

Saul, L.R., & Petit, R.E.,
2001

Invertebrate Paleontology
Earth Sciences Division
Natural History Museum

THE VELIGER
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The Veliger 44(3):261-270 (July 2, 2001)

A New Species of the Aporrhaid Gastropod Genus *Goniocheila* Gabb, 1868, from the Late Oligocene of North Carolina

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Abstract. Description of the new species *Goniocheila wilsoni* increases to three the number of species of this aporrhaid genus present in the Gulf Coast and southern Atlantic Coast Oligocene faunas of North America. *Goniocheila wilsoni* clearly exhibits characteristics of *Goniocheila* Gabb, a genus that has from its inception been considered close to *Aporrhais*, *Arrhoges*, and widely recognized European Paleogene aporrhaid forms close to or referred to "*Aporrhais*" *sowerbii* and "*Aporrhais*" *speciosa*. These species have been referred to *Aporrhais*, *Drepanocheilus*, and *Goniocheila*; and "*A.*" *speciosa* s.l. has been considered to include forms having a multidigitate wing as in *Aporrhais*, as well as an unidigitate wing as in *Drepanocheilus*. *Goniocheila* shares more characteristics with *Drepanocheilus*, especially early Tertiary *Drepanocheilus*, than with *Aporrhais* and *Arrhoges*.

INTRODUCTION

An undescribed species of *Goniocheila* Gabb, 1868, from the "Silverdale beds" was mentioned by MacNeil (in MacNeil & Dockery, 1984), but the specimens available to him were inadequate to serve as the basis of a species. Richard and Liz Petit recovered excellent specimens of this species, herein described as *Goniocheila wilsoni*, from the "Silverdale beds" on Webb Creek, Silverdale, Onslow County, North Carolina.

The "Silverdale beds" were included in the Belgrade Formation by Ward et al. (1978), and the Belgrade Formation was considered to be of earliest Miocene age. However, the Haywood Landing Member (= the "Silverdale beds") of the Belgrade Formation is now dated as latest Oligocene, late Chattian stage (Rossbach & Carter, 1991, planktic foraminifera zone N 3; Ward, 1992, Depositional Event 1).

In North America only two other species of *Goniocheila* have been recognized: *Goniocheila lirata* (Conrad, 1848) the type species, and *G. menthafontis* (MacNeil, in MacNeil & Dockery, 1984) are both from the Vicksburg Group in Mississippi and of earlier Oligocene age, *G. lirata* being from the Byram Formation and *G. menthafontis* from the Mint Spring Formation. The new species is readily recognized as congeneric with *G. lirata* and *G. menthafontis*, and *G. wilsoni* is especially similar to *G. menthafontis*.

Position of *Goniocheila* relative to other aporrhaid forms is less clear. MacNeil (in MacNeil & Dockery, 1984) con-

sidered *Goniocheila* to be a subgenus of *Aporrhais* da Costa, 1778, as had Gabb (1868) when erecting the taxon. MacNeil also placed in *Goniocheila* all 10 of the Paleogene species referred to *Aporrhais* by Wrigley (1938)—including English Paleogene specimens identified as *Aporrhais speciosa* (Schlotheim, 1820), thus suggesting the inclusion of many European forms ranging in age from late Paleocene to late Oligocene in *Goniocheila*. Wenz (1940) placed *Goniocheila* as a subgenus of *Drepanocheilus* Meek, 1864, and Báldi (1973) placed "*A.*" *speciosa* in *Drepanocheilus* rather than in *Aporrhais*. MacNeil characterized *Aporrhais* (*Aporrhais*) as an aberrant group with fewer species and shorter geologic range than *Goniocheila*, but he did not define the geologic range of *Aporrhais* or *Goniocheila*. Several revisions of Tertiary chronologies cause Wrigley's "Eocene and Oligocene" species to be late Paleocene to late Eocene in age (e.g., Davies, 1975; Berggren, 1972; Berggren et al., 1985; Curry, 1992).

Roy (1994) indicated that *Aporrhais*, was present in the Cenomanian, thus giving it greater geologic range than *Goniocheila*. Furthermore, he divided aporrhaid forms into two groups: "M1" characterized by multidigitate wings, and including *Aporrhais*, and "M2" characterized by those with simple wings, and including *Arrhoges*, *Goniocheila*, and *Drepanocheilus*. Several European workers (e.g., Glibert, 1957; Báldi, 1973; Lozouet, 1986; Gitton, et al., 1986) have included within "*Aporrhais*" *speciosa* s.l. forms with both types of wing margins.

Characteristics of the European Paleogene species distributed among *Aporrhais*, *Arrhoges*, and *Drepanocheilus* by various workers are difficult to evaluate because many older descriptions are incomplete, and some figures do not clearly show the morphologic features. European workers studying this group of aporrhaiids have not commented on a resemblance to *Goniocheila*, although Lozouet (1986) notes the Oligocene presence of *Goniocheila* (as a subgenus of *Aporrhais*) in Mississippi. Nor have European workers commonly recognized a generic distinction (or even a specific distinction) among forms having a multidigitate rather than a simple outer lip. Conversely, the multidigitate wing is viewed as being derived from the simple outer lip (Lozouet, 1986). *Goniocheila* is most similar to *Drepanocheilus* using the characteristics of Table 1, but with its outer lip features ignored is most similar to *Aporrhais* (Table 2).

The fauna of the Haywood Landing Member of the Belgrade Formation in North Carolina has a tropical aspect, having provided a large number of unusual genera and species of muricids (Vermeij & Vokes, 1997). Rossbach & Carter (1991) suggested a climate for North Carolina Oligocene faunas similar to that of today with warm temperate mollusks inshore and more tropical forms at depths exceeding 25 m. They recognized a reduction in tropical genera between the faunas of the Lower River Bend Formation of early Oligocene age and the Upper River Bend Formation of late Oligocene age, and a further reduction in the fauna of the Belgrade Formation which shows an even stronger Western Atlantic influence. The rarity of *Drepanocheilus*, *Aporrhais*, and *Goniocheila* in late early and middle Eocene faunas (MacNeil in MacNeil & Dockery, 1984) is perhaps related to a warming climate in the early Eocene, and the return of these aporrhaiids, to a cooling climate in the Oligocene. Lozouet (1986) commented on the loss of aporrhaiids in the Eocene and their abundance in the European Oligocene. Sohl (1967) noted that although *Drepanocheilus* is widely distributed, it is much more abundant from cooler water faunas than from subtropical and tropical faunas.

A distinctive feature on a mature *Goniocheila* is the bulbous callus anteriorly situated on the body whorl adjacent to the inner lip (Figures 1G, 20). This bulbous callus assists in distinguishing *Goniocheila* from *Drepanocheilus* and *Aporrhais*. Similar callosities are present in some other genera of aporrhaiids that are clearly distinct from *Goniocheila* and each other (e.g., *Anchura* Conrad, 1860, *Tessarolax* Gabb, 1864, *Pietteia* Cossmann, 1904, and *Platyoptera* Conrad, 1855). In all cases the callosities appear functionally related to the position of the aporrhaid gastropod on the substrate and its mode of locomotion. Recent aporrhaiids move forward in a "leap" that involves upward extension of the foot stalk followed by a forward topple of the animal and shell (Perron, 1978). In the Recent aporrhaid *Arrhoges occidentalis* (Beck, 1836) this "leap" results in speed greater than that of its

molluscan predators (Perron, 1978). Both during the animal's browse on the substrate and at a landing from a forward topple, the callus on the body whorl elevated the anterior end of the shell. With the anterior elevated, the animal would have been both ready to browse and able to recover more rapidly from its forward topple and more quickly take its next leap.

Abbreviations: The following institutional abbreviations are used: LACM = Natural History Museum of Los Angeles County, Malacology; LACMIP = Natural History Museum of Los Angeles County, Invertebrate Paleontology; NHM = The Natural History Museum (Great Britain); PRI = Paleontology Research Institute; TU = Tulane University; UF = Florida Museum of Natural History; USNM = United States National Museum of Natural History.

SYSTEMATIC PALEONTOLOGY

Placement of Aporrhaidae follows that of Ponder & Warén (1988).

Phylum MOLLUSCA Linnaeus, 1758

Class GASTROPODA Cuvier, 1797

Superorder CAENOGASTROPODA Cox, 1960

Order NEOTAENIOGLOSSA Haller, 1888

Superfamily STROMBACEA Rafinesque, 1815

Family APORRHAIIDAE Gray, 1850

Genus GONIOCHEILA Gabb, 1868

Alipes Conrad 1865, p. 31 (non Imhoff, 1854, Myriopoda).
Goniocheila Gabb 1868, p. 144.

Type species: *Alipes liratus* (Conrad) (= *Chenopus liratus* Conrad, 1848), by subsequent designation, Cossmann (1904). Oligocene, Byram Formation, Mississippi.

Diagnosis: Small aporrhaiids with outer lip triangulately expanded, extended into distal posterior labral digitation and having initially appressed apical digitation; distal lip margin callused. Whorls with two or three strong cords that extend onto the wing; posterior cord at angulate shoulder of mature whorls and extended onto posterior labral digitation; mature whorls noded at cords. Rostrum short and curved. Inner lip callused and with additional adjacent bulbous callus anterior to the posterior cord.

Discussion: *Goniocheila* has been repeatedly linked to the aporrhaid supraspecific taxa, *Aporrhais*, *Arrhoges* Gabb, 1868, and *Drepanocheilus*. Gabb (1868) proposed *Goniocheila* as a subgenus of *Aporrhais* and included in it *A. (G.) lirata* and "*A. (G.) sowerbyi* Sby. = *A. Parkinsonii* Sby." (Gabb, 1868:144). Gabb (1868) reproduced Conrad's figures of *G. lirata* which overemphasize the axial and under-represent the spiral sculpture. Figures in

MacNeil & Dockery (1984: pl. 28, figs. 11, 12) are more useful for recognizing characteristics of *Goniocheila* and of its type species *G. lirata*.

Gabb perhaps included "A." *sowerbii* in *Goniocheila* on the basis of figures 1–5 of pl. 349 of Sowerby (1822). Both Fleming (1828) and Mantell (1829) recognized that these figures, labeled *Rostellaria parkinsoni* Mantell, were not that species, and each provided the name *Rostellaria sowerbii*. Fleming (1828:360) referred to figures 1 and 5 at the end of his brief species description; Mantell (1829:203) in a footnote, without description, provided the new name for figures 1, 3, 4. The specimen for fig. 4 of Sowerby, 1822: pl. 349 (NHM G.61992) was selected by Wrigley (1938) as lectotype for "*Aporrhais*" *sowerbii* (Mantell), but a lectotype does not seem to have been selected for "*R.*" *sowerbii* Fleming. Fleming's (1828) inclusion in his *Rostellaria sowerbii* of only figures 1 and 5 of Sowerby's plate 349 makes impossible designation of the lectotype of "A." *sowerbii* of Mantell as lectotype of "A." *sowerbii* (Fleming). Figure 5, based on a specimen from Folkstone, lacks features described by Fleming, and we here designate the specimen for figure 1, NHM 43750, as lectotype of *Rostellaria sowerbii* Fleming, 1828. The specimen came from "Maidenhead, between Bray and Windsor;" (Sowerby, 1822). According to Wrigley (1938), it was from the London Clay Basement Bed, which is either latest Paleocene (Berggren et al., 1985) or earliest Eocene (Curry, 1992). Wrigley included Sowerby's figure 1 in the synonymy of *Aporrhais triangulata* Gardner, 1884, which was based on specimens from the Oldhaven beds of Paleocene, Thanetian age. The specimen chosen as lectotype of "*Aporrhais*" *sowerbii* (Mantell) was from the upper London Clay (Wrigley, 1938) and is of Eocene, Ypresian age.

Wrigley (1938) considered "A." *sowerbii* (Mantell) and "A." *triangulata*, despite their similarities, to belong to two different lineages, with "A." *triangulata* (in which he included Sowerby's figure 1) an end member of one, and "A." *sowerbii* (Mantell) derived from "*Aporrhais clarendonensis* (and evolving into "*Aporrhais*" *speciosa* [Schlotheim]) a member of the other. Illustrations of "A." *triangulata* ? = "A." *sowerbii* (Fleming) are similar to *Drepanocheilus perveta* (Stanton, 1920) of Paleocene age from the Cannon Ball Member of the Fort Union Formation of North and South Dakota. Both "A." *triangulata* and *D. perveta* are similar to species of *Goniocheila* in overall shape, although in both the outer lip is more strongly embayed near the middle strong spiral than in *Goniocheila*. The anterior lip angulation is a feature noted by Gabb 1868, as characteristic of *Goniocheila*. "*Aporrhais*" *sowerbii* (Mantell) differs from the North American Oligocene species of *Goniocheila* in its longer straighter anterior rostrum, much broader and very shallow anterior sinus, and higher spire with more persistent *Drepanocheilus*-like arched axial ribbing. Wrigley (1938) considered "A." *sowerbii* (Mantell) congeneric with 10

other Paleogene species including "A." *speciosa* (Schlotheim, 1820). Some of Wrigley's (1938) figures give indications of developing an anterior labral digitation.

As Gabb (1868) indicated, the shell of *Goniocheila* resembles that of *Aporrhais* in having an angulate shoulder and a second weaker, more anterior angulation, both of which are commonly noded. The angulations coincide with major cords. The apical digitation is short and adnate to the spire in geologically older species (*G. menthafontis*), becoming longer and free at its tip in geologically younger species (*G. wilsoni*). The distal margin of the outer lip is slightly convex to straight, and thickened between the posterior labral digitation and the anterior strong cord, at which the margin is subangulate. The posterior labral digitation is grooved interiorly, and at the anterior cord is a short, faint interior groove. The anterior sinus bordering the rostrum is narrow in *Goniocheila* and much wider in *Aporrhais* and in the Paleogene forms illustrated by Wrigley.

The body whorl of *Drepanocheilus* is also angulate at the shoulder and at least subangulate anteriorly at a strong cord. *Aporrhais* s.s. has at least one additional labral digitation at the anterior angulation. Both *Aporrhais* and *Goniocheila* develop posterior digitations, *Aporrhais* in the Cretaceous (Sohl, 1967), and *Goniocheila* in the Oligocene. MacNeil (in MacNeil & Dockery, 1984) argued that *Arrhoges* did not differ from *Goniocheila*, but Table 1 shows *Goniocheila* and *Arrhoges* to differ on two-thirds (four-fifths according to Table 2) of their characteristics, and shows *Arrhoges* to be more similar to *Latala* Sohl, 1960.

Table 1 lists morphologic characteristics of the four genera: *Aporrhais*, *Arrhoges*, *Drepanocheilus*, and *Goniocheila*. This list of characteristics is modified from Roy (1994, 1996) to be pertinent to these four genera. Figure 1 illustrates some aporrhaid shell descriptive terms (see also Popenoe, 1983: fig. 2). The expanded outer lip (apertural process of Roy 1994, 1996) is commonly referred to as a wing. Wing shape is variable within species (e.g., the wing of *A. pespelecani* (Linnaeus, 1758) with variation in length and number of digitations), and wing form is difficult to describe succinctly. In *Drepanocheilus* and *Goniocheila* it is somewhat triangular to crescentic. *Arrhoges* has a more quadrate wing, and that of *Aporrhais* is splayed. The two directions on the wing, axial (height) and spiral (width), give proportional information. On Table 1, height is "tall" or "short" and width is "broad" or "narrow." Some species of *Aporrhais* (e.g., *Aporrhais serresiana* Michaud, 1828, Recent, Mediterranean to Iceland; *Aporrhais uttingeriana* [Risso, 1826], Pliocene, Europe) have long digitations, but several European Tertiary species have digitations of moderate length. Roy (1994) considered *Aporrhais* to have a multidigitate (more than two digitations) wing, a criterion that would exclude from it most of the early Tertiary forms discussed by Gardner

Table 1
Morphologic characteristics of four aporrhaid genera.

Morphologic characters	<i>Aporrhais</i>	<i>Arrhoges</i>	<i>Drepanocheilus</i>	<i>Goniocheila</i>
* 1. Shell shape: elongate//short and stout	elongate	elongate	both	short and stout
* 2. Relative spire height: high//moderate (= height of body whorl)	high	high	high	moderate
3. Sides of immature whorls: angular//rounded	both	rounded	rounded	both
4. Sides of mature whorls: angular//rounded	angular	rounded	angular	angular
* 5. Rostrum: long//short (< half length of body whorl)	both	short	both	short
* 6. Rostrum: straight//curved	curved	straight	?straight	both
* 7. Rostrum width: narrow//broad	narrow	broad	narrow	narrow
* 8. Apical digitation adnate to spire: present//absent	partly	absent	if present	partly
9. Apical digitation: long//short//absent	long/short	absent	short/absent	short
*10. Apical digitation extending beyond spire: yes//no//absent	yes/no	absent	no	no
*11. Callus on spire: present//absent	present	absent	some	some
12. Callus knob on base near aperture: lumpy//present//absent	present	absent	present	lumpy
13. Callus knob on outer lip edge: present//absent	absent	absent	absent	present
14. Apertural expansion (wing): equant//inequant	equant	equant	inequant	equant
*15. Apertural expansion (wing): single//multidigitate	multidigitate	single	single	single
16. Apertural expansion (wing): tall//short	tall	tall	short	tall
*17. Apertural expansion (wing): broad//narrow	broad	broad	broad	broad
18. Distal margin of wing: convex//concave//straight	concave/straight	convex	convex	convex
*19. Number of digits: 1//1 or 2//2 or more	2 or more	1	1	1
20. Wing interior channeled opposite digitations	yes	no	yes	yes
21. Number of wing interior channels	2 or more	0	1	1
*22. Length of labral digitations: long//moderate//short	long	short	moderate	moderate
*23. Wing digitations: lobed//spiny//both	spiny	lobed	spiny	spiny
*24. Webb between digitations: present//absent	present	absent	absent	absent
*25. Concave posterior margin of wing	yes	no?	yes	yes
*26. Sculpture: strong//moderate//fine//absent	strong	moderate	moderate	strong
27. Dominant sculpture type on mature whorls: axial//spiral	spiral	axial	spiral	spiral
*28. Spiral body cords extending to wing: present//absent	present	absent	present	present
*29. Row of shoulder nodes: present//absent	present	absent	either	present
*30. Axial nodes: strong//weak//absent	strong	absent	weak	strong
31. Two-four strong cords on whorl: present//absent	present	absent	present	present
Similarity to <i>Goniocheila</i>	0.64	0.32	0.77	1.00
Similarity to <i>Aporrhais</i>	1.00	0.26	0.55	0.64
Similarity to <i>Arrhoges</i>	0.26	1.00	0.45	0.32
Similarity to <i>Drepanocheilus</i>	0.55	0.45	1.00	0.77

Morphologic characters * from lists of Roy, 1994, 1996.

(1884) and Wrigley (1938). The presence of two to four strong cords on the whorls (Figure 1H) is here considered significant as these cords commonly extend across the wing and onto digitations, suggesting that the cords reflect persistent features of the mantle.

Paleocene and Eocene species of *Drepanocheilus* are in general stouter and have thicker callus deposits about the aperture (e.g., *Drepanocheilus perveta* [Stanton, 1920], "A." *triangulatus* [Gardner, 1884] ? = "A." *sowerbii* [Fleming]) than do the more typical Cretaceous species. Species of Oligocene age referred to *Drepanocheilus* differ in several respects from typical *Drepanocheilus*. They are stouter, have a taller wing, have stronger nodes on the body whorl, usually have a posterior digitation adnate to the spire, some have a long posterior labral digitation, and some have an anterior labral digitation.

Most resemble more typical *Drepanocheilus* in the sculpture of the spire.

Cossmann (1904) included *Goniocheila* in *Arrhoges* (along with representatives of *Drepanocheilus*, *Latiala*, *Goniocheila*, and *Aporrhais*), but *Arrhoges* and *Latiala* lack the strong cords of *Goniocheila*, *Drepanocheilus*, and *Aporrhais*. The rostrum of *Goniocheila* is more bent and narrower than that of *Arrhoges*, and *Arrhoges* has a shallow and very broad anterior sinus. Sculpture exposed on early whorls of the spire of *Goniocheila*, *Arrhoges*, and *Drepanocheilus* consists of spiral cordlets and arched axial ribs, but anterior to the periphery, the sculpture of *Drepanocheilus*, *Aporrhais*, and *Goniocheila* is dominated by two or three strong cords, whereas whorls of *Arrhoges* are covered by many, more nearly uniform cordlets. Wrigley (1938) noted that *Aporrhais sowerbii* form

Table 2

Comparison of four aporrhaid genera omitting morphologic characteristics of wing and its digitations. Limiting characteristics to 16 characteristics (characteristics 1–7, 11–13, 26–31 of Table 1) makes *Goniocheila* and *Aporrhais* most similar.

Similarity to	<i>Aporrhais</i>	<i>Arrhoges</i>	<i>Drepanocheilus</i>	<i>Goniocheila</i>
<i>Goniocheila</i>	0.75	0.19	0.69	1.00
<i>Aporrhais</i>	1.00	0.31	0.81	0.75
<i>Arrhoges</i>	0.31	1.00	0.50	0.19
<i>Drepanocheilus</i>	0.81	0.50	1.00	0.69

clarendonensis Wrigley, 1938, of early Ypresian age, was an *Arrhoges*. The species resembles an *Arrhoges* in having spiral cordlets of roughly equal strength with barely stronger spiral cords positioned as in *Drepanocheilus*, *Aporrhais*, and *Goniocheila* (in which it was included by MacNeil (in MacNeil & Dockery, 1984). Unfortunately, all specimens of "A." *clarendonensis* from Clarendon in the LACMIP collection (Figures 6, 7) have a broken outer lip, but Gardner's (1884) illustration of the wing (pl. 17, figs. 5, 6) shows it, unlike that of *Arrhoges*, considerably expanded anteriorly.

Wrigley suggested that the better represented of his two lineages began with "A." *clarendonensis*, led into "*Aporrhais*" *speciosa*, and evolved toward a multidigitate aperture and typical *Aporrhais*. MacNeil (in MacNeil & Dockery, 1984) indicated that *Aporrhais* arose from *Goniocheila* and that *Aporrhais pespelecani* was aberrant. He did not mention that specimens resembling *Aporrhais* with angulated whorls, noded carinae, and more than two wing digitations are present in the Cretaceous (i.e., *Aporrhais drachuki* Saul, 1998, southern California, Turonian; *A. biangulata* [Meek & Hayden, 1856], Wyoming and Montana, Campanian; *Aporrhais* n. sp., Sohl, 1967, Alabama, early Campanian). MacNeil (in MacNeil & Dockery, 1984) suggested that *Aporrhais gracilis* Aldrich, 1886, from the Gulf Coast Eocene was more similar to early Eocene species figured by Wrigley (1938) (but did not specify which species) than are the southern U.S. species *G. lirata* and *G. menthafortis*. *Aporrhais gracilis* (in Harris, 1899) has a wing doubly digitated on its distal margin, and a whorl profile on the spire that is angulated, as are those of *Aporrhais pespelecani*. Among Wrigley's figures, *A. gracilis* is most similar to "A." *londiniensis* Wrigley, 1938, but differs in having the angulated whorl on the spire rather than the rounded whorl with sculpture resembling that of *Drepanocheilus* as in the English Paleocene and Eocene species (Wrigley, 1938).

Protoconchs, early sculpture, strong spiral cords, and wing shape of *Goniocheila*, *Drepanocheilus*, and some "A." *speciosa* are similar. If multidigitate *Aporrhais* ap-

pearing in the Late Cretaceous is monophyletic, rather than consisting of a series of iterative offshoots from a unidigitate lineage, it has greater antiquity than *Goniocheila* (unknown before Oligocene) and *Arrhoges* s.s. (Kollmann & Peel, 1983 recognize *Arrhoges (Latiala) palaeocaenica* Rosenkrantz, 1970, Paleocene, Greenland, as *Arrhoges* s.s. rather than as a *Latiala* Sohl, 1960; *Latiala*, proposed as a subgenus of *Arrhoges*, is known as early as the Aptian [Saul, 1998]).

In Table 1, *Goniocheila* is limited to characteristics evinced by *G. lirata*, *G. menthafortis*, and *G. wilsoni*. In these, the wing is, as described by Gabb, somewhat biangular with the posterior angle produced into a digitate process, and the anterior not produced, but having on its inner anterior face a faint, very short groove. Additionally, the distal wing margin is nearly straight to somewhat convex and heavily callused from the posterior digitation to the position of the middle cord. In *Aporrhais* this cord extends onto a labral digitation, and *Aporrhais* is largely defined by characteristics of *A. pespelecani* (Figures 2, 3, 8) and *A. serrisiana*. Characteristics of *Drepanocheilus* are those of the type species *D. evansi* Cossmann, 1904, (= *Rostellaria americana* Evans & Shumard, 1857 non d'Orbigny, 1842) (Figures 4, 5). *Arrhoges* is exemplified by its type species *A. occidentalis* (Figures 9–11).

Fifteen or nearly half of the characteristics of Table 1 pertain to the wing. Eight of these characteristics pertain to the digitations of the wing, which are probably variable. Digitations vary as to number and length from specimen to specimen within Recent species of *Aporrhais*, and the apical digitation arises through time in *Drepanocheilus*, *Aporrhais*, and *Goniocheila*. The wing is often missing from fossils, but as seen from Table 2, which lists comparisons of the four genera with the wing characteristics omitted, the genera can be distinguished upon the remaining characteristics. Without the wing characters, *Drepanocheilus*, *Aporrhais*, and *Goniocheila* are significantly more similar to each other than to *Arrhoges*, but *Goniocheila* is more similar to *Aporrhais* than to *Drepanocheilus*.

The three species of *Goniocheila* are a distinctive and compact group, showing far less morphologic diversity than has been ascribed to "A." *speciosa* s.l. Roy (1994) showed *Goniocheila* as present in the Turonian, based upon *Aporrhais (Goniocheila) castorensis* Whitfield, 1877, from the Benton Shale in the Black Hills, but the inadequately figured holotype (Whitfield, 1880: pl. 12, fig. 1; Stanton, 1893: pl. 31, fig. 1) lacks characteristics of *Goniocheila*, and appears closer to *Drepanocheilus*. Abbass (1967) referred an incomplete aporrhaid specimen from the Eocene of Egypt questionably to *Goniocheila orientalis*, but the fine arcuate ribbing of the spire is more suggestive of *Drepanocheilus* than of *Goniocheila*. At present, no specimens of earlier than Oligocene age can be assigned to *Goniocheila*, and the genus ranges from early to latest Oligocene or early Miocene age.

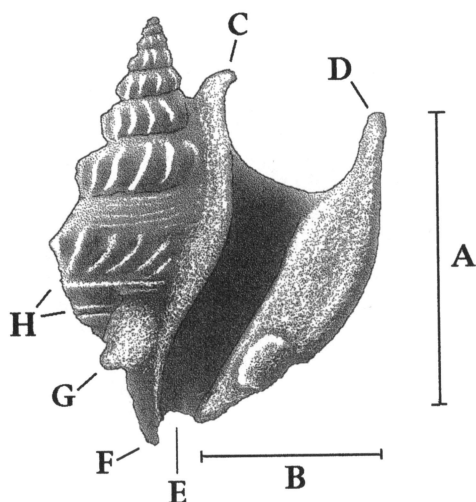


Figure 1. Some descriptive terms applied to *Goniocheila*. A = wing (expanded outer lip) height. B = wing (expanded outer lip) breadth. C = apical digitation. D = posterior labral digitation. E = anterior sinus. F = rostrum. G = bulbous callus on body whorl. H = strong spiral cords on anterior whorl slope.

Goniocheila wilsoni Saul & Petit, sp. nov.

(Figures 1, 12–22)

Aporrhais n. sp. Carter, Gallager, Valone, & Rossbach, 1988, p. 82, pl. 7, fig. 54.

Diagnosis: A *Goniocheila* having a well developed posterior digitation curling away from spire toward posterior lateral labral digitation and a deep, narrow anterior sinus immediately adjacent to the short rostrum. Whorl profile well angulated and noded especially on body whorl.

Description: Shell medium sized, fusiform with expanded outer lip, spire slightly less than half of shell height. Protoconch of three polished, globular whorls. Earliest sculpture on teleoconch of spiral ridges for about one half whorl, then fine, concavely arcuate axial ribs added. Ribs faint and moderately crowded, quickly becoming stronger, enlarged at shoulder, and reduced to half as many on second teleoconch whorl; following whorls with about 14 axial ribs per whorl. Whorl profile of first two post protoconch whorls convex, axials on next four spire whorls

weak near posterior suture and strongest at periphery, weakening toward anterior suture. Strength of axials at periphery producing concave whorl profile near posterior suture, subangulate at periphery, and convex between shoulder and anterior suture. Shoulder closer to posterior suture on earlier whorls becoming just below mid whorl on penultimate whorl. Ribs abruptly shorter on last whorl becoming nodes on peripheral cord. Cord extending to end of tip of wing. Two anterior cords present on body whorl. Spiral cordlets overall; on body whorl cordlets intermediate to anterior cords strengthen; three cordlets on whorl base nearly as strong as intermediate cordlets. Outer lip expanded into broad, somewhat crescentic wing with broadened distal edge posteriorly pointed by labral digitation, concave posterior edge, and curving posterior digitation adnate to two whorls but pointed away from spire at its tip. Two strong calluses developed, one at anterior end distal wing edge, other opposite on base of body whorl. Aperture elongate, sinused anteriorly and posteriorly with nearly parallel lips, angled about 25° to axis. Rostrum short, nearly straight, narrow with closely adjacent deep anterior sinus.

Holotype: USNM catalogue number 508381.

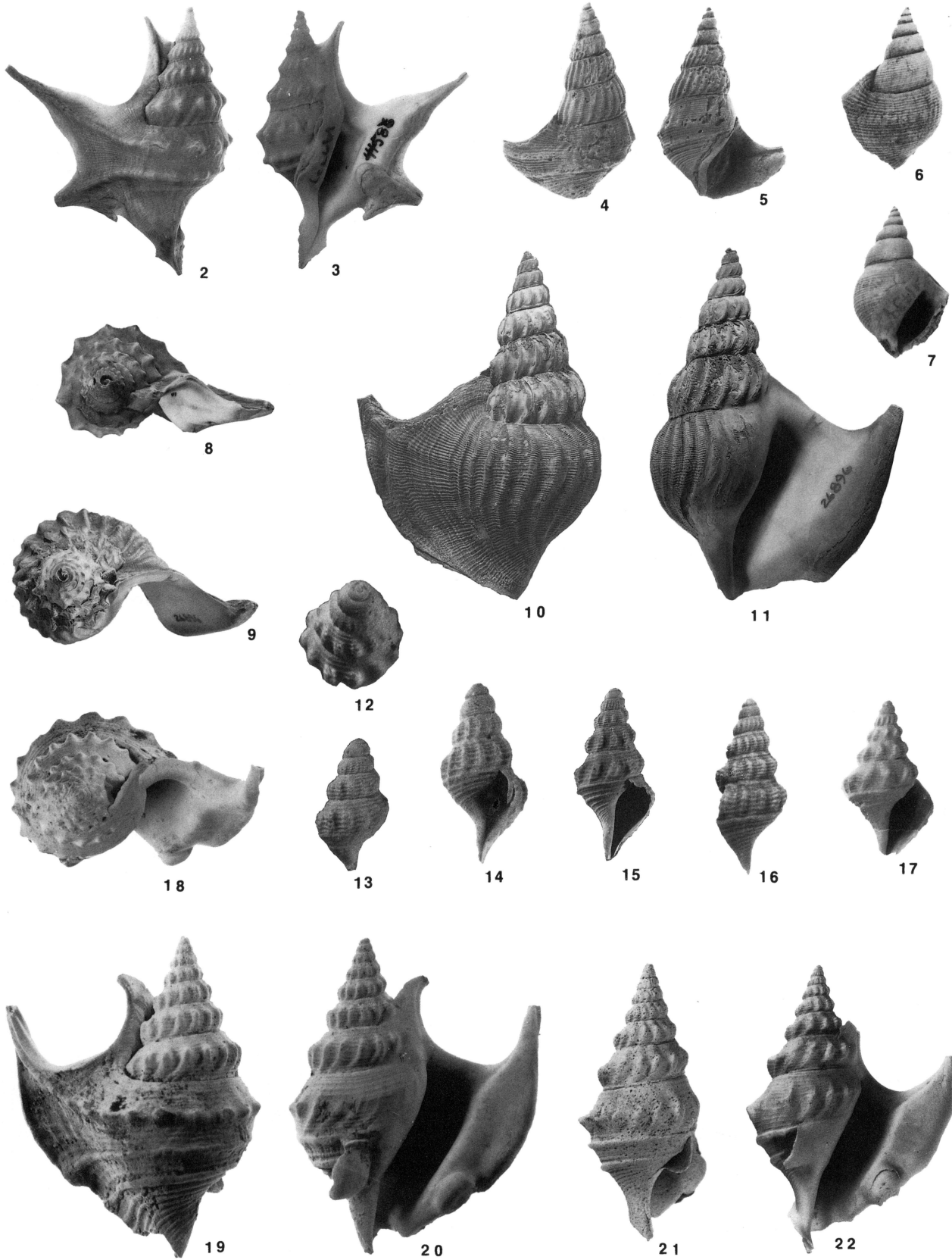
Type locality: "Silverdale Beds." Silverdale, North Carolina = Tulane loc. TU 866 (marl pit on north side of Webb Creek and east side of unnumbered county road, Silverdale, Onslow County, North Carolina [Vermeij & Vokes, 1997]). Coll. Dick & Liz Petit, 1968–1970. Belgrade Formation, Haywood Landing Member. Latest Oligocene

Paratypes: LACMIP catalogue numbers 12636–12642, PRI catalogue number 49395, UF catalogue number 102475, all from TU loc. 866.

Dimensions of holotype: Height 28.2 mm, diameter 21.8 mm. (last whorl and wing); diameter last whorl at 90° to wing 12.5 mm; height penultimate whorl 4.4 mm; diameter penultimate whorl 10 mm.

Height of paratypes: LACMIP 12636, 24.6 mm; LACMIP 12637, 3.8 mm; LACMIP 12638, 5.2 mm; LACMIP 12639, 7.0 mm; LACMIP 12640, 7.6 mm; LACMIP 12641, 9.5 mm; PRI 49395, 24.8 mm.

Figures 2–22. Figures 2–11, 19–22 coated with ammonium chloride. Figures 2, 3, 8, *Aporrhais pespelecani* (Linnaeus, 1758), hypotypes, from Mediterranean Sea, ×1; Figures 2, 3. LACM149737. Figure 2. Back. Figure 3. Aperture. Figure 8. LACM149738, apical view. Figures 4, 5. *Drepanocheilus evansi* Cossmann, 1904, hypotype, LACMIP 12643, from LACMIP loc. 25073, ×1.5. Figures 6, 7. "*Aporrhais*" *clarendonensis* Wrigley, 1938, hypotype, LACMIP 12644, from LACMIP loc. 28428, ×2. Figures 9–11. *Arrhoges occidentalis* (Beck, 1836), hypotype, LACM 152351, off Scantari Bank, Newfoundland, Canada at 250 fathoms, ×1; Figure 9. Apical view. Figure 10. Back. Figure 11. Aperture. Figures 12–22, *Goniocheila wilsoni* Saul & Petit, sp. nov. from TU loc. 866. Figures 12, 13. Paratype, LACMIP 12637. Figure 12. Protoconch, ×8. Figure 13. Back, ×6. Figure 14. Paratype, LACMIP 12638, aperture, ×6. Figure 15. Paratype, LACMIP 12640, aperture, ×4. Figure 16. Paratype, LACMIP 12639, labral side, ×4.4. Figure 17. Paratype, LACMIP 12641, ×3. Figures 18–20. Holotype, USNM 508381, ×2. Figure 18. Apical view. Figure 19. Back. Figure 20. Mature aperture. Figure 21. Paratype, PRI 49395, ablabral side, ×2. Figure 22. Paratype, LACMIP 12636, maturing aperture, ×2.



Discussion: The early *Drepanocheilus*-like spire sculpture is confined to about two whorls after which the axials coarsen, fade toward the sutures, especially the posterior suture, and strengthen on the shoulder. A series of specimens (Figures 13–16) shows that the strong anterior cords visible on the last whorl begin to be present on immature specimens at a height of 7 mm and are well developed at a height of 7.6 mm. The distal edge of the outer lip is considerably thickened between the labral digitation and the labral end of the more anterior cord. The wing is first thin and distally forward-facing. This forward-facing lip margin is slightly grooved and notched at the two strong cords of the exterior. Then the wing is thickened especially toward the distal margin to form a narrow parallel-sided aperture with a thick, broad, forward-facing outer lip with a callus knob adjacent to the two notches. The anterior grooves interior to the cords are filled, but the groove along the labral digitation remains, as does the groove along the posterior digitation. Both of these grooves face more laterally than ventrally, and the labral digitation groove is nearly hidden in apertural view by the distal labral callus. The anterior sinus of *G. wilsoni* is unusually narrow and deep for an aporhaid.

Goniocheila wilsoni has a more angulate whorl profile than either *G. menthfontis* or *G. lirata*. It has stronger and fewer axial ribs on the spire, a shorter spire, and a longer posterior digitation which, unlike that of the two geologically older species, curls away from the spire and points toward the posterior lateral labral digitation. In its strongly noded peripheral cord *G. wilsoni* is more similar to *G. menthfontis* than to *G. lirata*.

Etymology: The species is named for Druid Wilson of Lake Wales, Florida, stratigrapher and paleontologist, formerly of the Paleontology and Stratigraphy Branch of the U.S. Geological Survey, in appreciation for his many contributions to our knowledge of Tertiary Mollusca.

Acknowledgments. Lindsey T. Groves (LACMIP) provided access to collections and obtained some hard-to-find literature. Paul Jeffrey (NHM) kindly searched for, found the specimen figured by Sowerby (1822: pl. 349, fig. 1), and provided to us its Natural History Museum number. Photos for Figures 8–11 were taken by Takeo Susuki, and photos for Figures 12, 13, and 15 were provided by Richard L. Squires. We thank the reviewers and editor for helping us make this a more readable paper.

LITERATURE CITED

- ABBASS, H. L. 1969. A monograph on the Egyptian Paleocene and Eocene gastropods. United Arab Republic, Geological Survey, Geological Museum, Palaeontological Series, Monograph 4, 159 pp., 24 pls.
- ALDRICH, T. H. 1886. Preliminary report on the Tertiary fossils of Alabama and Mississippi. Alabama Geological Survey Bulletin 1:15–60, pls. 1–6.
- BÁLDI, T. 1973. Mollusc Fauna of the Hungarian Upper Oligocene (Egerian). Akadémiai Kiado: Budapest. 511 pp., 51 pl., 55 text-figs.
- BECK, H. H. 1836. *Rostellaria occidentalis*. Magasin de Zoologie (publié par F. B. Guérin-Méneville, v. 6, Classe 5, Notice LXXII (text), pl. 72.
- BERGGREN, W. A., 1972. A Cenozoic time-scale—some implications for regional geology and paleobiogeography. *Lethaia* 5:195–215.
- BERGGREN, W. A., D. V. KENT & J. J. FLYNN. 1985. Paleogene geochronology and chronostratigraphy. Pp. 141–186 in N. J. Snelling (ed.), *The Chronology of the Geological Record*. Geological Society of London Memoir 10.
- CARTER, J. G., P. E. GALLAGER, R. ENOS VALONE & T. J. ROSSBACH WITH CONTRIBUTIONS BY P. G. GENSEL, W. H. WHEELER & D. WHITMAN. 1988. Fossil collecting in North Carolina. North Carolina Geological Survey, Bulletin 89, 89 pp., 10 pls.
- CONRAD, T. A. 1848. Observations on the Eocene formation, and descriptions of one hundred and five new fossils of that period, from the vicinity of Vicksburg, Mississippi; with an appendix. *Academy of Natural Sciences of Philadelphia Proceedings* 3:280–299. [Reprinted 1848 in *Academy of Natural Sciences of Philadelphia Journal* (2) 1:111–134, pls. 11–14.]
- CONRAD, T. A. 1855. Observations on the Eocene deposit of Jackson, Mississippi, with descriptions of thirty-four new species of shells and corals. *Academy of Natural Sciences of Philadelphia Proceedings* for 1855:257–263. [Reprinted 1939 as, Reprint of Conrad's Jackson Eocene fossils as described and illustrated in the Philadelphia Academy of Natural History Proceedings for 1855, pp. 257–263 and Wailes Report on the Agriculture and Geology of Mississippi. 1854, pls. XIV–XVII. *Bulletins of American Paleontology* 24(86):341–359 (3–19), pls. 23–26 (1–4).]
- CONRAD, T. A. 1860. Descriptions of new species of Cretaceous and Eocene fossils of Mississippi and Alabama. *Academy of Natural Sciences of Philadelphia Journal* (2) 4:275–298. pl. 46–47.
- CONRAD, T. A. 1865. Catalogue of the Eocene and Oligocene Testacea of the United States. *American Journal of Conchology* 1:1–35.
- Cossmann, M. 1904. *Essais de Paléoconchologie Comparée*, Vol. 6. Paris. 151 pp., 9 pls.
- COX, L. R. 1960. Thoughts on the classification of the Gastropoda. *Malacological Society of London Proceedings* 33: 239–261.
- CURRY, D. 1992. Tertiary. Pp. 389–411 in P. McL. D. Duff & A. J. Smith, *Geology of England and Wales*. The Geological Society: London.
- CUVIER, G. 1797. *Tableau élémentaire de l'histoire naturelle des animaux*. Paris. 710 pp., 12 pls.
- DA COSTA, E. M. 1778. *Historia naturalis testaceorum Britanniae, or, the British Conchology*. London. xii + 254 + viii pp., 17 pls.
- DAVIES, A. M. 1975. (Revised by F. E. Eames & R. J. G. Savage). *Tertiary Faunas*, Vol. 2. George Allen & Unwin Limited: London. 447 pp., 34 figs.
- EVANS, J. & B. F. SHUMARD. 1857. On some new species of fossils from the Cretaceous formation of Nebraska Territory. *Academy of Sciences of St. Louis, Transactions* 1:38–42.
- FLEMING, J. 1828. *A History of British Animals*. Bell & Bradfute: Edinburgh. xxiii + 565 pp.
- GABB, W. M. 1864. Description of the Cretaceous fossils. *California Geological Survey, Paleontology*, 1:55–243, pls. 9–32, 1865.
- GABB, W. M. 1868. An attempt at a revision of the two families

- Strombidae and Aporrhaidae. *American Journal of Conchology* 4:137–149, pls. 13, 14.
- GARDNER, J. S. 1884. British Eocene Aporrhaidae. *Geological Magazine, New Series, Decade 3*, 1:529–534, pl. 17.
- GITTON, J. L., P. LOZOUET & P. MAESTRATI. 1986. Biostratigraphie et paléocologie des gisements types du stampien de la région d'Etampes (Essonne). France, Editions du Bureau des Recherches Géologiques et Minières, *Géologie de la France* no. 1–1986, 101 pp., 4 pls.
- GLIBERT, M. 1957. Pélécytopes et gastropodes du Rupélien supérieur et du Chattien de la Belgique. Institut royal des sciences naturelles de Belgique, *Mémoire* 137, 98 pp.
- GRAY, J. E. 1850. Systematic arrangement of the figures. Pp. 63–124 in M. E. Gray, 1850, *Figures of Molluscos Animals Selected from Various Authors; Etched for the Use of Students, Vol. 4*. Longman, Brown, etc: London, 219 pp.
- GRÜNDEL, J. 1997. Die Gastropodenfauna des Rupels von Amsdorf (Westlich Halle). *Palaeontographica, Abteilung A, Paläozoologie—Stratigraphie*: 1–36, 6 pls.
- HALLER, B. 1888. Die Morphologie der Prosobranchier. *Morphologisches Jahrbuch* 14: 54–169, pl. 3–9.
- HARRIS, G. D. 1899. The Lignitic Stage. Part II. Scaphopoda, Gastropoda, Pteropoda, and Cephalopoda. *Bulletins of American Paleontology* 3(11):1–128, pls. 1–12. [Reprinted by Kraus Reprint, 1964]
- KOLLMANN, H. A. & J. S. PEEL. 1983. Paleocene gastropods from Nigssuaq, West Greenland. København, Grønlands Geologiske Undersøgelse, *Bulletin* 146, 115 pp., 257 figs.
- LINNAEUS, C. 1758. *Systema naturae per regna tria naturae. Editio decima, reformata*. Stockholm, Vol. 1, *Regnum animale*. 824 pp.
- LOZOUET, P. 1986. Les gastropodes prosobranches de l'Oligocene Supérieur du bassin de l'Adour (Systematique, paléoenvironnements, paléoclimatologie, paléobiogéographie). Thèse Mémoire de l'école Pratique des Hautes Études (Paris), 475 pages, 34 pls.
- MACNEIL, F. S. & D. T. DOCKERY, III. 1984. Lower Oligocene Gastropoda, Scaphopoda, and Cephalopoda of the Vicksburg Group in Mississippi. *Mississippi Bureau of Geology Bulletin*, 124, 415 pp., 72 pls.
- MANTELL, G. 1829. A tabular arrangement of the organic remains of the County of Sussex. *Geological Society of London Transaction* (2)3:201–216.
- MEEK, F. B. 1864. Check-list of the invertebrate fossils of North America; Cretaceous and Jurassic. *Smithsonian Miscellaneous Collections* 7, no. 8 (Publ. 177), 40 pp.
- MEEK, F. B. & F. V. HAYDEN. 1856. Description of new species of Gastropoda from the Cretaceous formations of Nebraska Terr. *Academy of Natural Sciences of Philadelphia, Proceedings for 1856* 9:117–148.
- MICHAUD, A. G. L. 1828. Description de plusieurs espèces de coquilles vivantes de la Méditerranée. *Bulletin d'Histoire Naturelle de la Société Linnéenne de Bordeaux* 2:119–122.
- PERRON, F. E. 1978. Seasonal burrowing behavior and ecology of *Aporrhais occidentalis* (Gastropoda, Strombacea). *Biological Bulletin* 154:463–471.
- PONDER, W. F. & A. WARÉN. 1988. Classification of the Caenogastropoda and Heterostropha—a list of the family-group names and higher taxa. *Malacological Review* 4(Suppl.): 288–326.
- POPENOE, W. P. 1983. Cretaceous Aporrhaidae from California: Aporrhainae and Arrhoginae. *Journal of Paleontology* 57: 742–765, 6 figs.
- RAFINESQUE, C. S. 1815. *Analyse de la nature ou tableau de l'univers et des corps organisés*. Palermo. 224 pp.
- RISSE, J. A. 1810–1826. *Histoire naturelle des principales productions de l'Europe méridionale et particulièrement de celles des environs de Nice et des Alpes maritimes*. 5 Vols. Paris.
- ROSENKRANTZ, A. 1970. Marine Upper Cretaceous and lowermost Tertiary deposits in West Greenland. *Meddelanden fra Dansk Geologiske Forening* 19:406–453.
- ROSSBACH, T. J. & J. G. CARTER. 1991. Molluscan biostratigraphy of the Lower River Bend Formation at the Martin Marietta Quarry, New Bern, North Carolina. *Journal of Paleontology* 65:80–118.
- ROY, K. 1994. Effects of the Mesozoic marine revolution on the taxonomic, morphologic, and biogeographic evolution of a group: aporrhaid gastropods during the Mesozoic. *Paleobiology* 20:274–296.
- ROY, K. 1996. The roles of mass extinction and biotic interaction in large-scale replacements: a reexamination using the fossil record of stromboidean gastropods. *Paleobiology* 22:436–452.
- SAUL, L. R. 1998. Eight aporrhaid gastropod species from the Cretaceous of the Pacific Slope of North America and clarification of the type species of *Perissoptera*. *The Nautilus* 111:119–142.
- SCHLOTHEIM, E. F. VON 1820–1823. *Die Petrefactenkunde auf ihrem jetzigen Standpunkte durch die Beschreibung seiner Sammlung versteinerter und fossilier überreste des Theirund und Pflanzensreichs der Vorwelt erläutert*. Becker'schen Buchhandlung, Gotha, lxii + 437 pp. Atlas pls. 15–29 [1820]; pls. 1–21 [1822]; pls. 22–37 [1823].
- SOHL, N. F. 1960. Archaeogastropoda, Mesogastropoda, and stratigraphy of the Ripley, Owl Creek, and Prairie Bluff Formations. *United States Geological Survey Professional Paper* 331-A, 152 pp., 18 pls.
- SOHL, N. F. 1967. Upper Cretaceous gastropods from the Pierre Shale at Red Bird, Wyoming. *United States Geological Survey Professional Paper* 393-B: B1–B46, 11 pls.
- SOWERBY, J. 1822. *The Mineral Conchology of Great Britain, Vol. 4*. (pt. 61): London, 69–76, pls. 349–354.
- STANTON, T. W. 1893. The Colorado Formation and its invertebrate fauna. *United States Geological Survey, Bulletin* 106, 288 pp., 45 pls.
- STANTON, T. W. 1920. The fauna of the Cannonball Marine Member of the Lance Formation. *United States Geological Survey Professional Paper* 128-A. *Shorter Contributions to General Geology, 1920*: 1–60, pls. 1–9.
- VERMEIJ, G. J. & E. M. VOKES. 1997. Cenozoic Muricidae of the western Atlantic region. Part XII—The subfamily Ocenebrinae (in part). *Tulane Studies in Geology and Paleontology* 29:69–118.
- WARD, L. W. 1992. Molluscan biostratigraphy of the Miocene, middle Atlantic Coastal Plain of North America. *Virginia Museum of Natural History Memoir* 2, [vi] 159 pp, 26 pls.
- WARD, L. W., D. R. LAWRENCE & B. W. BLACKWELDER. 1978. Stratigraphic revision of the middle Eocene, Oligocene, and lower Miocene—Atlantic Coastal Plain of North Carolina. *United States Geological Survey Bulletin* 1457-F:F1–F23.
- WENZ, W. 1940. Superfamilia Strombacea. Pp. 905–948 in O. H. Schindewolf (ed.), *Handbuch de Paläozoologie, Band 6, Prosobranchia, Teil 3*. Gebrüder Borntraeger: Berlin. 1639 pp. [reprinted 1960–1961].
- WHITFIELD, R. P. 1877. Preliminary report on the geology of the Black Hills, containing descriptions of new species of fossils from the Potsdam, Jurassic, and Cretaceous formations of

the Black Hills of Dakota. United States Geographical and Geological Survey of the Rocky Mountain Region (Powell Survey), 49 pp.

WHITFIELD, R. P. 1880. Paleontology of the Black Hills of Dakota. Pp. 325–468 in H. Newton & W. P. Jenney, Report on the Geology and Resources of the Black Hills of Dakota. United States Geographical and Geological Survey of the Rocky Mountain Region (Powell Survey).

WRIGLEY, A. 1938. English Eocene and Oligocene Strombidae and Aporrhaidae. Malacological Society of London Proceedings 23:61–88, pls. 4–6.

APPENDIX

Locality descriptions for fossils illustrated.

866 TU: "Silverdale Beds." Silverdale, North Carolina (marl pit on north side of Webb Creek and east side of unnumbered county road, Silver-

dale, Onslow County, North Carolina. Coll. Dick & Liz Petit, 1968–1970. Belgrade Formation, Haywood Landing Member. latest OLIGOCENE, Chattian.

25073 LACMIP [= UCLA loc. 5073]: limey concretions in shale exposed on north bank Grand River about 762 m (2500') S, 427 m (1400') E of NW cor. sec. 24, T. 21 N, R. 24 E, Bullhead Quad. (USGS 1956), Corson County, South Dakota. Coll: T. Susuki, 1963. Fox Hills Formation, Trail City Member, *Protocardia* zone. CRETACEOUS, Maastrichtian.

28428 LACMIP: Clarendon, Wiltshire, England. Coll.? & id. Arthur Wrigley—sent by Wrigley to UCLA (exUCLA 11439). London Clay. EOCENE, Ypresian.