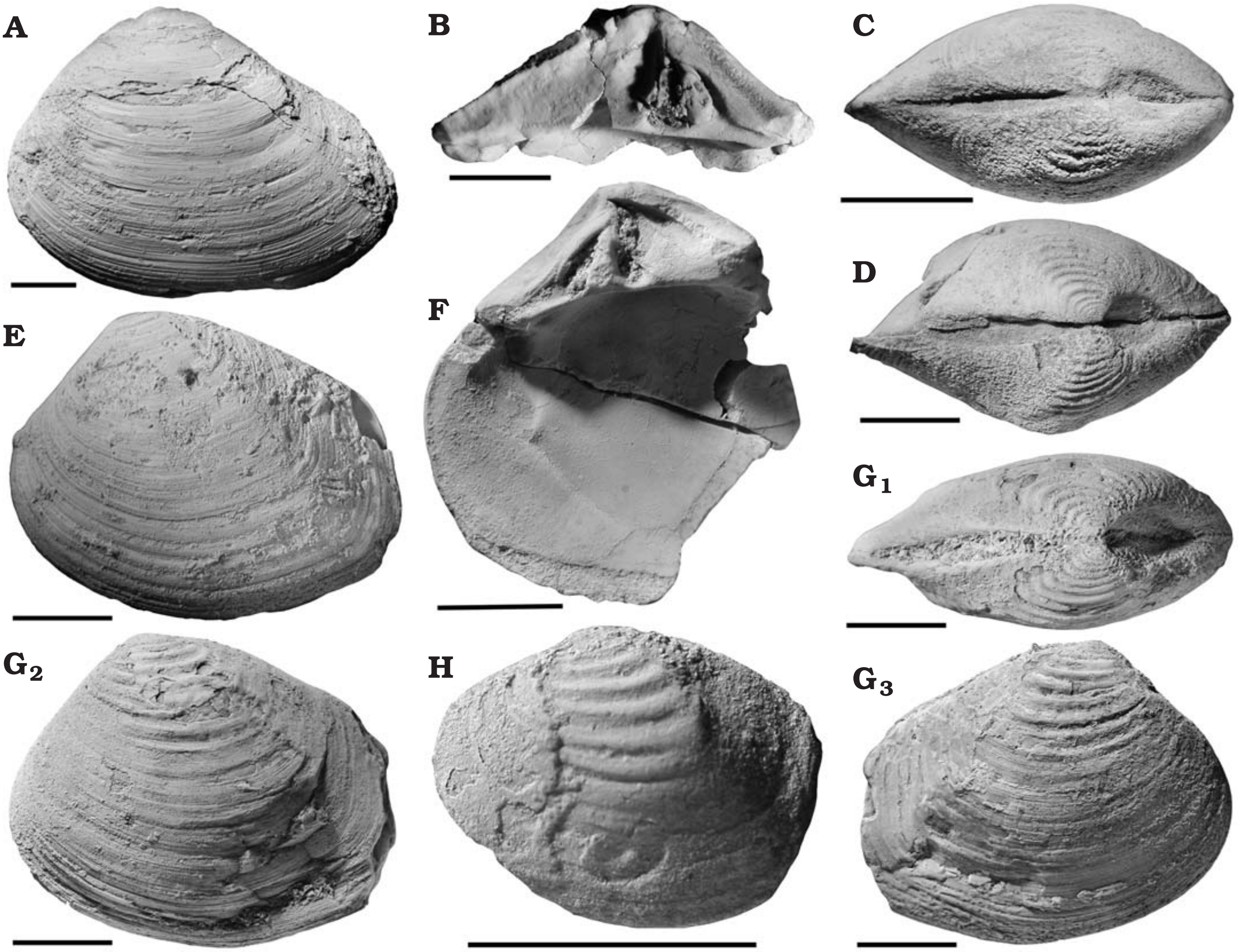

Fig. 6. Crassatellid bivalves from the late Eocene of south-central Peru. **A–F**, **H**. *Crassatella neorhynchus* (Olsson, 1931), Paracas depositional sequence. **A**. UWBM 101826, exterior of left valve. **B**. MUSM INV 203, left hinge plate. **C**. MUSM INV 208, dorsal margin, anterior at right. **D**. MUSM INV 206, dorsal margin, anterior at right. **E**. UWBM 101828, exterior of left valve. **F**. UWBM 101823, interior of right valve. **H**. MUSM INV 212, exterior of left valve, juvenile. **G**. *Crassatella pedroi* sp. nov., UWBM 101833, holotype, Otuma depositional sequence; exterior of left (G_1) and right (G_2) valves, dorsal view of paired valves (G_3), anterior at right. Scale bars 10 mm.

as the type horizon for *C. neorhynchus*, is not mapped near Mancora, despite being described from that stratotypic locality (Palacios 1994). Olsson's (1931) description of the area from which specimens of *C. neorhynchus* were collected corresponds to outcrop mapped as the upper Eocene Mirador Formation (Palacios 1994).

Stratigraphic and geographic range.—Lutetian, basal Paracas depositional sequence, East Pisco Basin, south-central Peru. Upper Eocene, Chira and Mirador Formations, Talara Basin, northern Peru.

Crassatella pedroi sp. nov.

Fig. 6G.

Etymology: From "Pedro", informal name for *Inkayacu paracasensis*, an Eocene penguin unearthed nearby.

Holotype: Articulated paired adult valves: UWBM 101833, L 38.4, H 30.8, T 8.6.

Type locality: B8341, near Playa Yumaque, East Pisco Basin, Peru.

Type horizon: Very base of Otuma depositional sequence, lower Priabonian.

Material.—B8329, six broken specimens.

Diagnosis.—Anterior of shell compressed. Commarginal ribs extend beyond umbo.

Description.—Shell about 40 mm long, quadrate, anterior compressed, L:H ratio 1.25, T:H ratio 0.2, maximum inflation ventral to beak. Anteriodorsal and posteriodorsal margins straight, anterior margin sharply rounded, posterior margin broadly truncate, ventral margin rounded with slight angulation. Weakly angular posterior ridge diverging 20–25° from posteriodorsal margin. Secondary posterior ridge obsolete. Lunule twice as wide as escutcheon; both about two-thirds the length of respective margins. Beak prosogyrate. Umbo rounded, orthogyrate, with broad com-

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marginal ribs extending ventrally 20 mm; ribs absent posterior to primary posterior ridge. Remainder of exterior with irregular commarginal growth lines. Interior of valves not visible. Inner ventral margin smooth.

Remarks.—Despite the absence of visible hinge characters, the paired specimen of *Crassatella pedroi* can be distinguished from specimens of *C. neorhynchus* by its anterior compression (Fig. $6G_1$) and commarginal ribs extending well beyond the umbo (Figs. $6G_2$, G_3). Furthermore, the lunule is narrowly cordate (Fig. $6G_1$) and both it and the escutcheon are proportionally longer than their counterparts on specimens of *C. neorhynchus*. The widely spaced umbonal ribs distinguish *C. pedroi* from the slightly younger *C. rafaeli* sp. nov. from the Otuma depositional sequence.

Stratigraphic and geographic range.—Priabonian, basal Otuma depositional sequence, East Pisco Basin, south-central Peru.

Crassatella rafaeli sp. nov.

Fig. 7.

Etymology: Named in recognition of Rafael Casas, driver and desert guide in the East Pisco Basin.

Type material: Holotype, adult right valve with exposed hinge and missing posterior: UWBM 101834, B8344, L (61.0), H (60.2), T 22.0. Paratypes: UWBM 101835, B8353, L 57.3, H 42.6, T 14.3; UWBM 101836, B8352, L 50.2, H 38.5, T 12.2; UWBM 101837, B8352, L 35.3, H 27.3, T 9.8; UWBM 101838, B8352, L (38.5), T 14.8; UWBM 101839, B8352, L (36.3), H 37.9, T 13.6; UWBM 101840, B8352, L (37.6), H 36.7, T 14.3; UWBM 101841, B8342, L 34.4, H 29.0, T 10.0; UWBM 101842, B8342, H (29.9), T 10.1; MUSM INV 210, B8334, L (55.8); MUSM INV 211, B8353, L 51.7, H 41.6, T 14.9; MUSM INV 212, B8352, L 45.3, H 36.6, T 10.6; MUSM INV 213, B8352, L (35.5), H (32.4), T 11.4; MUSM INV 214, B8352, L (35.4), H (31.5); from B8334, B8342, B8352, B8353; plain 4–10 km north of mine overlooking Bajada del Diablo, all material from the East Pisco Basin, Peru.

Type locality: B8344, 4 km north of mine that overlooks Bajada del Diablo, East Pisco Basin, Peru.

Type horizon: Lower Otuma depositional sequence, Priabonian.

Material.—Additional specimen from B8349, East Pisco Basin, Peru.

Diagnosis.—Umbo with closely spaced commarginal ribs. Resilifer extending half way or entirely to vmHP. Large specimens with crenulate inner ventral margin.

Description.—Shell to 80 mm long, elongate-ovate, L:H ratio 1.2, T:H ratio 0.3, maximum inflation ventral to beak. Anteriodorsal and posteriodorsal profiles usually slightly concave, anterior and ventral margins broadly rounded, posterior margin bluntly truncate, produced. Angular primary posterior ridge diverging 20–25°, weak secondary posterior ridge 5° from posteriodorsal margin. Lunule cordate, twice as wide as escutcheon; both about half the length of respective margins. Beak prosogyrate. Umbo rounded or slightly flattened, prosogyrate, with closely spaced commarginal ribs that disappear posterior to primary posterior ridge. Remainder of exterior with irregular commarginal growth lines. Resilifer extending half way or nearly entirely to vmHP. Left anterior cardinal tooth short, thick, wedge-shaped, inclined anteriorly 30°, separated from beak by lunule. Left posterior cardinal tooth wedge-shaped, inclined posteriorly 10°. Receptor pit absent. Right anterior pseudocardinal tooth lamellar, inclined anteriorly 70°, joining right cardinal tooth and lunule. Right cardinal tooth thick, wedge-shaped, inclined anteriorly 10°. Right posterior pseudocardinal tooth diverging 55° posteriorly from cardinal tooth, passing resilifer ventrally. Inner ventral margin crenulate in large specimens.

Remarks.–Specimens of *Crassatella rafaeli* are distinguished from those of the slightly older *C. neorhynchus* and *C. pedroi* by their closely spaced commarginal ribs on the umbo (Fig. $7F_1$). Large specimens of *C. rafaeli* become increasingly elongate and produced (Fig. $7F_2$, G). The crenulate ventral margin on the largest specimens is also visible externally as anteriodorsally-oriented parallel subsurface lineations that fade dorsally (Fig. 7C). Irrespective of shell size, some resilifers extend nearly fully from the beak to the vmHP (Fig. 7E, G). In contrast, for all specimens of all species of the younger *Tilicrassatella*, resilifers are broader and always extend entirely to the vmHP or nearly so.

Stratigraphic and geographic range.—Priabonian, Otuma depositional sequence, East Pisco Basin, south-central Peru.

Genus *Tilicrassatella* nov.

Etymology: From “Tili”, a 15th-century native chief from Chile’s Aconcagua Valley whose name, according to the 18th-century Spanish chronicler, Diego de Rosales, may have given rise to the country’s name.

Type species: *Crassatella ponderosa* Philippi, 1887; early to middle Miocene, Chile.

Species included: *Crassatella ponderosa* Philippi, 1887, *T. torrens* sp. nov., *T. sanmartini* sp. nov.

Diagnosis.—Umbo rounded, with very closely spaced commarginal ribs. Resilifer extending to vmHP. Left anterior cardinal tooth separated from beak by lunule. Inner ventral margin usually crenulate on large specimens.

Stratigraphic and geographic range.—Chattian to Langhian, south-central Peru to Chile.

Tilicrassatella ponderosa (Philippi, 1887)

Fig. 8A–C.

1887 *Crassatella ponderosa* sp. nov.; Philippi 1887: 166, pl. 38: 5, 5a.
?1887 *Venus medinae* sp. nov.; Philippi 1887: 115, pl. 17: 1.
?1974 *Crassatella medinae* (Philippi, 1887); Frassinetti 1974: 49, fig. 11.
1979 *Crassatella ponderosa* Philippi, 1887; Tavera 1979: 83, pl. 15: 35.
2003 *Eucrassatella ponderosa* (Philippi, 1887): DeVries and Frassinetti 2003: pl. 2: 3.

Type material: Lectotype, adult right valve with hinge partially obscured, herein designated: SGI. PI. 468, Navidad, Chile, L (95), H 76. Paralectotype, herein designated: SGI. PI. 4750, L (55), H (43). These type designations formalize unpublished notations on museum labels, most likely written by Juan Tavera. Paralectotypes: SGI. PI. 4749 and SGI. PI. 4751, unpublished designations of Juan Tavera, are not fragments of *T. ponderosa*, a fact noted on the museum labels by the late Daniel Frassinetti of the Museo de Historia Natural in Santiago, Chile.

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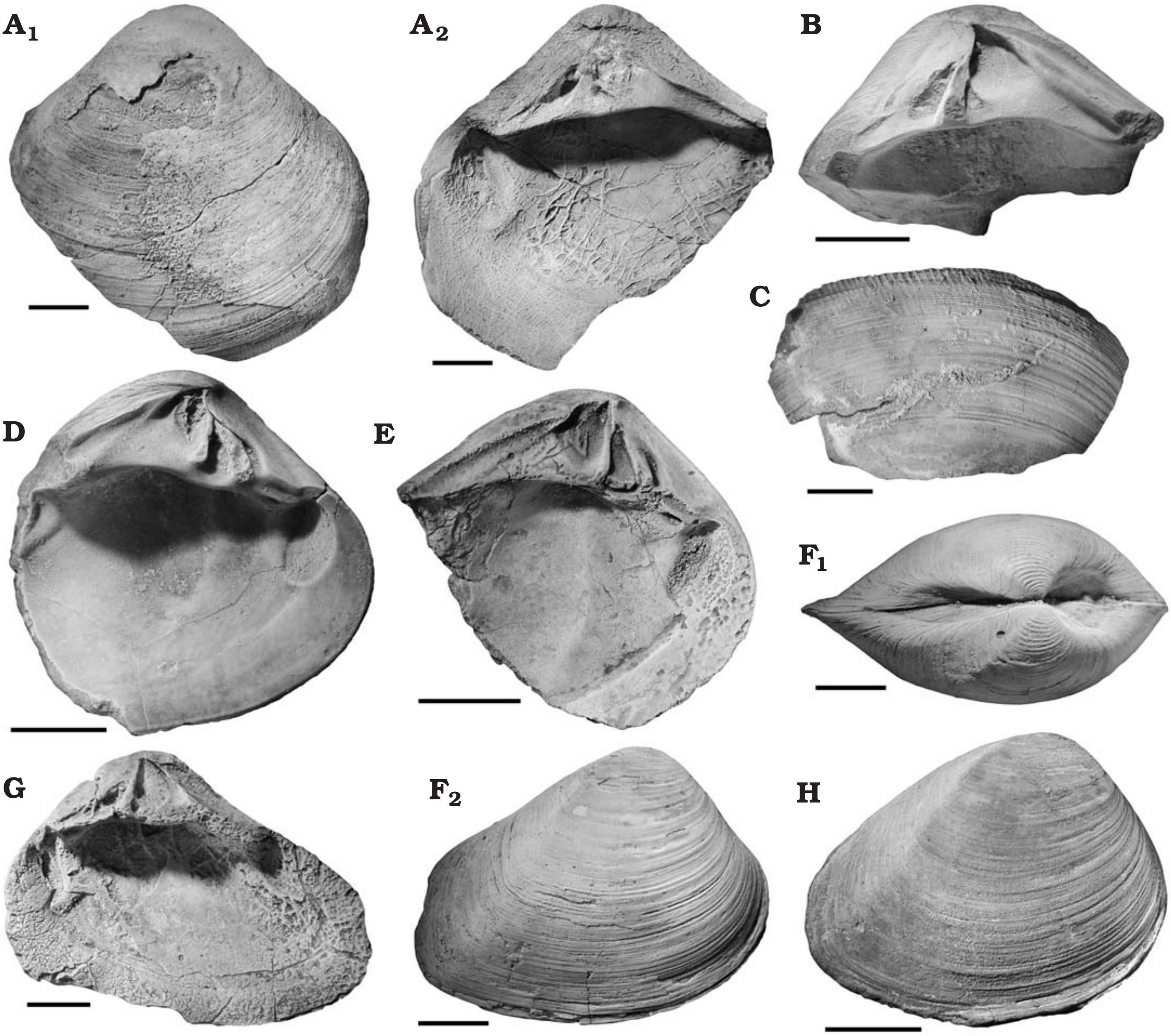

Fig. 7. Crassatellid bivalve *Crassatella rafaeli* sp. nov. from the late Eocene, Otuma depositional sequence, south-central Peru. **A**. UWBM 101834, exterior (A_1), and interior (A_2) of right valve. **B**. UWBM 101838, right hinge plate. **C**. MUSM INV 210, fragment of anterioventral margin showing striations terminating in marginal crenulations. **D**. UWBM 101840, interior of left valve with resilifer extending half way to the vmHP. **E**. MUSM INV 213, interior of left valve with resilifer reaching nearly to the vmHP. **F** UWBM 101836, dorsal margin of paired valves (F_1), anterior to right, exterior of right valve (F_2). **G**. UWBM 101835, interior of right valve. **H**. UWBM 101837, exterior of right valve. Abbreviation: vmHP, ventral margin of the hinge plate. Scale bars 10 mm.

Type locality: Navidad, Chile.

Type horizon: Navidad Formation, lower or middle Miocene.

Material.—UWBM 101843, B8314, L (76.7), H (70.5), T 25.4; UWBM 101844, B8328, L (59.8), H 58.3, T 21.6; UWBM 101845, B8332, H (29.6). Other specimens from B8315 (internal casts). Additional material from central Chile includes specimens from Maitenlahue (SGO. PI. 5517) and Rapel (Sven Nielsen, personal communication 2015), all from the Navidad Formation.

Emended diagnosis.—*Tilicrassatella* with shell posteriorly produced and strongly inflated.

Description.—Shell to 90 mm long, elongate-ovate, inflated, beak about one-third of length from anterior end, L:H ratio 1.3, T:H ratio 0.3, maximum inflation posterior to beak. Anteriodorsal and posteriodorsal profiles straight or slightly concave. Anterior and ventral margins rounded, posterior margin bluntly truncate, moderately produced. Rounded primary posterior ridge diverging 15°, weak secondary posterior ridge 5° from posteriodorsal margin. Lunule cordate, wider than escutcheon; both about half the length of respective margins. Beak prosogyrate. Umbo rounded, prosogyrate, with closely spaced commarginal ribs. Remainder of exterior with irregular commarginal

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growth lines. Resilifer extending nearly to vmHP. Left anterior cardinal tooth thick, wedge-shaped, inclined anteriorly 30°, separated from beak by lunule. Left posterior cardinal tooth narrow, wedge-shaped, straight, nearly orthocline. Right anterior pseudocardinal tooth short, narrow, inclined anteriorly 70°, joining cardinal tooth with lunule. Right cardinal tooth thick, wedge-shaped, inclined anteriorly 10°. Right posterior pseudocardinal tooth lamellar, diverging 20° from cardinal tooth, passing resilifer anteriorly. Inner ventral margin crenulate.

Remarks.—Like specimens of *Crassatella rafaeli*, those of *Tilicrassatella ponderosa* have closely spaced commarginal ribs on the umbo. Specimens of *T. ponderosa* differ from those of *T. torrens* sp. nov. by their anterior inflation and markedly inequilateral valves, resulting in a steeply descending anteriodorsal margin. The only known specimen of *T. sanmartini* is more elongate and less rostrate posteriorly and its resilifer is directed in a mostly posterior direction. An anterioventral fragment of a juvenile left valve of *T. ponderosa* (UWBM 101845) shows no evidence of ventral crenulations. A paired Miocene specimen of about 43 mm length (SGO. PI. 115), previously termed *Crassatella medinae* (Philippi, 1887) by Frassinetti (1974) and recently photographed by Leonardo Pérez (Universidad Austral de Chile, Valdivia), may be a juvenile example of *T. ponderosa*. Small specimens with exposed hinge plates are needed to make such a determination.

Stratigraphic and geographic range.—Chattian to Burdigalian, Chilcatay depositional sequence, East Pisco Basin, south-central Peru. Uppermost Chattian, basal Camaná Formation, southern Peru (Vega and Marocco 2004). Lower to lower middle Miocene, Navidad Formation, Chile.

Tilicrassatella torrens sp. nov.

Fig. 8D–G, I.

Etymology: From Latin *torrens*, torrent; referring to episodic flooding of the Rio Grande near the type locality.

Type material: Holotype, adult left valve with exposed hinge and ventral margin mostly missing: UWBM 101846, B8354, L (97.0), H (78.6), T 23.2. Paratypes: UWBM 101849, B8326, L (58.2), T 23.6; UWBM 101850, B8326, L (77.1), H (68.6), T 22.0; UWBM 101851, B8308, L (66.3), H 63.8, T 19.4; UWBM 101853, B8308, L (56.3); UWBM 101855, B8313, L (86.4), H 69.9, T 18.8; MUSM INV 217, B8326, L (52.9), T 22.0; MUSM INV 230, B8313, L (50.2). From Quebrada Gramonal (B8326), Carhuas-Comotrana road (B8308), Filudo depression (B8313). All material from the East Pisco Basin, Peru.

Type locality: B8354, east flank of Río Grande, across river from Cerro Terrestral, East Pisco Basin, Peru.

Type horizon: Chilcatay depositional sequence, lower Miocene.

Material.—UWBM 101847, B8330, L 55.9, H 45.9, T (15); UWBM 101848, B8330, H (44.1); UWBM 101852, B8324, L (74.1), H (55.9), T 19.8; UWBM 101854, B8304, H (55.4); UWBM 101856, B8305, H (39.9); MUSM INV 215, B8330, L (48.9), H (46.0); MUSM INV 216, B8330, L 57.2, H 46.3; MUSM INV 218, B8309, L (86.3), H 70.3. Other specimens from B8306, B8311, B8313, B8325, B8333, B8337. All material from the East Pisco Basin, Peru.

Diagnosis.—Shell trapezoidal, not inflated, nearly equilateral.

Description.—Shell to 100 mm long, trapezoidal, not inflated, beaks more than two-fifths of length from anterior end, L:H ratio 1.2, T:H ratio 0.2, maximum inflation ventral or posterior to beak. Anteriodorsal and posteriodorsal margins nearly straight, not steeply descending. Anterior and ventral margins broadly rounded, posterior margin broadly truncate, not produced. Primary posterior ridge rounded to obsolete, diverging 20–25° from posteriodorsal margin. Secondary posterior ridge usually obsolete. Lunule elongate-cordate, slightly wider than escutcheon, both about half the length of respective margins. Beak prosogyrate. Umbo slightly flattened, orthogyrate, with closely spaced commarginal ribs extending across primary posterior ridge. Remainder of exterior with irregular commarginal growth lines. Resilifer extending to vmHP. Left anterior cardinal tooth thick, elongate, wedge-shaped, inclined anteriorly 40–50°, separated from beak by lunule. Left posterior cardinal tooth narrow, straight, inclined anteriorly less than 20° or orthocline. Right anterior pseudocardinal tooth narrow, elongate, diverging from lunule margin and inclined anteriorly 70°. Right cardinal tooth thick, wedge-shaped, elongate, inclined anteriorly 20°. Right posterior pseudocardinal tooth lamellar, diverging 20° from cardinal tooth, passing resilifer anterioventrally. Inner ventral margin usually crenulate on large specimens.

Remarks.—Specimens of *Tilicrassatella torrens* are more equilateral than specimens of *T. ponderosa* and *T. sanmartini* and much less inflated than specimens of *T. ponderosa*. The presence of a crenulated inner ventral margin distinguishes specimens of *T. ponderosa* (and every species of *Tilicrassatella*) from specimens of *Hybolophus* in Miocene and Pliocene strata of the East Pisco Basin and northern Peru.

Stratigraphic and geographic range.—Aquitanian to Langhian, Chilcatay and basal Pisco depositional sequences, East Pisco Basin, south-central Peru.

Tilicrassatella sanmartini sp. nov.

Fig. 8H.

Etymology: Named in honor of José de San Martín (1778–1850), a liberator of Argentina and Peru.

Holotype: Adult right valve with damaged hinge and posterioventral portion missing: UWBM 101857, L (89.0), H (55.7), T 19.8.

Type locality: B8328, near confluence of Quebrada Gramonal and the Río Ica, East Pisco Basin, Peru.

Type horizon: Lower Chilcatay depositional sequence, Chattian or Aquitanian.

Diagnosis.—*Tilicrassatella* with posterior exceedingly elongate but not constricted. Resilifer directed more posteriorly than ventrally.

Description.—Shell to about 100 mm long, ellipsoidal, elongate, moderately inflated, beak less than one third distance

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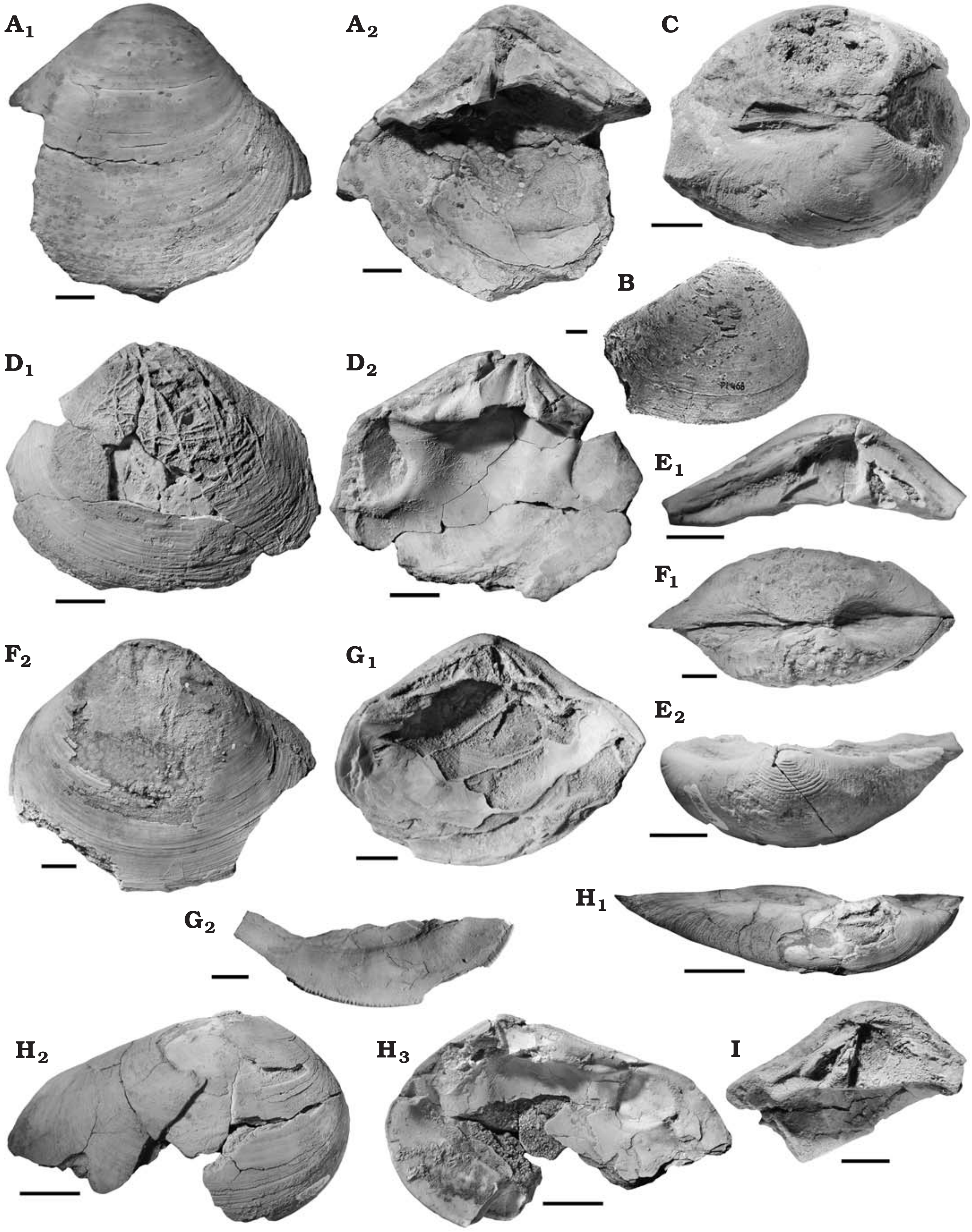

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from anterior end, L:H ratio 1.5, T:H ratio 0.2, maximum inflation posterior to beak. Anteriodorsal margin steeply descending, evenly convex; posteriordorsal margin straight. Anterior margin sharply and evenly rounded; posterior margin rounded ventrally, bluntly truncate dorsally. Ventral margin broadly rounded to straight, not constricted posteriorly. Primary posterior ridge weakly rounded, diverging 15–20° from posteriodorsal margin; secondary posterior ridge absent. Lunule elongate, narrow; escutcheon elongate, wider than lunule, about 40% length of posteriodorsal margin. Beak not preserved. Umbo rounded, orthogyrate, with closely spaced commarginal ribs. Remainder of exterior with irregular commarginal growth lines. Resilifer broad, slightly raised above hinge plate, inclined posteriorly 40°, extending nearly to vmHP. Right cardinal tooth thick, wedge-shaped. Right posterior pseudocardinal tooth starting at beak, passing resilifer anteriorly. Inner ventral margin crenulate.

Remarks.—This specimen differs from its sympatric congeners, *Tilicrassatella ponderosa* and *T. torrens*, by its extreme posterior elongation and posteriorly directed resilifer, features shared by many taxa attributed to *Bathytormus*, including the Eocene Argentinian *Bathytormus longior* (Ihering, 1897). One specimen of *B. longior* in particular, figured by Santelli and del Río (2014: fig. 6.7), greatly resembles the Peruvian specimen, although it is proportionally longer (L: H 1.7) with a less robust escutcheon, lunule, and umbo.

In addition to a full-length resilifer and crenulated inner ventral margin, Chavan (1939) attributed to *Bathytormus* a rostrate posterior, and Wingard (1993), a pronounced inequilaterality at all growth stages. Neither of the these characters describes the Peruvian specimen.

Chattian-Burdigalian specimens from the Guadal Formation of southern Chile attributed questionably to *Bathytormus longior* by Frassinetti and Covacevich (1999) are less elongate and more truncate posteriorly than specimens of *B. longior* described by Ihering (1897) and Santelli and del Río (2014). The Guadal specimens, with so few umbonal commarginal ribs (9–10 per 10 mm radially), are not examples of the contemporaneous *Tilicrassatella*, all three species of which have 17–25 umbonal ribs in the same radial interval.

Stratigraphic and geographic range.—Chattian to Aquitanian. Chilcatay depositional sequence, East Pisco Basin, south-central Peru.

Genus *Hybolophus* Stewart, 1930

Type species: *Crassatella gibbosa* Sowerby, 1832; original designation; Pacific coast of South America, Recent.

Remarks.—Stewart (1930) equivocated in his description of *Hybolophus*, focusing finally but with reservations on the opisthogyrate beaks (umbones?) of the new taxon. Thus, *Hybolophus* is better viewed through the descriptive prism of the type species, *H. gibbosus*. MacNeil (1936) and Ward and Blackwelder (1987) consequently leaned towards excluding less inflated and less posteriorly produced species that are herein placed in *Kalolophus*. Similarly, Marks (1951) expressed uneasiness about placing in *Hybolophus* his early Miocene species from Ecuador, which, being only slightly produced posteriorly and possessing a widely divergent and single posterior ridge, presents a veneriform profile. Marks (1951) would have been uneasier yet if Olsson (1964) had already published accounts of his late Miocene Ecuadorian *Eucrassatella picadera* and Colombian *E. tubera*. For now, considering the scarcity of exposed hinge plates and specimens of veneriform crassatellines, it is premature to assign the veneriform crassatellines to a separate genus or subgenus; they are included here within a more broadly conceived *Hybolophus*.

Stratigraphic and geographic range.—Upper Eocene to Recent, western North and South America, Caribbean.

Hybolophus disenum sp. nov.

Fig. 9A–D.

Etymology: From Latin *di*, two, and *senex*, old man; referring to Axel A. Olsson, then 69, and Wendell P. Woodring, then 67, who together collected the type specimens in 1958. Olsson had invited Woodring to Peru to show him evidence of incorrect foram-based Paleogene ages assigned by Robert M. Stainforth (Linda Hindall, personal communication 2015, citing a letter written by A.A. Olsson to Katherine Palmer).

Type material: Holotype, adult right valve with hinge mostly obscured and ventral margin missing: USNM 618239, L (33.9), T 12.6. Paratypes: USNM 618238, H (38.4), T 17.1; USNM 618240, H (25.7); USNM 618241, H (24.1), T (9.3).

Type locality: WP 28, minor tributary of Quebrada Mancora, 700 m S of bridge across Quebrada Mancora and about 100 m E of highway, 15 m higher in section that WP 27. Northern Peru.

Type horizon: Base of Heath Formation, lower Oligocene or lower Miocene (sensu Woodring 1958).

Diagnosis.—Shell veneriform, inflated. Beak situated nearly medially. Exterior with commarginal growth lines.

Description.—Shell to at least 40 mm, possibly 50–60 mm long, ovate, veneriform, nearly equilateral, L:H ratio 1.25;

← Fig. 8. Crassatellid bivalves *Tilicrassatella* from Peru and Chile. **A**–**C**. *Tilicrassatella ponderosa* (Philippi, 1887). UWBM 101843, early Miocene, Chilcatay depositional sequence, south-central Peru; exterior (A$_1$) and interior (A$_2$) of right valve. **B**. SGO. PI. 468, lectotype, early to middle Miocene, Navidad Formation, Chile; exterior of right valve. **C**. UWBM 101844, early Miocene, Chilcatay depositional sequence, south-central Peru; dorsal margin of paired valves, anterior at right. **D**–**G**, **I**. *Tilicrassatella torrens* sp. nov., early to middle Miocene, Chilcatay or basal Pisco depositional sequences, south-central Peru. **D**. UWBM 101846, holotype, exterior (D$_1$) and interior (D$_2$) of left valve. **E**. UWBM 101853, paratype, hinge plate of left valve (E$_1$), umbo (E$_2$). **F**. UWBM 101855, dorsal margin of paired valves (F$_1$), anterior at right, exterior of left valve (F$_2$). **G**. UWBM 101852, interior of left valve (G$_1$), anterioventral inner margin with crenulations (G$_2$). **I**. MUSM INV 230, paratype, hinge plate of right valve. **H**. *Tilicrassatella sanmartini* sp. nov., UWBM 101857, latest Oligocene to early Miocene, basal Chilcatay depositional sequence, south-central Peru; exterior (H$_1$) and interior (H$_2$) of right valve; dorsal margin (H$_3$), anterior at right. Scale bars 10 mm.

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T:H ratio 0.3–0.35, maximum inflation posterior to beak. Anteriodorsal and posteriodorsal margins nearly straight, not steeply descending ventrally. Anterior margin sharply rounded, ventral margin rounded with medial angulation, posterior margin very broadly truncate. Weakly angular primary posterior ridge diverging 20–25°, secondary posterior ridge less than 5° from posteriodorsal margin. Lunule narrowly cordate, escutcheon narrow. Beak prosogyrate. Umbo flattened, orthogyrate to opisthogyrate, with widely spaced commarginal ribs. Remainder of exterior with irregularly spaced commarginal growth lines. Resilifer narrow, extending to vmHP. Left anterior cardinal tooth narrow, wedge-shaped, inclined anteriorly 40°, dorsal intersection with lunule damaged. Left posterior cardinal tooth narrower, inclined anteriorly 10°, extending to beak. Right anterior pseudocardinal tooth joining proximal ends of lunule and cardinal tooth. Right cardinal tooth thick, wedge-shaped, inclined anteriorly 10–15°. Right posterior pseudocardinal tooth lamellar, diverging 45° posterioventrally from mid-point of cardinal tooth. Ventral margin not preserved.

Remarks.—Field notes of Woodring (1958: 8–9) put locality WP27 and the type locality of *Hybolophus disenum*, WP 28, close to the town of Mancora in soft sandstone beds of the basal Heath Formation, which were observed to overlie massive sandstone and conglomerate of the Mancora Formation. The two formations are lower and upper Oligocene, respectively (Higley 2004). Neither formation, however, is now mapped near Mancora (Palacios 1994; also, César Chalcatana [INGEMMET], personal communication 2015). Woodring's (1958) localities do plot in an area mapped by Palacios (1994) as the upper Eocene Mirador Formation. Adding to the confusion, distinctive black carbonaceous conglomerate near Mancora is attributed to the Mancora Formation by both Olsson (1931) and Palacios (1994).

Turritella woodsi Lisson, 1925 (= *T. conquistadorana* Hannah and Israelsky, 1925; see DeVries 2007) is found at locality WP 27. The gastropod also occurs about 30 km northeast at localities WP 31 and WP 32, near the mouth of Quebrada Plateritos (= Quebrada Culebra), an area mapped as the Mancora Formation by Palacios (1994). In southern Peru, *T. woodsi* is found in Priabonian to Chattian strata of the East Pisco Basin (DeVries 2007). Thus, specimens of *Hybolophus disenum* could have an age between late Eocene and latest Oligocene. The stratigraphic and paleontological evidence for locality WP 28 indicates a late Eocene or early Oligocene age.

In a related aside, Deniaud et al. (1999) assigned the Ecuadorian Subibaja Formation, in which are found specimens of *Turritella woodsi* and Marks's (1951) type specimens of *Hybolophus carrizalensis*, to the Langhian. In the Talara and East Pisco basins of Peru and Progreso Basin of Ecuador, *T. woodsi*-bearing beds underlie beds with specimens of the Langhian *T. infracarinata* Grzybowski, 1899 (Marks 1951; DeVries 2007). Therefore, *H. carrizalensis* might have an Oligocene to early Miocene age, not Langhian.

Hybolophus disenum may be contemporaneous or nearly so with *Crassatella neorhynchus*, being from the same outcrop area west of Mancora (Olsson 1931; Woodring 1958). Specimens of *H. disenum* have a flattened umbo, typical of *Hybolophus* but absent in *Crassatella*; are closer to being equilateral with dorsal margins descending ventrally less steeply than on specimens of *C. neorhynchus*; and have a less angular and more widely divergent posterior ridge. The damaged left anterior cardinal tooth (Fig. 9C) may be separated from the beak by the lunule, a feature typical of *Crassatella* but present in more than one species of *Hybolophus*. The inner ventral margin of *H. disenum* is not preserved and so cannot be compared with the crenulate margin in large specimens of East Pisco *C. neorhynchus*.

Stratigraphic and geographic range.—Upper Eocene or lower Oligocene, Mirador or Mancora Formation, northern Peru.

Hybolophus terrestris sp. nov.

Fig. 9E–J.

Etymology: Referring to Cerro Terrestral, the type locality.

Type material: Holotype, complete adult left valve with hinge exposed: UWBM 101871, L 57.3, H 51.0, T 15.4. Paratypes (all B8320): UWBM 101872, L (45.6), H 43.3, T 14.2; UWBM 101873, L 56.6, H 46.5, T 15.5; UWBM 101874, L 69.7, H 63.9, T 26.6; UWBM 101875, L 63.2, H 56.5, T 17.5; UWBM 101876, L 69.0, H 59.1, T 20.0; UWBM 101877, L 60.4, H 46.0, T 16.0; MUSM INV 224, L 58.3, H 47.6, T 16.5; MUSM INV 225, L (52.8), H (44.5), T 15.0; MUSM INV 226, L (68.9), H 58.9, T 18.5; MUSM INV 227, L 54.3, H 47.6, T 14.4; MUSM INV 228, L 64.1, H 51.7, T 17.3; MUSM INV 229, L 61.8, H 48.0, T 16.9.

Type locality: B8320, Cerro Terrestral, East Pisco Basin, Peru.

Type horizon: Upper Pisco depositional sequence, Tortonian or Messinian.

Material.—UWBM 101878, B8355, L 43.7, H 36.6, T 10.5; UWBM 101879, B8355, L 55.4, H 47.4, T 15.5. Other specimens from B8317 (molds) and B8319. All from material from the East Pisco Basin, Peru.

Diagnosis.—*Hybolophus* with shell veneriform, nearly circular, inflated, with irregular commarginal growth lines beyond the umbones.

Description.—Shell to 80 mm long, veneriform and nearly circular, rarely posteriorly produced, L: H ratio usually 1.0–1.1, T: H ratio 0.3, maximum inflation ventral or posterior to beak. Anteriodorsal and posteriodorsal margins straight to slightly convex, rarely slightly concave, anterior and ventral margins broadly rounded, posterior margin rounded to broadly truncate. Weakly angular primary posterior ridge diverging less than 20° from posteriodorsal margin, secondary posterior ridge bordering escutcheon. Lunule elongate-cordate, 60% length of anteriodorsal margin. Escutcheon 70–80% length of posteriodorsal margin, narrower than lunule. Beak prosogyrate. Umbo flattened, orthogyrate, rarely opisthogyrate, with widely spaced commarginal ribs. Remainder of exterior with irregular commarginal growth lines. Left anterior cardinal tooth narrow, wedge-shaped, inclined anteriorly 30–40°, extending from vmHP to beak. Left posterior cardinal tooth bladelike, straight, nearly ortho-

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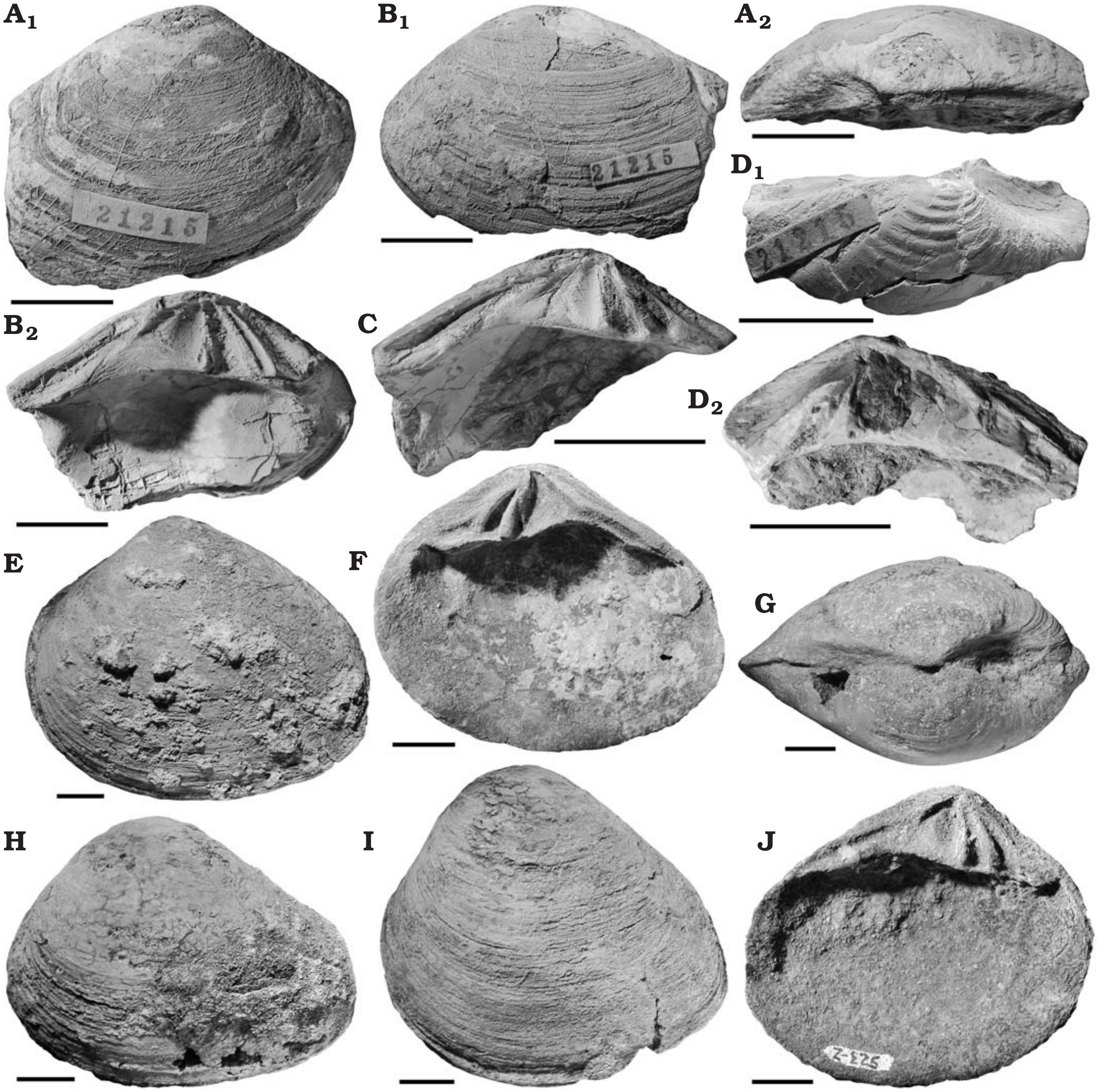

Fig. 9. Veneriform *Hybolophus* crassatellines from Peru. **A–D**. *Hybolophus disenum* sp. nov., late Eocene or Oligocene, Mancora, northern Peru. **A**. USNM 618239, holotype, exterior (A_1) and dorsal margin (A_2) of right valve. **B**. USNM 618238, paratype, exterior (B_1) and interior (B_2) of left valve. **C**. USNM 618241, paratype, hinge plate of left valve. **D**. USNM 618240, paratype, dorsal margin of right valve (D_1), anterior at right, hinge plate (D_2). **E–J**. *Hybolophus terrestris* sp. nov., late Miocene, mid-section in Pisco depositional sequence, south-central Peru. **E**. UWBM 101874, paratype, exterior of left valve. **F**. UWBM 101873, paratype, interior of right valve. **G**. UWBM 101879, dorsal margin of paired valves, anterior at right. **H**. UWBM 101877, paratype, exterior of posteriorly elongated left valve. **I**. UWBM 101875, paratype, exterior of left valve with posterior shortening. **J**. UWBM 101871, holotype, interior of left valve. Scale bars 10 mm.

cline. Right anterior pseudocardinal tooth narrow, diverging anteriorly from midpoint of lunule margin. Right cardinal tooth narrow, wedge-shaped, inclined anteriorly 30°. Right posterior pseudocardinal tooth lamellar, diverging 10–20° posteriorly from midpoint of right cardinal tooth, passing resilifer anteriorly. Inner ventral margin smooth.

Remarks.—Most specimens of *Hybolophus terrestris* have convex anteriodorsal and posteriodorsal margins, imparting a veneriform profile, yet individuals can be either trigonal or as elongate as some Miocene specimens of *H. gibbosus* and *H. nelsoni*, a pattern of variability also illustrated by Marks (1951) in *H. carrizalensis*. Like specimens of *H. gibbosus*,

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those of *H. terrestris* are inflated, thick, and have a flattened umbo, but the umbo is rarely as opisthogyrate. Also, specimens of *H. terrestris* lack the angular secondary posterior ridge of *H. gibbosus*.

Stratigraphic and geographic range.—Tortonian to Messinian, Pisco depositional sequence, East Pisco Basin, south-central Peru.

Hybolophus maleficae sp. nov.

Fig. 10A–G.

Etymology: From Latin malefica, witch; referring to the "La Bruja" (witch in Spanish), vertebrate level (Muizon and DeVries 1985), in which many specimens of this species were found.

Type material: Holotype, complete adult left valve with hinge exposed: UWBM 101858, B8338, L 44.5, H 38.8, T 11.4. Paratypes: UWBM 101859, B8338, L (25.2), H (18.0); UWBM 101860, B8338, L (24.3), H (16.1); UWBM 101861, B8338, L 37.0, H 29.4, T 10.0; UWBM 101862, B8312, L 57.9, H 41.9, T 13.0; UWBM 101863, B8312, L (35.9), H 31.5, T 10.1; UWBM 101865, B8312, L (41.0), H 36.2, T 12.7; MUSM INV 219, B8338, L 37.3, H 30.1, T 9.8; MUSM INV 220, B8338, L 24.9, H 18.7, T 6.6; MUSM INV 221, B8338, L 35.6, H 27.1, T 9.0; MUSM INV 222, B8312. L 54.8, H 43.7, T 13.2; MUSM INV 223, B8312, L 45.6, H 36.0, T 12.3. From B8338, B8312, Filudo depression, west of Pozo Santo, East Pisco Basin, Peru.

Type locality: B8338, knoll southwest of Cerro de Amara, Ica valley, East Pisco Basin, Peru.

Type horizon: Lower Pisco depositional sequence, Serravallian.

Material.—UWBM 101864, B8343, L (43.3), H 51.7, T 16.0; UWBM 101866, B8323, L 58.2, H 47.0, T 14.2; UWBM 101867, B8323, L 49.5, H 40.4, T 13.7; UWBM 101868, B8323, L 44.4, H 36.6, T 9.6; MUSM INV 231, B8323, L 48.0, H 37.9, T 11.5; MUSM INV 232, B8323, L (36.1); MUSM INV 233, B8356, L (39.5). Other specimens from B8307, B8310, B8316, B8321, B8335, B8345, B8350, B8351. All material from the East Pisco Basin, Peru.

Diagnosis.—Shell ovate. Resilifer narrow. Left anterior cardinal tooth separated from beak by lunule.

Description.—Shell to 70 mm long, trapezoidally ovate, moderately inflated, posterior variably elongate and produced, beak located two-fifths of length from anterior end, L:H ratio 1.2, T:H ratio 0.3, maximum inflation ventral or anterior to beak. Anteriodorsal and posteriodorsal profiles straight or slightly concave. Anterior margin rounded to bluntly rounded, ventral margin rounded and slightly angled, posterior margin bluntly truncate or produced. Moderately angular primary posterior ridge diverging 20° from posteriodorsal margin. Weak secondary posterior ridge nearly coincident with escutcheon margin. Lunule cordate, half the length of anteriodorsal margin. Escutcheon two-thirds the length of posteriodorsal margin, narrow, one-third width of lunule. Beak prosogyrate. Umbo flattened, prosogyrate to opisthogyrate with widely spaced commarginal ribs, latter sometimes extend ventrally across anterior of valve; remainder of exterior with irregularly spaced commarginal growth lines. Resilifer narrow. Left anterior cardinal tooth short, wedge-shaped, inclined anteriorly 30–35°, separated from beak by lunule. Left posterior cardinal tooth narrower, nearly orthocline. Right anterior pseudocardinal tooth short, diverging from lunule margin. Right cardinal tooth short, straight, wedge shaped, inclined anteriorly 20°. Right posterior pseudocardinal tooth lamellar, diverging 20° posterioventrally from midpoint of cardinal tooth. Inner ventral margin smooth.

Remarks.—Specimens of *Hybolophus maleficae*, like those of *H. picaderus*, have a left anterior cardinal tooth separated from the beak by the lunule, a character state not seen in specimens of the Peruvian Miocene *H. terrestris* sp. nov. and *H. nelsoni* and the younger Peruvian species, *H. gibbosus*. Otherwise, the smooth ventral margin and full-length resilifer are typical of posteriorly elongate *Hybolophus*. In the Filudo depression, strata with specimens of *H. maleficae* overlie by only a few meters beds with specimens of *Tilicrassatella torrens*. *Hybolophus maleficae* appeared in the East Pisco Basin at the same time as *Turritella infracarinata* and *Anadara sechurana* Olsson, 1932, two species with well established fossil records in the Talara and Sechura basins of northern Peru (Olsson 1932). Together, these species and others constituted a transitional fauna, younger than a Chilcatay fauna (with *Tilicrassatella* and many species also known in central Chile; DeVries and Frassinetti 2003) and older than an "early modern" fauna (with *Hybolophus* and many genera still extant in the modern Panamic Province of tropical western America).

Stratigraphic and geographic range.—Serravallian, lower Pisco depositional sequence, East Pisco Basin, south-central Peru. Tortonian, Pisco Formation, Sacaco Basin, southern Peru.

Hybolophus nelsoni (Grzybowski, 1899)

Fig. 10I.

1870 *Crassatella gibbosa* Sowerby; Nelson 1870: 203, pl. 7: 9; not *Crassatella gibbosa* (Sowerby, 1832).
1899 *Venus nelsoni* sp. nov.; Grzybowski 1899: 639, pl. 19: 2, 2a.
1922 *Crassatellites* (*Scambula*) *nelsoni* (Grzybowski); Spieker 1922: 128, pl. 7: 8.
1932 *Eucrassatella* (*Hybolophus*) *nelsoni* (Grzybowski); Olsson 1932: 87, figs. 1, 4.
1922 *Crassatellites charanensis* sp. nov.; Woods 1922: 112, pl. 19: 6; pl. 20: 1, 2, 3; not *Eucrassatella* (*Hybolophus*) *charanensis* (Woods, 1922); DeVries 1986: 429, pl. 13: 5, 8, 10 (= *Hybolophus gibbosus* [Sowerby, 1832]).
1925 *Crassatellites pizzaroi* sp. nov.; Hannah and Israelsky 1925: 46, pl. 7: 1.
1932 *Eucrassatella* (*Hybolophus*) *gibbosa tucilla* subsp. nov.; Olsson 1932: 88, pl. 6: 6.

Type material: Grzybowski's (1899) holotype not examined by the author. The whereabouts of every Grzybowski molluscan type from Peru is unknown. They do not reside in the collections of his home institution, the Jagiellonian University in Kraków (Jolanta Gruza, personal communication 15 February 2016). Emended description based on illustrations of Nelson (1870) and Grzybowski (1899) and Spieker's (1922) specimen.

Type locality: Caleta Grau, Peru.

Type horizon: Miocene, indeterminate formation.

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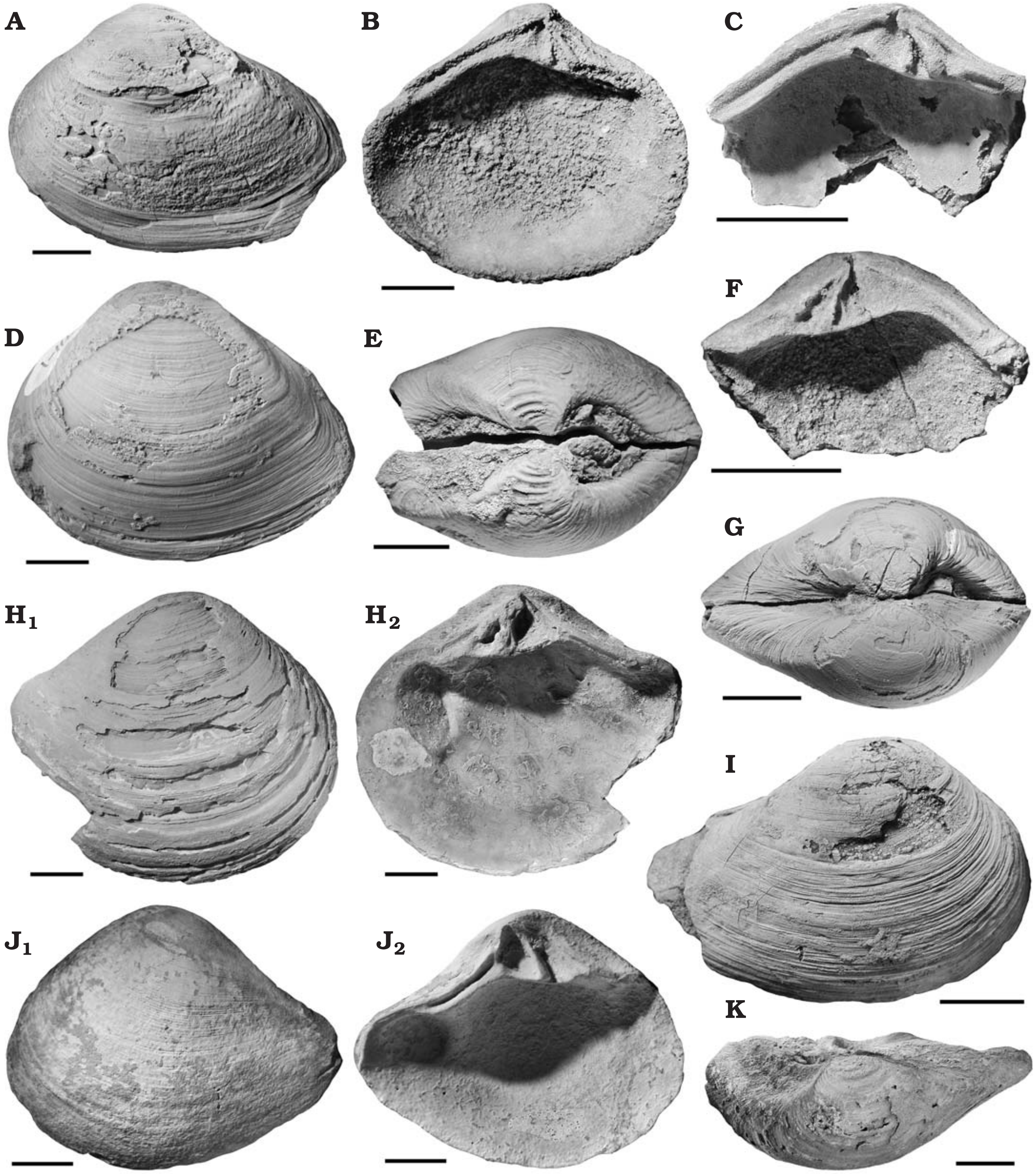

Fig. 10. *Hybolophus* crassatellines from Peru. **A**–**G**. *Hybolophus maleficae* sp. nov., middle Miocene, Pisco depositional sequence, south-central Peru. **A**. UWBM 101862, paratype, exterior of left valve. **B**. UWBM 101858, holotype, interior of left valve. **C**. UWBM 101860, paratype, interior of left valve. **D**. MUSM INV 222, paratype, exterior of left valve. **E**. UWBM 101864, dorsal margin of paired valves, anterior at right. **F**. UWBM 101859, paratype, interior of right valve. **G**. UWBM 101865, dorsal margin of paired valves, anterior at right. **H**, **J**, **K**. *Hybolophus gibbosus* (Sowerby, 1832), early to middle Pleistocene, tablazos, northern Peru. **H**. OSU 37600, exterior (H$_1$) and interior (H$_2$) of right valve. **J**. OSU 37597, exterior (J$_1$) and interior (J$_2$) of left valve. **K**. OSU 37601, dorsal margin of left valve, anterior at left. **I**. *Hybolophus nelsoni* (Grzybowski 1899), USNM 562398, late Miocene, Quebrada Heath, northern Peru; exterior of right valve. Scale bars 10 mm.

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Material.—USNM 562398, ridge at head of Quebrada Heath, northern Peru (Spieker 1922).

Emended diagnosis.—Shell inflated. Anteriodorsal margin straight to slightly convex. Posterior produced. Primary and secondary posterior ridges diverging by more than 10°, latter close to margin of escutcheon.

Emended description.—Shell to at least 70 mm long, ovate anteriorly, produced posteriorly, beak located two-fifths of length from anterior end, L:H ratio 1.2–1.4, T:H ratio 0.3, maximum inflation ventral to beak. Anteriodorsal margin straight to slightly convex, posteriodorsal margin concave. Anterior margin and ventral margin rounded, latter not constricted posteriorly; posterior margin weakly produced, bluntly truncate. Weakly angular primary posterior ridge diverging 15–20° from posteriodorsal margin, secondary posterior ridge obsolete or close to escutcheon. Lunule cordate, about 60% length of anteriodorsal margin. Escutcheon about 60% length of posteriodorsal margin, as wide or narrower than lunule. Beak orthogyrate to prosogyrate. Umbo flattened, opisthogyrate, with broad commarginal ribs. Remainder of exterior with irregular commarginal growth lines. Left hinge not available. Right anterior pseudocardinal tooth narrow, diverging from lunule margin, inclined 35° anteriorly. Right cardinal tooth wedge-shaped, inclined anteriorly 20°. Right posterior pseudocardinal tooth lamellar, diverging 10° posteriorly from midpoint of cardinal tooth. Inner ventral margin smooth.

Remarks.—*Hybolophus nelsoni* encompasses Miocene specimens from several localities in northern Peru. The oldest are attributed to the lower Miocene lower Zorritos Formation by Spieker (1922), although the specimens may have been collected from the middle Miocene Cardalitos Shale (Grzybowski 1899; Woods 1922; Hanna and Israelsky 1925; Olsson 1932). The youngest were collected from the upper Miocene Tumbez Formation (Olsson 1932).

Previous authors offer conflicting conclusions about the relationship between *Hybolophus nelsoni* and *H. gibbosus*. Quaternary specimens from northern Peru have closely spaced primary and secondary posterior ridges, producing an exceptionally narrow posterior truncation (i.e., the posterior nearly comes to a point), a deeply concave posteriodorsal margin, and an exceedingly opisthogyrate umbo; these are assigned to *H. gibbosus*. Specimens of *H. nelsoni* have a wider divergence between the primary and secondary posterior ridges, with the latter close to the margin of the escutcheon. The result is a broader posterior truncation, a straighter posteriodorsal margin, and a less opisthogyrate umbo.

Stratigraphic and geographic range.—Middle to upper Miocene, northern Peru.

Hybolophus gibbosus (Sowerby, 1832)

Fig. 10H, J, K.

1832 *Crassatella gibbosa* sp. nov.; Sowerby 1832: 56.

1843 *Crassatella gibbosa* Sowerby; Reeve 1843: vol. 1, pl. 1: 1a, b.

1909 *Crassatellites gibbosus* (Sowerby); Dall 1909: 260.

1930 *Crassatellites rudis* sp. nov.; Li 1930: 251, pl. 3: 16.

1961 *Crassatellites* (*Hybolophus*) *gibbosus* (Sowerby); Olsson 1961: 179, pl. 25: 1a, b.

1986 *Eucrassatella* (*Hybolophus*) *charanensis* (Wood, 1922): DeVries 1986: 429, pl. 13: 5, 8, 10. 1986 *Eucrassatella* (*Hybolophus*) *gibbosa* (Sowerby, 1832); DeVries 1986: 427, pl. 13: 6, 9.

1986 *Eucrassatella* (*Hybolophus*) *ovata* sp. nov.; DeVries 1986: 431, pl. 13: 1, 3, 7, 11, 12.

2012 *Eucrassatella gibbosa* (Sowerby, 1832); Coan and Valentich-Scott 2012: 398, pl. 130; not *Crassatellites charanensis* Wood, 1922 (= *Hybolophus nelsoni* Grzybowski, 1899).

See Coan (1984) for exhaustive synonymy.

Holotype: British Museum of Natural History, Zoology, 1953.4.15.15.

Type locality: Western coast of South America.

Type horizon: Recent.

Material.—UWBM 101880, Los Organos, northern Peru, Recent, L 55.4, H 38.4, T 13.7; UWBM 101881, Los Organos, northern Peru, Recent, L 36.4, H 24.7, T 11.1;UWBM 101882, Perlas Islands, Pacific coast of Panama, dredged 12–18 m, Recent, L 57.1, H 38.6, T 13.1; UWBM 101883, Perlas Islands, Pacific coast of Panama, dredged 12–18 m, Recent, L 46.4, H 32.4, T 11.1; OSU 37597, DV 245-2, Punta Organos Chico, Peru, late Pleistocene, L 54.2, H 42.6, T 14.9; OSU 37598, DV 245-2, L 48.9, H 32.2, T 11.6; OSU 37599, DV 241-2, near Los Organos, Peru, middle Pleistocene, L 49.8, H 38.2, T (15); OSU 37600, DV 328-3, west of Cerro El Nuro, Peru, late Pliocene, L (73), H 56.2, T 19.9; OSU 37601, DV 328-3, L (70), H (56), T 25.6; OSU 37602, DV 243-1, northeast of Cerro El Nuro, Peru, late Pliocene; OSU 37603, DV 244-2, south of El Alto, Peru, late Pliocene, L 58.0, H 43.4, T 13.7; OSU 37604, DV 244-2, L 54.8, H 38.7, T 12.0; OSU 37606, DV 244-2, H (41).

Emended diagnosis.—Closely spaced primary and secondary posterior ridge. Pointed posterior margin. Posteriodorsal margin deeply concave.

Description.—Shell to 90 mm long, ovate produced posteriorly, beak about one-third length from anterior end, L:H ratio 1.3–1.5, T:H ratio 0.2–0.25, maximum inflation ventral to beak. Anteriodorsal profile straight to slightly concave, posteriodorsal profile deeply concave. Anterior and ventral margin rounded, latter often constricted posteriorly; posterior margin produced, narrowly truncate. Angular primary posterior ridge diverging 15° from posteriodorsal margin, weaker angular secondary posterior ridge diverging only a few degrees less. Lunule cordate, escutcheon elongate, both equally wide and half the length of respective margins. Beak orthogyrate. Umbo flattened, strongly opisthogyrate, with broad, widely spaced commarginal ribs. Exterior with variably developed regular and irregular anterior commarginal ribs. Remainder of exterior with irregular commarginal growth lines. Left anterior tooth narrow, wedge-shaped, inclined anteriorly 50°, separated entirely from lunule by groove. Left posterior cardinal tooth smaller, wedge-shaped, inclined anteriorly 10–20°. Right anterior pseudocardinal tooth thick, diverging from lunule margin, inclined anteriorly 25–35°. Right cardinal tooth wedge-shaped, inclined anteriorly 20–30°. Right posterior pseudo-

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cardinal tooth lamellar, diverging 10° posteriorly from midpoint of cardinal tooth. Inner ventral margin smooth.

Remarks.—Specimens of *Hybolophus gibbosus* are found in northern Peru on the Mancora, Talara, and Lobitos tablazos of early, middle, and late Pleistocene age, respectively, and in the Golf Course Member of the upper Pliocene Taime Formation (DeVries 1986, 1988). A large unfigured specimen is reported from the Pliocene Canoa Formation of southwestern Ecuador (Pilsbry and Olsson 1941). *Hybolophus aviaguensis peruviana* (Olsson, 1932) from the middle Miocene (Dunbar et al. 1990) Montera Formation of the northern Peruvian Sechura Basin has an equally concave posteriodorsal margin and equally strongly opisthogyrate umbo, but the beak is more anteriorly located and the anterior margin consequently is more tightly circular in profile.

Stratigraphic and geographic range.—Pliocene, Canoa Formation, Manabí Province, Ecuador; Taime Formation, northern Peru. Pleistocene, Mancora, Talara, and Lobitos Tablazo, northern Peru. Recent, Baja California to Piura, Peru.

Genus *Kalolophus* nov.

Etymology: From Greek *kalo*, beautiful, and *lophus*, ridge; to echo the species name of the extant *Kalolophus speciosus* (Latin *speciosus*, beautiful).

Type species: *Crassatellites* (*Scambula*) *chipolanus* Dall, 1903; Chipola Formation, Florida, early Miocene.

Species included: *Crassatella antillarum* Reeve, 1842; *Crassatellites* (*Scambula*) *chipolanus* Dall, 1903; *Crassatellites densus* Dall, 1900; *Crassatellites* (*Scambula*) *jamaicensis* Dall, 1903; *Eucrassatella mansfieldi* MacNeil, 1936; *Crassatellites mediamericanus* Brown and Pilsbry, 1913; *Crassatella speciosa* Adams, 1854.

Diagnosis.—Shell trapezoidal. Posterior variably produced, bluntly truncate. Weakly to moderately inflated ventral to beak, flattening towards posterior ridge. Umbo orthogyrate to slightly opisthogyrate. Escutcheon often wider than lunule. Resilifer extending nearly or entirely to ventral margin of hinge plate. Left anterior cardinal tooth not separated from beak by lunule. Inner ventral margin not crenulate.

Stratigraphic and geographic range.—Lower Miocene to Recent, Florida, Caribbean, and western North and South America.

Kalolophus chipolanus (Dall, 1903)

Fig. 4E–H.

1903 *Crassatellites* (*Scambula*) *chipolanus* sp. nov.? [sic!]; Dall 1903: 1472, pl. 49: 12.

1926 *Crassatellites* (*Scambula*) *chipolanus* Dall; Gardner 1926: 86, pl. 16: 10.

Type material: Holotype, complete adult right valve with hinge exposed: USNM 114713a, L 43.8, H 33.3, T 11.3. Paralectotypes, designated herein, from the same type locality as the holotype: USNM 114713b, L 38.8, H (25.7), T 8.4; 114713c, L 24.5, H 19.8, T 5.2; 114713d, L 24.3, H 19.2, T 5.7; 114713e, L 18.4, H 14.3, T 4.6.

Type locality: No. 2212, Tenmile Creek, 1 mile west of Bailey's Ferry, Calhoun County, Florida (Gardner 1926: 86).

Type horizon: Chipola Formation, lower Miocene.

Material.—UF 85322a, L (40.0), H 30.7, T 10.6; UF 85322b, L 26.2, H 20.7, T 7.9; UF 85322c, L 40.6, H 28.0, T 9.1; UF 85322d, L 39.3, H 30.6, T 10.1; UF 85322e, L 45.5, H 31.8, T 10.6; UF 85322f, 48.2, H 30.7, T 10.3; UF 85322g, L 46.2, H 36.1, T 13.8; UF 85322h, L 41.7, H 27.9, T 8.9; UF 85322i, L 23.9, H 19.5, T 5.9; UF 85322j, L 26.3, H 18.7, T 5.8; UF 85322k, L (26.0); UF 85322l, L 39.4, H 30.7, T 10.3. All from Farley Creek 04 (CA012), Calhoun County, Florida; Tulane University locality TU821.

Emended diagnosis.—Umbo with widely spaced commarginal ribs. Exterior with closely spaced commarginal ribs, sometimes absent medially and posteriorly.

Description.—Shell length to 45 mm, trapezoidal, beak located two-fifths distance from anterior, L: H ratio 1.2–1.5, T: H ratio 0.2–0.25, maximum inflation ventral to beak, nearly as inflated posteriorly as medially. Anteriodorsal and posteriodorsal margins straight to slightly concave. Anterior margin sharply rounded, posterior margin variably produced, broadly truncate, ventral margin evenly rounded, slightly pinched posteriorly. Angular posterior ridge with sulcus on both sides, diverging 20–25°, weak secondary posterior ridge 5° from posteriodorsal margin. Lunule and escutcheon elongate, equally wide, about half the length of respective margins. Beak prosogyrate. Umbo flattened, slightly opisthogyrate to orthogyrate, with widely spaced commarginal ribs. Anterior with closely spaced commarginal ribs; shell medially and posteriorly ribbed or smooth with fine irregularly spaced growth lines. No commarginal ribs posterior to primary posterior ridge. Resilifer extending to or nearly to vmHP. Left anterior cardinal tooth narrow, wedge-shaped, inclined anteriorly 40°, extending from vmHP to beak. Left posterior cardinal tooth lamellar, inclined anteriorly 15–20°. Right anterior pseudocardinal tooth coalesced with lunule. Right cardinal tooth thick, wedge-shaped, inclined anteriorly 20–25°. Right posterior pseudocardinal tooth lamellar, diverging 10–15° from midpoint of cardinal tooth, orthocline. Inner ventral margin smooth.

Remarks.—Specimens of early Miocene Floridian *Kalolophus chipolanus* differ from the lower Oligocene Floridian *Crassatella portelli* precisely in the characters that distinguish the two genera: the presence of a non-truncate left anterior cardinal tooth and full-length resilifer in the former and crenulated inner ventral margin in the latter. Consistent differences between *K. chipolanus* and other circum-Caribbean species of *Kalolophus*, excepting *K. antillarum*, are not readily apparent.

Stratigraphic and geographic range.—Chipola Formation, lower Miocene, Florida.

Kalolophus antillarum (Reeve, 1842)

Fig. 3A, B.

1832 *Crassatella undulata* sp. nov.; Sowerby, 1832: 56, not Say 1824, not Lamarck 1801.

1842 *Crassatella antillarum* sp. nov.; Reeve 1842: 44.

1843 *Crassatella antillarum*; Reeve 1843: vol. 1, pl. 2: 8.

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1917 *Crassatella digueti* sp. nov.; Lamy 1917: vol. 62, 2, 7.
1931 *Crassatellites antillarum* (Reeve); Grant and Gale 1931: 271, pl. 13: 7a, b.
1961 *Eucrassatella* (*Hybolophus*) *diqueti* [sic] (Lamy); Olsson 1961: 180, pl. 25: 2.
1964 *Eucrassatella* (*Hybolophus*) *antillarum* (Reeve); Weisbord 1964: 194, pl. 25: 9, 10.
1979 *Eucrassatella* (*Hybolophus*) *antillarum* (Reeve); Gibson-Smith and Gibson-Smith 1979: 28.
1984 *Eucrassatella antillarum* (Reeve, 1842); Coan 1984: 160, figs. 12–16.
2012 *Eucrassatella antillarum* (Reeve, 1842); Coan and Valentich-Scott 2012: 398, pl. 130.

See Weisbord (1964) and Coan (1984) for more extensive synonymies.

Holotype: British Museum of Natural History, Zoology, 1953.4.15.10.

Type locality: Isla Margarita, West Indies.

Type horizon: Recent.

Material.—UWBM 101884, Coché, near Margarita Island, Venezuela, on muddy sand at depth of 20–25 m, Recent, L 68.6, H 49.0, T 12.1; UWBM 101885, Canal de Adentro Island, Bahia de Panama, western Panama, from depth of 80 m, Recent, L 46.6, H 31.1, T 9.9.

Emended diagnosis.—Exterior of shell with exclusively irregular commarginal growth lines.

Description.—Shell to 90 mm long, sharply ovate anteriorly, posterior variably produced, beak located two-fifths of distance from anterior L:H ratio 1.4–1.6, T:H ratio 0.2, maximum inflation ventral to beak, nearly as inflated posteriorly as medially. Anteriodorsal profile straight, posteriodorsal profile concave. Anterior margin rounded, ventral margin broadly rounded and slightly constricted posteriorly, posterior margin bluntly truncate. Angular primary posterior ridge diverging 20° from posteriodorsal margin and weakly sulcate on both sides, weaker angular secondary posterior ridge midway between primary posterior ridge and escutcheon. Lunule elongate, sometimes narrow, half the length of anteriodorsal margin. Escutcheon less than half the length of posteriodorsal margin, wider than lunule. Beak and umbo orthogyrate to opisthogyrate. Umbo flattened, with broad undulations, not entirely commarginal and fading posteriorly and anteriorly. Remainder of exterior with irregular commarginal growth lines. Left anterior cardinal tooth narrow, wedge-shaped, inclined anteriorly 50–60°, extending from vmHP to beak, separated entirely from lunule by groove. Left posterior cardinal tooth narrower, wedge-shaped, inclined anteriorly 20–30°. Right anterior pseudocardinal tooth narrow, straight, nearly coincident with lunule margin. Right cardinal tooth straight, wedge-shaped, inclined anteriorly 40°. Right posterior pseudocardinal tooth lamellar, diverging 20° from midpoint of cardinal tooth. Inner ventral margin smooth.

Remarks.—*Kalolophus antillarum* had become established in the Pacific and Atlantic during the Pliocene (Grant and Gale 1931; Weisbord 1964; Gibson-Smith and Gibson-Smith 1979). Specimens of the modern sympatric crassatelline in the Pacific Ocean, *Hybolophus gibbosus*, are more inflated anteriorly, more constricted posteriorly, and their two posterior ridges are more closely spaced, thereby creating a posterior margin that is almost pointed. Specimens of the modern sympatric congener in the Atlantic Ocean, *K. speciosus*, resemble those of *K. antillarum* in most respects, but the exterior is entirely covered with regularly spaced and pronounced commarginal ribs (Fig. 3H_1).

Stratigraphic and geographic range.—Pliocene–Pleistocene, Gulf of California, Venezuela. Recent, Gulf of California to Guayas, Ecuador, and Venezuela.

Discussion

Crassatelline phylogeny.—*Crassatella neorhynchus* from the East Pisco Basin inhabited the southern end of a Lutetian tropical faunal province centered in the Talara Basin (Olsson 1931; Rivera 1957; DeVries 2004). The East Pisco *C. pedroi* sp. nov., seven million years younger but nearly identical, is the likely descendant of *C. neorhynchus*. *Crassatella rafaeli* sp. nov., living in the East Pisco Basin less than one million years after *C. pedroi*, differs significantly from its East Pisco predecessors and most other American crassatellines because of its closely spaced commarginal umbonal ribs. A phylogenetic connection with Australian/New Zealand crassatellines cannot be ruled out, since many southwestern Pacific taxa have similar umbonal sculpture. The only contemporaneous southwestern Pacific species that, like *C. rafaeli*, also had a crenulate inner ventral margin was the New Zealand Eocene *Triplicitella australis* (Hutton, 1873) (Table 1). However, *T. australis* has a broad resilifer that always reaches the vmHP, a character present only on some specimens of *C. rafaeli*.

The only western American taxa with umbonal ribs identical with those of *Crassatella rafaeli* are species of the East Pisco and Chilean *Tilicrassatella* gen. nov. The uniquely shared umbonal sculpture of Priabonian *C. rafaeli* and Chattian–Burdigalian species of *Tilicrassatella* indicates that *Tilicrassatella* species may have evolved from *C. rafaeli*. Such a scenario is consistent with the shift from a full-length resilifer in just a few specimens of *C. rafaeli* to its invariable presence in species of *Tilicrassatella*.

The shape of *Tilicrassatella* species diversified dramatically in south-central Peru during the early Miocene. The gibbose species, *T. ponderosa*, flattened and nearly equilateral species, *T. torrens* sp. nov., and posteriorly elongate species, *T. sanmartini* sp. nov. mimic comparably shaped crassatelline genera *Hybolophus*, *Kalolophus* gen. nov., and *Bathytormus*, respectively. Before the end of the middle Miocene, all species of *Tilicrassatella* were extinct.

Species of crassatelline genera in Argentina fared little better than species of *Tilicrassatella*. Entirely different than the crassatelline fauna of western South America, the Argentine fauna (Santelli and del Río 2014) included veneriform and strongly crenulate *Crassatella* species that persisted until the late Miocene; early Miocene taxa as-

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signed by the two authors to *Talabrica* Iredale, 1924 and *Spissatella*, presumed to be emigrants and immigrants to and from New Zealand, respectively; and species assigned to *Bathytormus,* present from the Paleocene through the early Miocene. Every Argentinian crassatelline taxon was extinct by the end of the Miocene except *Riosatella*, an extant monospecific *Crassatella*-like genus of uncertain phylogenetic affinity (Vokes 1973).

Crassatelline lineages in the circum-Caribbean and tropical western America have proven longer lived than those in southern South America. *Kalolophus*, which probably evolved in Florida during the late Oligocene from the morphologically transitional *Crassatella portelli* sp. nov., has occupied the circum-Caribbean from the early Miocene (*K. chipolanus*) to the present (*K. speciosus*). Populations of *K. antillarum*, which appeared in the Caribbean during the Pliocene (Weisbord 1964; Gibson-Smith and Gibson-Smith 1979), had spread into the equatorial Pacific Ocean before the late Pliocene shallow-water closure of the Isthmus of Panama (Grant and Gale 1931; Leigh et al. 2014). *Kalolophus densus*, occurring in middle Miocene strata of Florida, exemplifies a morphology transitional between that of the small and thin *K. chipolanus* and the large, thick, and posteriorly elongate species from the Atlantic margin of North America assigned by Ward and Blackwelder (1987) to *Marvacrassatella* (Table 1). The oldest species of *Marvacrassatella* is the middle Miocene (Andrews 1976) *M. melinus* (Conrad, 1832); the youngest, the early Pleistocene (Blackwelder 1981) *M. kauffmani* Ward and Blackwelder, 1987.

The oldest known *Hybolophus* species is the veneriform late Eocene or Oligocene *H. disenum* sp. nov. from northern Peru, possibly a transitional species between *Crassatella* and *Hybolophus* if ventral crenulations can be found on specimens not yet discovered. The second oldest known *Hybolophus* species is the veneriform early Miocene Ecuadorian *H. carrizalensis*. The veneriform profile may be the ancestral state of *Hybolophus*, with posteriorly produced taxa evolving in Peru during the early Miocene (*H. nelsoni*) and spreading to the Caribbean (e.g., *H. aviaguensis*), sympatric with late Miocene veneriform taxa (*H. picaderus*, *H. tuberus*). The sole surviving veneriform species is the Quaternary *H. fluctuatus*, living sympatrically with the sole surviving posteriorly produced species, *H. gibbosus*.

A phylogenetic tree diagram for crassatelline genera discussed in this paper is presented in Fig. 11. Notably different than other treatments is the separation of large Neogene taxa into four independent lineages. The arrangement of New Zealand genera is adopted from Collins et al. (2014) except that the late Eocene species, *Spissatella media* (Marwick, 1926), is transferred to *Eucrassatella* based on a dorsally truncated left anterior cardinal tooth present on a specimen from the Geology Department, University of Otago (New Zealand) (OU8648, McCullough's Bridge; Katie Collins, personal communication 2015). The New Zealand species, *E. subobesa* (Marshall and Murdoch, 1919) and Australian *E. maudensis* (Pritchard, 1903) and (suggested herein) *E. oblonga* (Tenison Woods, 1876), all late Oligocene species (Darragh 1965; Collins et al. 2014) and all with a left anterior cardinal tooth extending to the beak, are candidates for the transitional taxon connecting late Eocene *Eucrassatella* and late Oligocene to middle Miocene *Spissatella*, some species of which have a left anterior cardinal tooth extending to the beak (Table 1).

The two sympatric lineages in the circum-Caribbean and tropical western America exhibit a number of convergent characters, including a flattened umbo, a full-size resilifer, a smooth inner ventral margin, and a dorsally extended left anterior cardinal tooth. These characters had appeared in *Hybolophus* species by the late Eocene or early Oligocene but were not all present in *Kalolophus* species until after the early Oligocene. Only one of the three characters was fully realized in the relatively short-lived latest Oligocene to middle Miocene *Tilicrassatella*.

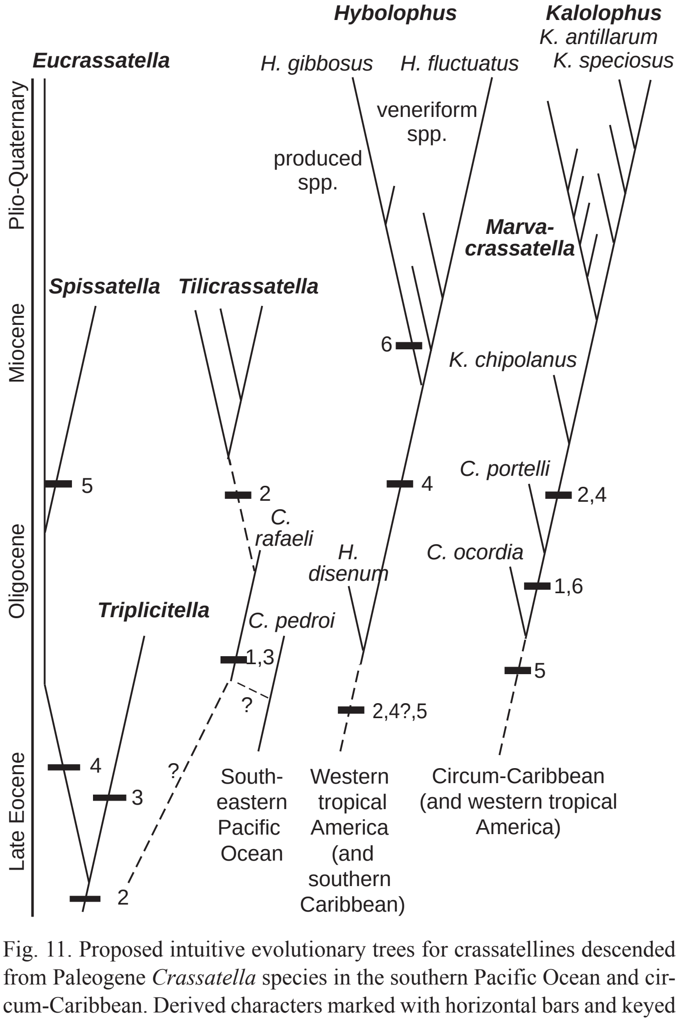

Fig. 11. Proposed intuitive evolutionary trees for crassatellines descended from Paleogene *Crassatella* species in the southern Pacific Ocean and circum-Caribbean. Derived characters marked with horizontal bars and keyed by number to list of characters: 1, occasional presence of large resilifer; 2, always presence of large resilifer; 3, occasional loss of ventral marginal crenulation; 4, always loss of ventral marginal crenulation; 5, occasional extension of left cardinal tooth to beak; 6, always extension of left cardinal tooth to beak. Dashed lines with question marks represent alternative hypotheses regarding origin of *Crassatella rafaeli* in south-central Peru. New Zealand tree modified from Collins et al. (2014).

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Impetus for crassatelline convergence.—Four independent crassatelline lineages evolved one or more identical features during the late Eocene and Oligocene. The most prevalent, seen in the southwestern Pacific genus, *Eucrassatella*, the southeastern Pacific genus, *Tilicrassatella*, and the North American genera, *Hybolophus* and *Kalolophus*, was a broader and longer resilifer. Nearly as prevalent was a smooth inner ventral margin, with ventral crenulations enduring only in the short-lived *Tilicrassatella*. A dorsally extended left anterior cardinal tooth appeared in *Hybolophus*, *Kalolophus*, and the southwestern Pacific *Spissatella* (Table 1).

The resilium, which nestles between facing resilifers, exerts an outward force to maintain a shell gape, counteracting a force exerted by the two adductor muscles to pull the valves closed (Kauffman 1969). The resilium also helps align the two valves and resists shear forces parallel to the plane of commissure that might arise while burrowing or being predated, as do the cardinal teeth (Stanley 1970). Ventral crenulations may also assist in aligning valves; they can also impede passage of sediment and debris when the valves are slightly open (Vermeij 2013), resist compressive pressure applied by predators (Thomas 2013), and thwart attempts by predators to drill or enter the bivalve through the valve margin (Vermeij 1983).

Two specimens with an anomalous cardinal tooth deserve mention. A left valve of the species *Tilicrassatella torrens* (UWBM 101852; see Fig. 8G_1) has a thin anterior cardinal tooth and anterior groove extending entirely to the beak, separated from a gracile lunule, much different than the truncated anterior cardinal tooth and robust lunule of all other left valves of all *Tilicrassatella* species. An extended left anterior cardinal tooth and anterior groove is also present on a specimen (USNM 618238; see Fig. 9B_2) of the species *Hybolophus disenum*, in which the two left cardinal teeth remain separated by an exceptionally wide socket terminating bluntly at the beak. Perhaps the expression of such phenotypic oddities reflects an underlying genetic propensity for an extended left anterior cardinal tooth, eventually realized as a ubiquitous character in the genera *Spissatella* and *Kalolophus* and present in the majority of *Hybolophus* taxa.

The late Eocene–Oligocene trend in crassatellines towards a ventrally elongated resilifer (and hence larger resilium) and dorsally extended left anterior cardinal tooth would have enhanced an animal's ability to align its valves and resist rotational forces in the plane of commissure. Ventral crenulations, already small in *Crassatella*, might have become less useful. The loss of crenulations might also signify that the passage of foreign material and predators across the shell margin had become less of a problem. A shift among crassatellines to burrowing in finer-grained and more cohesive sediment would be consistent with the morphological changes seen. Such sediment, probably medium- and fine-grained sand, would be encountered more often on the continental shelf or in lagoons and embayments than in the surf zone or well above wave base.

In the East Pisco Basin, specimens of *Crassatella neorhynchus* and *C. pedroi*, often paired, are found in coarse-grained and crossbedded transgressive sandstone beds of the upper Eocene Paracas and Otuma sequences, in the former case associated with the non-siphonate bivalve genera *Nucula*, *Ostrea*, *Glycymeris*, *Cucullaea*, and *Cyclocardia*. Specimens of *Tilicrassatella* species, often paired, similarly occur in coarse-grained bioclastic sandstone and gravelly sandstone of the uppermost Oligocene–lower Miocene Chilcatay depositional sequence and similar sediments of the basal Pisco depositional sequence, either in the basal transgressive unit, gravelly bioclastic intervals, or atop foreset beds. The *Tilicrassatella* specimens are associated with byssate, cemented, and non-siphonate *Ostrea*, *Glycymeris*, *Atrina*, and pectinid bivalves. Specimens of *C. rafaeli*, present throughout the Otuma depositional sequence and usually paired, occur in coarse-grained sandstone lenses interspersed with lenses of mudstone and large stranded tree trunks. Associated bivalves include *Ostrea*, *Cyclocardia*, *Corbula*, lucinids, and venerids. Based solely on sedimentological evidence, all the above-mentioned sediments are interpreted to have been deposited in shallow and agitated water, subject to reworking by waves, wave-induced currents, or in the case of beds with *C. rafaeli*, estuarine currents.

The oldest known and possibly transitional species of *Hybolophus*, the late Eocene or early Oligocene *H. disenum*, has a matrix of poorly sorted, bioclastic, coarse-grained sand and gravel, consistent with a high-energy depositional setting. Langhian and Serravallian specimens of *Hybolophus maleficae* from the East Pisco Basin, in contrast, occur in massive, bioturbated, and moderately well-sorted sandstone above basal transgressive deposits of the Pisco depositional sequence, associated with in situ paired valves of *Chione* and in situ paired valves and concentrated lags of disarticulated *Mulinia* and *Anadara sechurana*. A more diverse assemblage of in situ and transported venerids (*Chione*, *Chionopsis*, *Dosinia*, *Amiantis*) is associated with Tortonian paired and disarticulated valves of *H. maleficae* in winnowed tuffaceous sandstone of the Sacaco Basin and Messinian paired and disarticulated valves of *H. terrestris* in rippled and scoured tuffaceous silty sandstone in the East Pisco Basin. These middle and upper Miocene sediments, which in the Messinian example contain pelagic diatoms and clupeoid fish scales, are interpreted to have been deposited at inner and mid-shelf depths above storm wave base.

Modern specimens of *Hybolophus gibbosus*, *H. antillarum*, and *H. fluctuatus* are found in sand and less often gravel in water depths of 5–110 m and 5–206 m, respectively (Coan 1984; Coan and Valentich-Scott 2012), depths which are consistent with the occurrence of *H. gibbosus* in the upper Pliocene Taime Formation in massive, bioturbated, and moderately well-sorted medium-grained sandstone, associated with innumerable molds of *Mulinia* and *Pitar* valves (DeVries 1986). Single valves of *H. gibbosus* also constitute a small fraction of the bioclastic debris on the surface of Mancora and Lobitos tablazos of northern Peru and northern Peruvian modern beaches.

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In the circum-Caribbean region, the *Crassatella*-bearing upper Eocene Ocala limestone consists of packstone, wackestone, and grainstone with abundant foraminifera, echinoids, and mollusks (Carr and Alverson 1959; Scott et al. 2001), indicating a shallow high-energy depositional environment (Portell and Hulbert 2011). Shallow to moderate depth is indicated for the lower Oligocene Suwannee limestone and its fauna, including the transitional *Crassatella portelli* (Carr and Alverson 1959). The sandy and clayey limestone of the lower Miocene Chipola Formation, containing the oldest *Kalolophus*, *K. chipolanus*, are attributed to a nearshore shelf environment (Bryant et al. 1992) or, in the case of the Farley Creek deposits with specimens of *K. chipolanus*, a quiet-water embayment (Brown et al. 2013). Specimens of modern *K. speciosus* in collections of the Department of Invertebrate Zoology at the Smithsonian Museum of Natural History (e.g., USNM 833713, USNM 855600) were collected at depths of 10−60 m. The quieter waters successively occupied by Floridian crassatellines is reflected in the morphological transition from *Crassatella* to *Kalolophus* involving the cardinal teeth, resilifer, and ventral crenulation.

A similar pattern of crassatellines shifting to deeper waters during the Eocene and Oligocene is not so clearly demonstrated with the southwestern Pacific fossil record, since no Paleogene *Crassatella* have been found in Australia and New Zealand. It has been argued that species of *Spissatella*, a largely Neogene clade with full-sized resilifers, left anterior cardinal teeth extending to the beak, and smooth ventral margins, occupied deeper shelf environments than older and contemporaneous species of *Eucrassatella*, which retain truncated left anterior cardinal teeth (Beu and Maxwell 1990; Collins 2013).

Why crassatellines should have had less evolutionary success in shallow and/or more agitated environments following the Eocene is not known. Ocean cooling may have played an indirect role (Berggren and Prothero 1992), or a shift from predominantly benthic to planktonic primary production (Vermeij 2011), or the rapid diversification at the generic level of competing infaunal siphonate bivalves (Stanley 1968). Why Neogene crassatellines were able to occupy deeper or quieter water niches that they had not previously favored is also not known.

Conclusions

Evidence has been presented that most American, Australian, and New Zealand large crassatelline bivalves evolved from *Crassatella* forbears in one of four independent lineages, represented by the genera *Eucrassatella*, *Hybolophus*, and two new genera, *Tilicrassatella* and *Kalolophus*. During the late Eocene and early Oligocene, convergent changes in hinge structure and the ventral margin in two, three, or all four lineages coincided with and might explain the greater success of Neogene and modern large crassatellines in deeper or quieter waters, whether on the continental shelf or in lagoons and bays.

The classification scheme presented in this paper excludes a number of crassatellines and proposes phylogenetic connections that would bear testing by other means, including statistical cladistic methodologies and a comparison of mitochondrial DNA sequences. For example, comparing the genetic sequences of extant circum-Caribbean and tropical western American species (*H. gibbosus*, *H. fluctuatus*, *K. speciosus*, *K. antillarum*) would constitute an independent test of the phylogeny of *Hybolophus* and *Kalolophus* proposed here. Similar tests could be applied to extant *Crassatella*-like species found in the western Pacific, the northeastern Pacific (*Hybolophus fluctuatus*), the southwestern Atlantic, and South Africa. It is not known if these taxa are related to one another, are descendants of Neogene genera, or are independent lineages derived from Paleogene ancestors. Lastly, a stratophenotypic cladistic analysis of the diverse fauna of fossil and modern crassatellines in Australia, including a *Crassatella* of Miocene age (Darragh 1965), might show that the phylogeny of Australian crassatellines is more complex than previously perceived, if independent crassatelline lineages truly arose as readily as this study indicates.

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Appendix 1

Samples-locality.

Complete locality data available in Supplementary Online Material available at http://app.pan.pl/SOM/app61-DeVries_SOM.pdf

Abbreviations: Bxxxx, Burke Museum locality numbers; DV, DeVries numbers; JM, locality numbers of José Macharé, presently with the Instituto Geofísico del Perú, Lima.

DV 241-2, northern Peru, 4 km SE of Los Organos, a mesa SW Quebrada Carillos. Talara tablazo, middle Pleistocene (see DeVries 1986).

DV 243-1, northern Peru, about 1.5 km NE of Cerro El Nuro, six meters up in section. Taime Formation, upper Pliocene (see DeVries 1986).

DV 244-2, northern Peru, about 5 km S of El Alto, southernmost branch of Quebrada Taime, cliff face and dissected hills above cliffs, upper siltstone unit. Taime Formation, upper Pliocene (see DeVries 1986).

DV 245-2, northern Peru, Punta Organos Chico, 1 km SW of Los Organos, seaward edge of terrace. Lobitos tablazo, upper Pleistocene (see DeVries 1986).

DV 328-3, northern Peru, about 2 km W of Cerro El Nuro, cliff faces. Taime Formation, upper Pliocene (see DeVries 1986).

B8304, DV 377-2, 14°45’45” S, 75°30’27” W
B8305, DV 377-3, 14°45’45” S, 75°30’27” W
B8306, DV 386-1, 14°58’19” S, 75°19’49” W
B8307, DV 390-1, 14°09’50” S, 76°04’35” W
B8308, DV 396-1, 14°11’42” S, 76°06’57” W
B8309, DV 396-13, 14°11’20” S, 76°06’23” W
B8310, DV 397-1, 14°11’15” S, 76°05’35” W
B8311, DV 409-1, 13°54’08” S, 76°11’09” W
B8312, DV 411-1, 13°53’51” S, 76°09’22” W
B8313, DV 420-1, 13°57’48” S, 76°07’18” W
B8314, DV 441-12, 14°11’31” S, 76°06’56” W
B8315, DV 468a-1, 15°17’58” S, 75°08’26” W
B8316, DV 482-8, 14°30’41” S, 75°40’00” W
B8317, DV 482-12, 14°30’41” S, 75°40’00” W
B8318, DV 509-2, 14°39’50” S, 75°37’56” W
B8319, DV 523-1, 14°48’02” S, 75°23’02” W
B8320, DV 523-2, 14°48’02” S, 75°23’02” W
B8321, DV 542a-13, 14°35’31” S, 75°40’15” W
B8322, DV 544-1, 14°39’48” S, 75°37’57” W
B8323, DV 562-3, 15°29’13” S, 74°48’16” W
B8324, DV 574-2, 14°45’13” S, 75°30’39” W
B8325, DV 574-3, 14°45’13” S, 75°30’39” W
B8326, DV 575-3, 14°45’54” S, 75°30’53” W
B8327, DV 578-1, 14°46’28” S, 75°30’43” W
B8328, DV 598-1, 14°45’46” S, 75°30’58” W
B8329, DV 631-6, 14°09’48” S, 76°09’03” W
B8330, DV 632-3, 14°11’21” S, 76°08’22” W
B8331, DV 1174-1, 14°08’37” S, 76°10’16” W
B8332, DV 1272-1, 16°42’09” S, 72°26’57” W
B8333, DV 1320-1, 14°25’59” S, 75°49’19” W
B8334, DV 1650-1, 14°23’24” S, 75°53’52” W
B8335, DV 1655-4, 14°50’26” S, 75°27’38” W
B8336, DV 1732-1, 14°34’38” S, 75°51’37” W
B8337, DV 1805-1, 14°35’33” S, 75°40’18” W
B8338, DV 1809-1, 14°35’44” S, 75°41’33” W
B8339, DV 1816-1, 14°11’45” S, 76°08’40” W
B8340, DV 2023-1, 14°38’33” S, 75°47’31” W
B8341, DV 2040-1, 13°55’40” S, 76°16’00” W
B8342, DV 2255-1, 14°24’34” S, 75°53’49” W
B8343, DV 3004-1, 14°34’36” S, 75°39’55” W
B8344, DV 3022-1, 14°24’57” S, 75°55’13” W
B8345, DV 3039-1, 14°33’03” S, 75°43’45” W
B8346, DV 3078-1, 14°38’33” S, 75°49’03” W
B8347, DV 3080-2, 14°40’43” S, 75°50’04” W
B8348, DV 3096-1, 14°38’06” S, 75°47’30” W
B8349, DV 4042-1, 14°23’02” S, 75°54’00” W
B8350, DV 4088-1, 14°25’59” S, 75°49’20” W
B8351, DV 5041-1, 14°50’20” S, 75°27’59” W
B8352, DV 5092-1, 14°22’40” S, 75°54’50” W
B8353, DV 5115-1, 14°22’21” S, 75°54’24” W
B8354, JM 83 018-1, 14°51’30” S, 75°21’30” W
B8355, JM 83 020b-1, 14°52’30” S, 75°24’00” W
B8356, JM 84 323-1, 14°35’30” S, 75°41’00” W

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