

The *Cantharus* Group of Pisaniine Buccinid Gastropods: Review of the Oligocene to Recent Genera and Description of Some New Species of *Gemophos* and *Hesperisternia*

Geerat J. Vermeij¹

¹Department of Geology, University of California at Davis, One Shields Avenue, Davis, CA 95616, USA;
e-mail: vermeij@geology.ucdavis.edu

Received: 12 May 2004; revised version accepted 22 December 2004

The *Cantharus* group of pisaniine buccinid gastropods is represented in the Oligocene to Recent interval by twelve genera, two of which are extinct. I review the species composition, synonymy, characteristics, and fossil record of these genera: *Anna* Risso, 1826 (early Oligocene to Recent, eastern Atlantic); *Cancellopolia* Vermeij and Bouchet, 1998 (Recent, Indo-West Pacific); *Cantharus* Röding, 1798 (Pliocene to Recent, Indo-West Pacific); *Editharus* Vermeij, 2001a (early Eocene to early Oligocene, Europe); *Gemophos* Olsson and Harbison, 1953 (late Miocene to Recent, tropical and subtropical America, one species in West Africa); *Hesperisternia* Gardner, 1944 (late Oligocene to Recent, tropical and subtropical America); *Pollia* Gray in Sowerby, 1834 (early Miocene to Recent, Indo-West Pacific; one species in West Africa); *Preangeria* Martin, 1921 (early Miocene to Recent, Indo-West Pacific); *Prodotia* Dall, 1924 (?late Miocene to Recent, Indo-West Pacific); *Pusio* Gray in Griffith and Pidgeon, 1834 (?early and middle Miocene, late Miocene to Recent, eastern Pacific); *Solenosteira* Dall, 1890 (late Miocene to Recent, tropical America); and *Zeapollia* Finlay, 1927 (Oligocene to Pliocene, Australia and New Zealand). Besides many generic reassignments, I describe the following new species: *Gemophos basidentatus* (early Pleistocene, Florida); *G. crispatus* (late Pliocene, Florida); *G. filistriatus* (Recent, North Carolina to eastern Florida); *Hesperisternia binodosa* (late Pliocene, Atlantic Costa Rica); *H. distans* (early Miocene, Venezuela); and *H. petuchi* (late Miocene, Maryland). New morphological data are presented for *Gemophos tridentatus* (Tuomey and Holmes, 1857) from the late Pliocene of the southeastern United States.

Biogeographically, the *Cantharus* group conforms to many other shallow-water molluscan clades in having its highest diversity in the Indo-West Pacific (about 25 species), followed by the eastern Pacific (19), western Atlantic (7), and eastern Atlantic (5). Within the western Atlantic, a distinction at the species level between the Gatunian Province (Greater Antilles to Brazil) and the Caloosahatchian Province (southeastern United States) has existed throughout the Neogene. At least three invasions from the Gatunian to the Caloosahatchian Province are documented, two in *Gemophos* and one in *Solenosteira*. In addition, *Gemophos* spread across the Atlantic to West Africa, and *Pollia* extended its range from the Indian Ocean to West Africa. Neogene extinction was most intense in the western Atlantic, where the end of the Pliocene witnessed the regional or global extinction of at least two lineages of *Solenosteira* and one each of *Gemophos* and *Hesperisternia*. Warm-temperate members of the *Cantharus* group disappeared in the Pliocene and Pleistocene in California, Australia, New Zealand, and the northwestern Atlantic, and survive today only in the Mediterranean.

KEY WORDS: Buccinidae, Neogene, Gastropoda, taxonomy, biogeography.

Introduction

The history of the marine tropical biota is a complex tale of evolution, invasion, and extinction against a backdrop of climatic and tectonic change. One of the more effective tactics in telling this history is to interrogate the species taking part in it. This, in turn, requires a detailed understanding of the taxonomy and phylogenetic relationships of clades that have achieved a circumtropical distribution and for which a substantial fossil record is available.

This paper is a contribution to that end. In it, I examine

the genus-level taxonomy, morphology, biogeography, and evolution of the *Cantharus* group of pisaniine buccinid gastropods, and I complement a species-level summary for most of the genera with more detailed accounts of two American genera, *Gemophos* and *Hesperisternia*.

Systematic Palaeontology

Abbreviations – The following abbreviations are used to denote repositories for material referred to in the text.

ANSP	Academy of Natural Sciences, Philadelphia, PA, USA
NMB	Naturhistorisches Museum, Basel, Switzerland
PRI	Paleontological Research Institute, Ithaca, NY, USA
RGM	Rijksmuseum voor Geologie en Mineralogie (now Nationaal Museum voor Natuurlijke Historie), Leiden, The Netherlands
TU	Tulane University, New Orleans, LA, USA
UCMP	University of California Museum of Paleontology, Berkeley, CA, USA
UF	University of Florida (now Florida Museum of Natural History), Gainesville, FL, USA
USNM	United States National Museum of Natural History (Smithsonian Institution), Washington, DC, USA

Family Buccinidae Rafinesque, 1815
Subfamily Pisaniinae Gray, 1857

Remarks – As understood by Vermeij (2001a), the Pisaniinae comprises a group of mainly tropical, shallow-water predatory buccinid gastropods living on hard bottoms, in seagrass meadows, and occasionally on firm sand. The shell is small to medium-sized for the family (maximum length about 100 mm), ovate to fusiform, with a short siphonal canal, crenulated outer lip, rounded axial ribs (when present), and a columella with one or two weak basal folds. The square rachidian of the radula typically bears three cusps with fusiform bases, the central cusp generally being the largest and the lateral cusps, which sometimes bifurcate, being smaller (see Cernohorsky, 1971, 1975). The Pisaniinae extend back certainly to the late Cretaceous (Campanian), and possibly into the early Cretaceous (see Vermeij, 2001a).

Using Cernohorsky's (1971, 1975) scheme of classification as a point of departure, I divide the Pisaniinae informally into three groups, which may or may not be clades (Vermeij, 2001a). These are (1) the *Pisania* group, comprising Eocene to Recent species with generally thin shells having a terminal varix, fine to obsolete adult spiral sculpture, reduced axial sculpture, and a high spire; (2) the *Engina* group, also ranging from the Eocene to the Recent, having a narrow aperture, denticles on the inner (adaxial) side of the outer lip, a terminal varix, and distinct axial ribs on the teleoconch; and (3) the *Cantharus* group, ranging from the Cretaceous onward, in which the inner side of the outer lip is usually lirate rather than denticulate, the aperture is broadly ovate to ovate-elongate, the adult outer lip with or without a terminal varix; and spiral and axial sculpture is usually well developed on the teleoconch.

In an earlier paper (Vermeij, 2001a), I treated the pre-Oligocene members of the *Cantharus* group. Here, the focus shifts to species evolved during and after the Oligocene. Despite much previous confusion, this group of species comprises several distinct higher taxa, which I review below. In future papers, I plan to investigate the

phylogenetic relationships among these groups.

I currently recognize twelve genera in the *Cantharus* group with post-Eocene representatives. These are *Anna*, *Cancellopollia*, *Cantharus*, *Editharus*, *Gemophos*, *Hesperisternia*, *Polliia*, *Preangeria*, *Prodotia*, *Pusio*, *Solenosteira*, and *Zeapolliia*. *Preangeria*, an early Miocene to Recent genus of four fossil and one Recent species, diverges widely from other members of the *Cantharus* group, and was discussed by Vermeij (1998a, 2001b); I include it here only for completeness. *Prodotia* may be more closely related to the *Pisania* group. Although I shall characterize it briefly here, its taxonomy and scope require more research; I therefore confine myself to a general comparison to other genera.

Genus *Anna* Risso, 1826

Type species – *Anna massena* Risso, 1826, by monotypy.

Remarks – Based on my examination of most of the described species, the genus *Anna* is characterized by a fusiform, basally weakly constricted shell; weak to obsolete axial sculpture of 11 or more ribs on the last teleoconch whorl; ten or more weak spiral cords or threads, often with threads between and on the cords, on the last teleoconch whorl; a distinct parietal tooth at the adapical end of the inner lip; a terminal, varix-like outer lip with downwardly convex, crenate edge with the crenations unpaired and with six or more denticles or short lirae on its inner side; low siphonal fasciole often present; umbilical chink absent. No species I have seen exceeds a length of 27 mm. The genus ranges from the early Oligocene to the Recent in the Mediterranean, western Europe, and West Africa.

Well-known species include *A. assimilis* (Reeve, 1846), Recent, Senegal; *A. badensis* (Hörnes and Auinger, 1890) Badenian = Langhian middle Miocene, Vienna Basin; *A. bredai* (Michelotti, 1847), Tortonian late Miocene, Italy; *A. cancellarioides* (Basterot, 1825), Aquitanian and Burdigalian early Miocene, southern Europe; *A. consobrina* (Cossmann and Lambert, 1884), early Oligocene, France; *A. dorbignyi* (Payraudeau, 1826), late Miocene to Recent, Mediterranean region and Paratethys (likely with many synonyms named by Bellardi, 1873; and Hörnes and Auinger, 1890; see De Gregorio, 1885); *A. minutulus* (Baluk, 1995), Tortonian late Miocene, Poland; *A. massena* Risso, 1826 (= *Buccinum scacchianum* Philippi, 1844; see Dall, 1918; Arnaud, 1977), Recent, Mediterranean; *A. scabra* (Locard, 1886), Recent, Mediterranean; and *A. unifilosa* (Bellardi, 1873), Tortonian late Miocene, Italy.

Most fossil species of *Anna* were assigned by their describers to *Polliia*. *Anna* differs from the Indo-West-Pacific (IWP) genus *Polliia* by lacking a labral tooth at the edge of the outer lip and by having denticles or very short lirae instead of long lirae on the inner side of the outer lip. These same differences distinguish *Anna* from *Cancellopollia*. *Anna* differs from *Gemophos* by lacking

the latter's tubercle-like adapical extension of the adult varix, having crenations on the edge of the adult outer lip unpaired instead of paired, and having denticles or short lirae instead of long lirae on the inner side of the outer lip.

Glibert (1963) assigned most of the species of *Anna* to *Eocantharus* Clark, 1938 (type species: *Cantharus (Eocantharus) cowlitzensis* Clark, 1938). This early Paleocene to late Eocene genus differs from *Anna* by usually lacking an adult outer varix and by lacking a parietal tooth at the adapical end of the inner lip (see Vermeij, 2001a).

Many Oligocene to Pliocene species from Europe originally described as species of *Pollia* or *Tritonidea* (an objective junior synonym of *Pollia*) and therefore potentially assignable to *Anna* are in fact muricids belonging to the genus *Orania* Pallary, 1900. The tradition of considering these species as buccinids evidently began with Bellardi (1873), whose broad concept of *Pollia* was accepted by Fontannes (1882), Hörnes and Auinger (1890), Janssen (1984), and Chirli (2000), among others. *Orania* consistently differs from *Anna* and other members of the *Cantharus* group by having a planar outer lip, an adapical notch in the outer lip, and a more angular instead of a gradually concave basal constriction. Houart (1995, 1997, 2001) provides good descriptions of the genus *Orania* and of its Recent species.

Another related genus is *Aplus* De Gregorio, 1885 (type species: *Murex serzus* De Gregorio, 1885; see Vokes, 1971), a group I have provisionally assigned to the *Engina* group of Pisaniinae (Vermeij, 2001a). In fact, Monterosato (1917: 20) included *Anna dorbignyi* in *Aplus*, and many species described by Bellardi (1873) and Hörnes and Auinger (1890) under *Pollia* belong either to *Aplus* or to its possible junior synonym *Enginella* Monterosato, 1917 (type species: *Buccinum leucozonum* Philippi, 1844). In *Aplus*, denticles on the inner side of the outer lip are enlarged relative to those in *Anna*, and the aperture is much narrower. It is very likely that *Aplus*, which appears in the early Miocene (Aquitainian) of France (as *Nassa andrei* Basterot, 1825, placed in *Cantharus* by Lozouet *et al.*, 2001) and other Neogene members of the *Engina* group are derived from an ancestor with the characters of *Anna*.

Genus *Cancellopolia* Vermeij and Bouchet, 1998

Type species – *Cancellopolia gracilis* Vermeij and Bouchet, 1998, by original designation.

Remarks – Adult shells of this deep-water, Recent Indo-West Pacific (IWP) genus are characterized by small size (maximum length 31.8 mm in *C. gracilis*), with constricted base, rounded last teleoconch whorl, cancellate sculpture of 15 or more axial ribs and 18 or more spiral cords on the last whorl; prominent parietal tooth at the adapical end of the inner lip; terminal ascending varix with blunt labral tooth at the midpoint of the edge and a

few brief lirae on its inner side, narrowly elongate aperture tapering adapically, spirally threaded siphonal fasciole, and absence of an umbilical chink. There are two described species, *C. gracilis* and *C. ustulata* of Vermeij and Bouchet (1998), both from banks and seamounts near Vanuatu and New Caledonia.

Genus *Cantharus* Röding, 1798

Type species – *Buccinum tranquebaricum* Gmelin (1791), subsequent designation by Cossmann (1901).

Remarks – As narrowly defined by Vermeij and Bouchet (1998) and in this paper, *Cantharus* is a Pliocene to Recent IWP genus characterized by a large, ovate shell (maximum length more than 100 mm in *C. melanostomus*) with little or no basal constriction, whorls with more or less distinct angulation on upper part, strong, widely separated axial folds on upper part of last whorl, crossed by spiral cords and threads of varying sizes; weakly developed parietal tooth at adapical end of inner lip; ovate to narrowly elongate aperture not tapering adapically; outer lip weakly convex, typically thin, but occasionally varix-like (in some *C. leucotaeniatus* and *C. melanostomus*), with sharp unpaired crenulations at its edge and a distinct labral tooth formed as the fourth or fifth crenulation (counting from the abapical end) and situated at the end of an external groove; prominent spirally threaded siphonal fasciole; long prominent lirae on inner side of outer lip; umbilical slit open or closed.

I include the following taxa: *C. cecillei* (Philippi, 1848), Recent Japan to northernmost Australia; *C. erythrostomus* (Reeve, 1846), Recent, northwestern Australia; *C. erythrostomus mekranicus* Vredenburg, 1925, Pliocene, Pakistan; *C. leucotaeniatus* Kosuge, 1985, Recent, deep water, off the Philippines and Vanuatu; *C. melanostomus* (Sowerby, 1825), Recent, southeast Asia; *C. okinawa* MacNeil, 1961, Pliocene, Okinawa; *C. septemcostatus* Vermeij and Bouchet, 1998, Recent, north of New Caledonia; *C. spiralis* (Gray, 1839), Recent, Arabian Sea; ?*C. totomiensis* (Makiyama, 1927), Pliocene, Japan; and *C. tranquebaricus* (Gmelin, 1791), Recent, southeast India. There is an additional undescribed species closely related to *C. leucotaeniatus* and *C. septemcostatus* from the Pleistocene of Viti Levu, Fiji (Vermeij and Bouchet, 1998). A species similar to or the same as *C. tranquebaricus* occurs off Natal, south Africa.

I include *C. cecillei* and tentatively *C. totomiensis* in *Cantharus*, because these species lack a terminal varix, have a weak parietal tooth or none at all, and have the labral tooth in a relatively abapical position. These species, however, resemble *Pollia* in their fusiform shape, and may represent a morphology phylogenetically linking *Pollia* and *Cantharus*.

The taxon *Cantharus* has in the past been used very broadly for most or all members of the *Cantharus* group. Cernohorsky (1975) included in *Cantharus* not only the species related to *C. tranquebaricus*, but also eastern

Atlantic species of *Anna* and tropical American species of *Muricantharus* (= *Hesperisternia*). Vermeij and Bouchet (1998) restricted *Cantharus* to the *C. tranquebaricus* group, and Vermeij (2001b) suggested that *Cantharus* in this restricted sense forms a labral-tooth-bearing clade of mainly Indo-West Pacific species along with members of the genera *Polliia* and *Cancellopolliia*.

In overall shell form, *Cantharus* most closely resembles a group of tropical American species for which Olsson (1971) proposed the genus *Muricantharus* (type species: *Pseudoneptunea panamica* Hertlein and Strong, 1951). As noted below under *Hesperisternia*, I regard *Muricantharus* as a junior subjective synonym of *Hesperisternia* Gardner, 1944. The American species differ from *Cantharus* by lacking a labral tooth and by having a planar rather than a weakly convex outer lip whose edge bears weak paired or unpaired crenulations instead of sharp unpaired crenulations. The lirae of *Hesperisternia* tend to be brief and indistinct, whereas those of *Cantharus* are long and prominent. *Anna* differs from *Cantharus* by lacking a labral tooth, having denticles or brief lirae on the inner side of the outer lip, and having much finer spiral and axial sculpture. *Polliia* resembles *Cantharus* in having a labral tooth at the end of a spiral external groove, but the tooth in *Polliia* is situated at the midpoint of the outer lip rather than on the lip's abapical one-third. The tooth is an enlarged crenulation that is typically the seventh from the abapical end in *Polliia* instead of the fourth or fifth from the abapical end as in *Cantharus*. The parietal tooth of *Polliia* is generally prominent, and the aperture is adapically narrow and tapering, not broadly rounded as in *Cantharus*. The spire of *Polliia* is flat-sided, reflecting appressed or weakly impressed sutures, whereas that of *Cantharus* is stepped, reflecting deeper sutures and more angulate whorls. *Polliia* always has a terminal varix in the adult stage, whereas most *Cantharus* do not.

Genus *Editharus* Vermeij, 2001a

Type species – *Fusus polygonus* Lamarck, 1803 by original designation.

Remarks – When I treated this genus in detail (Vermeij, 2001a), I interpreted it as an exclusively Eocene group distributed in the European and North African Tethys, and ranging from the Ypresian to the latest Priabonian. Jacques Le Renard suggested to me that the genus continued into the Oligocene with *Engina heberti* Mayer, 1864. After examining specimens at RGM from Les Cours, St.-Hilaire, Essonne, France (Faluns de Pierrefitte, early Oligocene), I concur with Le Renard's view. Most species of *Editharus* are characterized by a fusiform, basally constricted shell, five to 12 strong axial ribs on the last teleoconch whorl, a decreasing number of axial ribs on the last whorl compared to earlier teleoconch whorls, a determinate adult outer lip with a distinct angle midway between the suture and the abapical ex-

tremity of the shell, and about eight denticles on the inner side of the outer lip. *E. heberti* differs from most Eocene species by having an evenly, strongly convex rather than angulate outer lip, and by having 14 axial ribs on both the penultimate and last whorls of the teleoconch. Cossmann (1893: 339), who regarded *E. heberti* as a species of *Tritonidea* (= *Polliia*), had already recognized the similarity of this Oligocene species with the Eocene *E. polygonus*. My inference (Vermeij, 2001a, b) that the labral tooth (medial angulation of the outer lip) of *Editharus* is confined to the Eocene remains correct, because *E. heberti* from the Oligocene replaces the tooth, formed as the angular junction between the adapical and abapical sectors of the outer lip, with an evenly convex transition.

Although *E. heberti* is the youngest known species of *Editharus*, it may have given rise to the European genus *Anna*. Both *Editharus* and *Anna* are characterized by relatively small shells, a determinate adult lip, and denticles on the inner side of the adult lip. *Editharus*, especially during the Eocene, has fewer axial ribs, but *E. heberti* from the Oligocene has 14, a large number for *Editharus* and near the lower end of the number of axial ribs in *Anna*. As noted in the remarks under *Anna*, the earliest species of that genus (*A. consobrina*) is from the same time and place as the youngest species of *Editharus*.

Genus *Gemophos* Olsson and Harbison, 1953

Type species – *Buccinum gemmatum* Reeve, 1846, by original designation.

Revised diagnosis – Shells of small to medium size, adults 18-42 mm in maximum length, broadly fusiform to ovate, abapically usually with a weakly constricted base; spire whorls flat-sided, periphery usually situated below lower suture; last teleoconch whorl with angulate or rounded shoulder-periphery; axial sculpture usually well developed, consisting of rounded ribs, strongest at the periphery and abapically fading out on base; spiral sculpture consisting of fine, strong cords, on and between which there may be secondary cords and threads; aperture ovate-elongate, which in the adult stage is variably extended adapically as a narrow channel between a well developed parietal rib on the adapical end of the inner lip and two to three enlarged denticles on the outer lip; adult outer lip downwardly convex, forming an externally thickened, adapically extended varix; edge of adult outer lip strongly crenulated by paired crenations; the three abapical-most crenations are separated from the others by a small gap, and are situated on a sector of the outer lip that is oriented toward the shell axis abapically; inner side of outer lip with strong, continuous lirae; siphonal fasciole prominent, spirally threaded; umbilical chink usually absent.

Remarks – I include the following species in *Gemophos*:

G. auritulus (Link, 1807), Recent, Caribbean region and Brazil; *G. basidentatus*, new species, late Pliocene to early Pleistocene, Florida; *G. cayapus* Olsson, 1964, late Miocene, Ecuador; *G. crispatus*, new species, late Pliocene, Florida; *G. filistriatus*, new species, Recent, deep-water, North Carolina to eastern Florida; *G. gemmatus* (Reeve, 1846), Recent, eastern Pacific; *G. janellii* (Kiener, 1835), Recent, Galápagos Islands and northern Peru; *G. pastinaca* (Reeve, 1846), Recent, eastern Pacific; *G. ringens* (Reeve, 1846), Pleistocene to Recent, eastern Pacific; *G. sanguinolentus* (Duclos, 1833), Recent, eastern Pacific; *G. tinctus* (Conrad, 1846), mid-Pleistocene to Recent, North Carolina to Florida and Bermuda; *G. tridentatus* (Tuomey and Holmes, 1857), late Pleistocene, North Carolina to Florida; and *G. viverratus* (Kiener, 1834), Pleistocene to Recent, West Africa (for fossil record of this species see Brébion, 1979).

Another possible member is *Cantharus (Pollia) advena* Malatesta, 1960, from the early Pleistocene of Catalarga, Sicily. Malatesta (1960) described this species as a small (length 18 mm) shell closely resembling *G. tinctus* from Florida. I have not seen material of *C. advena*, but this species may indeed represent a brief incursion of *Gemophos* into the Mediterranean.

Despite the distinctiveness of *Gemophos*, most authors who have treated American members of the *Cantharus* group have not understood the group well, and have therefore included species that I would unhesitatingly assign elsewhere. Dall (1889: 177) and Abbott (1974: 219) considered the species here assigned to *Gemophos* to belong to *Tritonidea* and *Pollia* respectively, which these authors treated as a subgenus of *Pisania* Bivona, 1832, because of similarities in the radula. Cernohorsky (1975: 197-198) likewise considered *Gemophos* a synonym of *Pollia*, which he treated as a subgenus of *Cantharus*.

When they proposed the genus *Gemophos*, Olsson and Harbison (1953: 225) introduced confusion by assigning not only *G. gemmatus* and the related *G. maxwelli* Olsson and Harbison, 1953 (= *G. tridentatus*; see below) and *G. tinctus* to *Gemophos*, but also "*G. cancellata*" (= *Pollia cancellaria* Conrad, 1846) and *Pisania (Tritonidea) lymani* M. Smith, 1936. These two nominal taxa, which likely represent a single species, belong instead to *Solenosteira* (Vermeij, 2001a; see below under *Solenosteira*).

Keen's (1971: 560-561) concept of *Gemophos* was similarly broad. Considering *Gemophos* as a subgenus of *Cantharus*, she included not only the eastern Pacific species listed above, but also five additional eastern Pacific species: *Cantharus (Gemophos) berryi* McLean, 1970; *Pusio elegans* Gray in Griffith and Pidgeon, 1834; *Buccinum lautum* Reeve, 1846; *Buccinum pagodus* Reeve, 1846; and *Murex vibex* Broderip, 1833. McLean (1970) had already noted the similarity of his species *C. (G.) berryi* from Banderas Bay, Mexico, to *B. lautum* and *M. vibex*, species which he, like Keen (1971), assigned to *Cantharus (Gemophos)*. These three species are here assigned to *Hesperisternia* (see Vermeij, 2001a, for

placement of *M. vibex* in *Hesperisternia*; see below under *Hesperisternia*). They lack a determinate outer lip, paired crenulations on the edge of the outer lip, abapical crenulations set off from other crenulations by a small gap, and an adapical apertural channel. The spire is characterized by impressed sutures and is stepped rather than flat-sided as in *Gemophos*. *Pusio elegans* is the type species of the genus *Pusio*. Its outer lip is indeterminate, not adapically extended as a channel, and is adorned with paired crenulations. The spire is stepped rather than flat-sided. *Buccinum pagodus* closely resembles *P. elegans* and is here assigned to *Pusio* (see below).

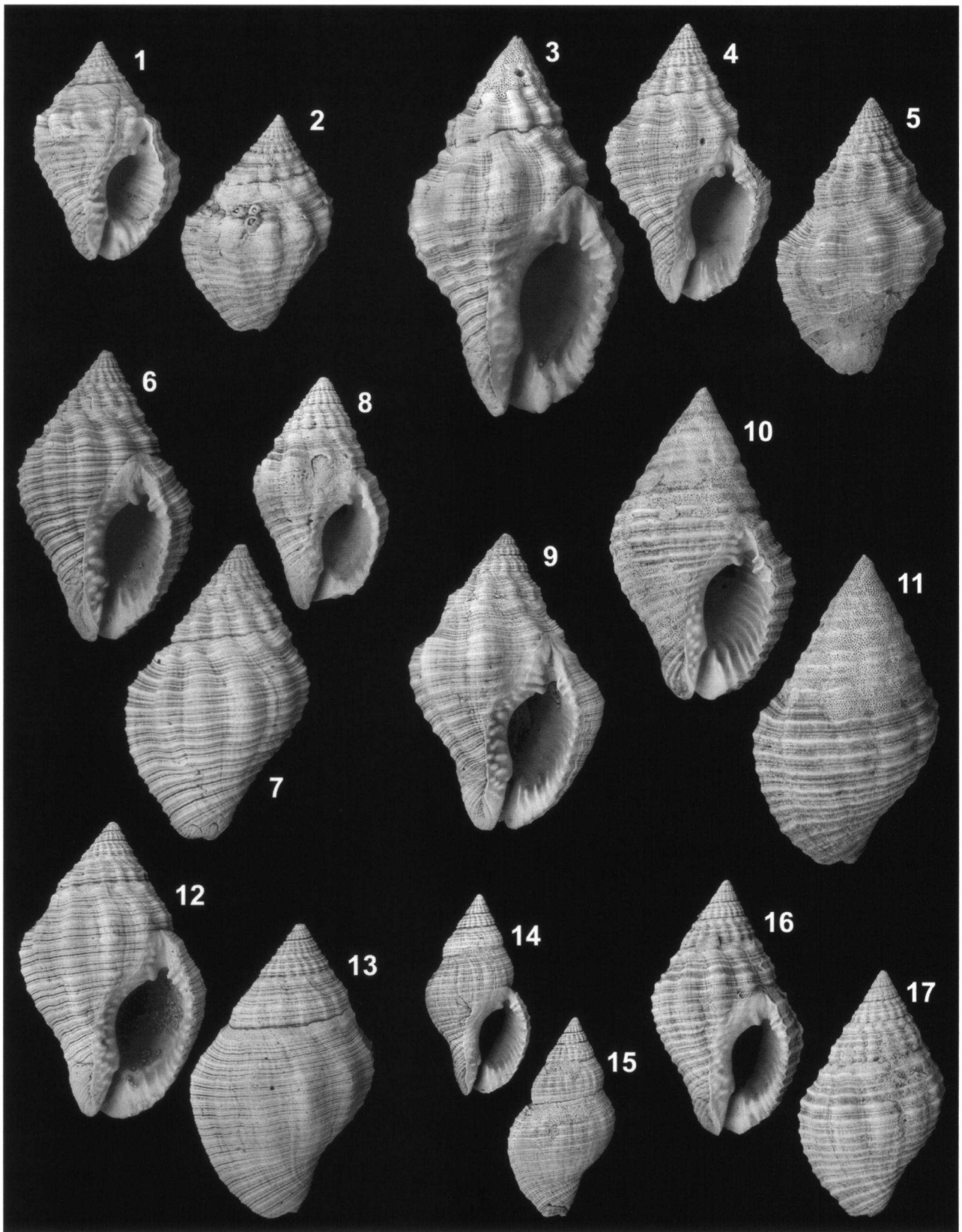
A previously unrecognized feature unique to *Gemophos* within the *Cantharus* group is the abapical sector of the adult outer lip. In an abapical direction, the edge of the outer lip curves toward the shell's axis of coiling. The three crenulations situated on the abapical sector are separated from the adapical crenulations by a slight gap. In other members of the *Cantharus* group, the abapical sector of the lip does not curve toward the axis, and there is no gap between crenulations on the lip's edge. *Gemophos* shares the adaxial curvature of the abapical sector of the outer lip with *Pisania*, especially the western Atlantic species *P. pusio* (Linnaeus, 1758). Species of *Pisania* have very fine to obsolete spiral sculpture, which is most strongly expressed abapically; and axial sculpture is confined to the upper whorls or is obsolete to absent throughout.

In most species of *Gemophos*, the three abapical crenulations on the outer lip are not enlarged and are therefore of the same size as the more adapical series of crenulations. In the late Pliocene to early Pleistocene *G. basidentatus* (Figures 3-5), however, the three abapical crenulations are enlarged, with the second crenation often forming a small, sharp labral tooth. When developed, this tooth has a different position from the labral tooth of *Cantharus* and *Pollia* (Vermeij, 2001b).

The crenulations on the outer lip of *Gemophos* are distinctly paired. *Gemophos* shares this trait with *Pusio*, but it differs from that genus by the presence of a terminal varix instead of an indeterminate outer lip. In other genera of the *Cantharus* group, crenulations are evidently unpaired. The American genera *Hesperisternia*, *Pusio*, and *Solenosteira* differ from *Gemophos* further by having the parietal tooth poorly expressed or absent, and by having a stepped spire in which the lower suture is situated below the shoulder angulation.

A second distinctive feature of *Gemophos* is the long adapical extension of the outer lip and of the adult aperture. The outer lip of the adult extends adapically up to a point quite high on the penultimate whorl, and in some species reaches the adapical suture of the penultimate whorl. The extension forms the abaxial margin of a narrow adapical channel of the aperture, constricted on its adaxial side by a very prominent parietal tooth. The adapical extension is better developed in *Gemophos* than in any other member of the *Cantharus* group.

Two groups of *Gemophos* are distinguishable according to how far toward the apex the adult outer lip extends.



Figures 1, 2. *Gemophos auritulus* (Link, 1807), length 24.7 mm, diameter 16.8 mm, Playa Adaro, Paraguaná Peninsula, state of Falcón, Venezuela, Vermeij collection.

Figure 3. *Gemophos basidentatus* n. sp., holotype, length 41.1 mm, diameter 23.7 mm, USNM 525689, Capeletti Pit no. 2, Dade County, Florida, lower Bermont Formation (early Pleistocene).

Figures 4, 5. *Gemophos basidentatus*, paratype, length 31.0 mm, diameter 19.1 mm, UF 58599, Hendry County Rock Pit, Hendry County, Florida, Caloosahatchee Formation (late Pliocene).

Figures 6, 7. *Gemophos crispatus* n. sp., holotype, UF 113283, length 29.9 mm, diameter 18.2 mm, Cochran Pit, Okeechobee

County, Florida; Caloosahatchee Formation (late Pliocene).

Figure 8. *Gemophos crispatus* n. sp., paratype, UF 113284, length 25.4 mm, diameter 15.1 mm, same locality.

Figure 9. *Gemophos tridentatus* (Tuomey and Holmes), "maxwelli" phenotype, Quality Aggregates Phase 9, Sarasota, Sarasota County, Florida; Fruitville Member, Tamiami Formation (late Pliocene); Vermeij collection.

Figures 10, 11. *Gemophos gemmatus* (Reeve, 1846), length 34.1 mm, diameter 20.3 mm, Playas del Coco, Guanacaste Province, Costa Rica; Vermeij collection.

Figures 12, 13. *Gemophos tridentatus* (Tuomey and Holmes, 1857), "watsonensis" phenotype, UF 48012, Fort Basinger, Kissimmee Valley, Florida, length 32.1 mm, diameter 19.8 mm.

Figures 14, 15. *Gemophos filistriatus* n. sp., holotype, USNM 801723, length 22.5 mm, diameter 11.9 mm, 64 km east of Daytona Beach, Florida, 68 to 72 m.

Figures 16, 17. *Gemophos tinctus* (Conrad, 1846), length 28.0 mm, diameter 16.6 mm, Gasparilla Island, Sarasota County, Florida; Vermeij collection.

In the typical Group 1 (that is, the group to which the type species, *G. gemmatus* [Figs. 10-11], belongs), the outer lip extends on to the shoulder-periphery of the penultimate whorl, where it forms a distinct tubercle. Other members of this group are the Atlantic *G. auritulus* (Figs. 1-2) and *G. crispatus* (Figs. 6-8) and the eastern Pacific *G. pastinaca*, *G. ringens*, and *G. sanguinolentus*. In Group 2, typified by *G. tinctus* (Figs. 16-17), the adult outer lip extends adapically to a point on the penultimate whorl well below the shoulder-periphery. It forms a small tubercle in the Floridian species *G. basidentatus* (Figs. 3-5) and *G. tridentatus* (Figs. 9, 12-13), but not in the other species, the Atlantic *G. filistriatus* (Figs. 14-15), *G. tinctus*, and *G. viverratus*, and the eastern Pacific *G. cayapus* and *G. janellii*. I surmise that the condition in Group 1 represents the derived state within *Gemophos*. Species in Group 1 appear later in the fossil record (late Pliocene), and the limited adapical extent of the adult outer lip in Group 2 (beginning in the late Miocene) more closely resembles the condition in other members of the *Cantharus* group than does the long adapical extension of group 1.

The long adapical extension of the outer lip seen in typical tropical American species of *Gemophos* has close parallels in at least two other epifaunal genera from the Neogene and Recent in tropical America. These are *Triumphis* Gray, 1857, tentatively assigned by Vermeij (1998a) to Pseudolividae, and *Gordanops* Olsson, 1964, synonymized with *Calophos* Woodring, 1964 by Allmon (1990) and assigned by him to the nassariid subfamily Dorsaninae. The adapical extension in these genera may reflect a strengthening of the adapical margins of the aperture. Some strombids and cerithiids also have substantial adapical extensions of the aperture, structures that deserve further functional study.

Detailed examination of fossil and Recent *Gemophos* reveals the existence of three undescribed species. Together with *G. tridentatus*, these three new species are treated below.

Gemophos tridentatus (Tuomey and Holmes, 1857)

Figures 9, 12, 13

1857 *Purpura tridentata* Tuomey and Holmes, p. 137, pl. 28, fig. 9.

1930 *Cantharus watsonensis* Mansfield, p. 72, pl. 9, fig. 6.

1953 *Gemophos maxwelli* Olsson and Harbison, pp. 226-227, pl. 35, fig. 7.

Material examined –

UF: TU Locality 870, pits on east side of North Carolina Highway 130, 1.8 miles north of Old Dock School, Old Dock, Columbus County, North Carolina; 24 specimens.

UF: Kissimmee Valley and Fort Basinger, Okeechobee County, Florida, spoil; UF 22095, 48012, 60557, 61027, 62825, 62506, 65876, 103188; TU locality 932; 37 specimens.

UF: MacAsphalt Pit (= Quality Aggregates), Sarasota, Sarasota County, Florida, UF 2225 and 29808; 4 specimens.

UF 103186, Cracker Swamp, Putnam County, Florida, Nashua Formation, 7 specimens.

Vermeij collection: Calabash, North Carolina, ex L. D. Campbell; 1 specimen.

Vermeij collection: Quality Aggregates Pit, Sarasota, Florida, upper Pinecrest (= Fruitville Member) beds, Tamiami Formation; ex G. S. Herbert; 8 specimens.

ANSP 18277 and 19309 (holotype and paratypes), *Gemophos maxwelli*, St. Petersburg, Florida; 1 holotype, 23 paratypes.

USNM 373131, Watson's Landing, Liberty County, Florida; holotype of *Cantharus watsonensis*.

Remarks – Tuomey and Holmes (1857) described and figured *Purpura tridentata* from fossil deposits at Black River, South Carolina. According to L. D. Campbell (personal communication, 17 September, 1999), the formation from which Tuomey and Holmes' specimen came could be either the lower Waccamaw Formation (late Pliocene) or the Duplin Formation (middle Pliocene). Campbell believes that the lower Waccamaw is the more likely provenance, because *G. tridentatus* has been encountered commonly at other localities in the lower Waccamaw Formation, such as Old Dock and Calabash (see material examined), whereas the species has not been collected in any locality of the Duplin Formation. The specimens from North and South Carolina I have examined are all characterized by numerous fine spiral sculptural elements, poorly differentiated into primary and secondary cords and threads, and by low rounded

axial ribs and a rounded shoulder angulation. Specimens very similar to the lower Waccamaw phenotypes occur in time-equivalent strata of the Fruitville Member of the Tamiami Formation (= upper Pinecrest beds) in the Kissimmee Valley and at Sarasota, Florida (for stratigraphy and correlations see Petuch, 2004) (Figures 12, 13). The same phenotype was named *Cantharus watsonensis* by Mansfield (1930) from the upper part (*Cancellaria* zone) of the Choctawhatchee (= Jackson Bluff) Formation in Liberty County, northwestern Florida. The holotype of *C. watsonensis* (USNM 373131) is a subadult specimen with obsolete axial ribs, and lies at one extreme of variation in sculpture observed in *G. tridentatus*. A lot from Cracker Swamp Ranch in the Nashua Formation (UF 103186) of eastern Florida, considered time-equivalent to the Caloosahatchee Formation (Petuch, 1997, 2004) and thus a little younger than the lower Waccamaw and Fruitville Member, is also of the *watsonensis* phenotype.

At the other extreme are strongly shouldered phenotypes with prominent, rounded axial ribs (Figure 9). These were named *Gemophos maxwelli* by Olsson and Harbison (1953) from St. Petersburg, Florida, in the lower Caloosahatchee Formation. Identical phenotypes occur commonly in the Fruitville Member at Sarasota, which are probably slightly older than the specimens at St. Petersburg. In this *maxwelli* phenotype, five or six primary spiral cords on the last whorl are more prominent than the prominent but narrower and lower secondary cords and tertiary threads intercalated between the primary cords. In many specimens from the Kissimmee Valley and Sarasota, the angular *maxwelli* phenotype is succeeded ontogenetically by a more rounded, less strongly sculptured *watsonensis-tridentatus* phenotype in later growth stages. I therefore interpret *Purpura tridentata*, *Cantharus watsonensis*, and *Gemophos maxwelli* as subjective synonyms representing a single rather variable species. This species, *Gemophos tridentatus*, is the only *Gemophos* occurring during that part of the late Pliocene represented by the lower Waccamaw Formation in North and South Carolina and by the Fruitville Member of the Tamiami Formation and the lower Caloosahatchee Formation in Florida. *G. tridentatus* is the oldest *Gemophos* in the southeastern United States, and is stratigraphically (and probably phylogenetically) succeeded by *G. basidentatus* n. sp.

Dall (1890: 130) synonymized *Purpura tridentata* with *Pisania (Tritonidea) auritula* (Link, 1807). *Gemophos tridentatus* differs from *G. auritulus*, a common Recent species from the Caribbean region and Brazil, by having stronger secondary spiral sculpture and by having the adult outer lip extended adapically only to the lower rather than to the upper part of the periphery on the penultimate whorl.

The largest specimen of *G. tridentatus* I have seen (length 36.0 mm) is from the Kissimmee Valley, Florida. *G. basidentatus* n. sp. attains somewhat larger sizes, whereas the late Pleistocene to Recent *G. tinctus* (Conrad, 1846) is generally smaller, reaching a maximum

length of 30.3 mm (Recent, Gasparilla, west Florida; Vermeij collection).

Sufficiently large samples were available from three localities to permit estimates of the frequency of specimens with at least one repaired injury. Shells repaired on the last whorl about for five of 24 specimens (21%) from the lower Waccamaw Formation at Old Dock, North Carolina; two of 40 specimens (2.5%) in the Kissimmee Valley (pooled from several localities), and none of 10 specimens from Sarasota.

Gemophos basidentatus n. sp.

Figures 3-5

2001 *Gemophos* n. sp., Vermeij (2001b), p. 497.

Diagnosis – Large *Gemophos* with angulate shoulder, weakly constricted base, adult outer lip extended adapically to the lower of two cords on penultimate whorl, and abapical crenations on adult outer lip enlarged relative to the adapical series.

Description – Shell large for genus, adults 25.4–41.1 mm in length, broadly fusiform, slightly abapically constricted; teleoconch consisting of up to seven whorls, flat-sided and with appressed sutures in early whorls, angulate and with more impressed suture in last three whorls; axial sculpture of teleoconch consisting of prominent, high, rounded ribs, eight to 11 on last whorl (ten in holotype); spiral sculpture consisting of two to six threads in concave subsutural sector on last whorl, six main cords on convex central sector of last whorl, and three narrower basal cords; cords on central sector separated by two to six secondary spirals; nodes form only at shoulder angulation; elsewhere, spiral sculpture crosses axial ribs without forming nodes; aperture elongate-ovate; outer lip downwardly convex, forming slightly externally thickened adult varix, its edge very sharply crenulated; abapical two to three crenations on adult outer lip enlarged (especially the second from the abapical end) relative to the 12 paired crenations on the central sector; the abapical crenations situated on sector of lip that slopes adapically toward shell axis, and separated from adapical series of crenations by small gap; three finer crenations on sector of outer lip corresponding to subsutural area; inner side of outer lip with about nine prominent, continuous lirae extending from lip's edge into aperture; the two or three adapical-most lirae thickened internally to form teeth opposite prominent parietal tooth; adapical extension of adult outer lip reaches the lower of two main cords on penultimate whorl; inner lip adherent, with two weak basal folds, including fold at entrance to short, narrow siphonal canal; siphonal fasciole rounded, with nine spiral threads; umbilical slit absent.

Holotype – USNM 525689; length 41.1 mm, diameter 23.7 mm, aperture length 26.0 mm, aperture width 9.6

mm.

Type locality – Capeletti Pit no. 11, Dade County, Florida, “Loxahatchee” beds, lower Bermont Formation (early Pleistocene).

Paratype – UF 58599, Hendry County Rock Pit, Hendry County, Florida, Caloosahatchee Formation (late Pliocene); length 31.0 mm, diameter 21.4 mm, aperture length 20.8 mm, aperture width 8.0 mm.

Other material examined –

UF 90646, Griffin Brothers Pit 1, Palm Beach County, Florida, Ayres Landing Member of Caloosahatchee Formation.

UF 53582, Capeletti Brothers Pit, one juvenile.

Vermeij collection, Cochran Pit, Okeechobee County, Florida, Caloosahatchee Formation; three specimens.

? UF 55432, Caloosahatchee River, lower Bermont Formation; one adult.

? UF 42171, Davis Pit, Caloosahatchee Formation; two specimens.

? UF 57058, Ortona Locks, Glades County, Florida; three specimens.

Vermeij collection, Miami Canal, Palm Beach County, Florida, Caloosahatchee Formation; one specimen.

UF 58516, De Soto Shell Pit, De Soto County, Florida; four specimens.

Petuch collection, near Miami Canal, Dade County, Florida; three specimens.

Vermeij collection, West Palm Beach Aggregates, Palm Beach County, Florida, two specimens.

Remarks – *G. basidentatus* is a distinctive species that is unique within the genus *Gemophos* in possessing two or three enlarged abapical crenations on the edge of the adult outer lip. The second of these crenations from the abapical end of the lip is the largest, and forms a very short but distinct labral tooth (Vermeij, 2001b, as *Gemophos* n. sp.).

In collections, this species has been confused with the Recent Caribbean and Brazilian *G. auritulus* (Link, 1807). The species differs most consistently in that the adult outer lip adapically extends to the upper of two cords on the penultimate whorl in *G. auritulus*, in which this extension forms a tubercle; whereas it extends only to the lower of two cords on the penultimate whorl in *G. basidentatus*, where it does not form a tubercle. *G. auritulus* also lacks the enlarged abapical crenations of *G. basidentatus*.

G. basidentatus has also been confused with the extremely similar but older *G. tridentatus*. The latter species differs from *G. basidentatus* in not having the abapical crenations enlarged on the adult outer lip and usually by having secondary spiral sculpture less clearly distinguished from primary cords. Moreover, *G. basidentatus* is always strongly shouldered, whereas *G. tridentatus* occurs in both a strongly shouldered form (*maxwelli* type) and as a form with more rounded whorls (*wat-*

sonensis and *tridentatus* phenotypes; see remarks under *G. tridentatus*).

Finally, *G. basidentatus* differs from the early Pleistocene to Recent *G. tinctus* (Conrad, 1846) by having much more prominent and generally fewer axial ribs (eight to 11 in *G. basidentatus*, ten to 15 in most *G. tinctus*), a much more prominent shoulder angulation so that the spire appears tabulate on later whorls rather than entirely straight-sided as in *G. tinctus*, and a greater differentiation between prominent primary and weaker secondary cords. The abapical crenations of *G. basidentatus* at the anterior end of the lip are enlarged relative to the adapical series, whereas in *G. tinctus* the crenations are of similar size over the entire length of the adult outer lip. *G. tinctus* is generally a much smaller species (adult length 17.6–30.3 mm as compared to 25.4–41.1 mm in *G. basidentatus*).

A few specimens (denoted by a question mark in the material examined) differ from typical *G. basidentatus* by not having the abapical crenations distinctly enlarged. In other respects, however, these specimens conform to the strongly sculptured, strongly shouldered phenotype characteristic of *G. basidentatus*.

No locality yielded enough specimens of *G. basidentatus* to allow for local estimates of the frequencies of repaired injury or drilling. Among 26 individuals I have examined from all localities in southeastern Florida, four had repaired injuries and two (both from the De Soto Shell Pit, UF 58516) had small drill holes. One specimen from the Griffin Brothers Pit (UF 90646) (length 31.0 mm) had a second varix at the position of the third axial rib behind the outer-lip adult varix.

Derivatio nominis – *basidentatus*: Latin basis (base) and dentatus (of tooth), referring to the basal labral tooth.

Gemophos crispatus n. sp.

Figures 6–8

Diagnosis – Medium-sized *Gemophos* distinguished by rounded last whorl, straight-sided conical spire, weak abapical constriction, sharp cords crossing broadly rounded axial ribs without forming nodes, and sharply crenulated adult outer lip extending adapically to the upper cord of rounded shoulder angulation on penultimate whorl.

Description – Shell medium-sized for genus, adults 25.4–29.9 mm in length, fusiform, weakly abapically constricted; teleoconch consisting of six whorls; spire flat-sided, conical, whorls separated by appressed sutures; last whorl with rounded shoulder angulation, evenly convex on central sector; axial sculpture consisting of low, very broad, rounded ribs, nine to ten on last whorl; spiral sculpture of last whorl consisting of 16 sharp cords, adjacent cords separated by two sharp threads; aperture elongate-ovate; outer lip downwardly convex, forming an externally slightly thickened, rounded adult varix; outer

lip edge with 16 crenations, the three abapical ones on a sector that slopes abapically toward shell axis; inner side of outer lip with prominent, continuous lirae, the two adapical-most lirae enlarged, forming prominent teeth opposite a prominent parietal tooth; adult outer lip adapically extended to the upper of two main cords on convex sector of penultimate whorl; siphonal fasciole indistinct; umbilical slit absent.

Holotype – UF 113283; length 29.9 mm, diameter 18.2 mm, aperture length 20.2 mm, aperture width 7.8 mm.

Type locality – Cochran Pit, Okeechobee County, Florida, Caloosahatchee Formation (late Pliocene)

Paratype—UP 113284, same locality; length 25.4 mm, diameter 15.1 mm, aperture length 16.2 mm, aperture width 6.0 mm.

Remarks – *Gemophos crispatus* is remarkably similar to the Recent tropical eastern Pacific type species of the genus, *G. gemmatus* (Reeve, 1846). Importantly, the two species resemble each other not only in most details of sculpture, but also in that the adult outer lip extends adapically to the upper part of the rounded shoulder angulation of the penultimate whorl. This latter character unites these two species with several other tropical American species of *Gemophos*, and contrasts markedly with the other fossil and living species of *Gemophos* from the southeastern United States including Florida: *G. basidentatus*, *G. filistriatus*, *G. tinctus*, and *G. tridentatus*. The only difference between *G. crispatus* and *G. gemmatus* is that the spiral cords of *G. gemmatus* are less prominent.

It is surprising that only two specimens of this distinct new species have come to light among the hundreds of thousands of fossil molluscs that have been collected from Plio-Pleistocene deposits in Florida. This circumstance may indicate a brief appearance of a tropical American taxon in southern Florida.

Derivatio nominis – *crispatus*: Latin, sharply crinkled, referring to the sculpture.

Gemophos filistriatus n. sp.

Figures 14, 15

Diagnosis – Small *Gemophos* characterized by numerous axial ribs that become obsolete on the last whorl, numerous fine undifferentiated spiral cords, and undifferentiated crenations on adult outer lip.

Description – Shell small for genus, adults 18.4–28.6 mm in length, fusiform, weakly abapically constricted; protoconch consisting of one low, broad, smooth whorl, 0.7 mm in maximum width; no obvious transition from protoconch to teleoconch; teleoconch consisting of six whorls; spire flat-sided, whorls separated by appressed

sutures; axial sculpture consisting of very low riblets confined to the sharply rounded peripheral area, about 23 on spire whorls, usually absent on last two whorls of adults; spiral sculpture consisting of very fine threads, about 15 on penultimate whorl, 35 or more on last whorl, not obviously differentiated into primary and secondary elements; aperture relatively broad for genus; outer lip of adult with about 21 subdued paired crenations at edge, all of similar size; outer lip extended adapically to a point just above suture and not reaching periphery of penultimate whorl; inner side of outer lip with 12 to 14 weak lirae, the two adapical-most lirae enlarged and situated opposite parietal tooth; inner lip adherent, with two basal folds; siphonal fasciole rounded, obsoletely spirally threaded; umbilical slit absent.

Holotype – USNM 801723; length 22.5 mm, diameter 11.9 mm, aperture length 14.0 mm; aperture width 5.4 mm.

Type locality – 40 miles (64 km) east of Daytona Beach, Florida, 29°09N, 80°12W, 36 to 40 fathoms (65 to 72 m), collected 5 October 1962.

Paratype – ANSP (IP) 80771; length 22.6 mm, diameter 13.0 mm, aperture length 14.6 mm, aperture width 5.4 mm.

Other material examined –

USNM 801723, type locality, 33 additional specimens.
USNM 801724, 40 miles (64 km) east of Daytona Beach, Florida, 29°16N, 80°11W, 38 to 50 fathoms (68 to 90 m), 17 specimens.

USNM 811506, 100 miles (140 km) east of Wilmington, North Carolina, 20 to 21 fathoms (36 to 38 m), 1 specimen.

Remarks – *Gemophos filistriatus* is a highly distinctive, deep-water Recent species of *Gemophos*, which lives sympatrically with the shallow-water *G. tinctus*. It differs from *G. tinctus* in having a thinner shell, larger protoconch, greatly reduced axial sculpture consisting of more numerous and much lower axial ribs that typically do not extend to the last two whorls of the teleoconch, and very fine spiral sculpture not differentiated into primary and secondary elements. The adult outer lip of *G. filistriatus* extends onto the penultimate whorl to a point just above the lower suture, rather than to the lower end of the periphery as in *G. tinctus*. In its numerous, poorly differentiated spiral sculptural elements, *G. filistriatus* resembles the *tridentatus* and *watsonensis* phenotypes of *G. tridentatus*, but the axial sculpture of *G. filistriatus* consists of more numerous, lower elements that are not expressed on the last two teleoconch whorls, and the adult outer lip extends less far adapically than in the late Pliocene species *G. tridentatus*.

In two lots (USNM 801723 and 801724) from east of Daytona Beach, Florida, only one of 52 shells examined (1.9%) was repaired. Specimens evidently collected

empty were encrusted by small barnacles.

Derivatio nominis – filistriatus: Latin, two-noded, referring to the sculpture.

Genus *Hesperisternia* Gardner, 1944 [= *Muricantharus* Olsson, 1971 (type species: *Pseudoneptunea panamica* Hertlein and Strong, 1951, by original designation)]

Type species – Hesperisternia waltonia Gardner, 1944, by original designation.

Remarks – This large, Late Oligocene to Recent genus from tropical and subtropical America has thin, rather large shells (maximum length 54.6 mm in *H. elegans*), ovate to fusiform in shape, characterized by an inflated last whorl sharply constricted near its abapical end; usually 12 or fewer high, strong axial ribs that extend on the last whorl from the suture to a variable distance above the basal constriction; axial ribs crossed by spiral cords and threads of varying sizes, often forming nodes at intersections with axial ribs; aperture broadly ovate to narrowly elongate, adapically broadly rounded; parietal tooth at adapical end of inner lip weak, occasionally absent; outer lip almost planar to very gently convex, usually thin and indeterminate but bearing a slightly thickened terminal varix in some species (e.g. *H. karinae*); edge of outer lip with fine, paired or unpaired crenulations, not separated into two series by a gap near the abapical end; inner side of outer lip with long or short lirae, often the adapical-most lira enlarged as a tooth; siphonal fasciole usually present; umbilical slit absent or present.

I include the following species in *Hesperisternia*: *H. amyca* (Olsson, 1942), early Pliocene, Pacific Panama; *H. bainbridgensis* Gardner, 1944, middle Miocene, Georgia; *H. berryi* (McLean, 1970), Recent, Pacific Mexico; *H. binodosa* new species, late Pliocene, Atlantic Costa Rica; *H. calusa* (Petuch, 1994), late Pliocene, Florida; *H. chipolana* Gardner, 1944, early Miocene, Florida; *H. corrugata* (Gabb, 1873), late Miocene to early Pliocene, Dominican Republic; *H. dadeensis* (Petuch, 1994), late Pliocene, Florida; *H. distans* new species, early Miocene, Venezuela; *H. elegans* (Dall, 1908), Pliocene to Recent, eastern Pacific (for fossil record see Olsson, 1942; for nomenclature see below); *H. filicata* (Conrad, 1843), middle to late Pliocene, Virginia to Florida; *H. harasewychi* (Petuch, 1987), Recent, northwestern Florida; *H. insula* (Olsson, 1922), late Miocene, Atlantic Costa Rica; *H. joelshugari* (Petuch, 1994), late Pliocene, Florida; *H. jugosa* (C. B. Adams, 1852), Recent, eastern Pacific; *H. karinae* (Nowell-Usticke, 1969), Recent, Caribbean and Brazil; *H. lauta* (Reeve, 1846), Recent, eastern Pacific; *H. lindae* (Petuch, 1994), middle Pliocene, Florida; *H. miamiensis* (Petuch, 1994), late Pliocene, Florida; *H. multangula* (Philippi, 1848), early Pleistocene to Recent, North Carolina to Florida, Bahamas, and Yucatan (for Recent distribution see Robertson, 1957); *H. olssoni* (Petuch,

1994), late Pliocene, Florida; *H. panamica* (Hertlein and Strong, 1951), Recent, eastern Pacific; ?*H. pauper* (Dall, 1890), late Oligocene, Florida; *H. pelicana* (Olsson, 1942), early Pliocene, Pacific Panama; *H. petuchi* new species, late Miocene, Maryland; *H. scissus* (Olsson, 1964), early Pliocene, Ecuador; *H. scrupus* (Olsson, 1964), early Pliocene, Ecuador; *H. shaskyi* (Berry, 1959), Recent, eastern Pacific; *H. tortugera* (Olsson, 1922), late Pliocene, Atlantic Costa Rica; *H. vibex* (Broderip, 1833), late Pleistocene to Recent, eastern Pacific (for fossil record, see Aguilar and Fischer, 1986); *H. waltonia* Gardner, 1944, middle Miocene, Florida. Several of these names may prove to be synonyms.

Gardner (1944: 445) originally named *Hesperisternia* as a genus of Fasciolariidae for Miocene fossils from Florida and Georgia. B. Smith (1946) transferred the genus implicitly to Buccinidae on the basis of the protoconch of the type species and of the Pliocene *H. filicata*. Robertson (1957) recognized that the Recent species *Fusus multangulus* Philippi, 1848, is related to *Pseudoneptunea panamica* Hertlein and Strong, 1951, and suggested that a new taxon might be needed for them, not realizing that fossil species similar to these Recent species had already been given the generic name *Hesperisternia*. When he created the genus *Muricantharus*, Olsson (1971: 61) was evidently also unaware of *Hesperisternia*. *Muricantharus* was originally conceived as an exclusively eastern Pacific genus, whose type species (*Pseudoneptunea panamica*) is one of several large, broad-apertured species with nodes where distant primary spiral cords cross high, narrow axial ribs. Although these species represent an extreme in size and nodosity, they are morphologically linked by intermediates to more typical species of *Hesperisternia* in which the cords do not form nodes where they intersect with axial ribs. The *H. multangula* group, confined to the southeastern United States and Yucatan, represents another extreme, in which the primary cords are generally low; but in such fossil members of this group as *H. lindae*, these cords nodulate the high, prominent, narrow axial ribs. Typically, there are three spiral rows of nodes in *H. lindae*, as there are in *H. corrugata* and other Recent and fossil species of the *Muricantharus* type. A third group comprises the Caribbean and Brazilian *H. karinae* and the eastern Pacific *H. lauta* and probably *H. jugosa*. This group is characterized by strong spiral cords and a narrow, dentate aperture convergent on that of *Engina*. Species lineages within *Hesperisternia* are surely recognizable, but for now I prefer to unite all the species into a single, quite possibly paraphyletic taxon *Hesperisternia*.

Axial sculpture in *Hesperisternia* typically consists of high, narrow, sharply rounded ribs, separated by broad interspaces. Ribs are lower and more crowded in *H. filicata* and *H. petuchi* n. sp. In some populations of *H. multangula* from northwestern Florida, which Abbott (1986) distinguished as the subspecies *grandanus*, axial sculpture on the last whorl is obsolete. More typical specimens of *H. multangula* with high, narrow axial ribs coexist with these *grandanus* phenotypes. Abbott (1986) already

suspected that the *grandanus* form might be little more than a minor variant of *H. multangula*, a position with which I concur. A similar but less extreme reduction in axial sculpture occurs in *H. binodosa* n. sp.

Although a minority of species here assigned to *Hesperisternia* have a determinate outer lip varix, this feature is present in the holotype of *H. waltonia* (type species of *Hesperisternia*), as well as in *H. binodosa* (Figures 18, 19), *H. corrugata* (Figures 20,21), *H. karinae*, and *H. pelicana*. When present, the varix is only slightly larger than preceding axial ribs, and has a modest adapical extension that does not form a channel at the adapical end of the aperture as it does in species of *Gemophos*. Moreover, a parietal tooth at the adapical end of the inner lip, which is prominent and which accentuates the adapical apertural channel in *Gemophos*, is generally weak or absent in *Hesperisternia*.

The oldest likely member of the genus *Hesperisternia* is the species described by Dall (1890) as *Pisania (Tritonidea) pauper*. The holotype (USNM 112055) from the "Silex beds" of the Tampa Limestone (late Oligocene) of Florida has low, weak axial ribs, about 13 spiral threads on the last whorl which do not form nodes where intersecting the axial ribs, a low but distinct parietal rib, and an indeterminate outer lip. Dall (1890: 129) suggested that this small species (shell length 9.5 mm) belongs to the *Pisania dorbignyi* group, which I assign to the genus *Anna*. Dall's species is in many ways a fitting intermediate between European species of *Anna* and later American species of *Hesperisternia*. Despite its poor preservation, *Pisania pauper* is here tentatively assigned to *Hesperisternia*.

Hesperisternia is the oldest post-Eocene genus of the *Cantharus* group in the Americas, and may well have given rise to the other American genera in the group. It is morphologically similar to *Pusio* and *Solenosteira*. *Pusio* differs from typical *Hesperisternia* by having strongly reduced axial sculpture on the later teleoconch whorls while maintaining prominent spiral cords. *Solenosteira* has a long siphonal canal and a tendency to form broader, more rounded axial ribs than is typical in axially ribbed *Hesperisternia*, in which the ribs are narrow and high. A species such as *H. distans* (early Miocene, Venezuela), in which the siphonal canal is long, could well have resembled the ancestor of the late Miocene to Recent genus *Solenosteira*.

***Hesperisternia elegans* (Dall, 1908)**

- 1908 *Solenosteira elegans* Dall, p. 300, pl. 5, fig. 6.
1962 *Cantharus rehderi* Berry, p. 130, replacement name for *Solenosteira elegans* Dall, 1908, secondary homonym of *Triton (Pusio) elegans* Griffith and Pidgeon, 1834.
1971 *Cantharus rehderi* Berry, 1962—Keen, p. 558, no. 1105.

Remarks – I here reinstate the name *Solenosteira elegans*

Dall, 1908, for an eastern Pacific species of *Hesperisternia* that Berry (1962) renamed *Cantharus rehderi* in the belief that Dall's taxon was a secondary homonym of *Triton (Pusio) elegans* Griffith and Pidgeon, 1834. Like Keen (1971), Berry (1962) regarded both species as belonging to the genus *Cantharus*. I reject the secondary homonymy because Griffith and Pidgeon's species is the type of *Pusio*, whereas the taxon Dall and Berry treated belongs to *Hesperisternia*. The correct name for the latter species is therefore *Hesperisternia elegans* (Dall, 1908).

***Hesperisternia binodosa* n. sp.**

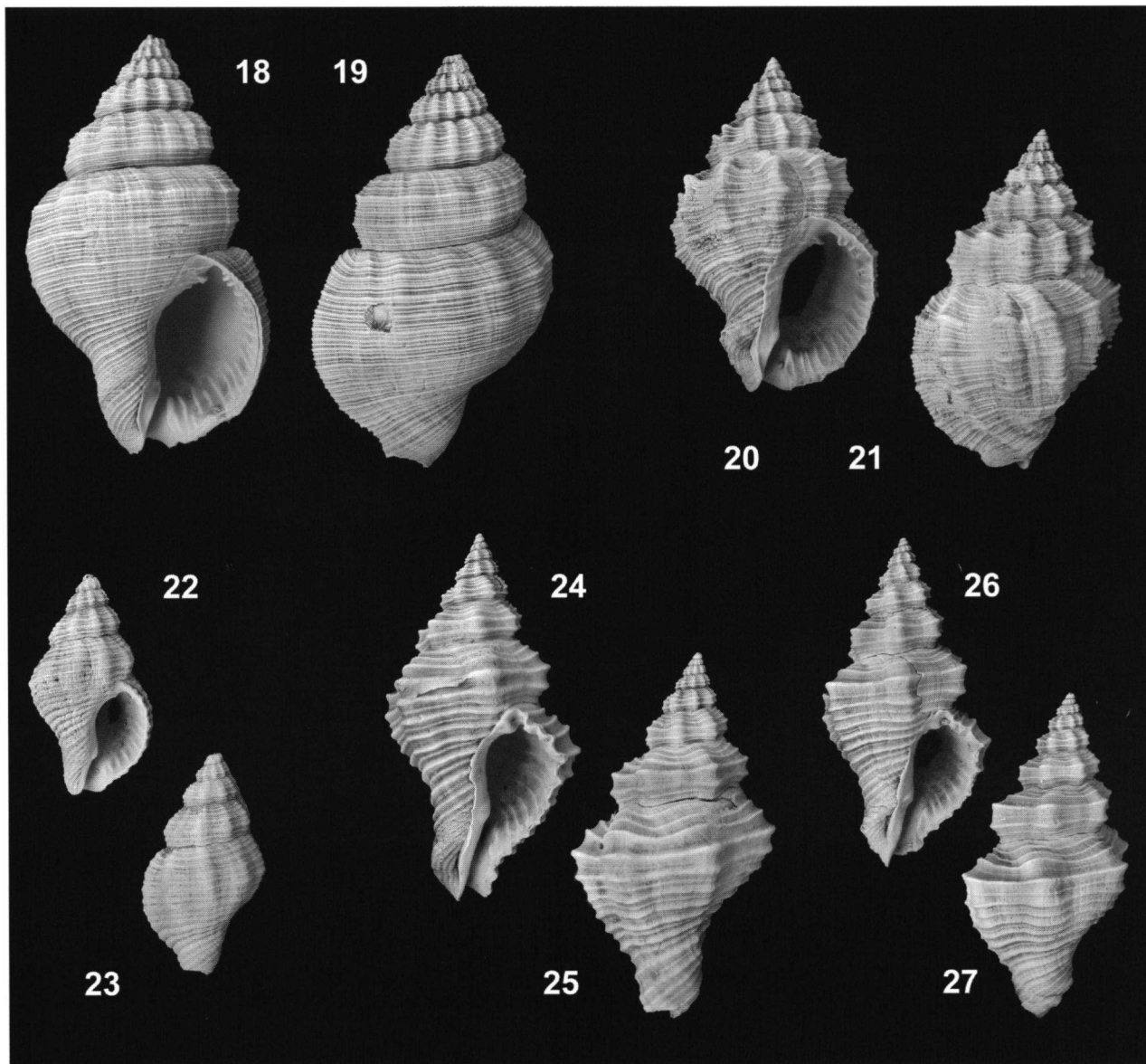
Figures 18, 19

Diagnosis – Medium-sized *Hesperisternia* characterized by numerous, low axial ribs confined to the shoulder and periphery, two spiral cords forming very low spirally elongate nodules at intersections with axial ribs, broad aperture, determinate outer lip, and deeply impressed sutures between later teleoconch whorls.

Description – Shell medium-sized, adult length 38.1 mm, broadly fusiform, basally slightly constricted; teleoconch consisting of six rounded whorls, the last three of which are separated by deeply impressed sutures; axial sculpture of last whorl consisting of 12 low, broad, rounded ribs extending from suture across convex subsutural area to a point just below the periphery; axial ribs on spire whorls extending from upper to lower suture; spiral sculpture consisting of low, sharp cords and threads, about six threads in subsutural area, two large cords forming periphery, and 25 poorly differentiated spiral elements below periphery; the two peripheral cords separated by three secondary cords and by tertiary threads; spirally elongate, low nodules forming where the peripheral cords cross axial ribs, but the cords and nodes not expressed on last quarter of body whorl; aperture broadly ovate, adapically rounded; outer lip and externally thickened varix, whose adapical extension reaches the lowest part of the penultimate whorl, well below the peripheral cords; edge of outer lip somewhat abraded, but apparently not crenate; inner side of outer lip with 21 prominent, continuous lirae extending from edge of lip into aperture; inner lip adherent, with two basal folds of which the more abapical one is very weak; low but distinct parietal tooth at adapical end of inner lip, flanking very short adapical channel of aperture; siphonal fasciole rounded, with nine spiral threads; umbilical slit absent.

Holotype – ANSP 80198; length 38.1 mm, diameter 22.3 mm, aperture length 22.5 mm, aperture width 9.5 mm.

Type locality – TU Locality 1240, Limon Province, Costa Rica, Moín Formation, collected by David G. Robinson.



Figures 18, 19. *Hesperisternia binodosa* n. sp., holotype, ANSP 80198, length 38.1 mm, diameter 22.3 mm, TU Locality 1240, Moín Formation, Costa Rica.

Figures 20, 21. *Hesperisternia corrugata* (Gabb, 1873), large mature specimen, length 30.1 mm, diameter 19.1 mm, NMB Loc. 16833, Rio Gurabo, Dominican Republic; Cercado Formation (late Miocene).

Figures 22, 23. *Hesperisternia petuchi* n. sp., holotype, UF 113285, length 20.5 mm, diameter 11.7 mm; Windmill Point, St. Mary's County, Maryland; Windmill Point Member, St. Mary's Formation (late Miocene).

Figures 24, 25. *Hesperisternia distans* n. sp., holotype, NMB 18322, length 33.4 mm, diameter 18.5 mm; 10 km west of Pueblo Nuevo, state of Falcón, Venezuela; Cantaure Formation (early Miocene).

Figures 26, 27. *Hesperisternia distans*, paratype, PRI 50277, length 30.1 mm, diameter 16.4 mm; same locality.

Remarks – Although only a single specimen is available, *H. binodosa* is so distinctive that it deserves to be formally named. Superficially, the species resembles members of the genus *Gemophos* in having a distinct, broadly rounded adult varix, but *H. binodosa* differs from *Gemophos* in that the varix extends only slightly on to the penultimate whorl. Moreover, the suture between the last several teleoconch whorls is deeply impressed, and the aperture is adapically broadly rounded in *H. binodosa*, whereas in *Gemophos* the sutures tend to be appressed

and the aperture is adapically narrow and elongated. Although the edge of the outer lip in the single specimen of *H. binodosa* is slightly abraded, it appears not to be sharply crenate as it is in species of *Gemophos*.

H. binodosa differs from other species of *Hesperisternia* by its strongly reduced axial sculpture. The grandanus phenotype of *H. multangula* also has greatly reduced axial sculpture, but this form is much less inflated than *H. binodosa*, and the lirae on the inner side of the outer lip do not extend far into the aperture as they do in *H.*

binodosa. Moreover, *H. multangula* and its variations never have a determinate lip. There is a low but distinct parietal tooth in *H. binodosa*, a feature lacking in *H. multangula*. *H. corrugata* from the late Miocene to early Pliocene of the Dominican Republic sometimes develops a varix as does *H. binodosa*, but it differs from the latter species by much more prominent axial sculpture, sharp nodes, and smaller adult size.

Derivatio nominis – *binodosa*: Latin, two-noded, referring to the sculpture.

***Hesperisternia distans* n. sp.**

Figures 24-27

Diagnosis – Medium-large *Hesperisternia* with long siphonal canal, distinct parietal tooth, and very prominent sculpture consisting of six to eight high, narrow axial ribs and 13 spiral cords on last whorl, and with at most one secondary cord between adjacent primary cords.

Description – Shell medium-large for genus, maximum length 40.1 mm, thick, fusiform, strongly constricted at upper end of long siphonal canal; protoconch consisting of one and a half smooth whorls, maximum width 0.85 mm; transition from protoconch to sculptured teleoconch sharp; teleoconch consisting of six angulate whorls separated by impressed sutures; axial sculpture of first teleoconch whorl consisting of ten ribs; later whorls with six to seven high, rounded, narrow ribs separated by wide, deep, rounded interspaces; some gerontic individuals with eight axial ribs on last whorl, the last two to three ribs low and close together; spiral sculpture consisting of high, sharp cords, about 13 on last whorl, of which two are situated above shoulder angulation; third and fourth cords from suture form shoulder angulation and periphery; suture typically emerges below these peripheral cords; occasionally one secondary cord between adjacent primary cords; aperture relatively narrowly elongate; outer lip planar, indistinctly crenated at edge by paired crenations corresponding to primary cords, indeterminate; inner side of outer lip with about 11 prominent lirae; inner lip adherent; columella with weak fold immediately above large fold at entrance to siphonal canal; low but distinct parietal tooth at adapical end of inner lip; siphonal fasciole high, with about three to four weak cords; umbilical slit narrow.

Holotype – NMB H 18322; length 33.4 mm, diameter 18.5 mm, aperture length 20.1 mm, aperture width 6.4 mm.

Type locality – NMB Locality 17516, lower shell bed, 1 km west of Casa Cantaure, about 10 km west of Pueblo Nuevo, Paraguaná Peninsula, state of Falcón, Venezuela; Cantaure Formation (early Miocene: Burdigalian).

Paratype – PRI 50277; length 30.1 mm, diameter 16.4 mm, aperture length 16.5 mm, aperture width 6.0 mm.

Other material examined – NMB: Locality 17516, 84 specimens; Locality 17518, upper shell bed, Cantaure Formation, 13 specimens; Locality 17519, 34 upper shell bed, Cantaure Formation, 48 specimens; Locality 17521, La Candelaria beds, 16 specimens.

Distribution – La Candelaria beds and Cantaure Formation (early Miocene: Burdigalian), Paraguaná Peninsula, Venezuela.

Remarks – *Hesperisternia distans* is an abundant species in the Cantaure Formation and La Candelaria beds (early Miocene) of Venezuela. It ranks as one of the most strongly sculptured fossil members of the genus. It has a comparatively longer siphonal canal than other species of *Hesperisternia*. *H. distans* differs from the contemporaneous *H. chipolana* (early Miocene, northwestern Florida) by reaching a much larger size (maximum length 40.1 mm as compared to 19.1 mm), having a longer siphonal canal, much more prominent spiral cords, a more prominent parietal tooth, and especially by having two of the upper cords forming a distinct peripheral angulation.

Derivatio nominis – *distans*: Latin, distant, referring to the axial ribs, which are far apart.

***Hesperisternia petuchi* n. sp.**

Figures 22, 23

1993 *Solenosteira cumberlandiana* (Gabb, 1860)—Petuch, p. 171; not *Cantharus cumberlandianus* Gabb, 1860.

Diagnosis – Small *Hesperisternia* with rounded periphery, low rounded axial ribs, low cords, indeterminate outer lip, and moderately strong parietal tooth.

Description – Shell small for genus, maximum length 21.1 mm, broadly fusiform, basally constricted, with rounded periphery; early whorls worn on all specimens; five preserved teleoconch whorls separated by impressed sutures; axial sculpture of last whorl consisting of eight to 13 low, narrow, rounded ribs, extending from suture to upper end of constriction; holotype with the last three axial ribs closely spaced; spiral sculpture of last whorl consisting of low cords, 12 to 14 on central sector of whorl, three to four narrow cords on base; a secondary thread between some adjacent cords; penultimate whorl with five to six cords; aperture relatively broad; outer lip indeterminate, weakly convex, indistinctly crenate at edge, and with about ten brief lirae on its inner side; inner lip adherent, with strong fold at entrance of siphonal canal and with parietal tooth at adapical end; siphonal fasciole rounded, with five to six spiral threads; umbilical slit absent.

Holotype – UF 113285; length 20.5 mm, diameter 11.7 mm, aperture length 12.7 mm, aperture width 5.0 mm.

Type locality – Windmill Point, St. Mary's River, St. Mary's County, Maryland; Windmill Point Member, St. Mary's Formation (late Miocene: Tortonian).

Paratype – UF 113286; length 21.1 mm, diameter 11.6 mm, aperture length 13.3 mm, aperture width 4.9 mm.

Remarks – The available specimens of *H. petuchi* are all somewhat worn, and show little variation. The species appears to be most similar to *H. filicata* (Conrad, 1843) from the Pliocene of Virginia to Florida. *H. petuchi* is smaller, has a generally lower spire, and has lower, less sharp spiral cords and a more prominent parietal tooth. Material in my collection of *H. filicata* from the Yorktown Formation (Pliocene, Virginia) reaches a maximum shell length of 25.4 mm. Specimens from the Pinecrest Member (middle Pliocene) of the Tamiami Formation in Sarasota, Florida, reach a similar size, but those from the Jackson Bluff (= Choctawhatchee Formation) of northern Florida (UF 7661, 79216, 79424, and 80276) reach a length of 35.6 mm. Whether *H. petuchi* is ancestral to *H. filicata* is uncertain. No species of *Hesperisternia* have yet been reported from the Eastover Formation, which lies stratigraphically between the St. Mary's and Yorktown Formations.

Petuch (1993) confused this species with *Cantharus cumberlandianus* Gabb, 1860. The latter species was named from the Kirkwood Formation (early Miocene) of New Jersey. Gabb's type specimen (ANSP 4314) and a second specimen (ANSP 14337), also from the Kirkwood Formation, in my view belong to the ocenebrine muricid genus *Urosalpinx* Stimpson, 1865. The determinate outer lip of this form is extremely thick (2.7 mm in the holotype, 3.1 mm in the second specimen), planar, and beset with eight strong denticles on its inner side. The ventral face of the siphonal area is flattened, as in many ocenebrines, and the siphonal canal is narrow. Whitfield (1984:103, pl. 17, figs. 3-6) illustrated the second specimen, and like Gabb (1860) considered the species a member of the genus *Cantharus*. The new species *H. petuchi* is from the St. Mary's Formation (late Miocene: Tortonian) of Maryland, and differs from the early Miocene *U. cumberlandianus* by having an indeterminate, briefly lirate instead of denticulate outer lip, and a more open, not ventrally flattened siphonal canal.

Derivatio nominis – named after E.J. Petuch of the Florida Atlantic University, Florida.

Genus *Pollia* Gray in Sowerby, 1834 (= *Tritonidea* Swainson, 1840, and *Aplus* De Gregorio, 1885, both with type species *Buccinum undosum* Linnaeus, 1758, by original designation)

Type species – *Buccinum undosum* Linnaeus, 1758, by

monotypy.

Remarks – This early Miocene to Recent, mainly Indo-West Pacific (IWP) genus is characterized by a fusiform, basally constricted, medium-sized shell (maximum length about 34 mm in *P. fumosa* and *P. undosa*); whorls in spire flat-sided, separated by appressed sutures; last whorl angulate or rounded in upper part, with variably developed, broadly rounded axial ribs and numerous, lower spiral cords and threads, which may form nodes at the shoulder angulation; aperture narrowly elongate, tapering adapically; adult outer lip an externally thickened, adapically somewhat extended varix, with erect, sharply crenulated edge and with long lirae on its inner side; crenations unpaired; labral tooth formed as enlarged seventh crenulation from abapical end, at apertural end of deep groove on shell exterior; inner lip with strong parietal tooth at adapical end; siphonal fasciole distinct; umbilical slit absent.

Several of the characters of *Pollia* are variably expressed. Axial ribs on the last whorl or the last two whorls of the adult shell are obsolete or absent in *P. undosa* and *P. wrightae*. In some adult specimens of *P. undosa*, the labral tooth is absent, but other individuals in the same population possess a small distinct labral tooth. A shoulder angulation is most strongly expressed in typical *P. fumosa* from the central IWP region, but is less distinct in other species, in which it is often replaced by an evenly rounded sector. The sense in which I use *Pollia* in this paper is identical to that in Vermeij and Bouchet (1998).

I include the following species in *Pollia* (see Vermeij and Bouchet, 1998, for discussions of *P. delicata* and *P. vicdani*): *P. angstanana* (Martin, 1921), early Miocene, Indonesia; *P. bucklandi* (d'Archiac, 1850), early middle Miocene to late Miocene, south and east Asia; *P. delicata* (E. A. Smith, 1899), Recent, Indian Ocean; *P. everwijni* (Martin, 1906), late Miocene, Indonesia; *P. fumosa* (Dillwyn, 1817), late Miocene to Recent, IWP; *P. fusiformis* (Martin, 1883), late Miocene, Indonesia; *P. insculpta* (Sowerby, 1900), Recent, southeast Africa; *P. martini* Shuto, 1969, early to late Miocene, Indonesia and the Philippines; *P. mollis* (Gould, 1860), Pliocene to Recent, east Asia; *P. njalindungensis* (Martin, 1921), early Miocene, Indonesia; *P. pellita* Vermeij and Bouchet, 1998, Recent, Loyalty Ridge and Lord Howe Rise; *P. rubens* (Küster, 1858), Recent, Red Sea; *P. rubiginosa* (Reeve, 1846), Recent, Indian Ocean; *P. sondeana* (Martin, 1895), Pliocene, Indonesia; *P. sowerbyana* (Melvill and Standen, 1903), Recent, Gulf of Oman; *P. subcostata* (Krauss, 1848), Recent, southeast Africa; *P. subrubiginosa* (E. A. Smith, 1879), Recent, Japan; *P. undosa* (Linnaeus, 1758), Recent, IWP; *P. vermeuleni* Knudsen, 1980, Recent, West Africa; *P. vicdani* (Kosuge, 1984), Recent, Vanuatu and Philippines and perhaps Mozambique Channel; *P. wrightae* (Cernohorsky, 1974), Recent, Fiji. Some of these taxa may prove to be synonyms. For example, *P. sondeana* is so similar to *P. undosa* that it may represent Pliocene occurrences of the

latter species. On the other hand, some taxa may comprise more than one species. Even with the removal of *P. subrubiginosa* as an Indian-Ocean species (usually synonymized with *P. fumosa* by modern authors), the tropical Pacific *P. fumosa* seems to comprise at least two species, an angular, large species in the central IWP and a more rounded, higher-spined form in Oceania.

I have given comparative remarks for *Polia* under *Cancellipolia*, *Cantharus*, and *Gemophos*. As noted under *Cantharus*, *Polia* represents the likely ancestral condition of the IWP clade of species with a labral tooth.

Genus *Preangeria* Martin, 1921 (= *Acantinella* Shuto, 1969; type species *Acanthina javana* Martin, 1899, by original designation)

Type species – *Preangeria angsanana* Martin, 1921, by original designation.

Remarks – This genus of Indo-West Pacific buccinids, represented by one living species, *P. dentata* (Schepman, 1911) and four fossil species ranging from the early Miocene to the Pliocene, diverges substantially from other members of the *Cantharus* group. It is characterized by a moderately small shell (maximum height 30.4 mm in *P. javana*), with rounded whorls, basal constriction weak or absent, numerous low axial ribs that are often absent on the last whorl, sharp cords of a single size, a narrowly elongate aperture, parietal tooth absent, outer lip indeterminate, its edge convex and finely crenulated, with nine to ten long lirae extending into aperture on inner side of outer lip beginning on a deeply recessed ridge, a sharp labral tooth at apertural end of groove situated abapical to all external cords, a distinct fasciole, and without umbilical slit. I have treated this genus fully in a previous paper (Vermeij, 1998) and have nothing new to add here.

Genus *Prodotia* Dall, 1924

Type species – *Pisania billeheusti* Petit de la Saussaye, 1853, by original designation (= ? *Triton iostomus* Gray in Griffith and Pidgeon, 1834).

Remarks – This early Miocene to Recent Indo-West Pacific genus consists of small species (maximum length about 32 mm) with slender shells, characterized by rounded whorls, a weakly constricted base, fine axial ribs and spiral cords and threads; outer lip of adult an externally thickened, adapically extended varix, finely crenulated at its convex edge and ornamented with long lirae on its inner side; parietal tooth and siphonal fasciole present; adapical edge of inner lip often erect; umbilical slit absent.

The genus differs from similarly sized species of *Anna* by having long lirae instead of denticles on the inner side of the outer lip, having a more narrowly elongate aper-

ture, and a generally more slender form. Much more taxonomic work will be necessary to determine the species composition of this group and to ascertain its relationships to the *Cantharus* and *Pisania* groups of pisanines.

Species I would include in *Prodotia* include *P. castanea* (Melvill, 1912), Recent, Persian Gulf; *P. gracilis* (Reeve, 1846), Recent, IWP; *P. iostoma* (Gray in Griffith and Pidgeon, 1834), Recent, IWP; *P. townsendi* (Melvill, 1918), Recent, Arabian Sea; *P. waluensis* (Ladd, 1977), early Miocene, Fiji; and *P. wanneri* (Fischer, 1927), late Miocene to Pliocene, Indonesia. Although Cernohorsky (1986) treated *P. gracilis* as a single species, the taxon may in fact comprise several more local units that likely deserve specific status.

Genus *Pusio* Gray in Griffith and Pidgeon, 1834 (= *Calicantharus* Clarke, 1938; type species *Pisania fortis* Carpenter, 1866, by original designation)

Type species – *Triton (Pusio) elegans* Gray in Griffith and Pidgeon, 1834, by monotypy.

Remarks – This early Miocene to Recent eastern Pacific genus is characterized by large shells (length greater than 100 mm in *P. humerosus*), angulate whorls in the relatively high spire, basal constriction weak or absent; axial ribs 15 or fewer in number per whorl, either absent on last whorl or confined to sector near shoulder angulation, which is situated about one-third of the distance from the suture to the abapical tip of the shell; spiral sculpture consisting of well developed alternating cords, not forming nodes at intersections with axial sculpture; aperture broadly ovate, adapically broadly rounded; parietal tooth at adapical end of inner lip small; outer lip indeterminate, gently convex, with low paired crenulations at edge and bearing long lirae on its inner side; siphonal fasciole prominent; umbilical slit open or closed.

I assign the following species to *Pusio*: *P. angulata* (Arnold, 1908), Pliocene, California (perhaps a synonym of *P. humerosus*); *P. elegans avus* (Pilsbry and Olsson, 1941), late Miocene, Ecuador; *P. elegans* (Gray in Griffith and Pidgeon, 1834), early Pleistocene to Recent, eastern Pacific; *P. fortis* (Carpenter, 1866), early Pleistocene, California; *P. humerosus* (Gabb, 1869), Pliocene, California; *H. kernensis* (Anderson and Martin, 1914), middle Miocene, California; *P. kettlemanensis* (Arnold, 1909), late Miocene, California; *P. pagodus* (Reeve, 1846), Recent, eastern Pacific; *P. rancherianus* (Addicott, 1970), early Miocene, California; *P. woodfordi* (Addicott, 1970), middle Miocene, California.

With some exceptions (Wenz, 1938-44; Robertson, 1957; Cernohorsky, 1975), most authors have overlooked *Pusio* as an available name for members of the *Cantharus* group. Wenz (1983-44) considered *Pusio* a synonym of *Pisania*, whereas Cernohorsky (1975) synonymized it with *Polia*.

Pusio differs from *Pisania* and *Polia* by having an inde-

terminate outer lip whose edge bears paired instead of unpaired crenulations, and by having angulate whorls. Species of *Pusio* lack a labral tooth, which is present in *Polia*. *Pusio* differs further from *Polia* by having a relatively broader aperture with a wider, more rounded adapical end. *Pusio* closely resembles *Hesperisternia* and *Solenosteira*. The spiral cords in *Pusio* never form nodes when they cross axial ribs, as they do in many species of *Hesperisternia* and *Solenosteira*; and axial sculpture tends to be greatly reduced in *Pusio* on the last one or two whorls of the adult shell. *Solenosteira* usually has a relatively much longer siphonal canal, and bears unpaired instead of paired crenulations at the edge of the outer lip.

When he described *Pisania fortis* (the type species of *Calicantharus* Clark, 1938), Carpenter (1866: 247) noted the close similarity of his species to *Buccinum insigne* Reeve, 1846 (a junior synonym of *Pusio elegans*), the type species of *Pusio*. Grant and Gale (1931: 647) noted this resemblance as well. Clark (1938: 712) nonetheless proposed *Calicantharus*, evidently being unaware of the earlier name *Pusio*.

In his genus *Calicantharus*, Clark (1938) also included *Cantharus* (*Calicantharus*) *californicus* Clark, 1938, from the Markley Formation (middle Eocene) of California. The fine spiral cords of this species appear to be somewhat stronger in the basal constriction than on more adapical sectors of the last whorl, and a siphonal fasciole appears to be absent. The aperture is filled with matrix in the two specimens I have examined (UCMP 12468 and 12469), so that nothing more can be said about the sculpture on the inner side of the outer lip. Both specimens are somewhat worn, but the greater development of cords abapically is inconsistent with assignment to the *Pisaniinae*.

Addicott (1970) included in *Calicantharus* several species that belong elsewhere. Some species were assigned to *Searlesia* Harmer, 1914 by earlier authors, but Vermeij (1991b) assigned these to the photine buccinid genus *Lirabuccinum* Vermeij, 1991b (see also Amano and Vermeij, 2003). *Chrysodomus carlsoni* Anderson and Martin, 1914, assigned by Addicott (1970) to *Calicantharus*, is a turrid (Amano and Vermeij, 2003). I tentatively include *Calicantharus woodfordi* Addicott, 1970, in *Pusio*, but the inner side of the outer lip appears to be smooth instead of lirate as in other species of *Calicantharus*.

Genus *Solenosteira* Dall, 1890 (= *Fusinosteira* Olsson, 1932; type species *Purpura fusiformis* de Blainville, 1832, by original designation)

Type species – *Pyrula anomala* Reeve, 1847, by original designation.

Remarks – The late Miocene to Recent genus *Solenosteira* is today found mainly in the tropical eastern Pacific, although there is one living Atlantic species (*S.*

cancellaria). Diversity was high in both the eastern Pacific and western Atlantic during the late Miocene and Pliocene. The shell is fusiform, often large (maximum length 65 mm in *S. fusiformis*), with angulate whorls in the spire, a strongly constricted base, and a relatively long siphonal canal; strong axial ribs often form nodes at the shoulder angulation, but generally do not extend to the constricted base; they are crossed by sharp cords, themselves covered and separated by finer spiral elements in many species; aperture elongate-ovate, adapically broad; outer lip thin, indeterminate, generally convex, usually with unpaired crenulations at edge but lacking a labral tooth, and usually with long lirae on its inner side; parietal tooth at adapical end of inner lip weakly developed; siphonal fasciole prominent; umbilical slit often present.

Species in the *S. cancellaria* group, including *S. floridensis* and *S. lymani*, differ from most other species of *Solenosteira* by having rounded rather than shouldered whorls, and by exhibiting a tendency for the axial ribs on the last whorl to become very broad and very low. This is especially noticeable in *S. floridensis*. The spiral sculpture and long canal of species in this group are very similar to those of *S. acclinensis*, *S. caloosana*, *S. mengeana*, and *S. vaughani*, which together with several other taxa named by Petuch (1994) comprise a distinctive group of *Solenosteira* from the Pliocene of Florida. I interpret *S. cancellaria* as the sole surviving species of this once diverse assemblage in Florida.

The following taxa, some of which are likely to be synonyms, belong to *Solenosteira*: *S. acclinensis* Tucker and Wilson, 1932, Pliocene, Florida; *S. alta* Petuch, 1994, early Pliocene, Florida; *S. alternata* (Nelson, 1870), late Miocene, Peru and Venezuela; *S. anomala* (Reeve, 1847), Pliocene to Recent, eastern Pacific (= ? *S. pallida*); *S. anomala buricana* (Olsson, 1942), Pliocene, Pacific Panama; *S. boggsi* (Pilsbry and Olsson, 1941), Pliocene, Ecuador; *S. caloosana* Tucker and Wilson, 1932, Pliocene, Florida; *S. cancellaria* (Conrad, 1846), Recent, Gulf of Mexico; *S. chiriquiensis* Olsson, 1922, late Miocene, Atlantic Costa Rica; *S. cochlearis* Guppy, 1911, late Miocene, Trinidad and early Pliocene, Venezuela (= *S. semiglobosa*); *S. cymioides* (Pilsbry and Olsson, 1941), late Miocene, Ecuador; *S. dalli* Brown and Pilsbry, 1911, late Miocene, Atlantic Panama and Colombia; *S. ecuadorensis* (Pilsbry and Olsson, 1941), late Miocene, Ecuador; *S. falconensis* Weisbord, 1929, late Miocene, Colombia and Venezuela; *S. floridensis* (Tucker and Wilson, 1932), Pliocene, Florida; *S. fusiformis* (de Blainville, 1832), Pliocene to Recent, eastern Pacific; *S. gatesi* Berry, 1963, Pleistocene to Recent, eastern Pacific; *S. gavilanensis* (Rutsch, 1934), early Pliocene, Venezuela; *S. hasletti* Anderson, 1929, early Pliocene, Colombia; *S. lymani* (M. Smith, 1936), Pliocene, Florida (= ? *S. cancellaria*); *S. macrospira* (Berry, 1957), Recent, Gulf of California; *S. magdalenensis* Weisbord, 1929, late Miocene, Colombia; *S. medioamericanus* Olsson, 1922, late Miocene, Atlantic Costa Rica to Venezuela; *S. mendozana* (Berry, 1959),

Recent, northwestern Mexico; *S. mengeana* Dall, 1890, late Pliocene, Florida; *S. mulepenensis* Petuch, 1994, late Pliocene, Florida; *S. multilineata* Petuch, 1994, late Pliocene, Florida; *S. pallida* (Broderip and Sowerby, 1829), Pleistocene to Recent, eastern Pacific; *S. sanctaerosae* Anderson, 1929, early Pliocene, Colombia; *S. sarasotaensis* Petuch, 1994, Pliocene, Florida; *S. sechurana* Olsson, 1932, late Miocene, Peru; *S. semiglobosa* Guppy, 1911, late Miocene to early Pliocene, Trinidad; *S. transitoria* Petuch, 1994, late Pliocene, Florida; *S. urumacoensis* H. K. Hodson in Hodson and Hodson, 1931, late Miocene, Venezuela; *S. vaughani* Dall, 1903, Pliocene, Florida.

Loel and Corey (1932) described *Solenosteira venturana* from the "Vaqueros" stage (late Oligocene) of Ventura County, California. This assignment was likely prompted by the apparent absence of the diagnostic, prominent, central columellar fold of the otherwise very similar rapanine muricid genus *Cymia* Mörch, 1860. The holotype of *S. venturana* (UCMP 31880), however, has the aperture filled with matrix, and the columella appears to be partly broken away, so that the presence or absence of a columellar fold cannot be ascertained. The massive siphonal fasciole, two rows of nodes centrally situated on the last whorl, and spiral cords above and below these nodes indicate to me that *S. venturana* belongs to *Cymia*. As already noted by Loel and Corey (1932), the species closely resembles the early Miocene *C. heimi* Hertlein and Jordan, 1927, from the Isidro Formation of Baja California, Mexico. It may well be a junior synonym of that species.

Two Oligocene species from Florida have also been described as members of *Solenosteira*, but are here excluded from that genus. *Solenosteira inornata* Dall, 1890, from the Tampa Limestone, is too poorly preserved to permit any definitive placement. Unlike species of *Solenosteira*, the inner side of the outer lip of this species is smooth. This is true also for *S. suwanneensis* Petuch, 1998, from the Suwannee Limestone (earliest Oligocene). This species, moreover, differs from *Solenosteira* by having a distinct crease or groove separating the convex part of the last whorl from the excavated base, and by having seven high axial ribs whose abapertural face is steeper than the adapertural face. In *Solenosteira*, axial ribs are rounded and more symmetrically constructed. No species of *Solenosteira* is known from the extremely rich Chipola Formation (early Miocene) of Florida. Given the excellent late Miocene to Recent fossil record of the genus, and the atypical nature of the Oligocene species, I suggest that the Oligocene taxa belong to another genus.

Mansfield (1937) assigned *Fusus quinquespina* Dall, 1890, from the Tampa Limestone (late Oligocene) of Florida, to *Solenosteira* on the basis of a close superficial resemblance to *S. turbinelloides* (Reeve, 1847) (= *S. pallida*). Dall (1890) compared his species to the melongenids *Papillina papillosa* (Conrad, 1833) from the middle Eocene and *Melongenella sculpturata* Dall, 1890, from the late Oligocene. My examination of the holotype of *F.*

quinquespina (USNM 12053) reveals that this species is indeed a melongenid. The shell has a smooth columella, lacking the one or two basal folds near the abapical end of Pisaninae; a low rounded rather than keel-like siphonal fasciole; an outer lip lacking lirae on its inner side; and axial ribs that connect an upper row of spines at the shoulder angulation with a more basal row of lower nodes, a feature never observed in Pisaninae.

These American Oligocene species are perhaps related to a series of Eocene species that several European authors (Glibert, 1963; Dolin *et al.*, 1980; Merle and Pacaud, 2002) have assigned to *Solenosteira* or to *Hanetia* (at the time considered a senior synonym of *Solenosteira*; see below). These species include *Poirieria braumuelleri* Traub, 1979, from the Oiching beds (late Thanetian or early Ypresian) of Austria; *Pugilina palissy* Pezant, 1908, from the early late Eocene of the Paris Basin, France; and *Fusus subcarinatus* Lamarck, 1803, from the Lutetian (middle Eocene) of the Paris Basin. These species have a more or less planar outer lip without lirae on its inner side, an adapical sinus on the outer lip corresponding to the basal constriction of the last whorl, and an inner lip lacking a parietal tubercle. Further work is needed to clarify the taxonomic position, scope, and age range of this group, but it cannot be assigned to *Solenosteira* (see also Vermeij, 2001a).

Many authors (Rutsch, 1934; Pilsbry and Olsson, 1941; Olsson, 1942, 1964; Berry, 1957, 1959; Woodring, 1964; Jung, 1969) used the name *Hanetia* Jousseume, 1880, for species of *Solenosteira*. Berry (1962), however, noted that the type species of *Hanetia*, *Murex haneti* Petit de la Saussaye, 1856, is a Brazilian muricid. Comparative remarks are given under *Hesperisternia* and *Pusio*. Berry (1962) believed that *Solenosteira* is unique among Buccinidae in using the (male) shell as the site of deposition for egg capsules. McLean (1970), however, noted that *Hesperisternia berryi* also has this habit.

Genus *Zeapollia* Finlay, 1927

Type species – *Tritonidea acuticingulata* Suter, 1917.

Remarks – This Oligocene to Pliocene genus from temperate Australia and New Zealand comprises small species (maximum length 13 mm in *Z. purpuroides*); shell weakly constricted at base, with shouldered whorls; last whorl with 11 or fewer prominent axial ribs crossed by several sizes of cords; aperture ovate; outer lip determinate, planar to weakly convex, bearing five to seven denticles on its inner side; adapical end of inner lip with two parietal denticles; siphonal fasciole rounded; umbilical slit absent.

According to Darragh (1970) and Beu and Maxwell (1990), the following described species belong to *Zeapollia*: *Z. acuticingulata* (Suter, 1917), middle Miocene (Altonian), New Zealand; *Z. brevis* (Tate, 1888), Miocene and Pliocene, Victoria; *Z. obliquecostata* (Tate, 1888), Pliocene, Victoria; *Z. purpuroides* (Johnston,

1880), Oligocene to early Miocene, southern Australia. *Zeapollia* appears to be most similar to the eastern Atlantic genus *Anna*. It shares with *Anna* the presence of denticles on the inner side of the outer lip, but differs by having fewer, more prominent axial ribs and by having two enlarged denticles in the parietal area.

Historical Biogeography

The Oligocene to Recent members of the *Cantharus* group chronicle an eventful history of diversification, invasion, and extinction. Although a formal phylogenetic analysis will be needed to document some of these events, the taxonomic revisions and additions documented in the present paper allow some conclusions to be drawn.

Number of species	Eastern Atlantic	Western Atlantic	Eastern Pacific	Indo-West Pacific
<i>Anna</i>	4	0	0	0
<i>Cancellopollia</i>	0	0	0	2
<i>Cantharus</i>	0	0	0	7
<i>Gemophos</i>	1	3	5	0
<i>Hesperisternia</i>	0	3	6	0
<i>Pollia</i>	1	0	0	13
<i>Preangeria</i>	0	0	0	1
<i>Prodotia</i>	0	0	0	4
<i>Pusio</i>	0	0	2	0
<i>Solenosteira</i>	0	1	6	0

Table 1. Summary of Recent diversity of genera in the *Cantharus* group.

The modern distribution of the *Cantharus* group conforms to that of many other shallow-water circumtropical clades of animals (Table 1). The highest diversity is found in the tropical Indo-West Pacific (IWP) region (27 species), followed by the eastern Pacific (19), western Atlantic (7), and eastern Atlantic including the Mediterranean (5).

In the IWP region, the *Cantharus* group is represented by three highly distinctive groups: the *Cancellopollia*-*Cantharus*-*Pollia* group, *Preangeria*, and *Prodotia*. The majority of species belong to the probable clade comprising *Cancellopollia*, *Cantharus*, and *Pollia*, together accounting for 22 IWP species (Table 1). Species in this group have a predominantly continental distribution, but two species of *Pollia* (*P. fumosa* in the broad sense, and *P. undosa*) extend to islands in Oceania. The genus *Pollia* does not, however, occur at such outposts as Easter Island, the Hawaiian Islands, and the Marquesas Islands. *Preangeria* is represented in the Recent fauna by a single continental species. Of the four currently recognized species of *Prodotia*, two extend to the furthest reaches of Oceania.

Much of the Recent diversity in the IWP is allopatric, that is, many of the species have mutually exclusive ranges. For example, no one site has more than one spe-

cies of *Cantharus*. Individual islands in the western Pacific support as many as three species of *Pollia* and two species of *Prodotia*.

In the eastern Pacific, one endemic genus (*Pusio*) and three genera with a broader tropical American distribution (*Gemophos*, *Hesperisternia*, and *Solenosteira*) comprise a largely continental fauna in which sympatric diversity is high. Only two species (*Gemophos janellii* and *G. sanguinolentus*) are known from the Galápagos Islands, but neither is endemic there. Distributional data point to a two-fold division of the eastern Pacific into a northern region, encompassing southern Baja California and the Gulf of California southward to Guatemala (with the species *Hesperisternia berryi* and *Solenosteira macrospira*), and a more diverse southern region extending from El Salvador to northern Peru (with *Gemophos janellii*, *G. pastinaca*, *G. ringens*, *Hesperisternia elegans*, *H. lauta*, and *Solenosteira fusiformis*). Twelve of the 20 members of the *Cantharus* group, however, occur in parts of both the northern and southern regions of the eastern Pacific. A similar north-south differentiation has been noted for other molluscs in the eastern Pacific (Vermeij, 1991a, 2001c; Reid, 2002). Sympatric diversity within the eastern Pacific reaches a peak in Panama, where two species of *Pusio*, four of *Gemophos*, six of *Hesperisternia*, and two or three of *Solenosteira* co-occur. In Panama, species of *Hesperisternia* and *Solenosteira* tend to live below the low tide line, whereas *Gemophos* and *Pusio* are more apt to be intertidal. No other part of the world has a higher sympatric diversity of species in the *Cantharus* group than Pacific Panama.

Western Atlantic species fall into two distinct biogeographic groups. One is confined to the subtropical coasts of the southeastern United States. This group includes *Gemophos filistriatus*, *G. tinctus*, *Hesperisternia harasewychi*, *H. multangula*, and *Solenosteira cancellaria*. The second, surprisingly small group, occurs in the Caribbean region and Brazil. This group comprises *Gemophos auritulus* and *Hesperisternia karinae*. There are no Brazilian endemic species. No genus in the *Cantharus* group is represented by more than one species at any given site, although regionally the genera *Gemophos* and *Hesperisternia* are each represented by two species in Florida. In both instances, the two sympatric species occur at different water depths; *Gemophos filistriatus* and *Hesperisternia harasewychi* are deep-water, whereas *G. tinctus* and *H. multangula* occur in the intertidal zone and shallow subtidal.

The *Cantharus* group is least well represented in the eastern Atlantic. There are four species of *Anna*, and one each of *Gemophos* and *Pollia*. Little can be said about the biogeographic subdivision of the eastern Atlantic until the Recent species of *Anna* are studied in more detail.

As noted in the remarks under *Anna* and *Editharus*, the post-Eocene members of the *Cantharus* group may have had an eastern Atlantic origin during the early Oligocene. At that time, the group was represented by two species in France, *Anna consobrina* and *Editharus heberti*, the lat-

ter being the youngest member of an otherwise Eocene genus. Unfortunately, no late Oligocene species of *Anna* has yet been confirmed. The next member of that genus to appear is the early Miocene (Aquitanian and Burdigalian) *A. cancellarioides* in southern Europe (see Lozouet *et al.*, 2001). By the late Oligocene, the *Cantharus* group had reached the Americas, the oldest species there being *Hesperisternia pauper*, and Australia.

The early to middle Miocene represents a time of modest diversification of the *Cantharus* group. In Europe, the group was represented by the genus *Anna*. The pattern of diversification in *Anna* remains unclear, because a revision of the many taxa for middle and late Miocene species will be needed to sort out how many species existed at any given time and place. In the Americas, the *Cantharus* group was represented in early and middle Miocene time by a few species of *Hesperisternia* (one at any given site and time in the southeastern United States and Venezuela) and perhaps by *Pusio* in the temperate north-eastern Pacific. The genera *Gemophos* and *Solenosteira* arose in the late Miocene. In the IWP, three clades (*Polia*, *Preangeria*, and *Prodotia*) were already present by early Miocene time.

Today's biogeographic distinction in the western Atlantic between a subtropical region centered on the southeastern United States and a tropical region centered on the Caribbean and Brazil was already evident in the *Cantharus* group during the early Miocene. Petuch (1982) referred to these regions as the Caloosahatchian and Gatunian Provinces respectively. Two genera (*Gemophos* and *Solenosteira*) appear to have originated in the Gatunian portion of tropical America. The Pliocene witnessed substantial diversification in the *Cantharus* group. In the southeastern United States, at least three lineages of *Solenosteira* (typified by *S. acclinensis*, *S. floridensis*, and *S. vaughani*) had differentiated by early Pliocene time, and locally coexisted until the end of the time interval represented by the Golden Gate and Fruitville Members of the Tamiami Formation. In the succeeding Caloosahatchee Formation (late Pliocene), only two of these lineages (represented by *S. lymani* or *S. cancellaria* and by *S. mengeana*) persisted. In the genus *Hesperisternia*, two lineages (*H. filicata-olssoni* and *H. lindae-multangula*) coexisted locally in Florida throughout the middle and late Pliocene, but only one lineage (typified by *H. multangula*) survived into the Pleistocene. Petuch (1994) described three sympatric species of *Hesperisternia* from the Golden Gate Member near Miami, but I suspect some of these taxa will prove to be synonyms, representing just two species. The genus *Gemophos* was represented during most of its history in Florida by a single species in the *G. tridentatus-basidentatus-tinctus* lineage, but during a brief interval of the late Pliocene, represented by the Caloosahatchee Formation, a second species (*G. crispatus*) caused the number of co-occurring species of *Gemophos* to climb to two.

In the Gatunian Province of tropical America, most sites had only one species each of *Gemophos*, *Hesperisternia*, *Pusio*, and *Solenosteira*. Two species of *Hesperisternia*

co-occurred in the Esmeraldas Formation and in the Jama Formation (both early Pliocene) of Ecuador. Two species of *Solenosteira* appear to have coexisted in the Jama Formation. Much of the high Gatunian diversity within the *Cantharus* group was, in other words, allopatric. The genus *Solenosteira* seems always to have had a strictly continental distribution. The genus was absent from the well sampled and well studied Pliocene faunas of the Gurabo Formation of the Dominican Republic and the Bowden Formation of Jamaica. Whether the very high sympatric diversity of Recent eastern Pacific members of the *Cantharus* group is a holdover from the Pliocene or is a Pleistocene to Recent development is difficult to infer, because intertidal species do not readily fossilize. However, given that two Atlantic species of *Gemophos* appear to very closely related to (and probably sister species of) eastern Pacific species (the fossil *G. crispatus* in Florida almost indistinguishable from the Pacific *G. gemmatus*; the Caribbean *G. auritulus* close to the Pacific *G. ringens* and *G. sanguinolentus*), I surmise that at least two species of *Gemophos* co-occurred in the eastern Pacific part of the Gatunian Province before the Central American isthmus rose to form an impenetrable barrier during the late Pliocene. This inference therefore suggests that sympatric diversity in the *Cantharus* group was already high in the eastern Pacific during the early Pliocene, though perhaps not as high as it became later.

In the IWP, the continentally distributed genus *Cantharus* appears to have originated from a *Polia*-like ancestor during the Pliocene. Although fossil evidence is scanty, the pattern of sympatric diversity observed in the IWP today is likely not to have been radically different in the Pliocene.

Based on sites of first appearance of genera in the fossil record, I recognize at least five instances of invasion of members of the *Cantharus* group from one tropical region to another. In the Americas, the genus *Solenosteira* appears later in Florida (*S. acclinensis* in Bed 10, lower Pinecrest beds or Buckingham Member of the Tamiami Formation; see Petuch, 2004) than in the Gatunian Province (late Serravallian or earliest Tortonian Miocene, *e.g.* *S. dalli protera* in the lower Gatun Formation of Panama). The genus *Gemophos* appears to have invaded the Caloosahatchian Province twice, once during the late Pliocene interval represented by the Fruitville and Golden Gate Members of the Tamiami Formation (*G. tridentatus*), and a second time a little later during the late Pliocene (*G. crispatus* in the Caloosahatchee Formation). The genus *Gemophos* invaded West Africa (as *G. viverratus*) during the Pleistocene. Finally, the IWP genus *Polia* also invaded West Africa (as *P. vermeuleni*). Although the *Cantharus* group is largely tropical, invasions of warm-temperate seas have occurred at least five times. *Zeapollia* reached temperate Australia by the late Oligocene. The eastern Pacific genus *Pusio*, today represented by two tropical to subtropical species, occurred in California from early to middle Miocene to Pleistocene times. In the western Atlantic, the genus *Hesperisternia* occurred as far north as Maryland during the Tortonian

(late Miocene: *H. petuchi*) and Virginia during the middle Pliocene (*H. filicata*). It is not known whether these two northern species belong to a single warm-temperate lineage or whether they represent independent northward extensions of subtropical lineages. The largely European genus *Anna* extended as far north as Poland during the Tortonian (*A. minutulus*). In the IWP, several species of *Pollia* are endemic to warm-temperate Japan (*Pollia mollis* and *P. subrubiginosa*) and southeastern Africa (*P. insculpta* and *P. subcostata*).

Late Neogene extinction in the *Cantharus* group was most intense in the western Atlantic. In Florida, only one lineage each of *Gemophos*, *Hesperisternia*, and *Solenosteira* survived beyond the late Pliocene. The lineages of *Hesperisternia filicata-olssoni*, *Gemophos crispatus*, *Solenosteira acilensis*, and *S. vaughani-mengeana* all disappeared above the Caloosahatchee Formation. Contrary to Petuch (1995), no lineages in this group became extinct between the Pinecrest Member and the overlying Fruitville (and time-equivalent Golden Gate) Member of the Tamiami Formation, nor between the Fruitville Member and the overlying Caloosahatchee Formation, although morphological shifts do occur within each of the surviving lineages. In the Atlantic part of the Gatunian Province, extinction was also severe. Some time during the Pliocene, the genus *Solenosteira* became regionally extinct, as did one or more lineages of *Hesperisternia* represented in the Pliocene by such species as *H. binodosa*, *H. corrugata*, *H. tortugera*, and an undescribed species (Jung, 1969) from Trinidad. A single species of *Hesperisternia* (*H. karinae*) persists in the Caribbean and Brazil today.

The tropical eastern Pacific acts as a major refuge for several lineages of the *Cantharus* group that had late Miocene or Pliocene representatives in the Atlantic. Refugial eastern Pacific groups include *Gemophos gemmatus*, the *Hesperisternia elegans-panamica-shaskyi* complex (represented in the Pliocene Atlantic by *H. corrugatus*), and two or more lineages of *Solenosteira*.

Temperate members of the *Cantharus* group also fared badly during the late Neogene. *Pusio* disappeared from California after the early Pleistocene, and survives today in the tropical and subtropical eastern Pacific. *Zeapollia* became extinct in Australia and New Zealand during the Pliocene, and the *Hesperisternia filicata* line disappeared after Yorktown Formation time (3.2 Ma) in the temperate northwestern Atlantic. The only warm-temperate members surviving today occur in the Mediterranean (species of *Anna*) and marginal parts of the IWP (species of *Pollia*).

The one region to escape any apparent extinctions during the late Neogene is the IWP. All genera recovered from that region in the early Miocene to Pliocene persist there today.

Acknowledgments

I thank Janice Cooper for technical assistance, and Greg

S. Herbert for technical assistance, photography of specimens, and helpful discussions. M. G. Harasewych, P. Jung, E. J. Petuch, R. W. Portell, and G. Rosenberg kindly made specimens available for study.

References

- Abbott, R.T. 1974. *American seashells (second edition)*, 663 pp. New York (Van Nostrand Reinhold).
- Abbott, R.T. 1986. *Cantharus multangulus* new subspecies *grandanus* from northwest Florida (Buccinidae). *Nautilus* 100, 120-121.
- Adams, C.B. 1852. Catalog of shells collected at Panama, with notes on synonymy, station, and habitat. *Annals of the Lyceum of Natural History of New York* 5, 229-566.
- Addicott, W.O. 1970. Miocene gastropods and biostratigraphy of the Kern River area, California. *United States Geological Survey Professional Paper* 642, 1-174.
- Aguilar, T. and Fischer, R. 1986. Moluscos de la Formación Montezuma (Plioceno-Pleistoceno; Costa Rica). *Geologie und Palaeontologie* 20, 209-241.
- Allmon, W.D. 1990. Review of the *Bullia* group (Gastropoda: Nassariidae) with comments on its evolution, biogeography, and phylogeny. *Bulletins of American Paleontology* 99, 1-179.
- Amano, K. and Vermeij, G.J. 2003. Evolutionary adaptation and geographic spread of the Cenozoic buccinid genus *Lirabuccinum* in the North Pacific. *Journal of Paleontology* 77, 863-872.
- Anderson, F.M. 1929. Marine Miocene and related deposits of North Colombia. *Proceedings of the California Academy of Sciences (Fourth Series)* 18, 73-213.
- Anderson, F.M. and Martin, B. 1914. Neocene in the Temblor Basin, California, and Neocene deposits of the San Juan district, San Luis Obispo County. *Proceedings of the California Academy of Sciences (fourth Series)* 4, 15-112.
- d'Archiac, A. 1850. Formation nummulitique roches ignées ou pyrogènes des époques quaternaire et tertiaire. *Histoire des progrès de la Géologie de 1834 à 1849* 3, 1-304.
- Arnaud, P.M. 1977. Révision des taxa malacologiques méditerranéens introduits par Antoine Risso. *Annales du Muséum d'Histoire Naturelle de Nice* 5, 101-150.
- Arnold, R. 1908. New and characteristic species of fossil mollusks from the oil-bearing Tertiary formations of Santa Barbara County, California. *Smithsonian Miscellaneous Collections* 4, 419-447.
- Arnold, R. 1909. Paleontology of the Coalinga district, Fresno and Kings Counties, California. *United States Geological Survey Bulletin* 396, 1-173.
- Baluk, W. 1995. Middle Miocene (Badenian) gastropods from Korytnica, Poland. Part II. *Acta Geologica Polonica* 45, 153-255.
- Basterot, B. de 1825. Description géologique du bassin Tertiaire du sud-ouest de la France. Première partie, comprenant les observations générales sur les mollusques fossiles, et la description particulière de ceux qu'on rencontre dans ce bassin. *Mémoires de la Société d'Histoire Naturelle de Paris* 2, 1-100.
- Bellardi, L. 1873. I molluschi dei terreni Terziarii del Piemonte e della Liguria. Parte 1: Cephalopoda, Pteropoda, Heteropoda, Gasteropoda (Muricidae e Tritonidae). *Memorie della Reale Accademia delle Scienze di Torino* (2) 27, 33-294.

- Berry, S.S. 1957. Notices of new eastern Pacific Mollusca. — I. *Leaflets in Malacology* 1, 75-82.
- Berry, S.S. 1959. Notices of new eastern Pacific Mollusca. — III. *Leaflets in Malacology* 1, 107-114.
- Berry, S.S. 1962. A note on *Cantharus*, with proposal of a new specific name. *Leaflets in Malacology* 1, 129-130.
- Berry, S.S. 1963. Notices of new eastern Pacific Mollusca. — V. *Leaflets in Malacology* 1, 139-146.
- Beu, A.G. and Maxwell, P.A. 1990. Cenozoic Mollusca of New Zealand. *New Zealand Geological Survey, Paleontological Bulletin* 58, 1-518.
- Bivona, A. 1832. Caratteri d'un nuovo genere di conchiglie della famiglia delle Columellarie del Signor de Lamarck. *Effemeridi Scientifiche e Letterarie per la Sicilia* 2, 8-13.
- Blainville, H. de 1832. Disposition méthodique des espèces Récentes et fossiles des genres pourpre, ricinule, licorne et concholépas de M. de Lamarck et description des espèces nouvelles ou peu connues faisant partie de la collection du Muséum d'Histoire Naturelle de Paris. *Nouvelles Annales du Muséum d'Histoire Naturelle de Paris* 1, 189-263.
- Brébion, P. 1979. Étude biostratigraphique du Quaternaire marocain. *Annales de Paléontologie Invertébrés* 65, 1-42.
- Broderip, W.J. 1833. Characters of new species of Mollusca and Conchifera, collected by Mr. Cuming. *Proceedings of the Zoological Society of London for 1833*, 173-179.
- Broderip, W.J. and Sowerby, G.B. 1829. Observations on new or interesting Mollusca contained, for the most part, in the museum of the Zoological Society. *Zoological Journal, London*, 4, 359-379.
- Brown, A.P. and Pilsbry, H.A. 1911. Fauna of the Gatun Formation, Isthmus of Panama. *Proceedings of the Academy of Natural Sciences of Philadelphia* 63, 336-373.
- Carpenter, P.P. 1866. On the Pleistocene fossils collected by Col. E. Jewett at Sta. Barbara (California); with descriptions of new species. *Annals and Magazine of Natural History, Including Zoology, Botany, and Geology*, 17 (third Series), 274-278.
- Cernohorsky, W.O. 1971. Indo-Pacific Pisaninae (Mollusca: Gastropoda) and related buccinid genera. *Records of the Auckland Institute and Museum* 8, 137-167.
- Cernohorsky, W.O. 1974. The taxonomy of some Indo-Pacific Mollusca. Part II. *Records of the Auckland Institute and Museum* 11, 121-132.
- Cernohorsky, W.O. 1975. Supplementary notes on the taxonomy of buccinid species of the subfamily Pisaninae (Mollusca: Gastropoda). *Records of the Auckland Institute and Museum* 12, 175-211.
- Cernohorsky, W.O. 1986. A taxonomic study on two Indo-Pacific species of *Cantharus* (*Prodotia*) (Mollusca: Buccinidae). *Records of the Auckland Institute and Museum* 23, 59-65.
- Chirli, C. 2000. *Malacofauna Pliocenica Toscana Vol. 2: Superfamiglia Muricoidea Rafinesque, 1815*, 142 pp. (Chirli).
- Clark, B.L. 1938. Fauna from the Markley Formation (upper Eocene) on Pleasant Creek, California. *Bulletin of the Geological Society of America* 47, 683-730.
- Conrad, T.A. 1833. *Fossil shells of the Tertiary formations of North America, illustrated by figures drawn on stone by T. A. Conrad. Vol. 3, no. 3*, pp. 29-38.
- Conrad, T.A. 1843. Description of a new genus, and of twenty-nine new Miocene and one Eocene fossil shells of the United States. *Proceedings of the Academy of Natural Sciences of Philadelphia* 1, 305-311.
- Conrad, T.A. 1846. Descriptions of new species of fossil and Recent shells and corals. *Proceedings of the Academy of Natural Sciences of Philadelphia* 3, 19-27.
- Cossmann, M. 1893. Révision sommaire de la faune du terrain Oligocène marin aux environs d'Etampes (suite). *Journal de Conchyliologie* 41, 297-363.
- Cossmann, M. 1901. *Essais de Paléoconchologie comparée. Vol. 4*, 293 pp. Paris (Cossmann).
- Cossmann, M. and Lambert, J. 1884. Étude paléontologique et stratigraphique sur le terrain Oligocène marin aux environs d'Etampes. *Mémoires de la Société Géologique de France, Troisième Série*, 3, 1-187.
- Dall, W.H. 1889. Reports on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico (1877-78) and in the Caribbean Sea (1879-80) by the U.S. Coast Survey Steamer "Blake," Lieut. Commander C.D. Sigsbee, U.S.N. and Commander J.R. Bartlett, U.S.N., Commanding. XXIX Report on the Mollusca, Part II, Gastropoda and Scaphopoda. *Bulletin of the Museum of Comparative Zoology at Harvard College* 18, 1-492.
- Dall, W.H. 1890. Contributions to the Tertiary fauna of Florida, with especial reference to the Miocene Silex-beds of Tampa and the Pliocene beds of the Caloosahatchee River. Part I. Pulmonate, opisthobranchiate and orthodont gastropods. *Transactions of the Wagner Free Institute of Science, Philadelphia*, 3, 1-200.
- Dall, W.H. 1903. Contributions to the Tertiary fauna of Florida, with especial reference to the Silex-beds of Tampa and the Pliocene beds of the Caloosahatchee River, including in many cases a complete revision of the generic groups treated of and their American Tertiary species. Part VI. Concluding the work. *Transactions of the Wagner Free Institute of Science of Philadelphia* 3, 1219-1655.
- Dall, W.H. 1908. Reports on the dredging operations off the west coast of Central America to the Galapagos, to the west coast of Mexico, and in the Gulf of California, in charge of Alexander Agassiz, carried on by the U.S. Fish Commission Steamer "Albatross," during 1891, Lieut. Commander Z.L. Tanner, U.S.N., commanding. XIV. The Mollusca and Brachiopoda. *Bulletin of the Museum of Comparative Zoology of Harvard College* 43, 205-487.
- Dall, W.H. 1918. Changes in and additions to molluscan nomenclature. *Proceedings of the Biological Society of Washington* 31, 137-138.
- Dall, W.H. 1924. Notes on molluscan nomenclature. *Proceedings of the Biological Society of Washington* 37, 87-90.
- Darragh, T.A. 1970. Catalogue of Australian Tertiary Mollusca except chitons. *Memoirs of the National Museum of Victoria* 31, 125-212.
- De Gregorio, A. 1885. Studi su talune conchiglie mediterranee viventi e fossili con una rivista del gen. *Vulsella*. *Bullettino della Società Malacologica Italiana* 10, 36-288.
- Dillwyn, L.W. 1817. *A descriptive catalogue of recent shells, arranged according to the Linnean method; with particular attention to the synonymy. Vol. II*, pp. 581-1092. London (John and Arthur Arch).
- Dolin, C., Dolin, L. and Le Renard, J. 1980. Inventaire systématique des mollusques de l'Auvergnien "Faciés Charnié" de Baron (Oise), et remarques paléontologiques. *Bulletin d'Informations des Géologues du Bassin de Paris* 17, 26-48.
- Duclos, P.B. 1833. Pourpre. *Purpura*. *Magasin de Zoologie Journal* 3, text and plate 22.
- Finlay, C.J. 1927. A further commentary on New Zealand molluscan systematics. *Transactions and Proceedings of the*

- New Zealand Institute* 57, 320-485.
- Fischer, P.J. 1927. Beitrag zur Kenntnis der Pliozän-Fauna der Mollukken-Inseln Seram und Obi. *Paläontologie von Timor* 15, 1-179.
- Fontannes, F. 1882. *Les mollusques Pliocènes de la vallée du Rhône et du Rousillon. Tome 1. Gastéropodes*, 276 pp. Lyon (Georg, Libraire).
- Gabb, W.M. 1860. Descriptions of new species of American Tertiary and Cretaceous fossils. *Journal of the Academy of Natural Sciences of Philadelphia* 4 (2nd series), 375-406.
- Gabb, W.M. 1869. Cretaceous and Tertiary fossils. Section I: Tertiary invertebrate fossils. Part II: description of new species (continued). *Palaeontology of California* 2, *Geological Survey of California* 2, 39-63.
- Gabb, W.M. 1873. On the topography and geology of Santo Domingo. *Transactions of the American Philosophical Society, new series* 15, 49-259.
- Gardner, J. 1944. The molluscan fauna of the Alum Bluff Group of Florida. Part VII. Stenoglossa (in part). *United States Geological Survey Professional Paper* 142-G, 437-491.
- Glibert, M. 1963. Les Muricacea et Buccinacea fossiles du Cénozoïque étranger des collections de l'Institut Royale des Sciences Naturelles de Belgique. *Mémoires de l'Institut Royale des Sciences Naturelles de Belgique* (2) 44, 1-179.
- Gmelin, J.F. 1791. *Systema naturae per regna tria naturae. Editio decim tertia*, pp. 3021-3910. Lipsiae.
- Gould, A.A. 1860. Descriptions of new shells collected by the United States North Pacific Exploring Expedition. *Proceedings of the Boston Society of Natural History* 7, 323-340.
- Grant, U.S. IV and Gale, H.R. 1931. Catalogue of the marine Pliocene and Pleistocene Mollusca of California and adjacent regions. *Memoirs of the San Diego Society of Natural History* 1, 1-1035.
- Gray, J.E. 1839. Molluscous animals and their shells. In: F. W. Beechey (ed.). *The zoology of Captain Beechey's voyage; compiled from the collections and notes made by Captain Beechey, the officers and naturalist of the expedition, during a voyage to the Pacific and Behring's Straits performed in His Majesty's ship Blossom, under the command of Captain F. W. Beechey, R.N., F.R.S., etc., etc., in the years 1825, 26, 27 and 28*, pp. 103-155. London (Henry G. Bohn).
- Gray, J.E. 1857. *Guide to the systematic distribution of Mollusca in the British Museum Part I*, 230 pp. London (British Museum).
- Griffith, E. and Pidgeon, E. 1834. *The Mollusca and Radiata. Arranged by the Baron Cuvier, with supplementary additions to each order*, 601 pp. London (Whittaker and Company).
- Guppy, R.J. 1911. Fossils from Springvale near Couva, Trinidad. — Second report — in continuation on Society Paper no. 440. *Agricultural Society of Trinidad and Tobago Paper* 454, *Proceedings of the Agricultural Society of Trinidad and Tobago* 11, 1-10. (Reprinted in Harris, G.D. 1921. A reprint of the more inaccessible paleontological writings of Robert John Lemere Guppy. *Bulletins of American Paleontology* 8, 149-346.)
- Harmer, F.W. 1914. *The Pliocene Mollusca of Great Britain, being supplementary to S.V. Wood's Monograph of the Crag Mollusca. 1*, 200 pp. Palaeontographical Society of London.
- Hertlein, L.G. and Jordan, E.L. 1927. Paleontology of the Miocene of Lower California. *Proceedings of the California Academy of Sciences* 16, 605-647.
- Hertlein, L.G. and Strong, A.M. 1951. Eastern Pacific expeditions of the New York Zoological Society. XLIII. Mollusks from the west coast of Mexico and Central America. Part X. *Zoologica, New York*, 36, 67-120.
- Hodson, F. and Hodson, H.K. 1931. Some Venezuelan mollusks. Part 2. *Bulletins of American Paleontology* 16: 95-132.
- Hoernes, R. and Auinger, M. 1890. *Die Gasteropoden der Meeres-Ablagerungen der ersten und zweiten Miocän Mediterran-Stufe in der Österreichisch-Ungarischen Monarchie*, pp. 233-282. Wien (Hölder).
- Houart, R. 1995. The Ergalataxinae (Gastropoda, Muricidae) from the New Caledonia region with some comments on the subfamily and the description of thirteen new species from the Indo-West Pacific. *Bulletin du Muséum National d'Histoire Naturelle, Paris* (4) 16 (Section A), 245-297.
- Houart, R. 1997. The West African Muricidae Part II. Ocenebrinae, Ergalataxinae, Tripterotyphinae, Typhinae, Trophoninae & Rapaninae. *Apex* 12, 49-91.
- Houart, R. 2001. *A review of the Recent Mediterranean and northeastern Atlantic species of Muricidae*, 227 pp. Rome (Evolver).
- Janssen, A.W. 1984. *Mollusken uit het Mioceen van Winterwijk-Miste*, 451 pp. Koninklijke Nederlandse Natuurhistorische Vereniging.
- Johnston, R.M. 1880. Third contribution to the natural history of the Tertiary marine beds of Table Cape with a description of 30 new species of Mollusca. *Monthly Notices of Papers and Proceedings and Report of the Royal Society of Tasmania for 1879*, 29-41.
- Jousseume, F.P. 1880. Division méthodique de la famille des Purpuridae. *Le Naturaliste, Journal des Echanges et des Nouvelles* 2, 335-336.
- Jung, P. 1969. Miocene and Pliocene mollusks from Trinidad. *Bulletins of American Paleontology* 55, 293-657.
- Keen, A.M. 1971. *Seashells of tropical West America: marine mollusks from Baja California to Peru (second edition)*, 1064 pp. Palo Alto, CA (Stanford University Press).
- Kiener, L.C. 1834. *Spécies général et iconographie des coquilles vivantes comprenant la collection du Muséum d'Histoire Naturelle de Paris, la collection de Lamarck, celle de Masséna (appartenant maintenant M. le Baron B. Delessert), et les découvertes récentes des voyageurs. Genre Buccin, Buccinum de Linné*, pp. 1-104. Paris (Rousseau Libraire).
- Kiener, L.C. 1835. *Ibid. Genre pourpre (Purpura, Lam.)*, pp. 1-151. Paris (Rousseau Libraire).
- Knudsen, J. 1980. *Cantharus (Pollia) vermeuleni* n.sp. (Mollusca, Prosobranchia, Buccinidae) from West Africa. *Beaufortia* 30, 11-15.
- Kosuge, S. 1984. Studies of the collection of Mr. Victor Dan (6). Descriptions of new species of the genera *Pterochelus*, *Takia*, *Muricopsis* and *Cantharus*. *Bulletin of the Institute of Malacology, Tokyo* 1: 143-146.
- Kosuge, S. 1985. New name for the genus *Cantharus*. *Bulletin of the Institute of Malacology, Tokyo* 2, 20.
- Krauss, F. 1848. *Die südafrikanischen mollusken. Ein Beitrag zur Kenntnis der Mollusken des Kap- und Natal-Landes und zur geographischen Verbreitung derselben, mit Beschreibung und Abbildung der neuen Arten*, pp. 1-140. Stuttgart (Ebner und Seubert).
- Küster, H.C. 1858-1860. *Die Gattungen Buccinum, Purpura*,

- Concholepas und Monoceros. Systematisches Conchylien-Cabinet von Martini und Chemnitz Küster edition, volume 7, part 2, 296 pp. [1858].*
- Ladd, H.S. 1977. Cenozoic fossil mollusks from western Pacific islands; gastropods (Eratoidae through Harpidae). *United States Geological Survey Professional Paper 533*, 1-84.
- Lamarck, J.B.P.A. de Monet de 1803. Mémoires sur les fossiles des environs de Paris, comprenant la détermination des espèces qui appartiennent aux animaux marins sans vertébrés, et dont la plupart sont figurés dans la collection des vélins du muséum. *Annales du Muséum d'Histoire Naturelle* 2, 315-321 (part of reprint of Lamarck, 1802-1809. Ithaca, NY: Paleontological Research Institute).
- Link, D.H.F. 1807. *Beschreibung der naturalien Sammlung der Universität zu Rostock. Teil 3*, pp. 101-165.
- Linnaeus, C. 1758. *Systema naturae per regna tria naturae: secundum classis, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Ed. 10, reformata. Holmiae (Salvii).*
- Locard, A. 1886. *Prodrome de Malacologie Française. Catalogue général des Mollusques vivants de France, Mollusque marins*, pp. 1-799. Paris, Baillière.
- Loel, W. and Corey, W.H. 1932. The Vaqueros Formation, Lower Miocene of California. I. Paleontology. *University of California Publications in Geological Sciences* 22, 31-410.
- Lozouet, P., Lesport, J.-F. et Renard, P. 2001. Révision des Gastropoda (Mollusca) du stratotype de l'Aquitainien (Miocène inf.): site de Saucats "Lariey", Gironde, France. *Cossmanniana*, Hors-Série no. 3, 1-189.
- MacNeil, F.S. 1961. Tertiary and Quaternary Gastropoda of Okinawa. *United States Geological Survey Professional Paper 339*, 1-148.
- Makiyama, J. 1927. Molluscan fauna of the lower part of the Kakegawa Series in the province of Tôtômi, Japan. *Memoirs of the College of Science, Kyoto Imperial University, Series B*, 3, 1-137.
- Malatesta, A. 1960. Malacofauna Pleistocenica di Grammichele (Sicilia). *Memorie per Servire alla descrizione della carta Geologica d'Italia* 12, 1-196.
- Mansfield, W.C. 1930. Miocene gastropods and scaphopods of the Choctawhatchee Formation of Florida. *Florida State Geological Survey Bulletin* 3, 1-185.
- Mansfield, W.C. 1937. Mollusks of the Tampa and Suwannee Limestones of Florida. *State of Florida, Department of Conservation, Geological Bulletin* 15, 1-334.
- Martin, K. 1883. Nachtraege zu den Tertiaerschichten auf Java. Erster Nachtrag: Mollusken. *Sammlungen des Geologischen Reichs-Museums in Leiden, erster Serie*, 1, 194-265.
- Martin, K. 1895. Die Fossilien von Java auf Grunde einer Sammlung von Dr. R.D.M. Verbeek und von Anderen. *Sammlungen des Geologischen Reichs-Museums in Leiden, Neue Serie*, 1 (5), 1-132.
- Martin, K. 1899. Die Fossilien von Java auf Grund einer Sammlung von Dr. R.D.M. Verbeek. *Sammlungen des Geologischen Reichs-Museums in Leiden, Neue Serie*, 1 (6), 133-280.
- Martin, K. 1906. Die Fossilien von Java auf Grund einer Sammlung von Dr. R.D.M. Verbeek. *Sammlungen des Geologischen Reichs-Museums in Leiden, Neue Folge* 1 (7).
- Martin, K. 1921. Die Mollusken der Njalindungschichten. *Sammlungen des Geologischen Reichs-Museums in Leiden, Neue Folge* 1 (2), 446-496.
- Mayer, C. 1864. Description de coquilles fossiles des terrains Tertiaires inférieurs. *Journal de Conchyliologie* 12, 168-181.
- McLean, J.H. 1970. New species of tropical eastern Pacific Gastropoda. *Malacological Reviews* 2, 115-130.
- Melville, J.C. 1912. Descriptions of thirty-three new species of Gastropoda from the Persian Gulf, Gulf of Oman, and northern Arabian Sea. *Proceedings of the Malacological Society of London* 10, 240-254.
- Melville, J.C. 1918. Descriptions of thirty-four species of marine Mollusca from the Persian Gulf, Gulf of Oman and Arabian Sea, collected by Mr. F.W. Townsend. *Annals and Magazine of Natural History, ninth Series*, 1, 137-158.
- Melville, J.C. and Standen, R. 1903. Description of sixty-eight new Gastropoda from Persian Gulf, Gulf of Oman, and north Arabian Sea, dredged by Mr. F.W. Townsend of the Indo-European Telegraph Service, 1901-1903. *Annals and Magazine of Natural History, seventh Series*, 12, 289-324.
- Merle, D. and Pacaud, J.-M. 2002. The Early Paleogene muricids (Mollusca, Neogastropoda) from the Oiching beds (Haunsberg area, Salzburg, Austria): revision and addition to the knowledge of the evolution of Paleocene and lower Eocene *Poirieria*. *Mitteilungen der Bayerischen Staatssammlung, Paläontologie und Historische Geologie*, 42, 3-14.
- Michelotti, G. 1847. Description des fossiles des terrains Miocènes de l'Italie septentrionale. *Natuurkundige Verhandelingen van de Hollandsche Maatschappij der Wetenschappen te Haarlem (tweede Verzameling)* 3 (2), 1-409.
- Monterosato, A. 1917. Molluschi viventi e quaternari raccolti lungo le coste della Tripolitania. *Bollettino della Società Zoologica Italiana (Ser. 3)* 3 (12), 1-25.
- Mörch, O.A.L. 1860. Beiträge zur Molluskenfauna Central-Amerika's. *Malakozoologische Blätter* 7, 66-106.
- Nelson, E.T. 1870. On the molluscan fauna of the later Tertiary of Peru. *Transactions of the Connecticut Academy of Arts and Sciences* 2, 186-206.
- Nowell-Usticke, G.W. 1969. *A supplementary listing of new shells (illustrated) to be added to the check list of the marine shells of St. Croix*, 32 pp. Privately published.
- Olsson, A.A. 1922. The Miocene of northern Costa Rica with notes on its general stratigraphic relations. *Bulletins of American Paleontology* 9: 174-482.
- Olsson, A.A. 1932. Contributions to the Tertiary paleontology of northern Peru: part 5, The Peruvian Miocene. *Bulletins of American Paleontology* 19, 1-272.
- Olsson, A.A. 1942. Tertiary and Quaternary fossils from the Burica Peninsula of Panama and Costa Rica. *Bulletins of American Paleontology* 27, 151-258.
- Olsson, A.A. 1964. *Neogene mollusks from northwestern Ecuador*, 256 pp. Ithaca, NY (Paleontological Research Institute).
- Olsson, A.A. 1971. Biological results of the University of Miami deep-sea expeditions. 77. Mollusks from the Gulf of Panama collected by R./V. John Elliott Pillsbury, 1967. *Bulletin of Marine Science* 21, 35-92.
- Olsson, A.A. and Harbison, A. 1953. Pliocene Mollusca of southern Florida with special reference to those from North Saint Petersburg. *Academy of Natural Sciences of Philadelphia Monograph* 8, 1-457.
- Pallary, P. 1900. Coquilles marines du littoral du département d'Oran. *Journal de Conchyliologie* 48, 211-422.
- Payraudeau, B.-C. 1826. *Catalogue descriptif et méthodique des annelides et des mollusques de l'île de Corse*, 218 pp.

- Petit de la Saussaye, S. 1853. Notice sur le genre *Phos* de Denys de Montfort, avec la description de deux espèces nouvelles. *Journal de Conchyliologie* 5, 87-92.
- Petit de la Saussaye, S. 1856. Description des coquilles nouvelles. *Journal de Conchyliologie* 5, 87-92.
- Petuch, E.J. 1982. Geographical heterochrony: contemporaneous coexistence of Neogene and Recent molluscan faunas in the Americas. *Palaeogeography, Palaeoclimatology, Palaeoecology* 37, 277-312.
- Petuch, E.J. 1987. *New Caribbean molluscan faunas*, 154 pp. Charlottesville, VA (Coastal Education and Research Foundation).
- Petuch, E.J. 1993. Patterns of diversity and extinction in Transmarian muricacean, buccinacean, and conacean gastropods. *Nautilus* 106, 155-173.
- Petuch, E.J. 1994. *Atlas of Florida fossil shells (Pliocene and Pleistocene marine gastropods)*, 394 pp. Evanston, IL (Chicago Spectrum).
- Petuch, E.J. 1995. Molluscan diversity in the Late Neogene of Florida: evidence for a two-stage mass extinction. *Science* 270, 275-277.
- Petuch, E.J. 1997. *Coastal paleoceanography of eastern North America (Miocene-Pleistocene)*, 373 pp. Dubuque, IA (Kendall/Hunt).
- Petuch, E.J. 1998. A new gastropod fauna from an Oligocene back-reef lagoonal environment in west central Florida. *Nautilus* 110, 122-138.
- Petuch, E.J. 2004. *Cenozoic seas: the view from eastern North America*, 308 pp. Boca Raton, FL (CRC).
- Pezant, A. 1908. Mollusques fossiles de Monneville (Oise) (suite). *La Feuille des Jeunes Naturalistes, Revue Mensuelle d'Histoire Naturelle (IV)* 38, 173-178.
- Philippi, R. 1844. *Fauna molluscorum viventium et in tellure Tertiaria fossilium regni utriusque Siciliae. Volumen secundum*, 304 pp. Halis Saxonum (E. Anton).
- Philippi, R. 1844. Nachtrag zum zweiten Bande der Enumeratio Molluscorum Siciliae. *Zeitschrift für Malakozoologie* 1 (3), 7-112
- 1848. Testaceorum novorum centuriae (continuatio). *Zeitschrift für Malakozoologie* 5, 17-27.
- Pilsbry, H.A. and Olsson, A.A. 1941. A Pliocene fauna from western Ecuador. *Proceedings of the Academy of Natural Sciences of Philadelphia* 93, 1-79.
- Rafinesque, C.S. 1815. *Analyses de la nature ou tableau du Univers et ces corps organises*, pp. 5-6, 136-149, 218-223. Palermo (Barravecchia).
- Reeve, L. 1846. Monograph of the genus *Buccinum*. *Conchologia Iconica* 3, pls. 1-12.
- Reeve, L. 1847. Monograph of the genus *Pyrula*. *Conchologia Iconica* 4, pls. 1-9.
- Reid, D.G. 2002. The genus *Nodilittorina* von Martens, 1897 (Gastropoda: Littorinidae) in the eastern Pacific Ocean, with a discussion of biogeographic provinces of the rocky-shore fauna. *Veliger* 45, 85-170.
- Risso, A. 1826. *Histoire naturelle des principales productions de l'Europe meridionale et particulièrement de celles des environs de Nice et des Alpes Maritimes. Vol. 4, Mollusca*, 412 pp. Paris.
- Robertson, R. 1957. A study of *Cantharus multangulus* (Philippi), with notes on *Cantharus* and *Pseudoneptunea* (Gastropoda: Buccinidae). *Notulae Naturae* 300, 1-10.
- Röding, P.F. 1798. *Museum Boltenianum e tribus regnis naturae quae olim collegerat Joa. Frid. Bolten, M.D.P.D. Pars Secunda*, 199 pp. Hamburg (J. Christi, Trappii).
- Rutsch, R. 1934. Die Gastropoden aus dem Neogen der Punta Gavilan in Nord-Venezuela. *Abhandlungen der Schweizerischen Palaeontologischen Gesellschaft* 54, 1-88.
- Schepman, M.M. 1911. Prosobranchia of the Siboga Expedition. Part IV: Rachiglossa. *Siboga-Expeditie* 49d, 247-363.
- Shuto, T. 1969. Neogene gastropods from Panay Island, the Philippines. *Memoirs of the Faculty of Science, Kyushu University, Series D Geology* 19, 1-250.
- Smith, B. 1946. Observations on gastropod protoconchs. Part III - Some protoconchs in *Busycon*, *Fusinus*, *Heilprinia*, *Hesperisternia*, and *Urosalpinx*. *Palaeontographica Americana* 3, 18-302.
- Smith, E.A. 1879. On a collection of Mollusca from Japan. *Proceedings of the Zoological Society of London for 1879*, 181-218.
- Smith, E.A. 1899. Natural history notes from H.M. Indian Marine Survey Steamer "Investigator," commander T. H. Heming, R.N. Series III, no. 1. On Mollusca from the Bay of Bengal and the Arabian Sea. *Annals and Magazine of Natural History, 7th Series*, 4, 237-251.
- Smith, M. 1936. New Tertiary shells from Florida. *Nautilus* 49, 135-139.
- Sowerby, G.B. 1825. *A catalogue of the shells contained in the collection of the late Earl of Tankerville, arranged according to the Lamarckian conchological systems; together with an appendix, containing descriptions of many new species*, 92 pp. London.
- Sowerby, G.B. 1834. New species of shells contained in the collection made by Mr. Cuming on the western coast of South America and among the islands of the South Pacific. *Proceedings of the Zoological Society of London for 1833*, Part i, 134-139.
- Sowerby, G.B. III 1900. On some marine shells from Ponderland and the Kowie, with descriptions of seventeen new species. *Proceedings of the Malacological Society of London* 4, 1-7.
- Stimpson, W. 1865. On certain genera and families of zoophagous gastropods. *American Journal of Conchology* 1, 55-64, pls. 8, 9.
- Suter, H. 1917. Descriptions of new Tertiary Mollusca occurring in New Zealand, accompanied by a few notes on necessary changes in nomenclature. Part I. *New Zealand Geological Survey, Paleontological Bulletin* 5, 1-93.
- Swainson, W. 1840. *A treatise on malacology; or the natural classification of shells and shellfish*, 419 pp. London (Longman, Orme, Brown, Green, and Longmans).
- Tate, R. 1888. The gastropods of the older Tertiary of Australia. (Part I.). *Transactions, Proceedings, and Report of the Royal Society of South Australia* 10, 91-176.
- Traub, F. 1979. Weitere Paläozän-Gastropoden des Haunsberges nördlich von Salzburg. *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und Historische Geologie* 19, 93-123.
- Tucker, H.I. and Wilson, D. 1932. Some new or otherwise interesting fossils from the Florida Tertiary. *Bulletins of American Paleontology* 18, 39-62.
- Tuomey, M. and Holmes, F.S. 1857. *Pleiocene fossils of South-Carolina containing descriptions and figures of the Polyparia, Echinodermata and Mollusca*, 152 pp. Charleston, SC (Russell and Jones).
- Vermeij, G.J. 1991a. Marine extinctions and their implications for conservation and biogeography. In: Dudley, E.C. (ed.). *The unity of evolution. Proceedings of the fourth international congress of systematic and evolutionary biology*.

- Vol. 1, pp. 143-148. Portland, OR (Dioscorides Press).
- Vermeij, G.J. 1991b. Generic identity and relationships of the northeastern Pacific buccinid gastropod *Searlesia dira* (Reeve, 1846). *Veliger* 34, 264-271.
- Vermeij, G.J. 1998a. Generic revision of the neogastropod family *Pseudolividae*. *Nautilus* 111, 53-84.
- Vermeij, G.J. 1998b. The systematic position of *Tritonidea dentata* Schepman, 1911 (Gastropoda, Prosobranchia: Buccinidae). *Basteria* 62, 25-34.
- Vermeij, G.J. 2001a. Taxonomy, distribution, and characters of pre-Oligocene members of the *Cantharus* group of Pisaninae (Neogastropoda: Buccinoidea). *Journal of Paleontology* 75, 295-309.
- Vermeij, G.J. 2001b. Innovation and evolution at the edge: origins and fates of gastropods with a labral tooth. *Biological Journal of the Linnean Society* 72, 461-508.
- Vermeij, G.J. 2001c. Distribution, history, and taxonomy of the *Thais* clade (Gastropoda: Muricidae) in the Neogene of tropical America. *Journal of Paleontology* 75, 697-705.
- Vermeij, G.J. and Bouchet, P. 1998. New Pisaninae (Mollusca, Gastropoda, Buccinidae) from New Caledonia, with remarks on *Cantharus* and related genera. *Zoosystema* 20, 471-485.
- Vokes, E.H. 1972. Catalogue of the genus *Murex* Linné (Mollusca: Gastropoda); Muricinae, Ocenebrinae. *Bulletins of American Paleontology* 61, 1-141.
- Vredenburg, E. 1925. Descriptions of Mollusca from the post-Eocene Tertiary formation of north-western India, Cephalopoda, Opisthobranchiata, Siphonostomata. *Memoirs of the Geological Survey of India* 50, 1-350.
- Weisbord, N.E. 1929. Miocene Mollusca of northern Colombia. *Bulletins of American Paleontology* 14, 234-306.
- Wenz, W. 1938-44. *Gastropoda. Teil I: Allgemeiner und Prosobranchia. Handbuch der Paläozoologie* 6. Berlin (Bonntraeger).
- Whitfield, R.P. 1894. *Mollusca and Crustacea of the Miocene formations of New Jersey*, 195 pp. Washington, DC (United States Geological Survey)
- Woodring, W.P. 1964. Geology and paleontology of Canal Zone and adjoining parts of Panama: description of Tertiary mollusks (gastropods: Columbelloidea to Volutidae). *United States Geological Survey Professional Paper* 306-C, 241-297.