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Review and revision of the Olivoidea (Neogastropoda) from the Paleocene and Eocene of the U.S. Gulf Coastal Plain

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Abstract.—Numerous species of "oliviform" gastropods have been recognized in the Paleogene of the U.S. Gulf Coastal Plain, many of which have previously been allied to the "*Bullia* group" in the family Nassariidae, and placed in a variety of poorly defined genera. We review these species, revise their generic and familial placement, and present a phylogenetic analysis. Of 19 species considered valid, all are assigned to Olivoidea, six to Olividae—one to *Oliva*, five to *Agaronia*—and the rest to Ancillariidae. The highly variable species *Ancillaria altile* Conrad is referred in the genus *Ancillopsis* and appears to have evolved anagenetically over an interval of perhaps 20 million years. *Ancillaria tenera* Conrad and *Ancillaria scamba* Conrad are placed in the new genus *Palmoliva*. *Monoptygma* Lea is demonstrated to belong to Ancillariidae, and to contain only a single species. Specimens assigned to *Lisbonia expansa* Palmer are split into adults assigned to *Ancillopsis altilis* and juveniles (together with several other species) in the long-lived species *Anbullina elliptica* (Whitfield). Coastal Plain ancillariids may have evolved from one or more species of the Cretaceous–Paleocene genus *Eoancilla*. We agree with previous authors who have suggested that the late Eocene species *Oliva mississippiensis* Conrad is the earliest known representative of this genus and the subfamily Oliviinae, perhaps derived from a species of *Agaronia*. The oldest *Agaronia* is lower Eocene (Ypresian).

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Introduction

Neogastropods known as "olive shells" and their relatives (Superfamily Olivoidea, sensu Kantor et al., 2017) have been common components in many shallow marine communities for much of the past 50 million years. They include the families Olividae Latreille, 1825 (including the subfamilies Olivinae Latreille, 1825, Olivellinae Troschel, 1869, and Agaroniinae Olsson, 1956), Pseudolividae de Gregorio, 1890, Ancillariidae Swainson, 1840, Bellolividae Kantor et al., 2017, and Benthobiidae Kantor et al., 2017 (Fig. 1). Olivoidea includes ∼460 extant species (WoRMS, 2021). Ancillariidae, which is of particular interest in this paper, includes at least 100 extant species and subspecies (Kilburn, 1981).

The earliest known members of Olivoidea appear to have been ancillariids, which may include the stem group of the larger clade (Riedel, 2000; Vermeij, 2001, p. 507). The oldest ancillariids date to no later than the Late Cretaceous (Maastrichtian) (Sohl, 1964, p. 247–248; Kilburn, 1981; Tracey et al., 1993, p. 152). Kilburn (1981, p. 356) suggested that, based on poorly preserved material from the Cretaceous of Burma, *Ancilla* (*Sparellina*) *poenitens* Vredenburg (1923, p. 251, pl. 14, figs 5a, b) "was either an *Ancilla* or an *Ancillarina*". Voskuil et al. (2011) mentioned four other species of likely Cretaceous Ancillariidae: *Tanimasanoria japonica* (Kase, 1990), Upper Cretaceous (lower Maastrichtian), Azenotani Mudstone Member, near Osaka, Japan; *Eoancilla acutula* Stephenson, 1941, Upper Cretaceous (Maastrichtian), Owl Creek Formation, Mississippi and Kemp Clay, Texas; *Tanimasanoria* sp. (Basse, 1932), Upper Cretaceous, Manja, Madagascar; and *Oliva vetusta* Forbes, 1846, Arriyalur Group, Upper Cretaceous (Maastrichtian), Pondicherry, India. Garvie (2013, p. 61) indicated that a Lower Cretaceous (Albian) fauna from Texas described by McCall et al. (2008) contains "a species that appears to be an ancestral *Ancilla*," potentially extending the history of the group still further.

Numerous ancillariid species have been reported from the Paleocene and Eocene of Europe. Schnetler and Nielsen (2018, pl. 7, fig. 2) reported *Ancilla* from the Selandian of Denmark, and other European Paleogene species are discussed by Lozouet (1992), Pacaud et al. (2013), and Pacaud (2014). Eocene species from New Zealand are discussed by Olson (1956), Michaux (1987, 1991), and Beu and Maxwell (1990). Kilburn (1981, p. 356) suggested that the "earliest-known true *Ancilla* is probably *A. boettgeri* Martin (1914, p. 133, pl. 2, fig. 67) of the upper Eocene Nanggoelan beds of Java." The genus *Ancillarina* Bellardi, 1882 (Selandian–Bartonian; type species *Ancilla canalifera* Lamarck, 1803) is also present in these beds; it includes "*Ancilla*-like species with a similarly divided fasciolar band but a total lack of callus on the spire whorls and sutures" (Kilburn, 1981, p. 356).

Numerous species of "oliviform" gastropods (sensu Kantor, 1991) have been recognized in the Paleogene of the

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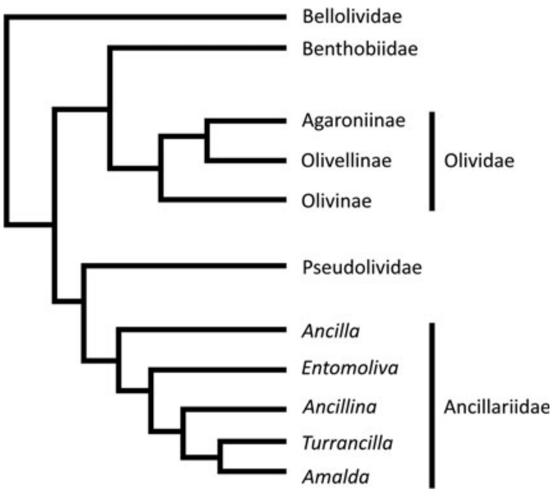

Figure 1. Phylogenetic relationships among living families of olivoid gastropods (based on Kantor et al., 2017).

U.S. Gulf Coastal Plain over almost 200 years, many of which previously have been allied to the "*Bullia* group" in the family Nassariidae, and placed in a variety of poorly defined genera. Previous work (Allmon, 1990) argued that these forms were not, in fact, related to *Bullia* s. s., but did not assign them to any other group. Here we review these forms and revise their generic and familial placement (Table 1). We place most of them in Olivoidea and present a phylogenetic analysis. Figure 2 shows the geological context and stratigraphic ranges of the species discussed here. We also discuss one species from the Eocene of France and the U.K., which we conclude is closely related to Coastal Plain species previously assigned to "*Bullia*." The expanded calluses on the shells of some of the species discussed here make them almost spherical, and recently have been analyzed as examples of homoplasy (convergence and parallelism); the phylogenetic analysis presented here supports those conclusions (Pietsch et al., 2021).

Table 1. Species of olivoid gastropods from the Paleocene and Eocene of the Gulf Coastal Plain (and U.K. and France) discussed in this paper.

Family	Subfamily	Genus	Species
Olividae	Olivinae	*Oliva* Bruguière, 1789	*mississippiensis* Conrad, 1848
	Agaroniinae	*Agaronia* Gray, 1839	*alabamensis* Conrad, 1833
			bombylis Conrad, 1833
			inglisia Palmer in Richards and Palmer, 1953
			media Meyer, 1885
		Bulovia Palmer, 1937	*weisbordi* Palmer, 1937
Ancillariidae		*Anbullina* Palmer, 1937	*ancillops* Heilprin, 1891
			ellipticum Whitfield, 1865
		Ancillopsis Conrad, 1865a	*altilis* Palmer, 1937
			patula Deshayes, 1835
		Monoptygma Lea, 1833	*lymneoides* Conrad, 1833
		Olivula Conrad, 1832	*staminea* Conrad, 1832
		Palmoliva n. gen.	*tenera* Conrad, 1834a n. comb.
			scamba Conrad, 1832 n. comb.
		Eoancilla Stephenson, 1941	*acutula* Stephenson, 1941
			mediavia Harris, 1896
			hordea Garvie, 2013
			lapicidina Garvie, 2021
		Micrancilla Maxwell, 1992	*alibamasiana* Pacaud, Merle, and Pons, 2013

Biology, shell morphology, and systematic characters

Living olivoids in general, and ancillariids in particular, are burrowing, sand-dwelling carnivores and scavengers (Kilburn, 1981; Cyrus et al., 2012; Kantor et al., 2017, p. 495; Robinson and Peters, 2018). The animal usually has a large foot with multiple folds that frequently extend far outside of, and may completely cover, the shell (Fig. 3) (Kilburn, 1981; Kantor et al., 2017, p. 519–522). Some species use the foot to swim or "surf" in turbulent water (Wilson, 1969).

The shell of Olivoidea (Fig. 4) is callused to different degrees, the functional significance and mode of formation of which remain poorly understood (Kantor et al., 2017, p. 519; Pietsch et al., 2021), and this has been described in numerous ways. Sometimes the callus is limited to the inner (parietal) wall of the aperture, but often it extends adapically, sometimes reaching or covering most or all of the spire, leaving only the protoconch and a part of the body whorl exposed. In many cases, the callus overlays or is associated with the sutures, which therefore may not be clearly visible externally. The callus may be uniform or consist of multiple layers, and these may vary throughout ontogeny. Kilburn (1977) and Kantor et al. (2017) have distinguished "primary" from "secondary" callus, with the primary usually forming a band around the anterior portion of each spire whorl, parallel to the suture, and the secondary callus located on the parietal wall of the aperture (ventral side of the shell), sometimes extending onto the spire, where it can cover primary callus. The primary callus, in this terminology, is therefore the secondary callus of earlier ontogenetic stages. Here we use a slightly different terminology, distinguishing spire callus from body whorl callus (Fig. 4.2), with the former forming a band on the anterior (abapical) part of each spire whorl, causing callusing associated with the sutures. For the body whorl callus, we distinguish the lateral extent (over the body whorl) from the posterior extent (extending posteriorly from the aperture toward the spire, sometimes covering the suture). Posterior body whorl callus will become spire callus as a subsequent whorl is added. Extensive posterior body whorl callus on subsequent whorls may then overlie spire callus of previous whorls. "Extreme parietal callus" (EPC) refers to the condition in which callus covers >50% of the ventral surface of the body whorl, which occurs on both olivoid and non-olivoid gastropods (Pietsch et al., 2021).

The anterior end of the olivoid shell bears a complex structure commonly referred to as the fasciole, formed by successive accretions of the anterior siphonal notch, which surrounds the anterior canal and its associated callus (Tursch and Greifeneder, 2001, p. 114–115; Kantor et al., 2017, p. 513–519). In all olivoids, the fasciole includes several more or less discrete zones or bands, which have been variously named in the literature

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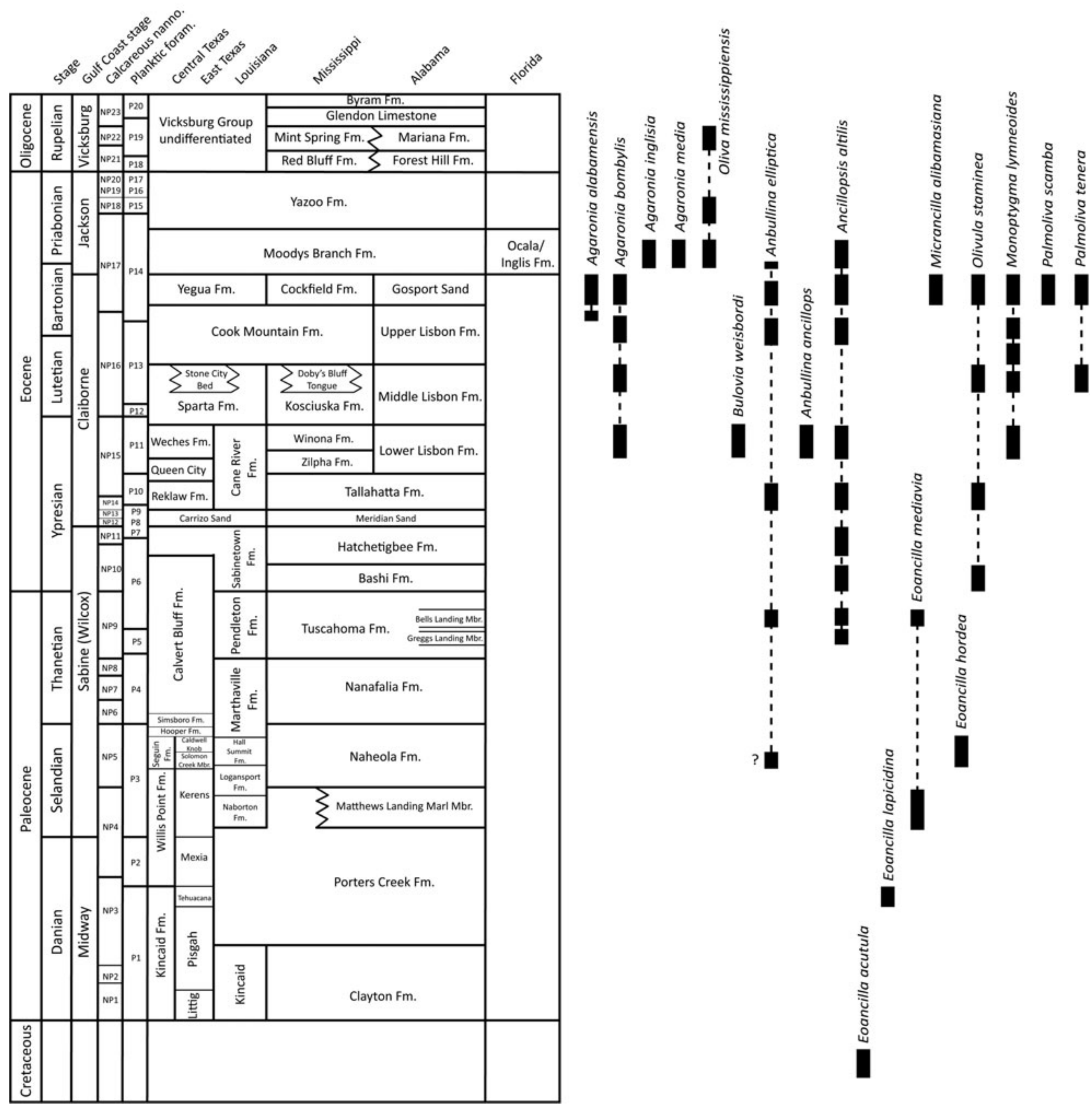

Figure 2. Paleocene and Eocene stratigraphic units in the U.S. Gulf Coastal Plain (based on Garvie, 2013; Dockery and Thompson, 2016; Garvie et al., 2020) and stratigraphic ranges of the species discussed in this paper.

(e.g., Kilburn, 1981; López et al., 1988; Tursch and Greifeneder, 2001; Pacaud et al., 2013). Here we use the terminology proposed by Kantor et al. (2017) (Fig. 4.1). The structure of the fasciole is important in discriminating olivoid shells from those of other neogastropods. For example, all representatives of the family Nassariidae lack the olivoid and anterior bands and show at least a slight terminal fold on the end of the fasciole (Allmon, 1990; Galindo et al., 2016).

Species of Ancillariidae can be distinguished conchologically from other olivoids by characters of callusing on the shell (Kantor et al., 2017, p. 535). Ancillariids are generally more strongly callused than other Olivoidea (but see Tursch and Greifeneder, 2001, p. 107–110), especially on the body whorl, and the suture between the spire and body whorl is usually overlaid with callus to varying degrees.

In this paper, we use the conception of fossil species advocated by Allmon (2016), which includes reference to morphological differences between extant species of a clade. The value of shell characters for recognition of species and genera in living olivoids remains unclear and is likely variable across the group. A number of modern olivid genera are distinguished only by non-shell characters. For example, some species of *Oliva* can be distinguished from species of *Agaronia* and *Ancilla* only by the radula (Zeigler and Porreca, 1969, p. 21). Kantor and Bouchet (2007, p. 27) described a new genus of Recent olivids, *Calyptoliva*, noting that it differs from the very similar *Belloliva* mainly

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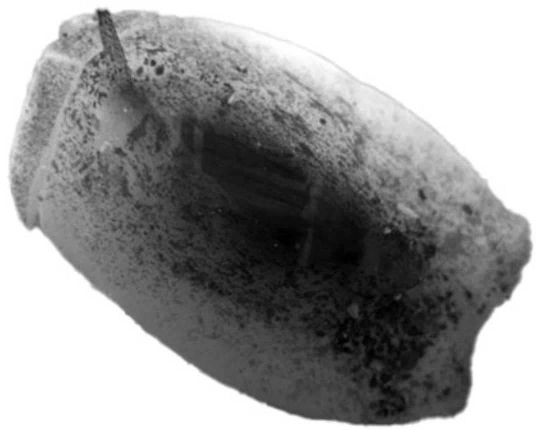

Figure 3. Live ancillariid gastropod showing large foot covering the entire shell. *Amalda australis* collected from New Zealand (illustration from https://en.wikipedia.org/wiki/Amalda_australis#/media/File:Amalda_australis1.jpg).

"by the absence of a mantle filament and the presence of a mantle lobe." Tursch and Greifeneder (2001) argued that morphospecies of *Oliva* are highly variable but frequently recognizable. Michaux (1987) showed that species of *Amalda* distinguished by electrophoresis also were distinguishable morphologically, but Kantor et al. (2016) found that several molecularly distinct species of *Ancilla* were morphologically cryptic. Thus, it is possible that morphospecies recognized here based solely on fossils include more than a single biological species.

Phylogenetic analysis

Methods.—Our preliminary phylogenetic analysis included 19 Paleocene–Eocene species representing three genera of Olividae and seven genera of Ancillariidae. We also included the Recent species *Agaronia testacea* (Lamarck, 1811) and *Oliva sericea* (Röding, 1798) for comparison. We used type and figured material to code each species for the following discrete character suites: (1) suture; (2) callus; (3) bands (including the olivoid, anterior, subsutural, and body whorl bands); (4) columella and plications; (5) ornamentation and texture; and (6) shell shape. In instances where museum specimens were unavailable, taxa were coded using primary taxonomic figures and literature. Species were coded for 27 discrete characters (10 binary and 17 multistate) (Table 2) that were selected to capture morphological variation among the clades and are inferred to represent homologous structures among sampled taxa. *Eoancilla* was designated as the outgroup because the genus is a putative ancestor of the other ancillariids (Garvie, 2013).

A parsimony analysis was conducted in PAUP* v. 4.0a147 (Swofford, 2003) using a heuristic search with 10,000 random addition sequences. TBR (tree bisection reconnection) was used for the branch-swapping algorithm with no reconnection limit and collapsing all branches with a maximum branch length of zero. All characters were left unordered and equally weighted. Nexus files utilized are provided as Supplement 1. Values for consistency index (CI) and retention index (RI) were recorded for recovered trees, and bootstrap values and Bremer support were calculated using PAUP*.

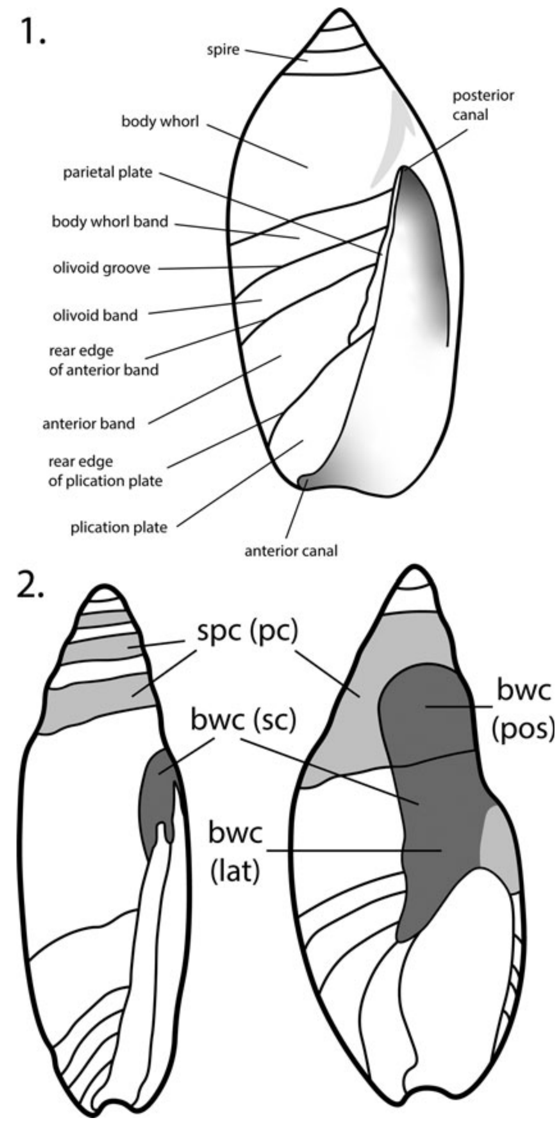

Figure 4. Shell morphological terminology used in this paper. (**1**) Modified from Kilburn (1981). (**2**) Terminology of the callus; lighter shading is spire callus (spc); darker shading is body whorl callus (bwc); bwc (lat) = body whorl callus, lateral; bwc (pos) = body whorl callus, posterior; (sc) = secondary callus; (pc) = primary callus; sc and pc are the terminology of Kantor et al. (2017); bwc (sc) means that the terms "body whorl callus" and "spire callus" are synonymous; spc (pc) means that the terms "spire callus" and "primary callus" are synonymous. See text for further discussion.

Results.—The parsimony analysis recovered 82 most parsimonious trees with tree lengths of 111 steps (CI 0.485, RI 0.541). Strict and semi-strict consensus of the most parsimonious trees resulted in a tree topology with poor resolution (Fig. 5.1). The 50% majority rule consensus tree (Fig. 5.2) gives better resolution and was plotted against the observed stratigraphic ranges of sampled genera to produce a time-scaled phylogeny (Fig. 20).

Material

Repositories and institutional abbreviations.—Academy of Natural Sciences of Drexel University, Philadelphia, PA, USA (ANSP); Alabama Museum of Natural History, Tuscaloosa, AL, USA (ALMNH); Bureau of Economic Geology, Austin,

Table 2. Characters scored for phylogenetic analysis (see Figure 4 for shell terminology).

1) Form of suture: 0 depressed; 1 channeled; 2 callused.
2) Lateral extent of callus: 0 absent; 1 limited to within aperture; 2 less than halfway across body whorl; 3 extreme parietal callus (EPC).
3) Vertical extent of callus: 0 absent; 1 limited to within aperture; 2 barely past posterior canal; 3 well past posterior canal; 4 covers preceding suture; 5 covers spire.
4) Inductura: 0 absent; 1 present
5) Olivoid groove (rear edge of olivoid band): 0 absent; 1 faint; 2 sharp.
6) Olivoid groove and band on dorsal side: 0 absent; 1 persists; 2 fades.
7) Width of plication plate compared to anterior band (as seen on left edge in apertural view): 0 narrower; 1 wider; 2 equal or close to.
8) Plication plate plications: 0 absent; 1 present.
9) Number of plications: 0 absent; 1 solitary plication; 2 multiple plications.
10) Rear edge of plication plate: 0 invisible, callused; 1 groove; 2 ridge.
11) Strength of groove: 0 faint; 1 sharp.
12) Strength of ridge: 0 faint; 1 sharp.
13) Width of anterior band compared to olivoid band: 0 narrower; 1 wider; 2 equal to.
14) Rear edge of anterior band: 0 groove; 1 ridge; 2 line (note: if anterior band is raised, code as groove).
15) Fasciolar ridge: 0 absent; 1 groove; 2 ridge; 3 line.
16) Body whorl texture: 0 smooth; 1 reticulate.
17) Axial folds on early teleoconch: 0 absent; 1 present.
18) Axial folds on body whorl: 0 absent; 1 present.
19) Shouldering: 0 absent; 1 present.
20) Shape of columellar tip: 0 pointed; 1 blunt.
21) Subsutural band: 0 absent; 1 present.
22) Body whorl band: 0 absent; 1 present.
23) Parietal plate: 0 absent; 1 present.

Four additional characters code for ratios based upon continuous measurements:

24) Maximum width/total Height.
25) Spire height/total Height.
26) Aperture width/Height.
27) Distance from posterior canal to suture/body-whorl Height.

TX, USA (BEG; collections now referred to as NPL); Florida Geological Survey, Tallahassee, FL, USA (FGS; collection now at Florida Museum of Natural History, Gainesville); Field Museum, Chicago, IL, USA (FMNH); Geological Survey of Alabama (Type Cabinet), Tuscaloosa, AL, USA (GSA (GSATC)); Museum of Geosciences, Louisiana State University, Baton Rouge, LA, USA (LSU); Department of Invertebrate Paleontology, Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA (MCZIP); Mississippi Geological Survey collection, Jackson, MS, USA (MGS); Muséum National d'Histoire Naturelle, collection de Paléontologie, Paris, France (MNHN); Paleontological Research Institution, Ithaca, NY, USA (PRI); Non-Vertebrate Paleontological Laboratory, University of Texas, Austin, TX, USA (NPL = NVPL of some previous authors); Texas Memorial Museum, Austin, TX, USA (TMM; collections now referred to as NPL); Université Claude Bernard, Lyon, France (UCBL); Florida Museum of Natural History, University of Florida, Gainesville, FL, USA (UF); National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM).

Systematic paleontology

In the species accounts below, morphological terminology follows Figure 4. Specimen measurements for all species are given in Table 3.

Phylum Mollusca Linnaeus, 1758
Class Gastropoda Cuvier, 1797
Family Olividae Latreille, 1825
Subfamily Olivinae Latreille, 1825
Genus *Oliva* Bruguière, 1789

Type species.—*Voluta oliva* Linnaeus, 1758; subsequent monotypy by Lamarck, 1799.

Remarks.—Conchologically, the genus *Oliva* is distinguished by having a "[p]lication plate subdivided into parietal plate,

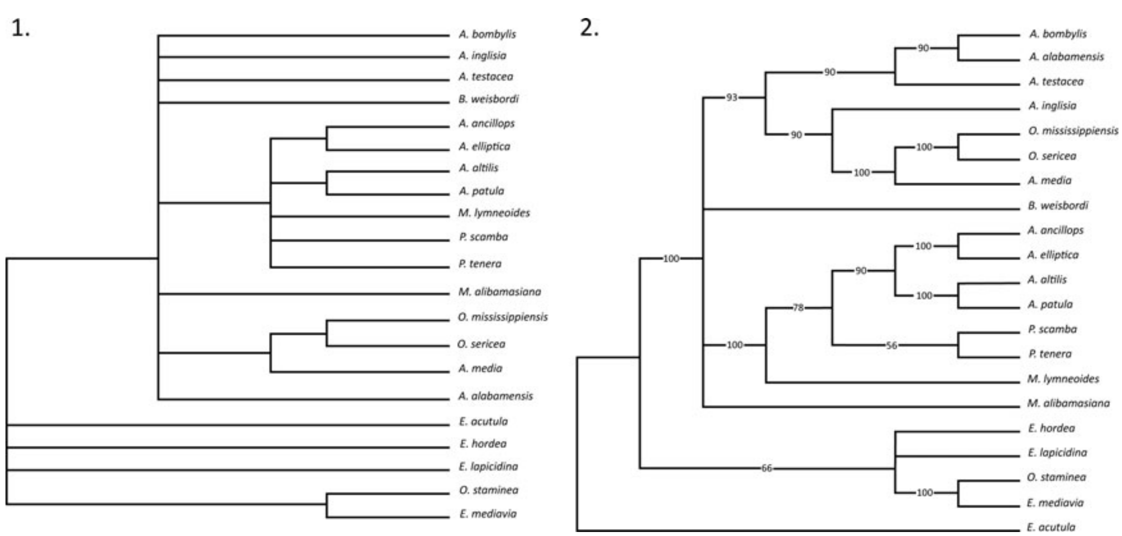

Figure 5. Phylogenetic relationships among the fossil species discussed in this paper. Numbers on branches are the number of trees with that arrangement. (**1**) Strict consensus of 82 equally parsimonious trees. (**2**) 50% majority-rule consensus of 82 equally parsimonious trees. Sister taxa are relatively well supported with four of the six pairs appearing in all of the most parsimonious trees, although support was lowest for the *Palmoliva* n. gen. pair. As the only representatives of their genera, *M. alibamasiana* and *B. weisbordi* support their genus' distinction from the other genera (*Agaronia*, *Oliva*, *Anbullina*, *Monoptygma*, and *Palmoliva* n. gen.) in their larger clade. See text for further discussion.

Table 3. Measurements for representative specimens.

Species	specimen	Total Height	Maximum width	Aperture Height	Spire height
Oliva mississippiensis	ANSP 13450	27.1	12.1	18.2	5
Agaronia alabamensis	ANSP 14649	41.0	17.0	27.0	8.0
	ANSP 5914	10.0	3.7	5.2	2.5
	ANSP 5916	42.0	16.5	25.5	8.5
	ANSP 5920	39.0	15.5	25.0	6.0
	PRI 3290	48.1	19.7	28	10.7
Agaronia bombylis	ANSP 14627	22.3	7.1	13.7	5
Agaronia inglisia	UF 108756	29.4	10.9	19.2	6
Agaronia media	MGS 2074	19.5	7.5	11.6	5.5
	PRI 20009	8.6	3.0	4.0	2.2
Bulovia weisbordi	PRI 3048	22.2	9.1	14.2	4.3
Ancillaria expansa	USNM 638775	50.5	38.0	31.0	7.5
Ancillina ancillops	PRI 3045	28.8	13.1	16.8	6.8
Ancillina ellipticum	PRI 30410	23.5	12.6	15.2	4.4
	PRI 83937	16.4	7.8	8.5	2.9
	FMNH 24670	17.0	8.8	8.5	2.5
Ancillopsis altilis	ANSP 14644	37.7	22.2	24	7.4
	PRI 356	16.8	13.5	13.2	0
	PRI 357	20.0	16.0	--	--
	PRI 360	15.3	9.8	10.8	1.0
	PRI 3037	26.6	20.3	21.6	1.5
	PRI 3038	25.0	20.0	15.5	1.0
	PRI 3039	27.0	18.0	15.5	5.4
	PRI 3040	44.7	28.5	24.3	7.5
	PRI 3042	50.0	39.0	33.0	2.9
	PRI 3043	31.0	22.0	20.2	1.0
	PRI 3044	20.0	14.0	--	--
	PRI 3047	78.4	57.0	50.8	4.4
	PRI 4659	14.8	6.5	6.8	2.8
	PRI 30022	27.0	22.5	20.5	0
	ALMNH 15246	69.2	49.4	46.9	6.4
	USNM 638776	51.4	38.6	32.1	7.8
	GSA-I17344	28.0	17.9	20.1	1.4
	GSA-I17579	23.2	16.6	--	1.4
Ancillopsis patula	UCBL EM30549	28	19.3	23.4	2.4
	PRI 83935	30.7	20.7	20.7	1.6
Monoptygma lymneoides	PRI 3026	22.5	9.9	15.2	3.6
	PRI 3027	22.4	10.6	13.2	5.1
	PRI 3036	36.2	16.6	24.6	4.9
	ANSP 5929	12.0	5.3	6.5	--
	ANSP 5930	8.2	4.0	5.0	--
	ANSP 13274	17.0	8.5	--	--
	ANSP 15618	11.8	5.5	8.0	2.5
Olivula staminea	ANSP 14670	31.8	11.8	25.9	3.4
	PRI 3282	25.3	8.5	14.8	4.7
	PRI 3283	21.6	6.8	14.9	2.0
Palmoliva tenera n. comb.	ANSP 14646	29.7	13.7	20.3	4.9
	ANSP 14647	35.0	16.0	18.5	10.0
	PRI 3064	26.0	15.0	17.4	2.1
	PRI 3065	23.3	14.4	13.3	3.6
	PRI 3066	41.0	22.0	--	--
Palmoliva scamba n. comb.	ANSP 14647	36.7	16.5	20.2	9.9
	PRI 3082	35.9	14.6	19.1	8.5
Eoancilla acutula	USNM 77126	9.3	4	5.2	2.5
Eoancilla mediavia	PRI 57647	17.4	5.0	8.2	3.9
Eoancilla hordea	NPL 37709	11.5	4.8	7.3	2.6

Table 3. Continued.

Species	specimen	Total Height	Maximum width	Aperture Height	Spire height
Eoancilla lapicidina	NPL 93694	11.1	4.1	5.7	2.8
Micrancilla alibamasiana	MNHN.F.H13251	5.0	1.4	1.4	1.0

shoe and belt. Filament channel well defined, eventually overlaid by primary spire callus on upper spire whorls, but free at least on last whorl" (Kantor et al., 2017, p. 526). Tursch and Griefender (2001) recognized 74 extant morphospecies.

Oliva mississippiensis Conrad, 1848
Figure 6.1, 6.2

1848a *Oliva mississippiensis* Conrad, p. 289.
1848b *Oliva mississippiensis* Conrad, p. 119, pl. 3, figs. 6, 38.
1865a *Lamprodoma Mississippiensis*; Conrad, p. 22.
1866 *Lamprodoma Mississippiensis*; Conrad, p. 30.
1903 *Oliva mississippiensis*; Casey, p. 281.
1945 *Oliva mississippiensis*; Gardner, p. 216.
1947 *Agaronia mississippiensis*; Harris and Palmer, p. 410, pl. 63, figs. 17–19.
1966 *Agaronia mississippiensis*; Palmer and Brann, p. 487.
1977 *Agaronia mississippiensis*; Dockery, p. 79, pl. 11, fig. 3A, B.
1981 *Strephonella mississippiensis*; Drez, p. 105.
1984 *Oliva* (*Strephonella*) *mississippiensis*; MacNeil and Dockery, p. 157, pl. 33, figs. 17, 18, pl. 56, figs. 13, 14.

Type material.—Lectotype ANSP 13450; hypotypes (Harris and Palmer, 1947, pl. 63) PRI 20010, 20011, 20012.

Occurrence.—Louisiana: upper Eocene (Bartonian–Priabonian), Moodys Branch and Yazoo formations (Loc. LA-GR-1); Mississippi: lower Oligocene (Rupelian), Mint Springs Formation (Loc. MS-WA-23).

Remarks.—Drez (1981) and Petuch and Sargeant (1986, p. 10–11) identified this species as the earliest olivid; Drez placed it in the genus *Strephonella*, and Petuch and Sargeant in *Oliva*. MacNeil and Dockery (1984, p. 157) placed *Strephonella* as a subgenus of *Oliva*, and recognized a second similar species, *O.* (*Strephonella*) *affluens* Casey, 1903, in the Moodys Branch Formation. Both of these forms appear to be closer to *Oliva* than to *Agaronia*, due to their inflated body whorl, wide and complex plication plate bearing sharp plications, and presence of a parietal plate posterior of the plication plate (see Tursch and Greifeneder, 2001, p. 112). Given its similarity to *Agaronia*, it is possible that this species (and therefore the clade Olivinae) is derived from a species of that genus (see further discussion below).

Subfamily Agaroninae Olsson, 1956
Genus *Agaronia* Gray, 1839

Type species.—*Voluta hiatula* Gmelin, 1791, by monotypy.

Remarks.—Conchologically, the genus *Agaronia* is distinguished by having a "[p]lication plate not distinctly subdivided, with distinct spiral plicae. Olivoid groove present, shallow. Olivoid band differing or not in color from cloak of last whorl. Filament channel well defined, free on most spire whorls" (Kantor et al., 2017, p. 526). The shell is less glossy than in *Oliva*, with a taller, more acuminate spire and slightly flaring outer apertural lip. López et al. (1988, p. 296) suggested that the "count of lirae [on the inner lip of the aperture]" and the "height and shape of the spire" provide useful specific characters in *Agaronia*.

Agaronia was originally described by Gray (1839) as a subgenus of *Olivancillaria*, which was accepted by some later authors. It was elevated to a separate genus by Olsson (1931), and this has been more widely accepted. *Agaronia* is most often placed in a monotypic subfamily, Agaroniinae (Olsson, 1956; Ponder and Warén, 1988; Sterba, 2003; Kantor et al., 2017), although Bouchet and Rocroi (2005) and Cilia (2012) placed it in Olivinae. The majority of the ~20 described extant species occur on low-latitude coasts of west Africa, western Central America, and the eastern Indian Ocean (see López et al., 1988; Cilia, 2012). The oldest recognized species is *Agaronia bombylis* (Conrad, 1833) from the Lower Eocene (Ypresian) (see below).

We recognize four species of *Agaronia* in the Paleogene of the Coastal Plain and Florida: *A. alabamensis* (Conrad, 1833), *A. bombylis* (Conrad, 1833), *A. media* (Meyer, 1885), and *A. inglisia* (Palmer in Richards and Palmer, 1953). We follow Garvie (2021) in placing the species *A. mediavia* (Harris, 1896) in the genus *Eoancilla* Stephenson, 1941.

Our phylogenetic analysis (see below) indicates that *Agaronia* is paraphyletic and includes the ancestry of *Oliva mississippiensis*. Since a thorough phylogenetic analysis of all fossil and extant *Agaronia* is beyond the scope of this paper, we use the name *Agaronia* sensu lato to include all Coastal Plain Paleogene species.

Agaronia alabamensis (Conrad, 1833)
Figure 6.7–6.14

non 1829 *Oliva gracilis*; Broderip and Sowerby, p. 379.
1833 *Oliva alabamensis* Conrad, p. 32.
1833 *Oliva Greenoughi* Lea, p. 183, pl. 6, fig. 197.
1833 *Oliva dubia* Lea, p. 183, pl. 6, fig. 198.
1833 *Oliva Phillipsii* Lea, p. 184, pl. 6, fig. 199.
1833 *Oliva gracilis* Lea, p. 182 [in part], pl. 6, fig. 196.
1834b *Oliva Phillipsii*; Conrad, p. 5.
1834b *Oliva alabamensis*; Conrad, p. 5.
1835 *Oliva alabamensis*; Conrad, p. 41, pl. 16, fig. 3.
non 1835 *Ancillaria dubia*; Deshayes, p. 734.
non 1835 *Oliva nitidula* Deshayes, p. 741.
1835 *Oliva alabamiensis* [sic]; Duclos, pl. 18, figs. 13, 14.

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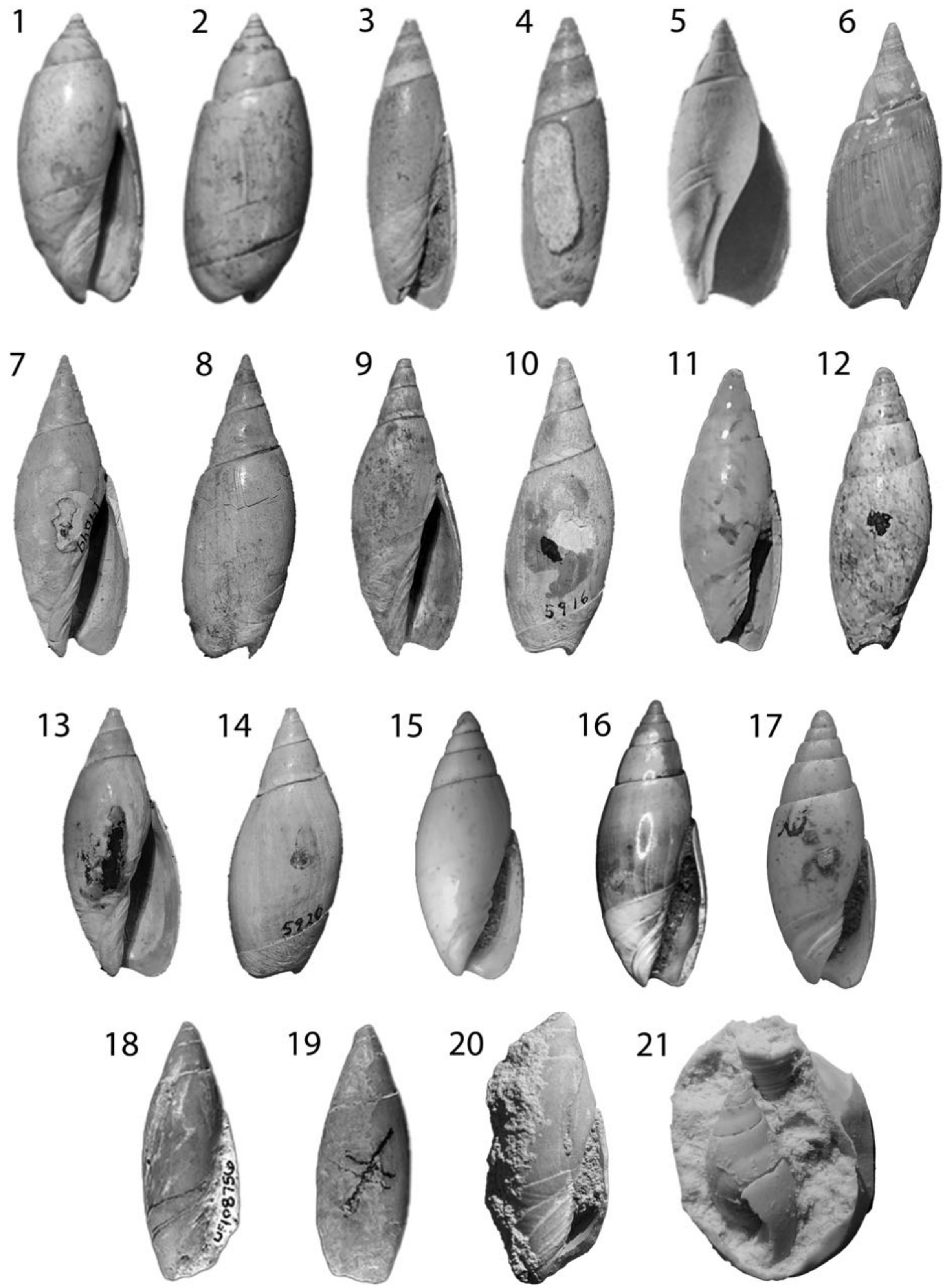

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Figure 6. *Oliva*, *Bulovia*, and *Agaronia*. (**1, 2**) *Oliva mississippiensis* lectotype ANSP 13450; height 27.1 mm. (**3, 4**) *Agaronia bombylis* (*Oliva bombylis* lectotype ANSP 14627); height 22.3 mm. (**5, 6**) *Bulovia weisbordi* holotype PRI 3048; height 22.2 mm. (**7–14**) *Agaronia alabamensis*: (**7, 8**) *Oliva alabamensis* lectotype ANSP 14649; height 41 mm. (**9, 10**) *Oliva greenoughi* holotype ANSP 5916; height 42 mm. (**11, 12**) *Oliva gracilis* holotype ANSP 5914. (**13, 14**) *Oliva dubia* holotype ANSP 5920; height 39 mm. (**15–17**) *Agaronia media*: (**15**) lectotype GSA-I17375; height 7 mm. (**16**) hypotype MGS 2074; height 19.5 mm. (**17**) hypotype (Harris and Palmer, 1947) PRI 20009; height 9 mm. (**18–21**) *Agaronia inglisia*: (**18, 19**) holotype UF 108756; height 29.4 mm. (**20**) UF 5455; height 38 mm. (**21**) UF 66680 silicone cast of mold in limestone. Cast measures 40 × 50 mm.

1844 *Oliva alabamiensis* [sic]; Duclos, p. 11, pl. 20, figs. 13, 14.
1846 *Oliva alabamensis*; Conrad, p. 220.
1849 *Oliva alabamensis*; Lea, p. 103.
1849 *Oliva Greenoughi*; Lea, p. 103.
1849 *Oliva dubia*; Lea, p. 103.
1849 *Oliva Phillipsii*; Lea, p. 103.
1849 *Oliva gracilis*; Lea, 1849, p. 103.
1850 *Oliva Phillipsii*; d'Orbigny, p. 351.
1850 *Oliva alabamensis;* d'Orbigny, p. 351.
1858 *Oliva alabamensis*; Tuomey, p. 266.
1865a *Lamprodoma alabamiensis* [sic]; Conrad, p. 22.
1865a *Lamprodoma gracilis*; Conrad, p. 22.
1865a *Lamprodoma Phillipsii*; Conrad, p. 22.
1866 *Lamprodoma alabamiensis* [sic]; Conrad, p. 17.
1866 *Lamprodoma gracilis*; Conrad, p. 17.
1866 *Lamprodoma Phillipsii*; Conrad, p. 17.
1890 *Oliva Phillipsii*; de Gregorio, p. 53, pl. 3, fig. 66 [copied Lea, 1833].
1890 *Oliva gracilis*; de Gregorio, p. 52, pl. 3, fig. 50, 51 [copied Lea, 1833].
1890 *Oliva nitidula*; de Gregorio, p. 51, pl. 3, figs. 36–42.
1890 *Oliva mitreola* Lamarck; de Gregorio, p. 51, pl. 3, fig. 47, 48 [not Lamarck, 1803, p. 391].
1890 *Oliva antelucana*; de Gregorio, p. 54, pl. 3, figs. 58–61.
1890 *Oliva pinaculica*; de Gregorio, p. 54, pl. 3, figs. 63–65.
1891 *Oliva gracilis*; Heilprin, p. 397.
1893 *Olivella alabamiensis* [sic]; Cossmann, p. 40.
1893 *Olivella Phillipsi*; Cossmann, p. 40.
1895b *Oliva alabamensis*; Harris, p. 3.
1899 *Olivancillaria* (*Agaronia*) *alabamiensis* [sic]; Cossmann, p. 51.
non 1899 *Oliva parisiensis*; Cossmann, p. 178.
1926a *Oliva alabamensis*; Cooke, pl. 95, fig. 5.
1935 *Olivancillaria* (*Agaronia*) *alabamiensis* [sic]; Davies, p. 306.
1937 *Agaronia alabamensis*; Palmer, p. 431, pl. 68, figs. 14–16, 18–22, pl. 89, fig. 5.
non 1937 *Oliva parnensis*; Palmer, p. 431.
1944 *Olivella* (*Agaronia*) *alabamensis*; Shimer and Shrock, p. 511, pl. 210, fig. 13 [copied Conrad, 1935a].
1947 *Agaronia alabamensis*; Harris and Palmer, p. 408.
1960 *Agaronia alabamensis*; Brann and Kent, p. 29.
1960 *Olivancillaria* (*Agaronia*) *alabamiensis* [sic]; Glibert, p. 19.
1966 *Agaronia alabamensis*; Palmer and Brann, p. 484.

Type material.—Lectotype + 8 specimens ANSP 14649; holotype *Oliva greenoughi* ANSP 5916; holotype *Oliva dubia* ANSP 5920; holotype *Oliva phillipsii* ANSP 5926; holotype *Oliva gracilis* ANSP 5914; hypotypes *Agaronia alabamensis* (Palmer, 1937) PRI 3288, 3289, 3290, 3291, 3292, 3293.

Occurrence.—Alabama: middle Eocene (Lutetian–Bartonian), Lisbon Formation, Gosport Sand (Locs. AL-CL-1, AL-MO-2a, b); South Carolina: middle Eocene (Bartonian), McBean Formation (Loc. SC-OR-1); Texas, Louisiana, Mississippi: middle Eocene (Lutetian–Bartonian), Cook Mountain Formation (see Palmer, 1937, p. 434).

Revised description.—Shell large. Protoconch of one and a half or two smooth whorls, and the sutures are indistinct, not channeled as on teleoconch whorls. Spire up to ∼0.25 total height in adults, shorter in juveniles. Sutures channeled. Shell smooth. Callus extends only slightly laterally out of aperture over body whorl and posteriorly toward spire, creating narrow callus band, often of lighter color, above sutures. Aperture ∼0.6 total height, narrowing posteriorly into a sharp channel and widening anteriorly to a broad channel. Olivoid band distinct and continuing on dorsal side, with sharp posterior margin. Another band often present posterior to olivoid band, consisting of smooth stripe or slight concavity on body whorl, bounded posteriorly by slight rounded ridge. Anterior band distinct, separated from olivoid band by faint line. Plication plate distinct, slightly inflated, bearing multiple plications, separated from anterior band by deep groove.

Other material examined.—MCZIP 29246 (5 specimens); PRI 14142 (172 specimens); PRI 104503 (2 specimens); PRI 104693 (2 specimens).

Remarks.—This species is one of the most common large gastropods in the upper middle Eocene Gosport Sand of Alabama (CoBabe and Allmon, 1994; Pietsch et al., 2016). Kelley and Swan (1988) noted that *Agaronia alabamensis* shows a single pigmented spiral band parallel to the suture. Gosport specimens are larger than those from other stratigraphic units (Haveles and Ivany, 2010).

Agaronia bombylis (Conrad, 1833)
Figure 6.3, 6.4

non 1829 *Oliva gracilis*; Broderip and Sowerby, p. 379 [fide Palmer and Brann, 1966, p. 486].
1833 *Oliva bombylis* Conrad, p. 32.
1833 *Oliva constricta* Lea, p. 182, pl. 6, fig. 195.
1833 *Oliva gracilis*; Lea, p. 182 (part).
1835 *Oliva bombylis*; Conrad, p. 42, pl. 16, fig. 4.
1835 *Oliva bombylis*; Duclos, pl. 18, figs. 7, 8.
1846 *Oliva bombylis*; Conrad, p. 220.

1849 *Oliva bombylis*; Lea, p. 103.
1849 *Oliva constricta*; Lea, p.103.
1850 *Oliva bombylis*; d'Orbigny, p. 351.
1865a *Lamprodoma bombylis*; Conrad, p. 22.
1866 *Lamprodoma bombylis*; Conrad, p. 17.
1879 *Oliva bombylis*; Heilprin, p. 223.
non 1886 *Oliva bombylis*; Aldrich, p. 53 [fide Palmer and Brann, 1966, p. 485].
non 1886 *Oliva gracilis*; Aldrich, p. 56 [fide Palmer and Brann, 1966, p. 486].
1890 *Oliva bombylis*; de Gregorio, p. 52, pl. 3, fig. 49, [copied Conrad, 1835], fig. 52 [copied *Oliva constricta* Lea, 1833].
1893 *Olivella bombylis*; Cossmann, p. 40.
1895b *Oliva bombylis*; Harris, p. 8.
1899 *Olivella bombylis*; Cossmann, p. 54.
1937 *Agaronia bombylis*; Palmer, p. 434, pl. 68, figs. 12, 13.
1960 *Olivancillaria* (*Agaronia*) *bombylis*; Glibert, p. 19.
1966 *Agaronia bombylis*; Palmer and Brann, p. 485.

Type material.—Lectotype ANSP 14627; holotype *Oliva constricta* ANSP 5911; hypotypes (Palmer, 1937) PRI 3286, 3287.

Occurrence.—Texas: middle Eocene (Ypresian–Bartonian), Weches Formation, Stone City Formation, Cook Mountain Formation (Locs. TX-BA-1); Alabama: middle Eocene (Lutetian–Bartonian), Upper Lisbon Formation, Gosport Sand (Locs. AL-MO-2a, AL-MO-5); South Carolina: middle Eocene (Bartonian), McBean Formation (Loc. SC-OR-1).

Revised description.—Shell small and elongate. Protoconch of one and one-half or two whorls. Spire 0.2–0.25 total height. Sutures channeled. Callus extends only slightly laterally out of aperture over body whorl and posteriorly toward spire, creating wide callus band, usually of lighter color, above sutures. Shell smooth. Aperture 0.5–0.6 total height. Aperture narrow, pinching to sharp channel posteriorly and wider anteriorly. Olivoid band distinct, bounded posteriorly by a sharp line or groove. Anterior band distinct, bounded posteriorly by rounded ridge. Plication plate distinct with multiple plications. Columellar terminus pointed.

Other material examined.—PRI 56684 (1 specimen), PRI 56028 (35 specimens).

Remarks.—As noted by Palmer (1937, p. 434–435), juvenile *A. alabamensis* and *A. bombylis* may be confused with each other, but are distinguishable by overall shell shape, with *A. bombylis* being consistently more slender in its bodywhorl. In *A. bombylis*, the callus band above the suture is also relatively wider and more conspicuous. *Agaronia bombylis* does not attain the size or abundance of *A. alabamensis*. Kelley and Swan (1988) noted that *Agaronia bombylis* shows a single pigmented spiral band parallel to the suture. Palmer (1937, p. 435; Palmer and Brann, 1966, p. 486) stated that it occurs in the Weches and Stone City formations of Texas, but we have not been able to locate these specimens in the PRI collection. These reported occurrences are important because they considerably extend the stratigraphic range of the species downward (see Fig. 2).

Agaronia inglisia Palmer in Richards and Palmer, 1953
Figure 6.18–6.21

1953 *Agaronia inglisia* Palmer in Richards and Palmer, p. 31, pl. 6, figs. 5, 8, 13.
1966 *Agaronia inglisia*; Palmer and Brann, p. 486.

Type material.—Holotype FGS I-7604 (UF 108756); paratypes FGS I-7605 (UF 108760), FGS I-7606 (UF 108764).

Occurrence.—Florida: upper Eocene (Bartonian–Priabonian), Inglis Formation (Loc. FL-LE-1).

Revised description.—Shell medium-sized. Protoconch bulbous, of ~1.5 whorls. Spire <0.2 total height. Sutures deeply grooved. Callus extends posteriorly from aperture about half-way to suture. Body whorl smooth, unsculptured. Aperture narrow, ~0.6 total height. Olivoid and anterior bands marked by strong grooves. Plication plate relatively wide.

Other material examined.—UF 5396 (1 specimen), UF 5448 (2 specimens), UF 5455 (2 specimens), UF 6794 (2 specimens), UF 12753 (1 specimen), UF 19132 (2 specimens), UF 66680 (1 specimen), UF 106738 (1 specimen), UF 107439 (1 specimen).

Remarks.—This is the only species of *Agaronia* known from the Eocene of Florida.

Agaronia media (Meyer, 1885)
Figure 6.15–6.17

1885 *Oliva media* Meyer, p. 465.
1926b *Olivella jacksonensis* Cooke, p. 134, fig. 5.
1947 *Agaronia jacksonensis*; Harris and Palmer, pl. 63, fig. 10.
1947 *Agaronia media*; Harris and Palmer, p. 407, pl. 63, figs. 7, 9, 11–13.
1966 *Agaronia media*; Palmer and Brann, p. 486.
1977 *Agaronia media*; Dockery, p. 79, pl. 11, figs. 1A, B, 2A, B.

Type material.—Syntypes and lectotype GSA-I17375 (includes "holotype" listed in Palmer and Brann, 1966, p. 486, as GSATC 78); hypotypes (Harris and Palmer, 1947) PRI 20009, (Dockery, 1977) MGS 2073, 2074.

Occurrence.—Mississippi: upper Eocene (Bartonian–Priabonian), Moodys Branch Formation (Locs. MS-CL-2, MS-HI-3, MS-HI-4); Arkansas, Louisiana, Texas: (see Palmer and Brann, 1966, p. 486).

Revised description.—Shell small. Protoconch spherical. Spire ~0.25 total height. Suture strongly channeled. Callus minimal. Shell smooth, shiny, unsculptured. Aperture narrow, ~0.5 total height. Olivoid and anterior bands well marked. Plication plate narrow.

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Remarks.—Meyer (1885) did not figure the species when he described it, nor did he designate a type specimen. According to Palmer (in Harris and Palmer, 1947, p. 408), the collection in the Alabama Museum of Natural History included eight specimens labeled as "types," probably by Alabama State Paleontologist Winnie McGlamery. From among these, Palmer selected one as a lectotype. Unfortunately, this specimen was not kept separate and was recombined with 52 others in a single vial, all being given the number GSATC 78; they have since been given the new number GSA-I17375 (T.L. Harrell, personal communication, October 21, 2021). From these, one specimen was identified by T.L. Harrell as the most likely to have been Palmer's lectotype, and it is figured here (Fig. 6.15). Harris and Palmer (1947, p. 407) reported this species to be "very common" in the Moodys Branch Formation at Jackson, MS.

Genus *Bulovia* Palmer, 1937

Type species.—*Bulovia weisbordi* Palmer, 1937, by original designation.

Remarks.—The shell is very distinctive, which led Palmer to put it in a new monotypic genus. It resembles species of *Agaronia* in its strong olivoid and anterior bands, aperture shape, and strongly channeled suture, and we have been tempted to place it in *Agaronia*. In our phylogenetic analyses (Fig. 5), however, *Bulovia weisbordi* consistently falls outside of *Agaronia* because of the unique shape of the anterior end of the shell, especially the deep groove separating the plication plate and anterior band. Despite it being represented by a single specimen, we therefore retain it in Palmer's monotypic genus *Bulovia*.

Bulovia weisbordi Palmer, 1937
Figure 6.5, 6.6

1937 *Bulovia weisbordi* Palmer, p. 293, pl. 40, figs. 10, 11.
1943 *Bulovia weisbordi*; Wenz, p. 1226, fig. 3489 [copied Palmer, 1937, pl. 40, fig. 10].
1960 *Bulovia weisbordi*; Brann and Kent, p. 140.
1966 *Bulovia weisbordi*; Palmer and Brann, p. 546.
1982 *Bullia* (*Bulovia*) *weisbordi*; Cernohorsky, p. 17.
1990 *Bulovia weisbordi*; Allmon, p. 60, pl. 9, fig. 5.

Type material.—Holotype PRI 3048.

Revised description.—Shell small and slender. Protoconch unknown. Spire ~0.2 total height. Sutures are callused, with a prominent sutural band and the last suture deeply channeled. Callus extends posteriorly from aperture almost to suture, and laterally over more than half of body whorl. Growth lines have prominent relief on spire and body whorl beneath a prominent smooth subsutural band. Aperture wide, just over half total height, with a wide anterior canal. Olivoid and anterior bands very prominent. Plication plate narrow and smooth, separated from anterior band by a very deep groove, almost a pseudoumbilicus.

Occurrence.—Texas: middle Eocene (Ypresian), Weches Formation (Loc. TX-BA-1).

Remarks.—*Bulovia weisbordi* is known only from its holotype specimen, from the now-inaccessible Smithville outcrop of the Weches Formation in Texas.

Family Ancillariidae Swainson, 1840
(= Ancillinae Adams and Adams, 1853)

Diagnosis.—(Kantor et al., 2017, p. 530) "Shell glossy or mat, lacking periostracum, fusiform to narrowly fusiform, with high last whorl, and medium broad-to-narrow aperture tapering adapically. Siphonal canal absent, anterior end of shell distinctly notched. Anterior shell end with well-defined anterior band, raised above the shell cloak and often strongly shagreened. Olivoid groove present (at least in some species) in all genera. Plication plate limited to columella, usually with spiral plicae. Primary spire callus well defined, covering most of, or even completely, the shell. Secondary spire callus from poorly defined to very strong. Suture always overlaid by the callus."

Genus *Ancillopsis* Conrad, 1865

Type species.—*Ancillopsis altilis* Conrad, 1865a, by subsequent designation (Cossmann, 1899, p. 45).

Diagnosis.—Shell medium to very large. Spire in juveniles one-fourth or less of total height; spire in adults may be only a tiny point above the expanded callus, which may make shell subspherical. Aperture one-half to two-thirds total height. Sutures simple in juveniles, heavily callused on adults. Shell in juveniles lanceolate in overall shape; in adults shell is oval to almost circular and may be dorso-laterally flattened. Olivoid band and anterior bands pronounced. Plication plate narrow and simple and usually callused. Anterior end of columella a simple point.

Remarks.—When he first introduced the name *Ancillopsis*, Conrad (1865a, p. 22) did not provide a description (he also erroneously gave the date of its introduction as 1864), but listed four species (*altile*, *scamba*, *subglobosa*, and *tenera*) (he had earlier [Conrad, 1832, 1834a] placed these in *Ancillaria*, but this name was already preoccupied by *Ancillaria* Lamarck, 1799). These species were allied with Nassariidae by Cossmann (1893), who placed them in the genus *Buccinanops*. Palmer (1937) agreed with this familial placement but moved them all into the nassariid genus *Bullia*. Gardner (1945, p. 199) rejected Palmer's judgement, suggesting that the "much smaller protoconch and the banding of the body by the change in direction of the growth lines are probably significant characters in separating *Ancillopsis* from *Bullia*." Allmon (1990) similarly argued that *Ancillopsis* and associated forms were not closely related to *Bullia*, but did not assign them to another group. Pacaud and Cazes (2014) reiterated the case for an assignment of *altilis* and similar forms to *Bullia*. Dockery (1980) figured a small specimen with axial ribs on early whorls from the Cook Mountain Formation of Mississippi, referring it to "*Bullia* sp.", which may belong to the species *A. altilis*.

Species assigned here to *Ancillopsis* have in common with other species of Ancillariidae the presence of olivoid and anterior bands, which are not present in Recent species of *Bullia* (Fig. 7). Furthermore, the form of the anterior end of the columella is different between *Ancillopsis altilis* and extant *Bullia* species (Fig. 7): in *A. altilis*, the end comes to an acute point, while in *Bullia*, it is terminated by a fold. For these reasons, *altilis* and related forms can be placed in the genus *Ancillopsis* in the family Ancillariidae.

Pacaud and Cazes (2014) reported preserved color patterns on specimens of the two species here included in this genus (*A. altilis* and *A. patula*).

Ancillopsis altilis (Conrad, 1832)
Figures 8.1–8.21, 9.1, 9.10, 9.13, 9.14, 9.16, 9.17, 10

1832 *Ancillaria altile* Conrad, p. 24, pl. 10, fig. 2.
1832 *Ancillaria subglobosa* Conrad, p. 25, pl. 10, fig. 3.
1833 *Anolax gigantea* Lea, p. 180, pl. 6, fig. 193.
1849 *Ancillaria subglobosa*; Lea, p. 96.
1850 *Ancyllaria subglobosa*; d'Orbigny, p. 352.
1862 *Tritia altilis*; Conrad, p. 562.
1865a *Ancillopsis subglobosa*; Conrad, p. 22.
1866 *Ancillopsis subglobosa*; Conrad, p. 17.
1867 *Ptychosalpinx altilis*; Gill, p. 154.
1880 *Ancillaria* (*Ancillopsis*) *subglobosa*; Heilprin, p. 364.
1886 cf. *Ancillaria subglobosa*; Aldrich, p. 50, 51, 58.
1886 *Expleritoma prima*; Aldrich, p. 29, pl. 5, fig. 1.
non 1886 *Ancillaria expansa*; Aldrich, p. 28, pl. 5, fig. 11.
1890 *Ancilla altilis*; de Gregorio, p. 55, pl. 3, figs. 21, 22, 57, 62, 67.
1890 *Ancilla subglobosa*; de Gregorio, p. 56, pl. 4, figs. 3,4,19,20.
1890 *Expleritoma prima*; de Gregorio, p. 108, pl. 8, figs. 26, 27.
non 1890 *Ancilla expansa*; de Gregorio, p. 55, pl. 4, fig. 1 [copied Aldrich, 1886].
1893 *Buccinanops altile*; Cossmann, p. 33.
1893 *Buccinanops subglobosum*; Cossmann, p. 33.
1895b *Ancillaria subglobosa*; Harris, p. 43.
1899 *Buccinanops altile*; Cossmann, p. 45.
1901b *Buccinanops* (*Brachysphingus*) *subglobosa*; Cossmann, p. 221, pl. 9, fig. 14 [captions for figs 14 and 23 reversed].
1911 cf.? *Buccinanops altile*; Veatch and Stephenson, p. 295.
1921 *Ancillopsis Tuomoyi* [sic]; Aldrich, p. 12, pl. 1, figs. 23, 24.
1928 *Bullia altile harrisi* Palmer in Price and Palmer, p. 29, pl. 7, figs. 7, 11, 12, 15.
1928 *Bullia altile*; Palmer in Price and Palmer, p. 28, pl. 6, figs. 13, 14, 16.
1928 *Bullia altile* (*B. subglobosum* form); Palmer in Price and Palmer, p. 29, pl. 7, figs. 13, 14, 16.
1937 *Bullia altilis*; Palmer, p. 287, pl. 39, figs. 7–9.
1937 *Bullia altilis subglobosa*; Palmer, p. 289, pl. 39, figs. 1, 4, 5, 6, 11, 12, pl. 40, figs. 1–3, 5.
1937 *Bullia altilis harrisi*; Palmer, p. 290, pl. 39, figs. 2, 3, 10, 13.
1937 *Lisbonia expansa* Palmer [in part], p. 295, pl. 40, figs. 8, 12, 13.
1943 *Lisbonia expansa*; Wenz, p. 1227, fig. 3491 [copied Palmer, 1937].
1945 *Ancillopsis subglobosa*; Gardner, p. 199, pl. 22, figs. 20, 21.
1945 *Ancillopsis harrisi*; Gardner, p. 200, pl. 22, figs. 22, 23.
1947 cf. *Bullia altilis*; Harris and Palmer, p. 347, pl. 45, figs. 22, 23.
1947 cf. *Bullia altilis subglobosa*; Harris and Palmer, p. 348, pl. 45, fig. 24.
1953 *Bulla* [sic] *altilis subglobosa*; Wilbert, p. 99.
1960 *Bullia altilis harrisi*; Brann and Kent, p. 139.
1960 cf. *Bullia altilis subglobosa*; Brann and Kent, p. 139.
1960 *Lisbonia expansa* [in part]; Brann and Kent, p. 500.
1966 *Bullia altilis harrisi*; Palmer and Brann, p. 543.
1966 *Bullia altilis subglobosa*; Palmer and Brann, p. 543.
1966 *Bullia tuomeyi*; Palmer and Brann, p. 545.
1966 *Lisbonia expansa* [in part]; Palmer and Brann, p. 740.
1977 *Bullia altilis*; Dockery, p. 73, pl. 14, figs. 8, 9.
1977 *Bullia altilis*; Toulmin, p. 276, pl. 45, fig. 9.
1977 *Bullia altilis subglobosa*; Toulmin, p. 205.
1980 *Bullia calluspira* Dockery, p. 109, pl. 3, figs. 4–7.
1990 "*Bullia*" *altilis*; Allmon, p. 56, pl. 9, fig. 10.
1990 "*Bullia*" *tuomeyi*; Allmon, p. 59, pl. 9, fig. 13.
1996 *Bullia altilis harrisi*; Garvie, p. 74, pl. 15, figs. 1, 2.
2014 *Bullia altilis subglobosa*; Pacaud and Cazes, p. 18, pl. 1, figs. 4, 5, pl. 2, figs. 10, 11.

Type material.—Lectotype (plus 8 specimens) *Ancillaria altile* (selected by Palmer, 1937, p. 289 [fide Moore, 1962, p. 36]) ANSP 14644; holotype *Anolax gigantea* Lea, 1833, ANSP 5909 (lost; J. Sessa, personal communication, 11/12/21); holotype *B. altilis harrisi* PRI 360; paratypes PRI 356, 357; hypotype (Garvie, 1996) PRI 33127; holotype *B. calluspira* PRI 30022; hypotypes *Lisbonia expansa* (Palmer, 1937) PRI 3046, 3047; hypotypes *B. altilis* (Palmer, 1937) PRI 3038, 3040, 3042, juvenile specimen 3039; juvenile specimen (Harris and Palmer, 1947) PRI 4659; hypotypes *B. altilis subglobosa* (Harris and Palmer, 1947) PRI 4660; (Palmer, 1937) PRI 3037, 3038, 3043; holotype *Ancillopsis tuomeyi* GSA-I17344, cotype GSA-I17579; holotype *Expleritoma prima* Aldrich, 1886, USNM 638776.

Occurrence.—Alabama: upper Paleocene (Thanetian), Nanafalia Formation, Bells Landing Marl, (AL-MO-3), lower Eocene (Ypresian), Bashi Marl, Hatchetigbee Formation (Locs. AL-CH-1, AL-CL-2, AL-CL-6, AL-WA-1), middle Eocene (Lutetian–Bartonian), Lisbon Formation, Gosport Sand (Locs. AL-CL-1, AL-CH-4, AL-MO-2, AL-MO-5, AL-PA-1); Mississippi: lower Eocene (Ypresian), Bashi Marl (Locs. MS-LA-1, MS-LA-2), upper Eocene (Bartonian–Priabonian),

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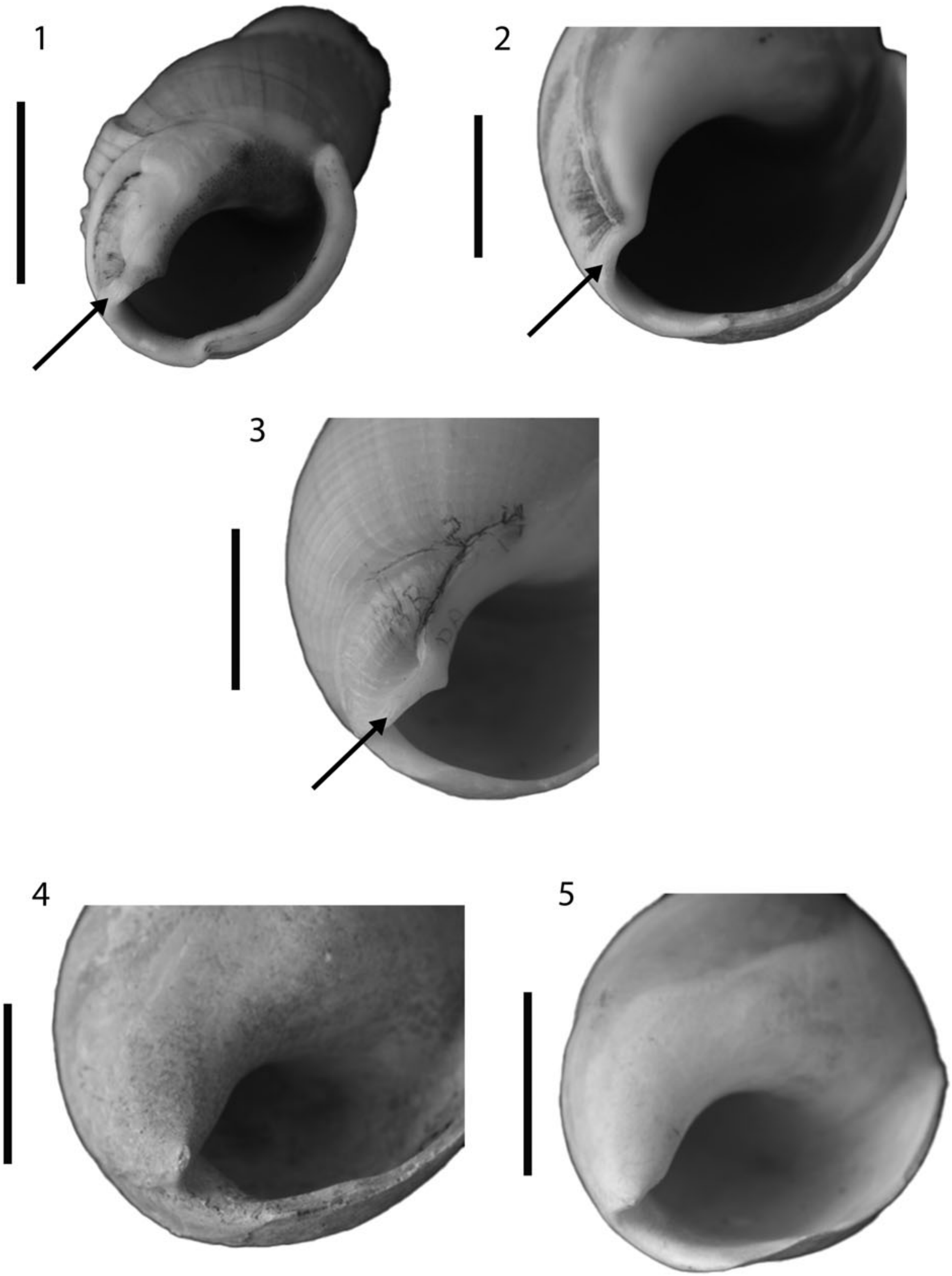

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Figure 7. Comparison of the anterior ends of the shell in three living species of *Bullia* and specimens of *Ancillopsis*, which have been placed by other authors in *Bullia*. The *Bullia* specimens (**1–3**) all show a terminal columellar fold (arrows), whereas the specimens of *Ancillopsis* (**4, 5**) do not. (**1**) *Bullia vittata* (Linnaeus, 1767), Sri Lanka, PRI 104508. (**2**) *Bullia laevissima* (Gmelin, 1791), South Africa, PRI 104509. (**3**) *Bullia annulata* (Lamarck, 1816), South Africa, PRI 104507. (**4**) *Ancillopsis altilis*, Gosport Sand, Alabama (Loc. AL-MO-2a), PRI 83941. (**5**) *Ancillopsis patula,* Eocene, Ducy, France (Loc. FR-1), PRI 83935. All scale bars = 1 cm.

Moodys Branch Formation (Loc. MS-YA-1); Texas: middle Eocene (Lutetian–Bartonian), Cook Mountain, Reklaw, Weches formations (Locs. TX-BA-4, TX-MI-1); Arkansas: upper Eocene (Priabonian), White Bluff Formation (Loc. AR-ST-1). Mexico: middle Eocene (Bartonian), Laredo Formation (Loc. MX-NL-1), upper Eocene (Priabonian), Jackson Formation (MX-TA-1).

Revised description.—Adult shell small to very large. Protoconch of 2–3 smooth whorls. Shell lanceolate with acute spire as juvenile, becoming rounded with lower spire with age. Spire in juveniles up to 0.25 total height, sometimes with faint axial ribs. In mature individuals, almost the entire ventral surface of shell covered by callus, with the early spire whorls sometimes barely or not at all protruding, producing a subspheroidal shape. Aperture lanceolate, 0.5–0.7 total shell height and ∼0.5 maximum width. Posterior canal usually conspicuous. Shell smooth except for growth lines. Anterior and olivoid bands covered by callus near aperture, well developed on dorsal side of body whorl, with pronounced ridge between them. Growth lines prominent, straight, and sharply angled in olivoid band, deeply curved concavely toward the anterior notch in the anterior band. Plication plate covered by callus and not visible. Anterior tip of columella simple and pointed. Some large individuals show slight shouldering on posterior of body whorl.

Other material examined.—PRI 64338 (1 specimen); PRI 83922 (10 specimens); PRI 83923 (1 specimen); PRI 83924 (1 specimen); PRI 83925 (4 specimens); PRI 83926 (2 specimens); PRI 83928 (1 specimen); PRI 83929 (1 specimen); PRI 83930 (1 specimen); PRI 83931 (15 specimens); PRI 83932 (3 specimens); PRI 83933 (1 specimen); PRI 83934 (16 specimens); PRI 83938 (4 specimens); PRI 83939 (1 specimen); PRI 83940 (1 specimen); PRI 83941 (1 specimen); PRI 83942 (1 specimen); PRI 83943 (2 specimens); PRI 83944 (1 specimen); PRI 83945 (1 specimen); PRI 83946 (12 specimens); PRI 104694 (1 specimen); ALMNH 15245 (27 specimens); ALMNH 15246 (1 specimen); MCZIP 24244 (53 specimens); MCZIP 29243 (21 specimens); MCZIP 29245 (1 specimen).

Morphometrics.—We measured 10 variables on a total of 211 specimens from localities in Alabama, Mississippi, and France (Fig. 11; Supplement 2). Measurements were taken with digital calipers. Data were analyzed by factor analysis, using the 4M program in the BMDP statistical package (Dixon, 1993). The first three factors reported explained 91.6% of the total variation in the dataset. The results (Fig. 12) indicate that the specimens cannot be clearly separated morphologically, and therefore reasonably can be included in a single species-level taxon. The specimens measured included the type specimen of *Bullia calluspira* Dockery, 1980 (from the Bashi Formation), and the European species *Buccinum patulum* Deshayes, 1835 (see below), both of which are morphometrically clustered among the other specimens.

Specimens from early in the history of the lineage (from the Tuscahoma, Bashi, and Hatchetigbee formations) do, however, differ in size and shape from those in the later Gosport Sand and Moodys Branch formations. Older specimens are smaller, and Gosport/Moodys specimens are larger (similar to the pattern reported in *Agaronia alabamensis* and other taxa; see Haveles and Ivany, 2010) (Figs. 13, 14). Price and Palmer (1928) described *harrisi* as a subspecies of *altilis* from the Queen City Formation at Smithville, Bastrop County, TX (Loc. TX-BA-4) (see Molineaux et al., 2013, about this locality), and Garvie (1996) reported it from the Reklaw Formation in Texas. Specimens of this form are especially small.

Shell shape and degree of callus lateral expansion over the body whorl also vary with time (Fig. 12). Specimens from the Bashi and Gosport are more inflated and have callus covering about half to three-fourths of the ventral side, while those from the Hatchetigbee are flatter and have callus on the entire ventral side and lapping over onto the dorsal side. Specimens from the Bashi, Hatchetigbee, and Queen City/Reklaw formations have low spires even as juveniles. The earliest known specimens, from the Greggs Landing bed of the Tuscahoma Formation (described as *Ancillopsis tuomeyi* Aldrich, 1921), are also distinctive in being dorso-ventrally flattened (Fig. 9.6–9.10).

Remarks.—This is one of the most distinctive gastropods in the Eocene of the Gulf Coastal Plain. It has received a large number of names, which has unfortunately obscured rather than clarified its manifest morphological variability and disparity through its extended stratigraphic range. Significantly, the numerous named forms do not overlap with each other in time, suggesting a single variable lineage showing considerable anagenetic change through time rather than multiple separate taxa (Figs. 13, 14).

One of the most conspicuous characteristics of these forms is the greatly expanded parietal callus on adult individuals, frequently extending over the apex giving the shells an almost spherical overall shape (see Pietsch et al., 2021) (e.g., Figs. 8, 9). Juveniles, in contrast, have attenuated spires and only narrow extent of callus on the body whorl and spire (Fig. 8.14, 8.21). A series of specimens from the Moodys Branch Formation shows this ontogenetic transition particularly well (Fig. 10).

Several specimens from the Gosport Sand also show enormously thickened shell inside the last whorl ending at the aperture. This includes the type specimen of *Explerotoma prima* (USNM 638776; Fig. 8.11–8.13), which is now unfortunately badly damaged, and a specimen that Palmer assigned to *Bullia altilis subglobosa* (PRI 3037; Fig. 8.19, 8.20). Palmer (1937,

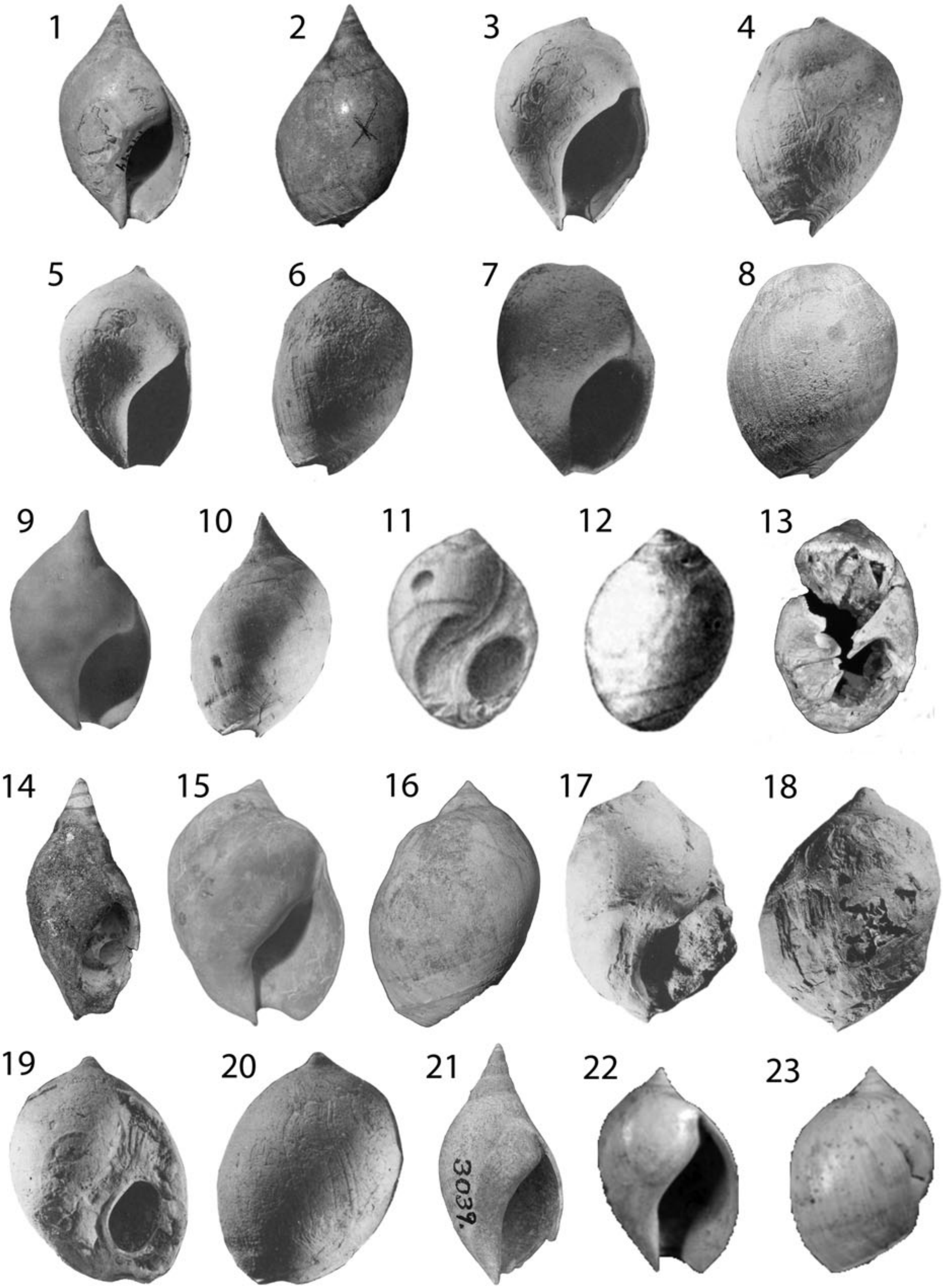

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Figure 8. *Ancillopsis*. (**1–20**) *Ancillopsis altilis*: (**1, 2**) *Ancillaria altile* lectotype ANSP 14644; height 37.7 mm. (**3, 4**) *Bullia altilis subglobosa* hypotype PRI 3044; height 20.0 mm. (**5, 6**) *Bullia altilis subglobosa* hypotype PRI 3043; height 31.0 mm. (**7, 8**) *Bullia calluspira* holotype PRI 30022; height 27.0 mm. (**9, 10**) *Bullia altilis* hypotype PRI 3040; height 44.7 mm. (**11–13**) *Expleritoma prima* holotype USNM 638776: (**11, 12**) drawings from Aldrich (1886); (**13**) photo of broken specimen; height 36.0 mm. (**14**) *Ancillopsis altilis* (juvenile) PRI 4659; height 15.2 mm. (**15, 16**) *Ancillopsis altilis* ALMNH 15246; height 69.2 mm. (**17, 18**) *Lisbonia expansa* hypotype PRI 3047; height 78.4 mm. (**19, 20**) *Bullia altilis subglobosa* hypotype PRI 3037; height 26.6 mm. (**21**) *Bullia altilis* (juvenile) hypotype PRI 3039; height 27.0 mm. (**22, 23**) *Ancillopsis patula* (*Bullia patula* lectotype UCBL EM30549; height 28.0 mm; from Pacaud and Cazes, 2014).

p. 289) described these specimens as "injured or diseased" individuals of *B. altilis subglobosa*.

Palmer (1937) named the genus *Lisbonia* for *Ancillaria expansa* Aldrich, 1886. She stated that young specimens had axial ribs on their early whorls and were relatively uncallused, but that adult specimens, "rivalling in size *B. altilis*" were heavily callused. Indeed, a large specimen assigned to *L. expansa* by Palmer (1937; Fig. 8.16, 8.17) is almost identical to large specimens of *altilis*. Palmer noted that such ribbing did not occur on early whorls of *altilis*, and that "[t]he life histories of the two species are different and show that the two belong to two different genera" (Palmer, 1937, p. 295). She stated that the holotype of *expansa* (Fig. 9.11, 9.12) "has longitudinal nodes and fine, spiral lines on the apical whorls" (Palmer, 1937, p. 295). This is true, but these nodes are not the same as the longer longitudinal ribs present in other specimens, which are herein assigned to *Anbullina elliptica* (Whitfield, 1865) (see below). The holotype of *Ancillaria expansa* Aldrich (Fig. 9.11, 9.12), furthermore, has a very different overall shell shape compared to specimens assigned here to *Ancillopsis altilis*. The former has a very prominent and sharp rear edge of the anterior band, and no olivoid band. The widest part of the body whorl is just beneath the spire, rather than adjacent to the aperture. It is clearly not *Ancillaria* (see discussion below), and is more similar to *Pseudoliva*, except that it does not have the "pseudolivid groove" (see Vermeij, 1998), and may belong in the family Pseudolividae.

Ancillopsis patula (Deshayes, 1835)
Figures 8.22, 8.23, 9.15

non 1758 *Buccinum patulum* Linnaeus, 1758 (see Pacaud and Cazes, 2014, p. 17).
1835 *Buccinum patulum*; Deshayes, p. 646, pl. 88, figs. 5, 6.
1844 *Buccinum patulum*; Deshayes and Milne Edwards, p. 211, n. 10.
1850 *Buccinanops palulum* [sic]; d'Orbigny, p. 420, n. 1556.
1850 *Pseudoliva ovalis* Sowerby, p. 106, pl. 7, fig. 13.
1854 *Pseudoliva ovalis*; Morris, p. 274.
1854 *Pseudoliva ovalis*; Edwards, p. 451.
1855 *Buccinum patulum*; Pictet, p. 44, pl. 67, fig. 4.
1865 *Buccinum patulum*; Deshayes, p. 495, n. 2.
1871 *Pseudoliva ovalis*; Briart and Cornet, p. 40.
1889 *Ancillaria cossmanni* Mayer-Eymar, p. 324, n. 88, pl. 14, fig. 1.
1889 *Buccinanops* (*Bullia*) *palulum* [sic]; Cossmann, p. 134.
1890 *Ancilla cossmanni*; de Gregorio, p. 56.
1891 *Pseudoliva ovalis*; Newton, p. 167.
1893 *Buccinanops* (*Bullia*) *palulum* [sic]; Cossmann, p. 33.
1900 *Buccinum* (*Buccinanops*) *palulum* [sic]; Dollfus, p. 135.
1901a *Buccinanops* (*Brachysphingus*) *patulum*; Cossmann, p. 48.
1901b *Buccinanops* (*Brachysphingus*) *palulum* [sic]; Cossmann, p. 222.
1901b *Buccinanops patulum*; Cossmann, p. 222.
1911 *Buccinanops* (*Brachysphingus*) *palulum* [sic]; Cossmann and Pissarro, pl. 36, fig. 175-1.
1937 *Bullia patula*; Palmer, p. 289.
1945 *Ancillopsis patula*; Gardner, p. 199.
1963 *Bullia patula*; Glibert, p. 98.
1990 "*Ancillopsis*" *patula*; Allmon, p. 86, pl. 9, fig. 12.
1995 *Bullia patula*; Le Renard and Pacaud, p. 114.
1995 *Bullia patula*; Pacaud and Le Renard, p. 167.
1996 *Ancillopsis patula*; Tracey et al., p. 120.
1997 *Ancillopsis patula*; Squires, p. 850.
2014 *Bullia patula*; Pacaud and Cazes, p. 17, text-fig. 1, pl. 1, figs. 1–3; pl. 2, figs. 1–9.

Type material.—Lectotype UCBL EM30549.

Occurrence.—France: upper Eocene (Auversian); UK: upper Eocene, Bracklesham Beds, Selsey Formation (Loc. UK-WS-1).

Revised description.—The shell is medium in size, oval, plump, with rounded curve at the back, dorso-ventrally depressed, with thick test. The spiral is short, pointed, composed of 3–4 very narrow whorls, separated by simple sutures and disturbed by the increments (disrupted by growth lines?). The whole of the teleoconch is devoid of sculpture; we observe only strong and numerous streaks of weakly opisthocyrtic growth lines, strongly sinuous in the peri-sutural adapical region, intersected by very fine barely visible spiral streaks. The body whorl, very large, constituting by itself almost the entire total height, shows a particularly convex profile; it ends without a neck, by a broad, clearly delimited fasciole. The body whorl presents in the abapical region above the fasciole, a wide band, slightly depressed, inducing a wide furrow on the edge of the labrum corresponding to the deviation of the streaks of growth. This band is separated from the fasciole by a space equal in width to the abapical band. The opening is large, ovoid, dilated, broad in front, narrow in the back, and terminated by a short and narrow anal canal. The columella, clearly excavated over the entire height, ends in an acute point; the columella also is cut by a wide and deep siphonal notch. The parietal and columellar calluses are thick, very widely spread laterally. The labrum is thin, smooth on the inside, slightly prosocline (translation of Pacaud and Cazes, 2014, p. 17–18).

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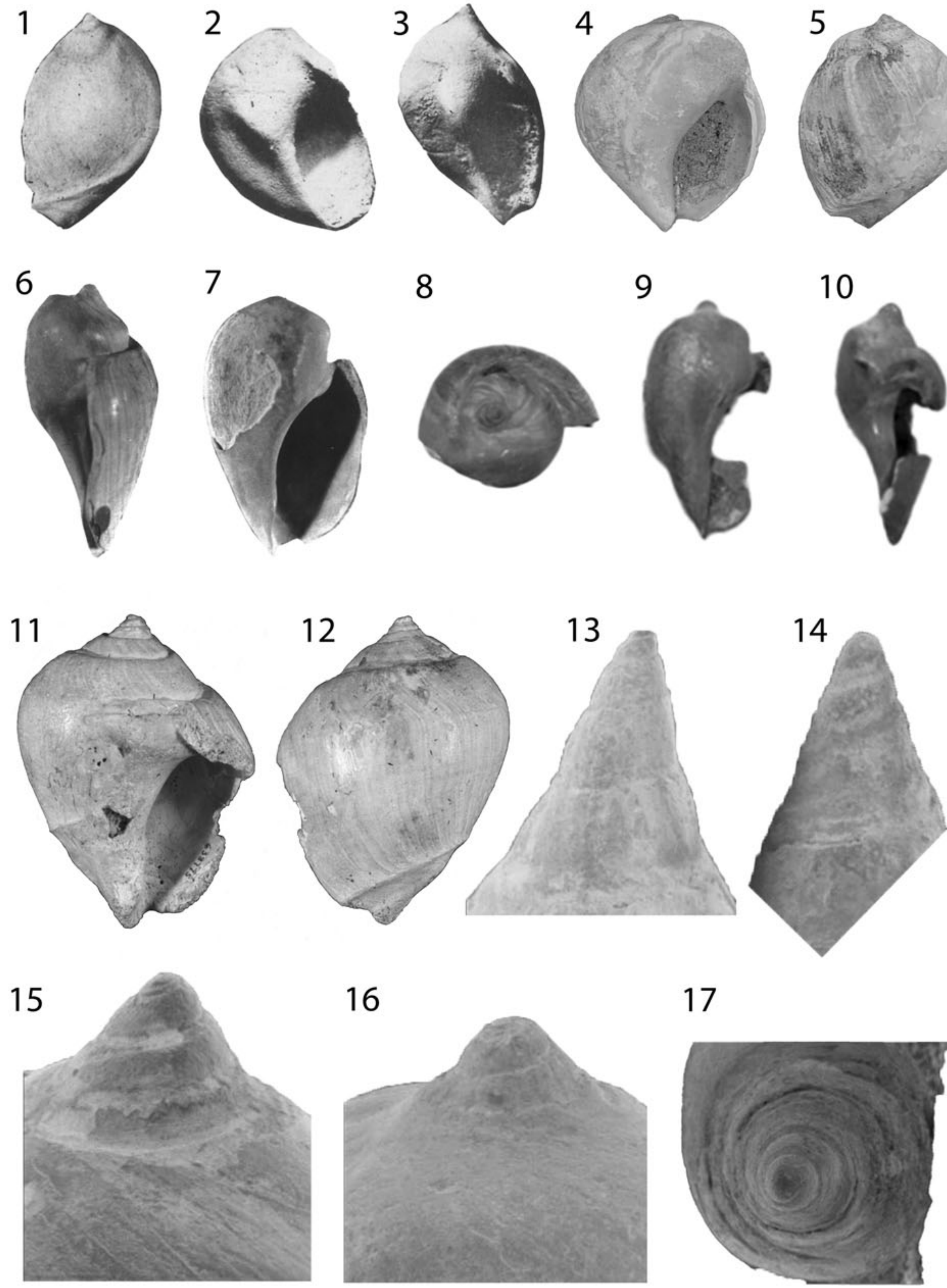

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Figure 9. *Ancillopsis altilis* (continued) and *Ancillaria expansa*. (**1–10, 13, 14, 16, 17**) *Ancillopsis altilis*: (**1**) *Bullia altilis harrisi* holotype PRI 360; height 15.3 mm. (**2**) *Bullia altilis harrisi* paratype PRI 356; height 16.8 mm. (**3**) *Bullia altilis harrisi* paratype PRI 357; height 20 mm. (**4, 5**) *Ancillopsis altilis* from Hatchetigbee Bluff, Alabama (Loc. AL-WA-1) PRI 104694; height 27.2 mm. (**6–8**) *Ancillopsis tuomeyi* holotype GSA-I17344; height 28 mm. (**9, 10**) *Ancillopsis tuomeyi* cotype GSA-I17579; height 23.2 mm. (**11, 12**) *Ancillaria expansa* holotype USNM 638775; height 51.4 mm. (**13**) Scanning electron micrograph of shell apex, *Bullia altilis* (juvenile) hypotype PRI 3039; height 27.0 mm. (**14, 17**) Scanning electron micrographs of shell apex, *Ancillopsis altilis* (juvenile) PRI 4659. (**15**) Scanning electron micrograph of shell apex, *Ancillopsis patula* PRI 83935. (**16**) Scanning electron micrograph of shell apex, *Ancillopsis altilis* PRI 83944.

Other material examined.—PRI 83935 (1 specimen) (Loc. FR-1).

Remarks.—As noted by Palmer (1937, p. 289), Allmon (1990, p. 86), and Squires (1997), *Ancillopsis patula* is almost identical to *Ancillopsis altilis* from the U.S. Gulf Coast in its subspherical but dorsoventrally flattened shape, minute spire, inflated, unsculptured body whorl, large aperture, expanded callus, and lack of terminal columellar fold; and in our morphometric analysis, it falls among Coastal Plain specimens (Fig. 12). It differs in being smaller than specimens of *A. altilis* of similar geological age and having a shinier shell (which might be partly an artifact of preservation). The most significant difference between the two species may be their pattern of remnant color on the body whorl; *A. patula* shows an olivoid band that appears purplish under UV light, whereas *A. altilis* does not (Pacaud and Cazes, 2014, p. 21).

As noted by Pacaud and Cazes (2014, p. 16), the species also exists in the Bartonian in England where it had been erroneously assigned to the genus *Pseudoliva* and described as *Pseudoliva ovalis* (Briart and Cornet, 1871; Newton, 1891). As the only representative of this clade outside of the Gulf Coast, this species has interesting paleobiogeographic implications.

Pacaud and Cazes (2014) argued that *patula* should be retained in *Bullia* in Nassariidae. Neither *patula* nor *altilis*, however, have terminal columellar folds, which are characteristic of all modern members of Nassariidae (Allmon, 1990; see Fig. 7).

Genus *Anbullina* Palmer, 1937

Type species.—*Ancillaria ancillops* Heilprin, 1891, by original designation (Palmer, 1937, p. 292).

Diagnosis.—Shell oval to lanceolate; spire low but acute. First three or four teleoconch whorls longitudinally ribbed, ribs becoming obsolete on later whorls of spire and body whorl. Spire and body whorls frequently slightly shouldered. Body whorl bears narrow band below suture, which bears sigmoidal growth lines of growth. Plication plate and anterior band faint to pronounced. Parietal callus extends less than halfway across ventral surface of body whorl, and only slightly posterior of aperture. Olivoid band present but faint. Anterior notch moderate to deep.

Remarks.—Palmer (1937) named *Anbullina* for the distinctive species *Ancillaria ancillops* Heilprin, 1891. This species was allied with the *Bullia* group in Nassariidae by Cossmann (1901b), who placed it in the genus *Buccinanops*, and Palmer proposed *Anbullina* as a subgenus within *Bullia* Gray, 1834. Its similarities to these genera of Nassariidae, however, consist of little more than overall shape (Allmon, 1990, p. 59). On the other hand, it shares with other ancillariids an (albeit very faint) olivoid band and (well-developed) anterior band. It therefore seems more likely assignable to the ancillariids, but does not agree with any other genus in that family. Recognition of a second species, *Anbullina elliptica* (Whitfield, 1865), further justifies continued recognition of a separate genus-level taxon.

Anbullina ancillops (Heilprin, 1891)
Figure 15.1, 15.2

	1891	*Ancillaria ancillops* Heilprin, p. 398, pl. 11, fig. 4.
	1901b	*Buccinanops* (*Bullia*) *ancillopsis* [sic]; Cossmann, p. 223, pl. 9, fig. 24.
non	1901b	*Anaulax ancillopsis*; Cossmann, p. 223.
	1937	*Bullia* (*Anbullina*) *ancillops*; Palmer, p. 292, pl. 40, figs. 4, 6.
	1943	*Bullia* (*Anbullina*) *ancillops*; Wenz, p. 1226, fig. 3488 [copied Palmer, 1937, pl. 40, fig. 6].
	1980	*Bullia* cf. *B.* (*Anbullina*) *ancillops* [misspelled in plate caption as "*Bucilla* cf. (*Anbullina*) *Ancillops*"]; Dockery, p. 110, pl. 17, fig. 4.
	1990	"*Bullia*" (*Anbullina*) *ancillops*; Allmon, p. 59, pl. 9, fig. 4.

Type material.—Holotype lost (fide Palmer, 1937, p. 293); hypotype (Palmer, 1937) PRI 3045.

Occurrence.—Texas: middle Eocene, Weches Formation (Loc TX-BA-1).

Revised description.—Shell lanceolate; spire low but acute. Protoconch of 1.5 whorls, smooth, rounded; first protoconch whorl flatly convex; first three or four teleoconch whorls longitudinally ribbed, the ribs becoming obsolete on the later whorls of the spire and the body whorl, which are smooth. Body whorl with narrow band below suture, which bears sigmoidal growth lines. Plication plate with sharp rear edge forming slight false umbilicus and square anterior edge; anterior notch deep.

Other material examined.—PRI 57311 (1 specimen).

Remarks.—*Anbullina ancillops* is known only from one locality, the now-inaccessible Smithville outcrop of the Weches Formation in Texas (Loc. TX-BA-1). Dockery (1980, p. 110, pl. 17, fig. 4) figured a poorly preserved specimen from the Doby's Bluff Tongue (see Fig. 3) in Mississippi and assigned it to "*Bullia* cf. *B.* (*Anbullina*) *ancillops*." This specimen (see Figure 15.11), however, has a relatively longer and wider aperture than the type of *ancillops*, the spire appears to be partially covered with parietal callus, and it

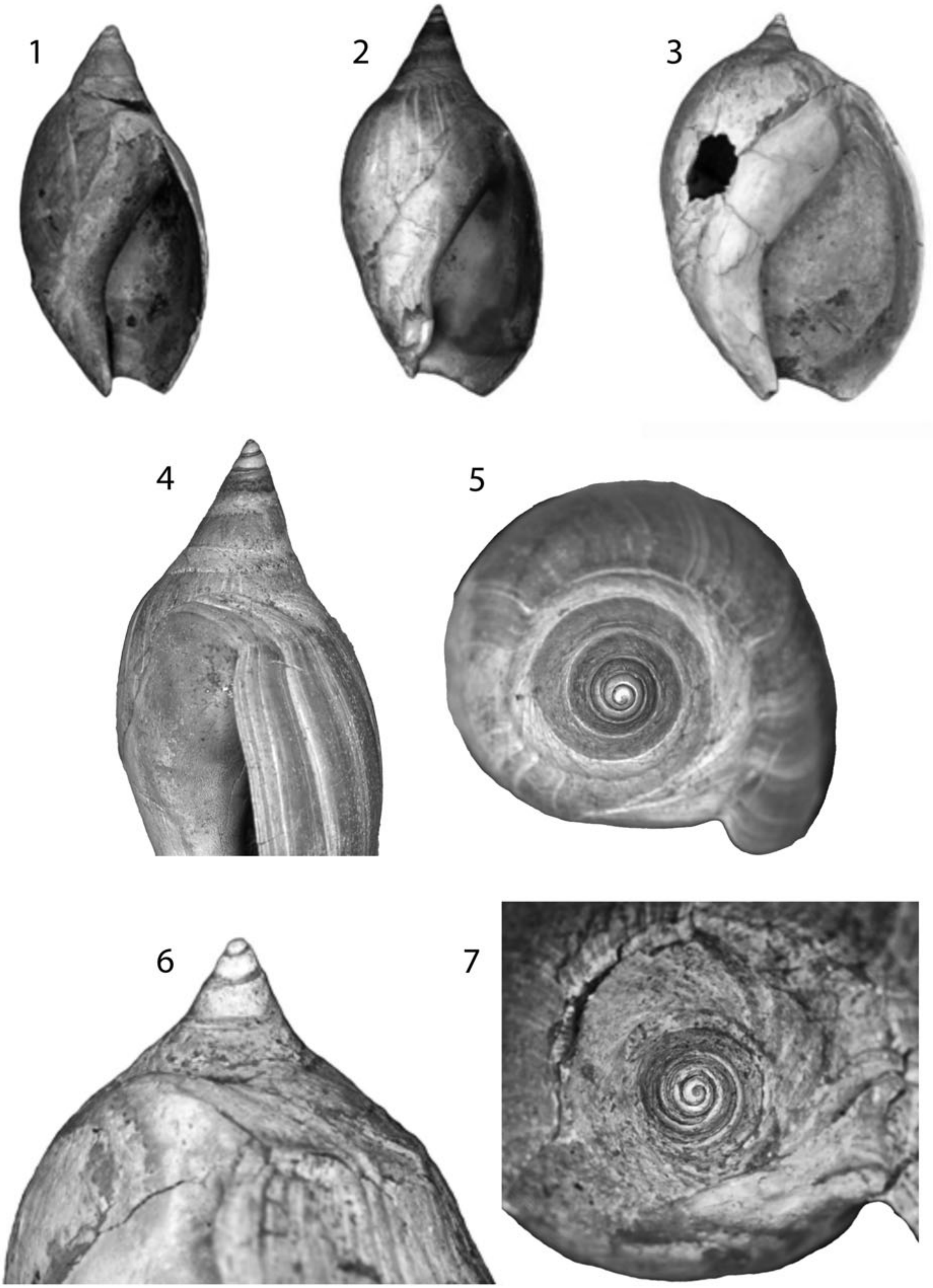

Figure 10. *Ancillopsis altilis* (continued), Moodys Branch Formation, Mississippi (Loc. MS-YA-1). (**1**) MGS 2103 Height 25.0 mm. (**2, 4, 5**) MGS 2104 Height 29.0 mm. (**3, 6, 7**) MGS 2386 Height 36.0 mm. Photos provided by David Dockery.

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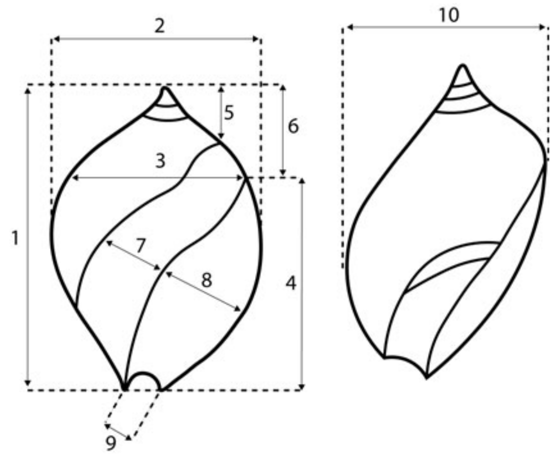

Figure 11. Measurements taken on specimens of *Ancillopsis altilis* for morphometric analysis. 1. Maximum height. 2. Maximum width in apertural view. 3. Width at posterior end of aperture. 4. Aperture length. 5. Height from posteriormost point of parietal callus. 6. Maximum height minus aperture length. 7. Maximum width of callus on ventral side. 8. Maximum width of aperture. 9. Width of anterior canal. 10. Maximum width from left side.

lacks the distinctive anterior end of the columella. It somewhat resembles modern and fossil species of *Baryspira* from New Zealand (see Beu et al., 1990), and resembles no other form in the Coastal Plain. No other similar specimens have been found in the Doby's Bluff (Dockery, personal communication, November 2, 2021). It may represent yet another otherwise unrecorded ancillariid lineage in the region.

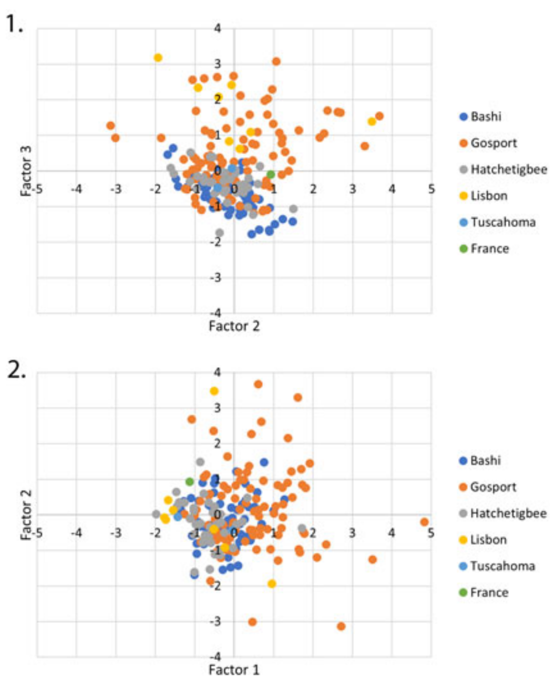

Figure 12. Results of factor analysis of morphometric data (Fig. 11; formations as indicated in Fig. 2; see Supplement 2 for data) from 211 specimens of *Ancillopsis altilis*. (**1**) Plot of scores on Factor 2 vs. Factor 3. (**2**) Plot of scores on Factor 1 vs. Factor 2.

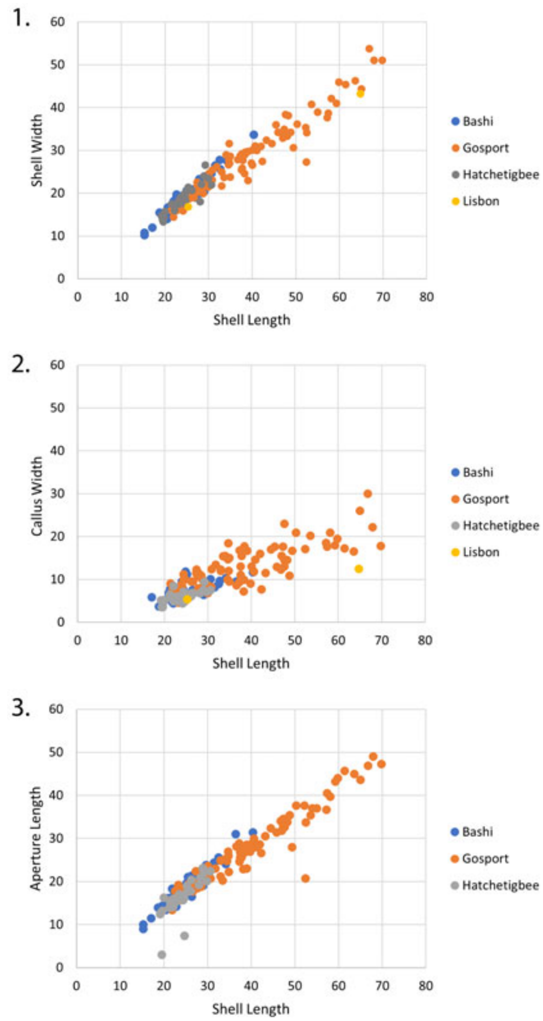

Figure 13. Anagenetic change in *Ancillopsis altilis* through time (formations as indicated in Fig. 2). (**1**) Shell height vs. shell width; (**2**) shell height vs. callus width; (**3**) shell height vs. aperture length. Measurements are in mm. See text for further discussion.

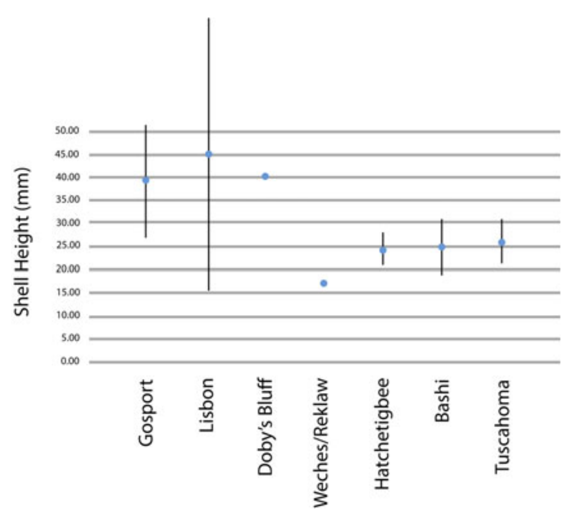

Figure 14. Height of *Ancillopsis altilis* through time (mean and +/− one standard deviation). Formations as indicated in Figure 2.

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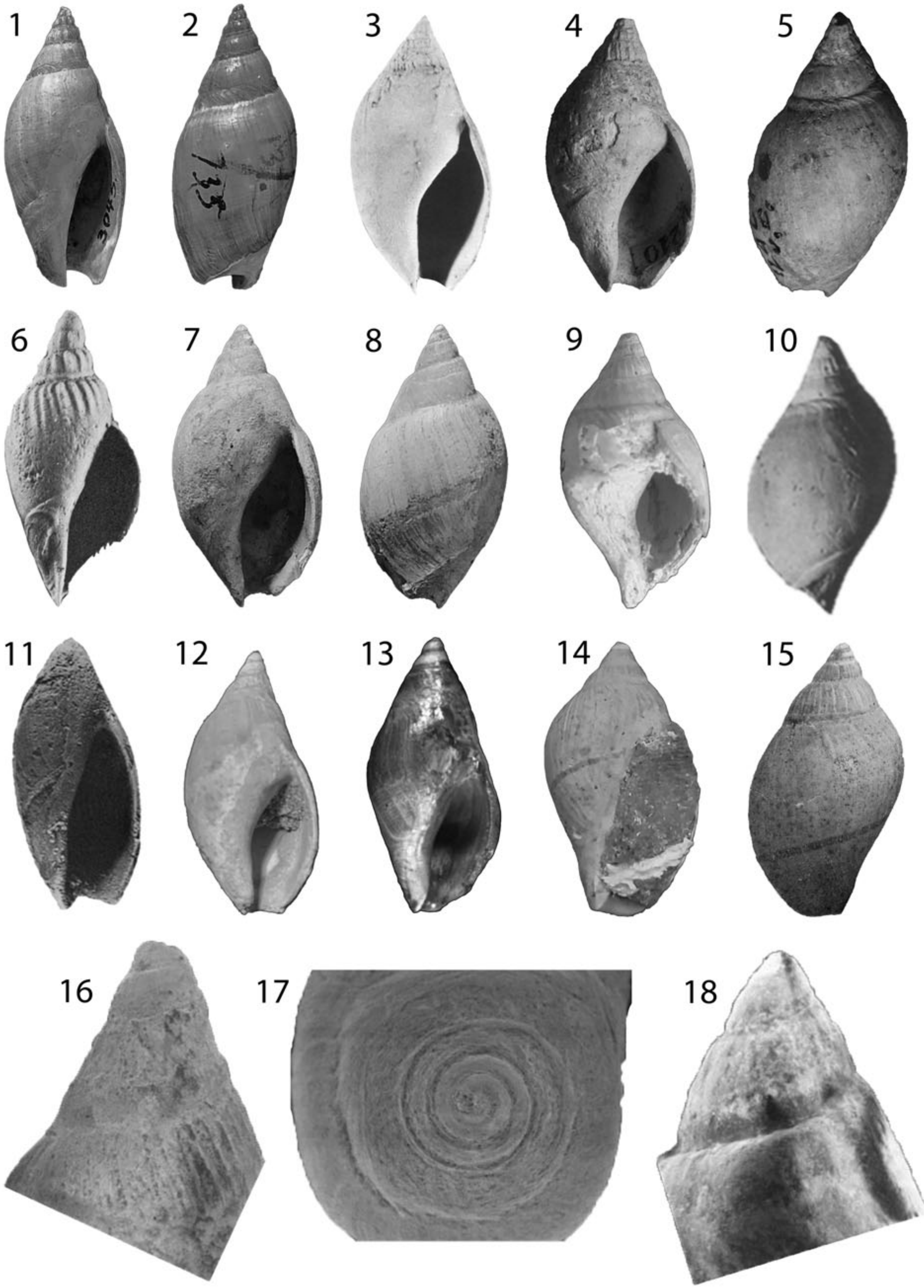

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Figure 15. *Anbullina*. (**1, 2**) *Anbullina ancillops*: *Bullia* (*Anbullina*) *ancillops* hypotype PRI 3045; height 28.8 mm. (**3–10, 12, 16–18**) *Anbullina elliptica*: (**3**) *Anbullina elliptica* (*Buccinanops ellipticum* hypotype [Barry and LeBlanc, 1942] LSU 6023; height 27.5 mm). (**4, 5**) *Pseudoliva elliptica*, holotype FMNH-UC 24670; height 17 mm. (**6**) *Bullia* sp. (from Dockery, 1980, pl. 37, fig. 7), MGS 523; height 11 mm. (**7, 8, 18**) "*Buccinanops*" *ellipticum reklawensis* holotype PRI 30410; height 23.5 mm); (**18**) scanning electron micrograph of shell apex. (**9, 10**) *Anbullina elliptica* (*Lisbonia expansa* hypotype [Palmer, 1937] PRI 3046; height 25 mm). (**11**) *Bucilla* [sic] cf. *B*. (*Anbullina*) *ancillops* (from Dockery, 1980, pl. 17, fig. 4), MGS 110; height 20.7 mm. (**12, 16, 17**) *Anbullina elliptica,* specimen from Bells Landing, AL (Loc. AL-MO-3), PRI 83937; height 18.4 mm; (**16, 17**) scanning electron micrographs of shell apex. (**13**) *Anbullina elliptica*? (*Pseudoliva ostrarupis pauper* holotype NPL 35590); height 18 mm. (**14, 15**) *Anbullina elliptica*? (*Lisbonia pauper* NPL 37825); height 13.2 mm.

Anbullina elliptica (Whitfield, 1865)
Figure 15.3–15.10, 15.12, 15.16–15.18

	1865	*Pseudoliva elliptica* Whitfield, p. 260.
	1886	*Pseudoliva elliptica*; Aldrich, p. 56.
	1887	*Pseudoliva elliptica*; Aldrich, p. 80 [not "1897" as in Harris, 1899a, and Barry and LeBlanc, 1942].
non	1895a	*Pseudoliva ostrarupis pauper* Harris, p. 76, pl. 8, fig. 4.
	1896	*Pseudoliva ostrarupis pauper*; Harris, p. 99, pl. 9, fig. 20.
	1899a	*Buccinanops ellipticum*; Harris, p. 30, pl. 3, figs. 14, 15.
	1899b	*Buccinanops ellipticum*; Harris, p. 305, pl. 54, figs. 4, 5.
	1923	*Pseudoliva ostrarupis pauper*; Trowbridge, p. 96.
	1933	*Pseudoliva ostrarupis pauper*; Plummer, p. 581.
	1935	*Pseudoliva ostrarupis pauper*; Gardner, p. 317.
	1937	*Lisbonia expansa* (Aldrich) [in part]; Palmer, p. 295, pl. 40, figs. 8, 12, 13.
	1942	*Buccinanops ellipticum*; Barry and LeBlanc, p. 117, pl. 15, figs. 1, 2.
	1945	*Pseudoliva elliptica*; Gardner, p. 195, pl. 27, figs. 3, 4.
	1945	*Pseudoliva ostrarupis pauper*; Gardner, p. 195.
	1960	*Buccinanops ellipticum*; Brann and Kent, p. 134.
	1966	*Buccinanops ellipticum*; Palmer and Brann, p. 533.
	1990	"*Buccinanops*" *ellipticum*; Allmon, p. 59, pl. 9, fig. 8.
	1996	"*Buccinanops*" *ellipticum reklawensis* Garvie, p. 74, pl. 15, figs. 14, 15.
	?2013	*Lisbonia pauper*; Garvie, p. 4, pl. 7, figs. 14, 15.

Type material.—Holotype FMNH-UC 24670; hypotype (Barry and LeBlanc, 1942) LSU 6023; holotype "*Buccinanops*" *ellipticum reklawensis*, PRI 30410; holotype *Pseudoliva ostrarupis pauper* TMM BEG 35590; hypotypes (Garvie, 2013) TMM NPL 37825, 37826.

Occurrence.—Texas: upper Paleocene (Selandian), Solomon Creek Member, Seguin Formation (Loc.TX-BA-2), upper Paleocene (Thanetian), Pendleton Formation (Loc. TX-SA-1), lower Eocene (Ypresian), Reklaw Formation (Loc. TX-MI-1); Louisiana: upper Paleocene (Selandian), Marthaville Formation (Locs. LA-NA-1, LA-SA-1, LA-SA-2); Alabama: upper Paleocene (Thanetian), Bells Landing Marl (Loc. AL-MO-3); middle Eocene (Lutetian–Bartonian), Lisbon Formation (Loc. AL-MO-5); Mississippi: upper Eocene (Bartonian–Priabonian), Moodys Branch Formation (Loc. MS-NE-1).

Revised description.—Shell medium sized, lanceolate to elliptical in shape, with an evenly curved profile attenuated at both apical and anterior ends. Protoconch incompletely known, but probably of 2–3 smooth whorls. Spire relatively low, comprising not more than one-fourth the total height, while the aperture comprises more than one-half the total height. Spire usually bears numerous faint straight axial ribs on early teleoconch whorls. Sculpture on body whorl lacking, other than growth lines. Olivoid band faint to pronounced. In the holotype, this band takes the form of an adapertural angular deflection of the growth lines, forming shallow chevrons. Specimens from the Moodys Branch Formation of Mississippi show a single shallow groove 1–2 mm wide. Body whorl may show minor shouldering beneath spire or be smoothly tapered. Posterior margin of parietal callus usually even with posterior end of aperture, rarely extending to spire. Anterior notch deep.

Other material examined.—PRI 83936 (3 specimens); PRI 83937 (1 specimen).

Remarks.—Whitfield (1865) stated that his type specimen (Fig. 15.4, 15.5) came from Vicksburg, Mississippi, but Aldrich (1887, p. 80; see Palmer and Brann, 1966, p. 533) argued that it likely came from the Bells Landing Marl Member of the Tuscahoma Formation in Alabama (AL-MO-3) (see Fig. 2), where other very similar specimens have been found (see Fig. 15.12). This variable species includes specimens that have been placed in a variety of taxa, including those identified by Palmer (1937) as juveniles of her *Lisbonia expansa* (see above, under *Ancillopsis altilis*).

Adults of *Anbullina elliptica* are similar to juveniles of *Ancillopsis altilis* (compare Figs. 8.14, 8.21, 10.1, 10.2 with 15.1–10, 15.12). Our phylogenetic analysis shows that the two species are closely related (Fig. 5).

Price and Palmer (1928, p. 23) listed but did not figure "*Bullia* sp. aff. *ellipticum* Whitefield" (sic) from Smithville, TX (Loc. TX-BA-1). Garvie (2013, p. 44–45) placed *Pseudoliva ostrarupis pauper* in the genus *Lisbonia*, arguing (based on material he said was in his collection but did not figure) that the genus is valid (see discussion of *Lisbonia* above under *Ancillopsis altilis*). The hypotype of *Lisbonia pauper* (NPL 37825) figured by Garvie (2013) shows axial ribs on the early teleoconch whorls, and may belong here, but the holotype of *Pseudoliva ostrarupis pauper* Harris, 1895a (NPL 35590; Fig. 15.13) lacks axial ribs, and may belong to *Pseudoliva*.

Genus *Eoancilla* Stephenson, 1941

Type species.—*Eoancilla acutula* Stephenson, 1941, by original designation.

Diagnosis.—From Garvie's (2013, p. 59) diagnosis: "Shell with high, smooth, evenly tapering spire; protoconch smooth, blunt, of 2 ¾ whorls; tip minute, partially immersed; callus band covering approximately lower 70% of spire whorls; columella strongly twisted; fasciolar band with 5–8 oblique narrow lirae, usually posterior ancillid band, and groove; anterior notch deep, internally thickened with callus; small low ridge of callus continuing posteriorly up inside of outer lip for ca. 1/3 of its height; small labral denticle present at end of line or kink in growth lines running from posterior end of aperture."

Remarks.—Stephenson described *Eoancilla* based on a Late Cretaceous species from Texas. As summarized by Garvie (2013, p. 59–60), Sohl (1964) synonymized *Eoancilla* with *Ancillus* Montfort, 1810, the type species of which is *A. buccinoides* Lamarck, 1803, from the Lutetian of the Paris Basin, "on the basis of the shared glazed whorls, the blunted apex, and apertural features." Garvie (2013, 2021) argued that *Eoancilla* was distinct from *Ancilla*. He also described two additional Paleocene species from Texas and Alabama, assigned the Paleocene species *Olivella mediavia* Harris, 1896, to *Eoancilla*, and said that he had "several specimens of *Eoancilla*, or a close relative thereof, from the middle Claibornian Weches Formation" (Garvie, 2013, p. 61), which he did not figure. He suggested that *Eoancilla* can "be taken as an ancestral Upper Cretaceous ancillid taxon that by Middle Eocene times had already spread to the Nangulaan Eocene of Java, because *A. songoensis* Martin, 1914… is remarkably close to *A. mediavia*" (Garvie, 2013, p. 61).

Eoancilla acutula Stephenson, 1941
Figure 16.1, 16.2

1941 *Eoancilla acutula* Stephenson, p. 361, pl. 69, figs. 8, 9.
1964 *Ancilla* (*Ancillus*) *acutula*; Sohl, p. 248, pl. 36, figs. 1–7, 10.

Type material.—Holotype USNM 77126; paratype USNM 77127; hypotypes (Sohl, 1964) USNM 130465–130467.

Occurrence.—Texas: Upper Cretaceous (Maastrictian), Kemp Clay (Loc. TX-TR-1); Mississippi: Upper Cretaceous (Maastrictian), Owl Creek Formation (Locs. MS-TI-1, MS-TI-2); Tennessee: Upper Cretaceous (Maastrictian), Clayton Formation (Owl Creek Formation reworked into base) (Loc. TN-HA-1).

Original description.—(Stephenson, 1941, p. 361) "Shell small, polished, with maximum inflation at about the midheight, from which region the surface slopes gently toward each extremity. Protoconch small smooth, trochoid, coiled about twice. Whorls four. Spire acute and a little less than half the total height of the shell; spiral angle about 45 degrees at the tip decreasing to about 40 degrees on the whorls below. Sides of whorls of spire nearly flat; the lower 7/10 of the surface of the penultimate whorl is covered with a smooth, nontumid, closely appressed band of callus, which is separated from the upper edge of the body whorl by a fine, sharp, slightly incised, but not canaliculate, suture; the upper edge of the band is gently undulating, but the band extends with about the same proportional width all the way back to the protoconch. The main surface of the shell is smooth, except for growth lines and an exceedingly faint indication of fine spiral lines, and one fine spiral groove at about the position of the periphery. The growth lines cross the body whorl in a gently sinuous trend, bending sharply backward before they join the suture above, and more gently backward near their junction with a sharply incised groove on the base below. The aperture is lenticular with a narrow, sharply upturned, posterior canal, and widens anteriorly to a short, wide, deeply notched, siphonal canal. Outer lip broadly arcuate and notched at the suture above; inner lip broadly excavated and forming on the parietal wall a band of callus which spreads forward a little and extends upward, becoming thicker in front of the posterior canal; this callus spreads upward across about 7/10 of the surface of the penultimate whorl and is continued backward forming the band of callus on that whorl already described. The columella is flattened anteriorly and is ornamented with a band of 7 or 8 closely spaced, small, narrow oblique ridges which continue forward on the sharply twisted anterior fasciole to the terminus of the shell. The anterior fasciole is bordered on the outer side by a deep, wide, round-bottomed spiral sulcus which is traceable backward until it is covered by the callus of the lip; the anterior edge of the callus of the inner lip follows down the bottom of the sulcus to the terminus of the shell; the sulcus is bordered in front on the base of the shell by a wide, smooth band which is limited both above and below by narrow sharply incised grooves."

Remarks.—This is the only Cretaceous species treated here and may be among the oldest known species of Ancillariidae.

Eoancilla hordea Garvie, 2013
Figure 16.8, 16.9

2013 *Eoancilla hordea* Garvie, p. 61, pl. 11, figs. 6, 7.

Type material.—Holotype TMM NPL 37709; paratype TMM NPL 37710.

Occurrence.—Texas: upper Paleocene (Selandian), Seguin Formation (Loc. TX-BA-2).

Original description.—(Garvie, 2013, p. 60) "Shell small, subcylindrical, smoothly rounded, barely contracted at suture; protoconch of ca. 2 whorls; tip somewhat oblique, partially immersed, with no demarcation transition to teleoconch whorls; suture defined by impressed line; spire whorls mostly covered with enamel-callus band; aperture slightly larger than ½ shell Height; columella spirally twisted; fasciolar band with 6 oblique narrow lirae; ancillid band wide; groove prominent; anterior notch deep, internally thickened with callus; thin line of callus continuing posteriorly up inside of outer lip; labral denticle small."

Remarks.—This species is known from 23 specimens from the type locality (Garvie, 2013, p. 61).

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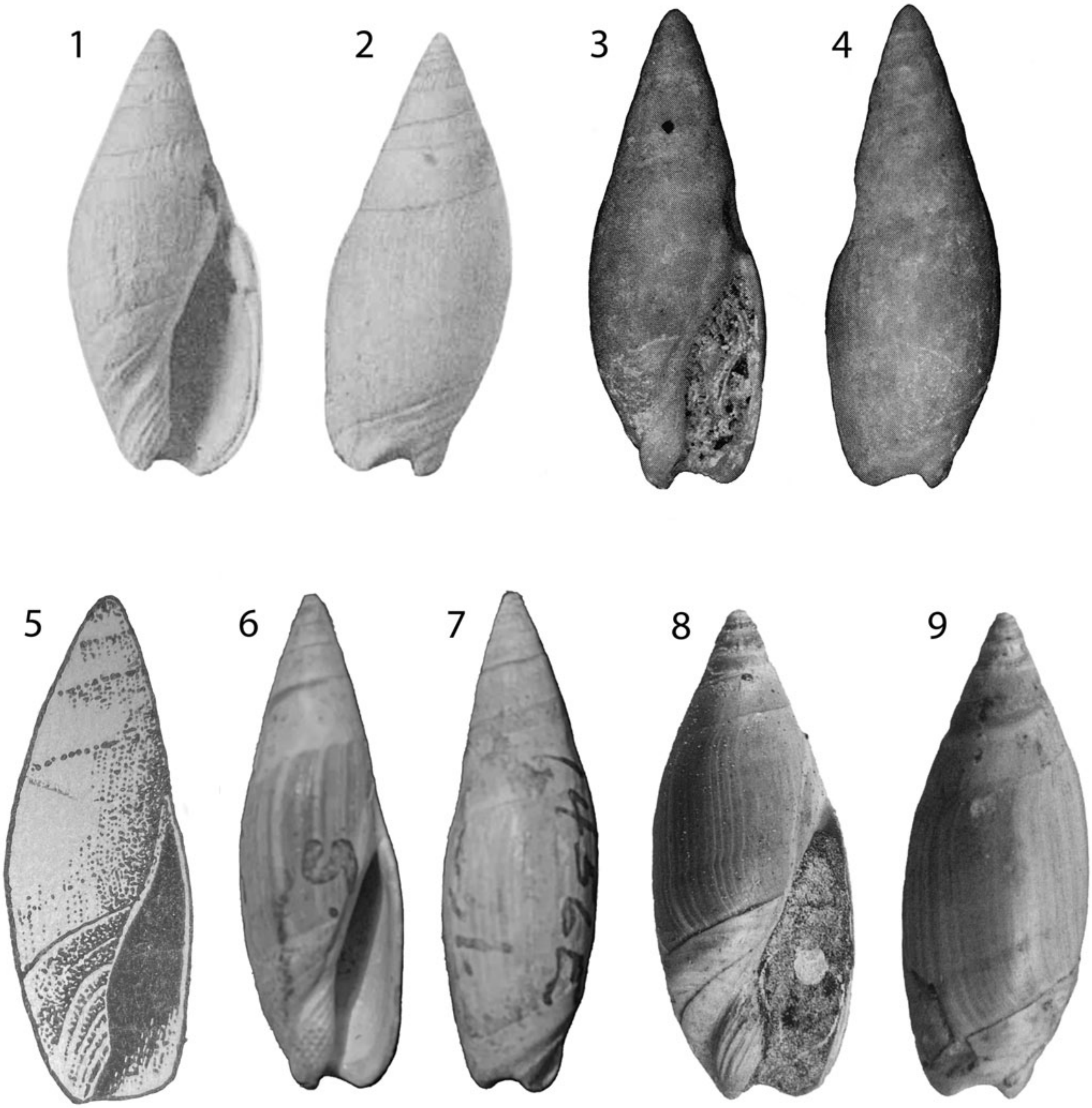

Figure 16. *Eoancilla.* (**1, 2**) *Eoancilla acutula* holotype USNM 77126 (from Stephenson, 1941); height 9.3 mm. (**3, 4**) *Eoancilla lapicidina* holotype NPL 93694 (from Garvie, 2021); height 11.1 mm. (**5**) *Eoancilla mediavia* (*Olivella mediavia*, drawing from Harris, 1896, of specimen in USNM). (**6, 7**) *Eoancilla mediavia* PRI 57647; height 17.4 mm. (**8, 9**) *Eoancilla hordea* holotype NPL 37709 (from Garvie, 2013); height 11.5 mm.

Eoancilla lapicidina Garvie, 2021
Figure 16.3, 16.4

2021 *Eoancilla lapicidina* Garvie, p. 138, pl. 14, figs. 11, 12.

Type material.—Holotype TMM NPL 93694; paratype TMM NPL 93695.

Occurrence.—Texas: lower Paleocene (Danian), Kincaid Formation (Loc. TX-FA-1).

Original description.—(Garvie, 2021, p. 139) “Shell small to medium sized, whorls feebly concave on upper half, feebly convex below; whorls covered with a light coating of callus; columella not or only weakly twisted, with 7 spiral ridges margined by a deep

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sulcus, sulcus forming the anterior part of the lower anterior band, upper anterior band well defined and posteriorly margined by a minute, impressed line, line only visible near the aperture, rapidly becoming obsolete adaperturally; olivid groove and band not visible; secondary callus thick where margining the upper part of the aperture, rapidly thinning and becoming the convex part of the spire, although not easily differentiated; protoconch of 2 whorls, somewhat flattened, and set at a slight angle to the shell axis."

Remarks.—This species is known from 18 specimens from the type locality (Garvie, 2021, p. 139).

Eoancilla mediavia (Harris, 1896)
Figure 16.5–16.7

	1896	*Olivella mediavia* Harris, p. 80, pl. 7, fig. 19.
non	1897	*Olivella mediavia*; Harris, p. 29, pl. 3, fig. 12 (fide Palmer and Brann, 1966, p. 486).
	1899	*Ancilla* (*Sparella*) *mediavia*; Cossmann, p. 62.
	1935	*Olivella mediavia*; Gardner, p. 230.
	1966	*Agaronia mediavia*; Palmer and Brann, p. 486.
	2021	*Eoancilla mediavia*; Garvie, p. 139.

Type material.—Holotype lost (fide Palmer and Brann, 1966, p. 487).

Occurrence.—Alabama: upper Paleocene (Selandian–Thanetian), Matthews Landing Marl, Bells Landing Marl (Locs. AL-MO-3, AL-SU-3, AL-WI-1, AL-WI-2).

Original description.—(Harris, 1896, p. 80) "…whorls about 7; the first extremely small, the second much larger, and the third still greater, producing a blunt appearance; remaining spiral whorls nearly or quite covered by the sutural callosity; body whorl smooth, but the direction of the lines of growth can be traced with a glass; growth lines slightly geniculated about three-fourths of the way from the suture to the anterior folds at a faint depression which produces a faint tooth on the margin of the outer lip; columella well twisted below where it is 7–8 striate; above on the columella there is often a large obtuse fold which marks a former position of the upper margin of the slit for the anterior canal."

Other material examined.—PRI 57647 (Bell's Landing, AL; Loc. AL-MO-3).

Remarks.—The type specimen was from Matthews Landing, AL (Loc. AL-WI-2). Gardner (1935, p. 230) said that this species "is widespread and fairly common" and Palmer and Brann (1966) listed it as coming from several other Alabama localities. Garvie (2013, p. 60–61) argued that its multispiral protoconch, callus that covers only a portion of the teleoconch whorls, and the lower inner lip callus support placing it in *Eoancilla*. Our phylogenetic analysis (see below) indicates that this species may be ancestral to *Olivula staminea* (Conrad, 1832).

Genus *Monoptygma* Lea, 1833

Type species.—*Monoptygma alabamiensis* Lea, 1833, by subsequent designation (Cossmann, 1899).

Remarks.—The name *Monoptygma* has a complicated history. It was first proposed by Isaac Lea (1833) for two fossil species from the Eocene of Alabama (*M. alabamiensis* and *M. elegans*), which do not especially resemble each other (Fig. 17.7, 17.8). G.B. Sowerby II (1839, p. 66) listed "*Monoptygma* Lea", but as including only "*M. elegans*," with a copy of Lea's illustration. Four lines later, he listed "*Monotigma* Gray" with no species name and referenced his figure 371, which shows a very different shell. According to van Aartsen and Hori (2006, p. 3), however, "there is no indication of involvement of Gray in Sowerby's Manual," and so "one has to consider Sowerby, 1839, as the author of *Monotigma*." Gray (1847, p. 140, 159), citing "J. Lea," distinguished "*Monop. alabamiensis*, J. Lea" and "?*Monoptygma* sp. Lea" from "*Monotigma* or *Monotygma*, G. Sowerby," the latter containing "*Mon. elegans*, Lea," and assigned the former to Pyramidellidae. Adams (1853, 1854), however, used *Monoptygma* for several modern species in Pyramidellidae. This was repeated by Smith (1872) and Mörch (1875). van Aartsen (1986) untangled these names, clarifying that *Monoptygma* Lea is a valid genus, and that *Monotygma* and *Monotigma* are both valid and distinct genera of pyramidellids.

Although some authors (e.g., Gabb, 1872) placed *Monoptygma* in Olividae, Palmer (1937, p. 296) allied it with *Bullia* in Nassariidae, writing that "[t]he columella is smooth as in *Bullia*." This was accepted by Glibert (1963). Cernohorsky (1984, p. 27) seemed to be agnostic about the placement in Nassariidae, writing that "*Monoptygma* lacks any characters which would suggest a relationship with the Dorsaninae" in Nassariidae.

Monoptygma (which means "single fold") is characterized by a single (very rarely double) fold or plication on the inner apertural lip. All species also show an olivoid band wrapping around the lower part of the body whorl. This combination of characters is unique and makes this taxon somewhat puzzling. Careful examination of all available specimens, however, indicates that the fold is continuous with the plication plate, and is therefore not homologous to the "columellar folds" of other taxa, such as species of Volutidae. We therefore conclude that it is assignable to Olividae.

The genus *Monoptygma* has been oversplit, and several species are represented by few or poorly known specimens. We synonymize all described forms into one somewhat variable species.

Monoptygma lymneoides (Conrad, 1833)
Figure 17.1–17.7, 17.9–17.18

1833	*Ancillaria lymneoides* Conrad, p. 44.
1833	*Monoptygma alabamiensis* Lea, p. 186, pl. 6, fig. 201.
1834b	*Ancillaria lymneoides*; Conrad, p. 5.
1835	*Ancillaria lymneoides*; Conrad, p. 42, pl. 16, fig. 6.
1849	*Ancillaria lymneoides*; Lea, p. 96.
1850	*Ancyllaria* [sic] *lymneoides*; d'Orbigny, p. 352.
1854	*Ancilla lymneoides*; Conrad, p. 30.
1860	*Monoptygma crassiplica* Conrad in Gabb, p. 384, pl. 67, fig. 37.
1865a	*Monoptygma crassiplica*; Conrad, p. 22.
1865a	*Monoptygma alabamiensis*; Conrad, p. 22.

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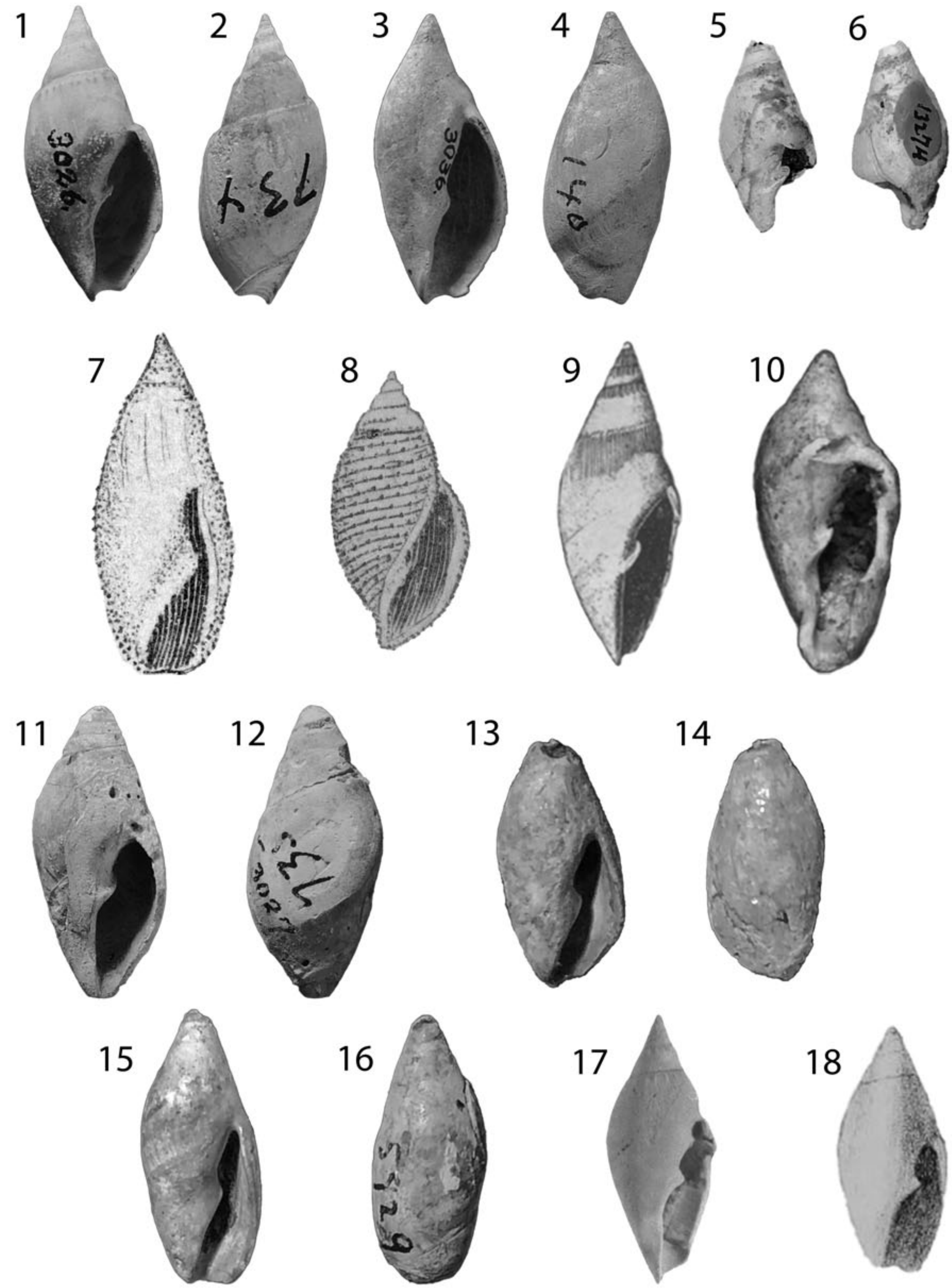

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Figure 17. *Monoptygma lymneoides*. (**1, 2**) *Monoptygma leai* PRI 3026; height 22 mm. (**3, 4**) *Monoptygma lymneoides* PRI 3036; height 35 mm. (**5, 6**) *Monoptygma crassiplica* ANSP 13274; height 17 mm. (**7**) *Monoptygma alabamiensis*, drawing from Lea (1833). (**8**) *Monoptygma elegans*, drawing from Lea (1833) (not *Monoptygma*). (**9**) *Monoptygma crassiplica*, drawing by G.D. Harris (from Palmer, 1937, pl. 38, fig. 4) of USNM specimen. (**10**) *Monoptygma curta* holotype ANSP 15618; height 11.6 mm. (**11, 12**) *Monoptygma crassiplica* hypotype PRI 3027; height 22.4 mm. (**13, 14**) *Monoptygma alabamiensis* paratype ANSP 5930; height 8.2 mm. (**15, 16**) *Monoptygma alabamiensis* holotype ANSP 5929; height 12 mm. (**17**) *Monoptygma leai* syntype FMNH 24671; height 19 mm. (**18**) *Monoptygma crassiplica,* drawing from Gabb (1860).

1865a *Monoptygma curta* Conrad, p. 22.
1865a *Monoptygma lymneoides*; Conrad, p. 23.
1865b *Monoptygma curta*; Conrad, p. 143, pl. 11, fig. 8.
1865 *Monoptigma* [sic] *leai* Whitfield, p. 261, pl. 27, fig. 7.
1866 *Monoptygma curta*; Conrad, p. 17.
1866 *Monoptygma lymneoides*; Conrad, p. 17.
1866 *Monoptygma curta*; Conrad, p. 17.
1866 *Monoptygma alabamiensis*; Conrad, p. 17.
1866 *Monoptygma crassiplica*; Conrad, p. 17.
1883 *Monoptygma lymneoides*; Tryon, p. 61, pl. 3, fig. 23.
1887 *Monoptygma leai*; Aldrich, p. 80.
1890 *Monoptygma alabamiensis*; de Gregorio, p. 58, pl. 4, fig. 10.
1890 *Ancilla* (*Monoptygma*) *curta;* de Gregorio, p. 58, pl. 4, fig. 11 [copied Conrad, 1865b, pl. 11, fig. 8].
1890 *Ancilla* (*Monoptygma*) *Alabamiensis*; de Gregorio, p. 58, pl. 4, fig. 10 [copied Lea, 1833, pl. 6, fig. 201].
1890 *Ancilla* (*Monoptygma*) *lymneoides*; de Gregorio, p. 58, pl. 4, fig. 14 [copied Conrad, 1835, pl. 16, fig. 6].
1890 *Monoptygma curta*; de Gregorio, p. 58, pl. 4, fig. 11.
1891 *Monoptygma crassiplica*; Heilprin, p. 398.
1893 *Monoptygma limneoides* [sic]; Cossmann, p. 41.
1895b *Monoptygma curta*; Harris, p. 14.
1895b *Ancillaria lymneoides*; Harris, p. 26.
1899 *Monoptygma curta*; Cossmann, p. 72.
1899 *Monoptygma limneoides* [sic]; Cossmann, p. 71, pl. 3, figs. 24, 25.
1937 *Monoptygma crassiplica*; Palmer, p. 298, pl. 38, figs. 3–5.
1937 *Monoptygma lymneoidies* [sic]; Palmer, p. 296, pl. 38, figs. 19, 20, pl. 85, figs. 3, 7.
1937 *Monoptygma curta*; Palmer, p. 298, pl. 85, fig. 8.
1937 *Monoptygma leai*; Palmer, p. 297, pl. 38, figs. 1, 2, 6, 8.
1943 *Monoptygma lymneoides*; Wenz, p. 1227, fig. 3492 [copied Palmer, 1937, pl. 38, fig. 19].
1945 *Monoptygma leai*; Gardner, p. 195, pl. 27, figs. 2, 5.
1960 *Monoptygma leai*; Brann and Kent, p. 567.
1966 *Monoptygma leai*; Palmer and Brann, p. 779.
1966 *Monoptygma curtum*; Palmer and Brann, p. 779.
1966 *Monoptygma crassiplicum*; Palmer and Brann, p. 778.
1990 *Monoptygma crassiplicum*; Allmon, p. 61.
1990 *Monoptygma curtum*; Allmon, p. 61.
1990 *Monoptygma leai*; Allmon, p. 60, pl. 9, fig. 9.
1990 *Monoptygma lymneoides*; Allmon, p. 60.

Type material.—Conrad (1832–1835) apparently did not designate a holotype for *M. lymneoides* (see Moore, 1962, p. 72); lectotype (ANSP 15619) selected by Palmer (1937, p. 297) with eight other specimens under the same number (all apparently lost; J. Sessa, personal communication, 11/12/21); holotype *M. alabamiensis* Lea, ANSP 5929; paratype ANSP 5930; hypotype (Palmer, 1937), PRI 3036; holotype *M. curta* ANSP 15618; syntypes *Monoptygma leai* FMNH-UC 24671 (5 specimens); hypotype (Palmer, 1937) PRI 3026; Conrad's holotype *Monoptygma crassiplica* probably lost (fide Palmer, 1937, p. 298; Moore, 1962, p. 51); hypotype (Palmer, 1937) PRI 3027.

Occurrence.—Alabama: middle Eocene (Lutetian–Bartonian), Upper Lisbon Formation, Gosport Sand (Locs. AL-MO-2a, AL-MO-5); Texas: middle Eocene (Ypresian–Luettian), Weches Formation, Stone City Beds (Loc. TX-BA-1, TX-RO-1); Louisiana: middle Eocene (Lutetian–Bartonian), Cook Mountain Formation (LA-BI-1, LA-OU-1).

Revised description.—Shell lanceolate in shape, with aperture equal to about two-thirds of shell height. Protoconch unknown. Body whorl profile usually grades smoothly into spire profile, but occasionally slightly shouldered. Single distinct columellar fold on the middle of the parietal lip. Spire slightly acuminate, with faint axial ribbing on adapical margins of the whorls. Spire sutures moderately callused. Parietal callus moderately developed, extending about one-half to one-third of the way across the body whorl and about halfway between posterior end of aperture and suture. Faint anterior band, consisting of slight deflection of the growth lines, on body whorl, sometimes with faint ridge on posterior edge. Anterior end of body whorl ends in a simple tapered point.

Other material examined.—PRI 56353 (7 specimens); MCZIP 29252 (1 specimen); MCZIP 29247 (1 specimen); ANSP 13274 (1 specimen); PRI 104504 (2 specimens); PRI 83948 (1 specimen); PRI 104514 (2 specimens).

Remarks.—Monoptygma lymneoides has been oversplit; the various named forms mostly do not overlap in time and grade into one another, forming a single variable lineage. *Monoptygma lymneoides* from the upper middle Eocene Gosport Sand is the largest form. *Monoptygma curta*, also from the Gosport, is known only from the holotype. Palmer (1937, p. 298) said that it "differs from the young of *M. lymneoides* in being broader and shorter" but also closely resembles some specimens of *M. leai* from the underlying Cook Mountain/Lisbon formations. Palmer (1937, p. 297) described *M. leai* as "beautiful and distinct," but it intergrades with specimens of *M. lymneoides* (compare Fig. 17.1–17.4). *Monoptygma crassiplica* occurs in the middle Eocene Weches and Stone City beds in Texas and the Cook Mountain Formation of Louisiana. It also intergrades with *M. lymneoides.* Palmer (1937, p. 298) mentioned that a specimen of *crassiplica* "in the U.S. Nat. Museum from Holstein's well, 5 miles southeast of Gibbsland, Bienville

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Parish, La. was drawn by G.D. Harris for his Texas Eocene MS" and published that figure as her pl. 38, fig. 4. We have not been able to locate Harris' specimen, and the drawing is reproduced here as Figure 17.19. The specimen ANSP 5929 (Figure 17.15, 17.16) was listed as the holotype of *Monoptygma alabamiensis* by Palmer (1937, p. 297). A query ("?") was added to this designation in Palmer and Brann (1966, p. 780). The specimen generally resembles Lea's figure (1833, pl. 6, fig. 201), but the apex may have been damaged.

As explained by Wheeler (1935, p. 103–105), Conrad (1833) was published on August 29, while Lea (1833) was published on December 2, therefore Conrad's name *lymneoides* has priority.

Genus *Olivula* Conrad, 1832

Type species.—*Ancillaria staminea* Conrad, 1832, by subsequent designation Cossmann (1899, p. 70).

Remarks.—Lamarck (1811) proposed the name *Ancillaria*, but it is generally synonymized with *Ancilla* Lamarck, 1799 (e.g., Kilburn, 1981, p. 358). In 1832, Conrad proposed the species *Ancillaria staminea* from the Claibornian Eocene of Alabama and said that it closely resembled *Ancillaria canalifera* (Lamarck, 1803), from the Eocene of France. But he then suggested (Conrad, 1832, p. 25) that "[t]hese two species do not correspond entirely with the genus *Ancillaria*, as the aperture is much longer, the shells are striated, and the suture is somewhat channeled;" he therefore stated that these two species "might constitute a separate genus by the name of *Olivula*." Cossmann (1899, p. 70) designated *A. staminea* Conrad as the type species of *Olivula*. Wenz (1943, p. 1277) and Glibert (1960, p. 19) also placed it there, as did Tracey et al. (1996) and Garvie (1996, p. 87), who made *Olivula* a subgenus of *Ancilla*. Meanwhile, as noted by Palmer (1937, p. 429), Bellardi (1882) had used *canalifera* as the type species of his genus *Ancillarina.* Palmer argued that *canalifera* and *staminea* differ enough to be separated at "sectional" (i.e., subgeneric) rank, and so retained *staminea* in *Olivula*, which she treated as a subgenus of *Ancilla*.

In his comprehensive review of the genus *Ancilla*, Kilburn (1981, p. 356) treated *Ancillarina* as a separate genus (possibly "a sister group" of *Olivula*) containing "*Ancilla*-like species with a similarly divided fasciolar band but a total lack of callus on the spire whorls and sutures," and represented by fossils from the Eocene of Java and possibly the Cretaceous of Burma.

Even though *canalifera* lacks the callused sutures characteristic of *staminea*, Garvie (2013, p. 60) assigned both *canalifera* and *staminea* to *Ancillarina*, suggesting that it be given subgeneric rank in *Olivula*. Garvie (2013, p. 60) also noted a change in the form of the suture callus or "collar band" over time in the three named subspecies of *staminea*, with *punctulifera* from the middle Eocene Claibornian and *maternae* from the lower Eocene showing "a steady decrease in the strength and sagittal angle of the [growth] lines" on the callus.

The marked callusing of the suture in *staminea* distinguishes it from *canalifera*, to which it is otherwise quite similar in overall shape, so we do not combine the two species in *Ancillarina*. It nevertheless seems useful to retain *Olivula* as a separate genus-level taxon, with a single, somewhat variable, species extending throughout much of the Gulf Coast Eocene.

The cancellate sculpture on the body whorl of *O. staminea* separates it from all other Coastal Plain olivoids. If, as implied by our phylogenetic analysis (Fig. 5), it is derived from *Eoancilla* (see Fig. 20), this would make *Eoancilla* paraphyletic. Further exploration of late Paleocene faunas in the Coastal Plain might further elucidate this relationship.

Olivula staminea (Conrad, 1832)
Figure 19.4–19.10

1832 *Ancillaria staminea* Conrad, p. 25, pl. 10, fig. 5.
1834b *Ancillaria staminea*; Conrad, p. 5.
1835 *Oliva staminea*; Duclos, pl. 18, figs. 9, 10.
1844 *Oliva staminea*; Duclos, p. 11, pl. 20, figs. 9, 10.
1846 *Ancillaria staminea*; Conrad, p. 220.
1849 *Ancillaria staminea*; Lea, p. 96.
1850 *Ancyllaria staminea*; d'Orbigny, p. 352.
1858 *Ancillaria staminea*; Tuomey, p. 264.
1858 *Anaulax staminea*; Conrad, p. 166.
1860 *Agaronia punctulifera* Gabb, p. 381, pl. 67, fig. 22.
1865a *Olivula punctulifera*; Conrad, p. 22.
1865a *Olivula staminea*; Conrad, p. 22.
1866 *Olivula staminea*; Conrad, p. 17.
1866 *Olivula punctulifera*; Conrad, p. 17.
1883 *Olivula staminea*; Tryon, p. 61, pl. 3, figs. 24, 25.
1886 *Ancillaria staminea*; Aldrich, p. 51.
1890 *Agaronia punctulifera*; de Gregorio, p. 54.
1890 *Ancilla* (*Olivula*) *staminea*; de Gregorio, p. 57, pl. 4, figs. 5–8, 17, 18 [copied Conrad, 1832, in part].
1891 *Olivula punctulifera*; Heilprin, p. 398.
1893 *Olivula staminea*; Cossmann, p. 41.
1895b *Ancillaria staminea*; Harris, p. 42.
1899a *Ancilla* (*Olivula*) *staminea*; Harris, p. 30, pl. 3, fig. 13.
1899 *Ancilla* (*Olivula*) *staminea*; Cossmann, p. 70, pl. 3, figs. 10, 11.
1937 *Ancilla staminea*; Palmer, p. 428, pl. 68, figs. 7, 9, 11.
1937 *Ancilla staminea maternae* Palmer, p. 430, pl. 68, figs. 3, 8.
1937 *Ancilla staminea punctulifera*; Palmer, p. 429, pl. 68, figs. 10, 17.
1943 *Ancilla* (*Olivula*) *staminea*; Wenz, p. 1277, fig. 3635 [copied Cossmann, 1899].
1944 *Olivula staminea*; Shimer and Shrock, p. 511, pl. 210, fig. 16 [copied Conrad, 1832].
1960 *Ancilla staminea*; Brann and Kent, p. 44.
1960 *Ancilla staminea maternae*; Brann and Kent, p. 44.
1960 *Ancilla staminea punctulifera*; Brann and Kent, p. 44.
1960 *Ancilla* (*Olivula*) *staminea punctulifera*; Glibert, p. 19.
1960 *Ancilla* (*Olivula*) *staminea*; Glibert, p. 19.
1960 *Ancilla* (*Olivula*) *staminea*; Brann and Kent, p. 44.
1966 *Ancilla* (*Olivula*) *staminea*; Palmer and Brann, p. 492.
1966 *Ancilla staminea maternae*; Palmer and Brann, p. 492.
1966 *Ancilla staminea punctulifera*; Palmer and Brann, p. 493.
1980 *Ancilla staminea punctulifera*; Dockery, p. 114, pl. 176, fig. 3.
1996 *Ancilla* (*Olivula*) *staminea reklawensis* Garvie, p. 87, pl. 19, figs. 15, 16.

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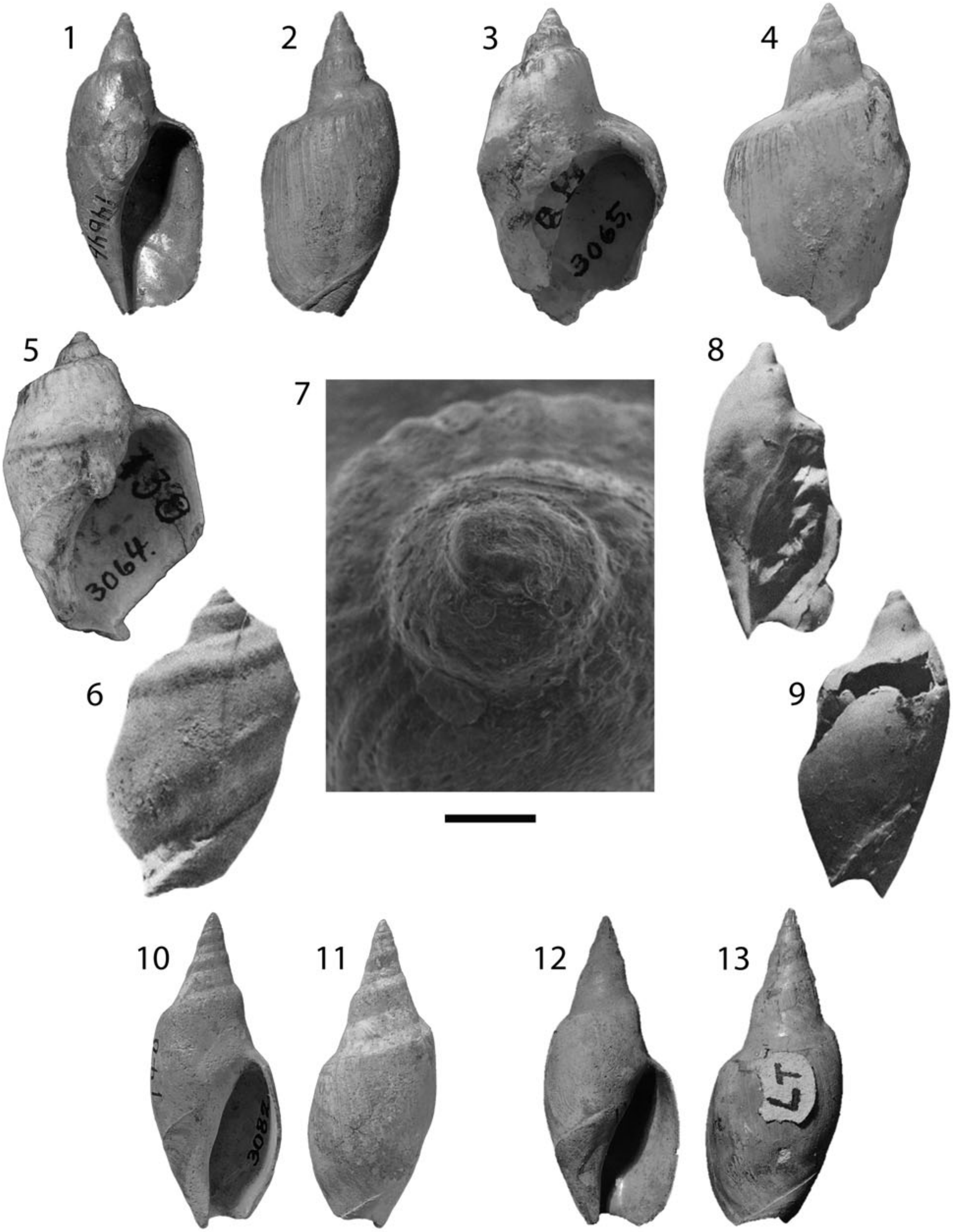

Figure 18. *Palmoliva* n. gen. (**1–9**) *Palmoliva tenera* n. comb.: (**1, 2**) *Ancillaria tenera* holotype ANSP 14646; height 29.7 mm. (**3, 4**) *Bullia tenera* hypotype PRI 3065 (from Palmer, 1937); height 23.3 mm. (**5–7**) *Bullia tenera* hypotype PRI 3064; height 26 mm; scale bar on (**7**) = 500 μm. (**8, 9**) *Bullia tenera* hypotype PRI 3066 (from Palmer, 1937); height 41 mm. (**10–13**) *Palmoliva scamba* n. comb.: (**10, 11**) *Bullia scamba* hypotype PRI 3082; height 35.9 mm. (**12, 13**) *Ancillaria scamba* lectotype ANSP 14647; height 36.7 mm.

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Type material.—Lectotype (Palmer, 1937, p. 429) ANSP 14670; hypotypes (Palmer, 1937) PRI 3284, 3285; holotype *Ancilla staminea maternae* PRI 3282; holotype *Agaronia punctulifera* ANSP 30729; hypotype (Palmer, 1937) PRI 3283; holotype *Ancilla staminea reklawensis* PRI 30425; paratype PRI 30426.

Occurrence.—South Carolina: middle Eocene (Bartonian), McBean Formation (Loc. SC-OR-1); Alabama: lower Eocene (Ypresian), Bashi Formation (Loc. AL-CL-2), middle Eocene (Lutetian–Bartonian), Lisbon Formation, Gosport Sand (Locs. AL-MO-2a, AL-MO-5); Mississippi: middle Eocene (Lutetian–Bartonian), Dobys Bluff Tongue, Cook Mountain Formation (Locs. MS-CL-1, MS-NE-1, MS-NE-2, MS-NE-3); Louisiana: middle Eocene (Lutetian–Bartonian), Cook Mountain Formation (Locs. LA-BI-2, LA-OU-2, LA-OU-3, LA-SA-3); Texas: middle Eocene (Ypresian–Lutetian), Stone City Beds, Reklaw Formation, Wheelock Member, Cook Mountain Formation (Locs. TX- RO-1, TX-BA-1).

Revised description.—(Revised by Palmer, 1937, p. 428–429) "Nucleus consists of two and a half smooth whorls; whorls of the spire crowded, those of the apex enveloped in the lower whorls; heavy, sutural callus collar extends over the upper margin of the lower whorl and lower margin of the preceding whorl with the suture a groove along the midline of the collar; the callus has deep sagittate longitudinal lines; in most cases the sutural collar covers most of the surface of the whorls of the spire' shell covered with coarse, longitudinal lines crossed by coarse, spiral lines which give the surface a fine, cancellated appearance."

Other material examined.—PRI 104505 (17 specimens); PRI 56421 (77 specimens).

Remarks.—*Olivula staminea* is a distinctive, abundant, long-lived, and widespread species. From youngest to oldest, in addition to *Ancilla staminea* s.s. from the Bartonian Gosport Sand, it includes three named temporal subspecies: *A. s. punctulifera* from the Lutetian Stone City Beds and the Wheelock Member of the Cook Mountain Formation in Texas; *A. s. reklawensis* from the upper Ypresian Reklaw Formation of Texas; and *A. s. maternae* from the lower Ypresian Bashi Formation of Alabama (Fig. 20).

Our phylogenetic analysis (see below) suggests that this species may have been derived from a species of *Eoancilla*, perhaps *E. mediavia*.

Genus *Palmoliva* new genus

Type species.—*Ancillaria tenera* Conrad, 1834a, by original designation herein.

Diagnosis.—Spire one-third or less of total shell height. Aperture one-half to one-third total shell height. Protoconch incompletely known, but probably of 2–3 smooth whorls. Sutures callused. Spire and body whorl strongly to moderately shouldered, with shoulders bearing faint to moderate axial sculpture. Shell otherwise smooth. Olivoid band moderate to faint, weakening but persisting on dorsal side. Anterior band pronounced, with posterior margin marked by a sharp ridge. Plication plate narrow and simple. Anterior end of columella a simple point.

Etymology.—Named in honor of Katherine Palmer, author of many of the taxa discussed in this paper.

Remarks.—Palmer (1937) placed two similar species, *Ancillaria tenera* Conrad, 1834a, and *Ancillaria scamba* Conrad, 1832, in *Bullia*, but they do not belong there because, although they both have simple, pointed anterior columellar ends, they both show well-developed olivoid and anterior bands, which are not present in *Bullia*. These two species share pronounced shouldering on spire and body whorls and faint to moderate axial sculpture on those shoulders, features that are not present together in any other taxa discussed here. We therefore place them both in a new genus, *Palmoliva*.

Palmoliva scamba (Conrad, 1832) new combination
Figure 18.10–18.13

1832 *Ancillaria scamba* Conrad, p. 25, pl. 10, fig. 4.
1833 ?*Anolax plicata* Lea, p. 181, pl. 6, fig. 194.
1849 ?*Anolax plicata*; Lea, p. 96.
1854 *Ancilla scamba*; Conrad, p. 30.
1865a *Ancillopsis scamba*; Conrad, p. 22.
1865a *Olivula* ? *plicata*; Conrad, p. 22.
1866 *Ancillopsis scamba*; Conrad, p. 17.
1866 *Olivula* ? *plicata*; Conrad, p. 17.
1883 *Ancillaria* (*Ancillopsis*) *scamba*; Tryon, p. 61, pl. 3, fig. 26.
1890 *Ancilla scamba*; de Gregorio, p. 55, pl. 4, figs. 12, 13, 15, 16 [copied Conrad, 1832, in part].
1890 *Ancilla* (*Olivula*) *plicata*; de Gregorio, p. 57, pl. 4, fig. 9 [copied Lea, 1833, pl. 6, fig. 194].
1893 *Ancillina scamba*; Cossmann, p. 40.
1893 *Ancillina* ? *plicata*; Cossmann, p. 40.
1895b ?*Anolax plicata*; Harris, p. 35.
1901b *Ancilla* (*Olivula*) *plicata*; Cossmann, p. 223.
1901b *Buccinanops* (*Bullia*) *scambum*; Cossmann, p. 223, pl. 9, fig. 23 [plate captions for figs. 23 and 14 are reversed].
1937 *Bullia scamba*; Palmer, p. 290, pl. 44, figs. 2, 7.
1960 *Bullia scamba*; Brann and Kent, p. 140.
1963 *Bullia scamba*; Glibert, p. 98.
1966 *Bullia scamba*; Palmer and Brann, p. 544.
1990 "*Bullia*" *scamba*; Allmon, p. 58, pl. 9, fig. 2.

Type material.—Lectotype (plus 10 specimens) (selected by Palmer, 1937, p. 291 [fide Moore 1962, p. 95]) ANSP 14647; hypotype (Palmer, 1937) PRI 3082.

Occurrence.—Alabama: middle Eocene; Gosport Sand (Locs. AL-CL-1; AL-MO-2a).

Revised description.—Protoconch unknown. Earliest known whorls smooth. Spire up to one-third of total height. Callus extending adapically of posterior end of aperture, giving sutures a callused form. Spire and body whorl moderately shouldered, with shoulders bearing faint to moderate axial sculpture. Posterior edge marked by ridge. Olivoid band faint and weakens

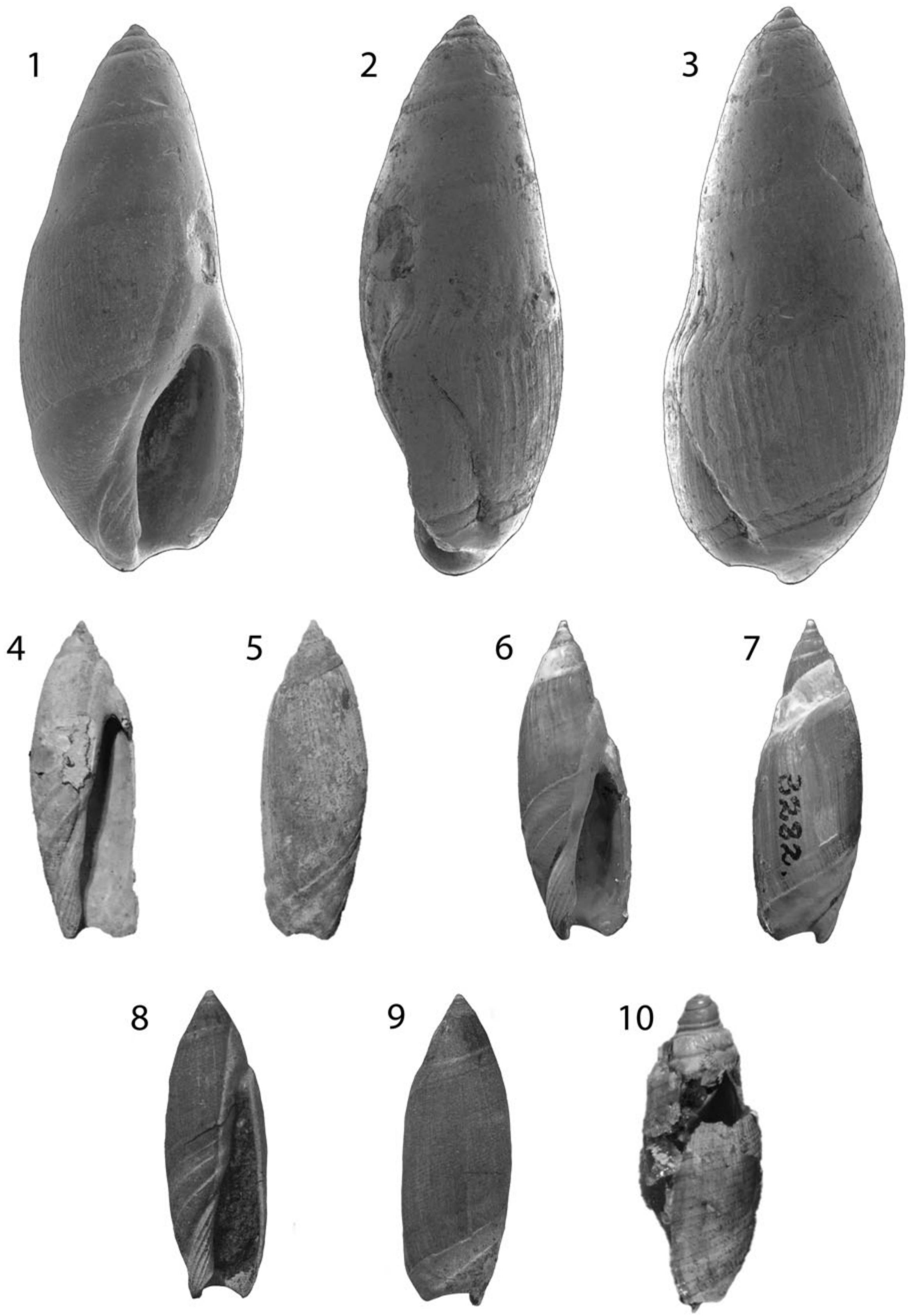

Figure 19. *Micrancilla* and *Olivula*. (**1–3**) *Micrancilla alibamasiana* holotype MNHN.F.J13251 (from Pacaud, 2014); height 5 mm. (**4–10**) *Olivula staminea*: (**4, 5**) *Ancillaria staminea* lectotype ANSP 14670; height 31.8 mm. (**6, 7**) *Ancilla staminea maternae* holotype PRI 3282; height 25.3 mm. (**8, 9**) *Ancilla staminea reklawensis* holotype PRI 30425; height 15.4 mm. **(10)** *Agaronia punctulifera* holotype ANSP 30729; height 6.8 mm.

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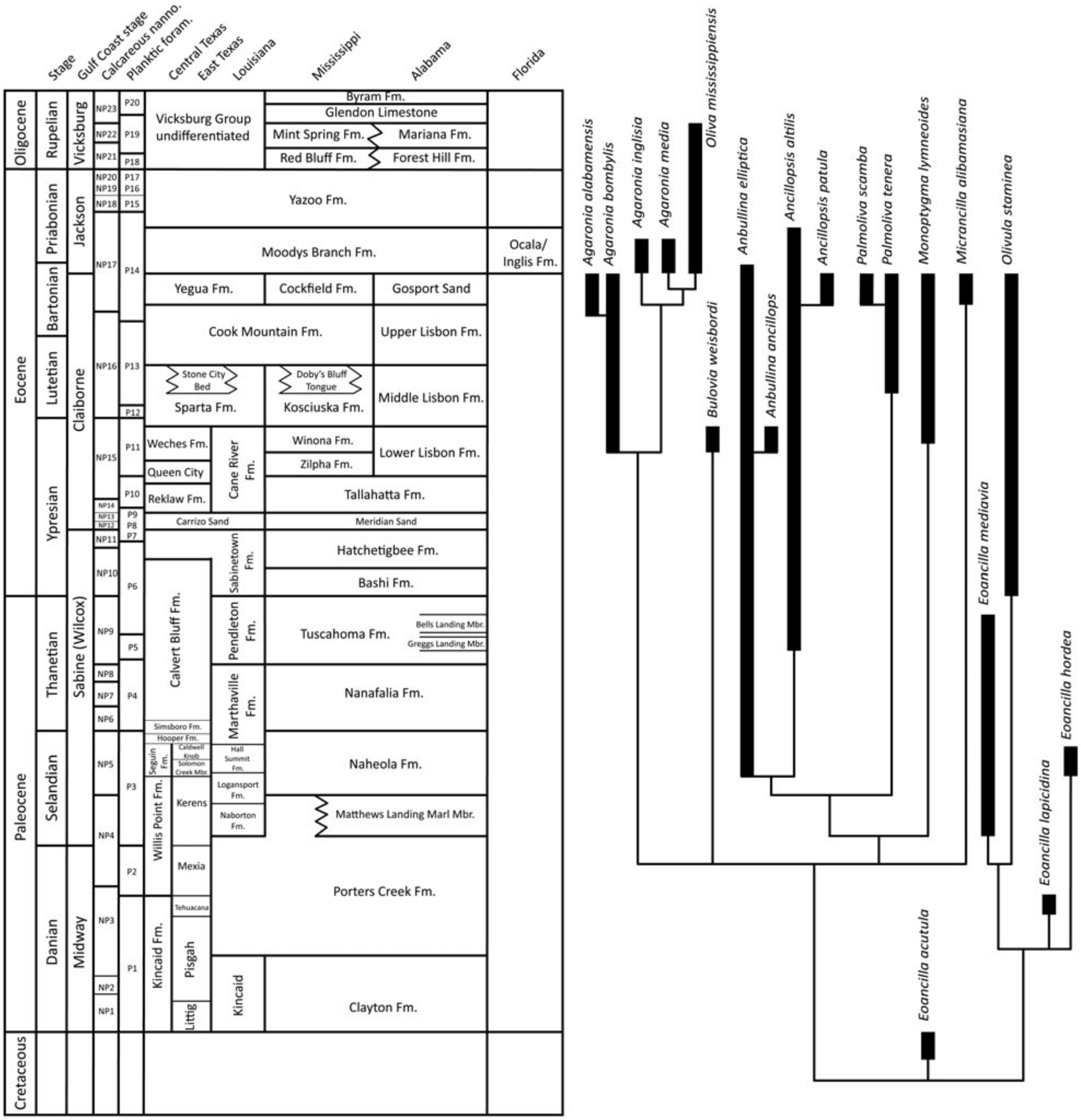

Figure 20. Evolutionary tree of the taxa discussed here, based on the cladogram in Figure 5.2 and the stratigraphic ranges in Figure 2.

but persists on dorsal side. Anterior band marked by strong growth lines, which are concave anteriorly. Posterior margin of anterior band is a sharp ridge, more pronounced in juvenile specimens. Plication plate narrow and simple. Anterior end of columella a simple point. Aperture height usually about half of total height; aperture usually about half or less of total maximum width.

Other material examined.—PRI 57505 (8 specimens); PRI 57499 (2 specimens); PRI 63642 (4 specimens); PRI 104511 (3 specimens); PRI 104512 (1 specimen); PRI 104513 (3 specimens).

Remarks.—Palmer (1937) noted that *scamba* is similar to *Monoptygma lymneoides* in having a similar overall shell shape and similar anterior notch and callused sutures but differs in lacking the single well-developed plication on the columella. Palmer (1937, p. 291) suggested that *Anolax plicata* Lea, 1833 (the lectotype of which, ANSP 5910, is lost; J. Sessa, personal communication, 11/12/21) may actually have been a juvenile of *tenera*.

Palmoliva tenera (Conrad, 1834) new combination
Figure 18.1–18.9

1834a *Ancillaria tenera* Conrad, p. 147.
1835 *Ancillaria tenera*; Conrad, p. 42, pl. 16, fig. 5.
1865a *Ancillopsis tenera*; Conrad, p. 22.

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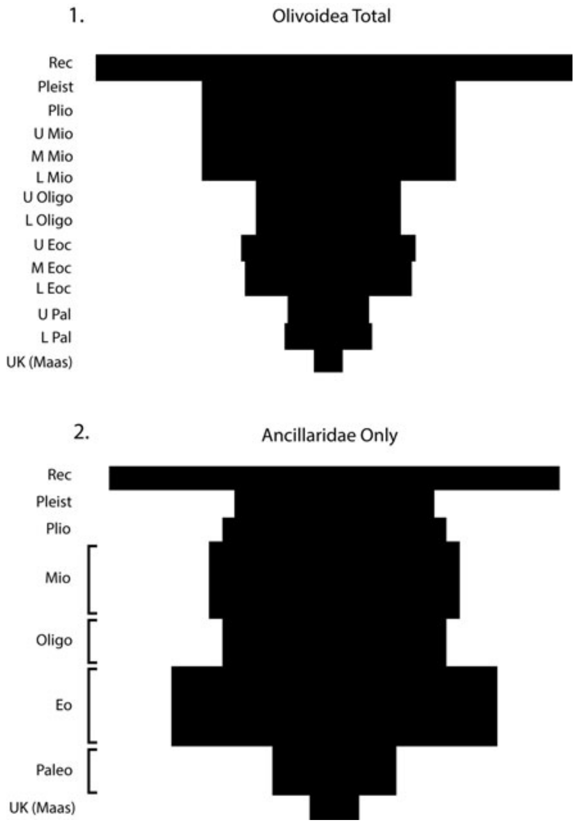

Figure 21. Global diversity of genera and subgenera since the late Cretaceous of (**1**) Olivoidea, and (**2**) only Ancillariidae. Data from Table 4.

1866 *Ancillopsis tenera*; Conrad, 1866, p. 17.
1890 *Ancilla tenera*; de Gregorio, p. 56, pl. 4, fig. 2 [copied Conrad, 1835, pl. 16, fig. 5]
1937 *Bullia tenera*; Palmer, p. 291, pl. 42, figs. 7–13.
1960 *Bullia tenera*; Brann and Kent, p. 140.
1966 *Bullia tenera*; Palmer and Brann, p. 54.
1990 "*Bullia*" *tenera*; Allmon, p. 58, pl. 9, figs. 1, 3.

Type material.—Holotype ANSP 14646; hypotypes (Palmer, 1937) PRI 3064 (not "3074" as in Palmer, 1937, p. 634), 3065, 3066.

Occurrence.—Alabama: middle Eocene (Bartonian), Gosport Sand (Loc. AL-MO-2a); Texas: middle Eocene (Lutetian), Stone City Beds (Loc. TX-RO-1); Louisiana: middle Eocene (PRI collection, exact localities unknown).

Revised description.—Protoconch incompletely known but probably of 2–3 smooth whorls. Spire less than one-fifth of total height. Callus extending adapically of posterior end of aperture, giving sutures a callused form. Spire and body whorl strongly shouldered, with shoulders bearing faint to moderate axial sculpture. Olivoid band more marked in juveniles. Posterior edge marked by ridge, more pronounced on posterior end. Olivoid band weakens on dorsal side but persists as a broad depression with moderately deflected growth lines. Anterior band marked by strong growth lines that are concave anteriorly. Posterior margin of anterior band is a sharp ridge, more pronounced in juvenile specimens. Plication plate narrow and simple. Anterior end of columella a simple point. Aperture width at least half of total maximum width.

Remarks.—The ANSP holotype is from the Gosport Sand of Alabama. PRI specimens are from older deposits to the west, including the Stone City Beds of Texas (PRI 3066) and "Louisiana. Exact data lost" (Palmer, 1937, p. 10, 292) (PRI 3064, 3065).

Palmoliva tenera n. comb. differs from *P. scamba* n. comb. mainly in having a lower spire, wider aperture, and more pronounced shouldering. Palmer (1937) noted that there was considerable variation in form among individuals in this species, but most of this variation appears to be ontogenetic. Younger individuals have lower spire, wider aperture, more pronounced olivoid and anterior bands, and more pronounced shoulders with stronger axial sculpture.

Genus *Micrancilla* Maxwell, 1992

Type species.—By original designation, *Amalda* (*Micrancilla*) *granum* Maxwell, 1992 (Priabonian, New Zealand).

Other included species.—*Micrancilla alibamasiana* Pacaud, Merle, and Pons, 2013 (Bartonian, Alabama); *M. antipodarum* Pacaud, 2014 (Lutetian, France); *M. dilatata* (Cossmann, 1886) (Lutetian, France); *M. guanensis* Pacaud, Merle, and Pons, 2013 (Ypresian, France); *M. oesiensis* Pacaud, Merle, and Pons, 2013 (Lutetian, France). Maxwell (1992, p. 143) stated that there are also undescribed species from New Zealand that belong to this taxon.

Original diagnosis.—(Maxwell, 1992, p. 143) "Shell very small for subfamily, narrowly ovate, spire elevated, apex rather broad, well-rounded. Parietal callus thin, ascending almost vertically from top of columella then bending back sharply, running parallel to and at some distance from base of callus band on posterior portion of whorls. Suture barely hidden by callus. Aperture small, narrowly ovate, columella short, nearly vertical with a few narrow plaits."

Micrancilla alibamasiana Pacaud, Merle, and Pons, 2013
Figure 19.1–19.3

Type material.—Holotype MNHN.F.J13251.

Occurrence.—Alabama: middle Eocene (Bartonian); Gosport Sand (Locs. AL-CL-1; AL-MO-2a).

Original description.—(Translation from Pacaud et al., 2013.) Small, narrow, elongated shell, cylindrical, thick test, consisting of about 5 whorls which are separated by indistinct suture lines in adulthood. The protoconch, with a pointed "button", consists of 2 whorls. The apical angle is 35°. The spire, high, is covered by a thick callus which hides the suture on the last turn, and which extends to the adapical part of the final whorl by forming a bead. The parietal callus is thin, rising almost vertically from the top of columella and then bending sharply backwards, runs parallel, at a certain distance

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Table 4. Described genera/subgenera (n = 84) in the Superfamily Olivoidea (sensu Kantor et al., 2017). References: (1) Kilburn (1981); (2) Sepkoski (2002); (3) Kollman and Peel (1983); (4) Ninomiya (1990); (5) Ninomiya (1988); (6) Kilburn (1977); (7) this paper; (8) Kantor et al. (2017); (9) Petuch and Sargeant (1986); (10) Vermeij (1998); (11) Olsson (1956); (12) Absalão and Pimenta (2003); (13) Watters and Fleming (1972); (14) Pacaud et al. (2000); (15) Tracey et al. (1996); (16) Pacaud et al. (2013); (17) Kantor and Bouchet (2007); (18) Klappenbach (1962); (19) Petuch (1988); (20) Drez (1981); (21) Voskuil (2018).

Family/Subfamily	Genus/Subgenus	Stratigraphic Range (reference)
Olividae Swainson, 1835		
Olivinae Latreille, 1825	*Oliva* Bruguière, 1789	Eocene–Recent (7)
	O. (*Acutoliva*) Petuch and Sargent, 1986	Recent (8, 9)
	O. (*Annulatoliva*) Petuch and Sargent, 1986	Recent (8, 9)
	O. (*Arctoliva*) Petuch and Sargent, 1986	Recent (8, 9)
	O. (*Cariboliva*) Petuch and Sargent, 1986	Miocene-Recent (8, 9)
	O. (*Carmione*) Gray, 1858	Recent (8, 9)
	O. (*Galeola*) Gray, 1858	Recent (8, 9)
	O. (*Lindoliva*) Petuch, 1988	Pleistocene (19)
	O. (*Miniaceoliva*) Petuch and Sargent, 1986	Recent (8, 9)
	O. (*Multiplicoliva*) Petuch and Sargent, 1986	Recent (8, 9)
	O. (*Musteloliva*) Petuch and Sargent, 1986	Recent (8, 9)
	O. (*Neocylindrus*) Fischer, 1883	Miocene–Recent (2)
	O. (*Oliva*) Bruguière, 1789	Lower Miocene–Recent (20)
	O. (*Omogymna*) von Martens, 1897	Lower Miocene–Recent (20)
	O. (*Parvoliva*) Thiele, 1929	Recent (8, 9)
	O. (*Porphyria*) Röding, 1798	Middle Miocene–Recent (9, 21)
	O. (*Proxoliva*) Petuch and Sargent, 1986	Recent (8,9)
	O. (*Rufoliva*) Petuch and Sargent, 1986	Miocene-Recent (8,9)
	O. (*Strephona*) Mörch, 1852	Miocene–Recent (8,9)
	O. (*Strephonella*) Dall, 1909	Upper Eocene–Recent (7)
	O. (*Viduoliva*) Petuch and Sargent, 1986	Recent (8, 9)
Agaroninae Olsson, 1956	*Agaronia* Gray, 1839	Lower Eocene–Recent (7)
Olivellinae Troschel, 1869	*Olivella* Swainson, 1831	Cretaceous (Senonian)–Recent (2)
	O. (*Anasser*) Absalão and Pimenta, 2003	Recent (12)
	O. (*Callianax*) Adams and Adams, 1853	Eocene-Recent (8)
	O. (*Cupidoliva*) Iredale, 1924	Recent (8)
	O. (*Dactylidia*) Adams and Adams, 1853	Miocene–Recent (8)
	O. (*Dactylidella*) Woodring, 1928	Miocene–Recent (2)
	O. (*Lamprodoma*) Swainson, 1840	Eocene–Recent (2)
	O. (*Macgintiella*) Olsson, 1956	Miocene–Recent (11)
	O. (*Minioliva*) Olsson, 1956	Pliocene–Recent (11)
	O. (*Niteoliva*) Olsson, 1956	Miocene–Recent (11)
	O. (*Olivina*) d'Orbigny, 1841	Recent (11)
	O. (*Orbignytesta*) Klappenbach, 1962	Recent (8, 18)
	O. (*Pachyoliva*) Olsson, 1956	Recent (8, 11)
	O. (*Zanoetella*) Olsson, 1956	Recent (8, 11)
Calyptolivinae Kantor et al., 2017	*Calyptoliva* Kantor and Bouchet, 2007	Recent (17)
Bellolividae Kantor et al., 2017		
	Belloliva Peile, 1922	Recent (8, 11)
	Olivellopsis Thiele, 1929	Recent (8)
	Jaspidella Olsson, 1956	Oligocene–Recent (11)
Ancillariidae Swainson, 1840		L
	Amalda Adams and Adams, 1853	Upper Cretaceous–Recent (2, 8)
	A. (*Alocospira*) Cossmann, 1899	Eocene–Pliocene (2, 8)
	A. (*Austrancilla*) Habe, 1959	Recent (8)
	A. (*Baryspira*) Fischer, 1883	Oligocene–Recent (2)
	A. (*Exiquaspira*) Ninomiya, 1988	Recent (8)
	A. (*Gracilispira*) Olsson, 1956	Eocene–Recent (2, 8)
	A. (*Mundaspira*) Ninomiya, 1990	Recent (8)
	A. (*Spinaspira*) Olsson, 1956	Miocene (2, 8)
	Anbullina Palmer, 1937	Lower Eocene (7)
	Ancilla Lamarck, 1799 (= *Anaulax* Roissy, 1805; *Ancillaria* Lamarck, 1799; *Ancillus* Montfort, 1810; *Sparella* Gray, 1857; *Sparellina* Fischer, 1883; *Ancillista* Iredale, 1936)	Upper Cretaceous/Eocene–Recent (1, 2, 8)
	Ancillarina Bellardi, 1882	Paleocene–Miocene (2, 3)
	Ancillina Bellardi, 1882	Oligocene–Miocene (8)
	Ancillopsis Conrad, 1865a	Upper Paleocene– Upper Eocene (7)
	Anolacia Gray, 1857	Recent (8)
	Chilotygma Adams and Adams, 1853	Recent (6)
	Eburna Lamarck, 1801	Miocene–Recent (2, 8)
	Entomoliva Bouchet and Kilburn, 1990	Recent (8)
	Exiquaspira Ninomiya, 1988	Recent (5)
	Gracilancilla Thiele, 1925	Recent (8)
	Hesperancilla Kilburn, 1981	Recent (8)
	Lamprodomina Marwick, 1931	Pliocene (8)
	Micrancilla Maxwell, 1992	Eocene–Recent (7, 8)
	Monoptygma Lea, 1833	Eocene (7)
	Olivella Swainson, 1831	Cretaceous–Recent (11)
	Olivula Conrad, 1832	Eocene (7)
	Palmoliva new genus	Eocene (7)

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Table 4. Continued.

Family/Subfamily	Genus/Subgenus	Stratigraphic Range (reference)
	Spirancilla Vokes, 1935	Paleocene–Eocene (16)
	Turrancilla von Martens in von Martens and Thiele, 1904	Recent (8)
Benthobiidae Kantor et al., 2017		
	Benthobia Dall, 1889	Recent (8)
	Fusulculus Bouchet and Vermeij, 1998	Recent (8)
Pseudolividae de Gregorio, 1880		
	Fulmentum Fischer, 1883	Recent (10)
	Fusopsis Ravn, 1939	Paleocene (10)
	Hubachia Etayo Serna, 1979	Paleocene (10)
	Luizia Douvillé, 1933	Lower Miocene–Recent (10)
	Macron Adams and Adams, 1853	Lower Miocene–Recent (10)
	Naudoliva Kilburn, 1989	Miocene–Recent (10)
	Ramoliva Cotton and Godfrey, 1932	Recent (8)
	Sulcobuccinum d'Orbigny, 1850	Upper Cretaceous–Lower Oligocene (10)
	Sulcoliva Vermeij, 1998	Lower–Upper Eocene (10)
	Pseudoliva Swainson, 1840	Miocene–Recent (10)
	Testalium Vermeij and DeVries, 1997	Lower Miocene–Upper Pliocene (10)
	Triumphis Gray, 1857	Lower Miocene–Recent (10)
	Zemira Adams and Adams, 1853	Upper Eocene–Recent (10)
Incertae sedis		
	Olivancillaria d'Orbigny, 1841	Oligocene–Recent (2, 8)
	O. (*Lintricula*) Adams and Adams, 1853	Pliocene–Recent (8, 13)
	O. (*Pseudolivella*) Glibert, 1960	Paleocene–Eocene (14, 15)

from the boundary of the spiral callus, and produces a narrow and unglazed spiral band on the adapical part of the spire. The callus extends over the neck, up to the fasciolar groove. The last whorl is elongated, cylindrical. The unglazed band is wide, well demarcated, strongly marked by the increments (growth lines), separated from the whorl by a clear limit of the spiral callus. The ancilline groove is well developed, narrow, linear, and deep. The ancilline band is very narrow, depressed, marked by the increases (growth lines). The neck is covered by a broad undivided fasciole. The posterior area is provided with a weak median ridge, blunt. Columellar torsion, short, slightly sinuous, not truncated and separated from the fasciole by a wide and deep fasciole groove, is decorated with 5 folds, wide and flat. The aperture, occupying a little less than half of the total height, is olivoid, contracted at its parietal angle. The siphonal notch is sinuous and widely marked. The labrum, beveled, orthoclinically oriented, is thickened in its terminal part. It presents an opisthocyrt outline in its adapical part, above the parietal angle of the opening. Exposure to UV light does not show residual colored pattern.

Remarks.—This is the only species of this genus in the Americas. It is apparently rare, as we have not encountered any specimens of it in the Gosport Sand, despite intensive sampling (e.g., CoBabe and Allmon, 1994; Pietsch et al., 2016).

Discussion and conclusions

An evolutionary tree based on the cladogram in Figure 5.2 and the stratigraphic ranges shown in Figure 2 are presented in Figure 20; they suggest that the basal diversification of ancillariids in the Coastal Plain occurred in the early to middle Paleocene. There are several significant ghost ranges, suggesting that the pre-middle Eocene record is less complete than that from the middle Eocene. This species-level diversification is slightly earlier than the Eocene global diversification of olivoid and ancillariid genera (Fig. 21).

Olivoids appear to have originated in the Cretaceous in the eastern Tethys, the region that now includes Madagascar, South Asia, and Japan, and soon spread to the Gulf Coast of North America and western Europe. These early olivoids were stem group ancillariids. The genus *Micrancilla* appears to have been part of this basal ancillariid radiation, perhaps originating in western Europe and spreading to New Zealand and America (Pacaud et al., 2013; Pacaud, 2014). This biogeographic history may explain the absence of *Micrancilla* in the Coastal Plain prior to the late middle Eocene.

The relative stratigraphic position of the four species of *Eoancilla* is consistent with them comprising a single ancestor-descendant lineage, perhaps including the ancestors of both *Olivula staminea* and all of the other species considered here.

The genus *Agaronia*, as presented here, is paraphyletic, and includes the ancestry of the oldest known species of the genus *Oliva*. *Agaronia* is widely distributed beyond the Coastal Plain up to the Recent; its comprehensive phylogenetic analysis is beyond the scope of this paper, so we have not subdivided it at the genus level.

Most of the species treated here have durations of <10 my (7 of 19 are known from a single formation), but three species are relatively long-lived (*Anbullina elliptica*, ca. 20–23 my; *Ancillopsis altilis*, ca. 20 my; *Olivula staminea*, ca. 18 my), and all three appear to show noticeable anagenetic change through these durations.

The Paleogene gastropods of the Coastal Plain are relatively well studied, but our analysis indicates that a significant number of taxonomic assignments should be changed. Nine of the 19 Coastal Plain species listed in Table 1 are here assigned to different genera and nine to different families than they were in the most recent authoritative summary more than 50 years ago (Palmer and Brann, 1966).

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Declaration of competing interests

The authors declare none.

Data availability statement

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.ffbg79cz6.

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Appendix

Locality register.—GSA = Geological Survey of Alabama localities; MGS = Mississippi Geological Survey localities (see Dockery, 1980); PRI = Paleontological Research Institution station numbers (see Palmer, 1937); TBEG = Texas Bureau of Economic Geology localities; USGS = U.S. Geological Survey station numbers.

Alabama.—Twenty-two localities.

AL-CH-1.—Choctaw County. Left (north) bank of Tuckabum Creek under Highway 114 bridge, between Pennington and Lavaca; Nanafalia Formation (PRI collection).

AL-CH-2.—Choctaw County. Jackson (Geological Survey of Alabama collection).

AL-CH-3.—Choctaw County. "West end of Butler Road bed and bank by Judge Lindsey's farm" (Geological Survey of Alabama collection).

AL-CH-4.—Choctaw County. "1 mile E of Butler on Mt. Sterling Road" (Geological Survey of Alabama collection).

AL-CL-1.—Clark County. Little Stave Creek. ∼3 miles north of Jackson, ∼0.75 mile west of Highway 43. Gosport Sand (MGS 29).

AL-CL-2.—Clarke County. Woods Bluff, left bank of Tombigbee River; Bashi Marl (PRI 749; USGS 262, 2667, 3099, 3100, 5470, 6205, 6206, 6207, 7482).

AL-CL-3.—Clarke County. Bashi Creek; Bashi Marl (PRI collection).

AL-CL-4.—Clarke County. Knight's Branch; Bashi Formation (Geological Survey of Alabama collection).

AL-CL-5.—Clarke County. "1 mile N of Campbell, Highway 79 roadcut" (Geological Survey of Alabama collection).

AL-CL-6.—Clarke County. Satilpa Creek (Aldrich, 1886; Palmer, 1937, p. 289).

AL-CL-7.—Clarke County. Cave Branch, several caves along a fork in a creek within the western half of S10-T11N-R2E; Bashi Marl (GSA 67).

AL-CO-6.—Coffee County. Elba Dam on Pea River; Bashi Marl (USGS 10013,10780).

AL-MA-1.—Marengo County. Nanafalia Landing, Tombigbee River; Nanafalia Formation (USGS 271, 5641).

AL-MO-2.—Monroe County. Claiborne Landing and Bluff, left bank Alabama River, downstream from Highway 84 bridge; 2a = Gosport Sand in bluff (MGS 28; PRI 104, 140; USGS 263, 2391, 2867); 2b = Upper Lisbon Formation exposed at base of bluff on river bank (PRI 103, 139; USGS 2395, 2396, 12171).

AL-MO-3.—Monroe County. Bell's Landing, left bank of Alabama River; Bells Landing Marl Member, Tuscahoma Formation (PRI 752; USGS 260, 2669, 3098, 5593, 5594, 5595).

AL-MO-4.—Monroe County. Gregg's Landing, right bank Alabama River just downstream of island; Greggs Landing Marl Member, Tuscahoma Formation (PRI 751; USGS 268, 2670, 3117, 3118, 3604, 5642).

AL-MO-5.—Monroe County. Lisbon Landing, Alabama River; Upper Lisbon Formation (USGS 3105, 5511, 6086).

AL-PE-1.—Perry County. "E.R. Showalter, Uniontown" (Geological Survey of Alabama collection).

AL-SU-3.—Sumter County. Black Bluff, Tombigbee River (PRI collection).

AL-WA-1.—Washington County. Hatchetigbee Bluff, right bank Tombigbee River; Hatchetigbee Formation (type section) (Toulmin, 1977, loc. Awa-1).

AL-WI-1.—Wilcox County. One mile W of Oak Hill, Naheola Formation (PRI collection).

AL-WI-2.—Matthews Landing. Nine miles W of Camden, right bank of Alabama River at bend; Matthews Landing Marl (USGS 3116, 2671, 5596).

Arkansas.—One locality.

AR-ST-1.—St. Francis County. Crow Creek. At bridge on Highway 70 ∼2 miles east of Forest City (PRI 894, 1046).

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Florida.—One locality.

FL-LE-1.—Levy County. Quarry 2.9 miles S of town of Gulf Hammock, SW of state road 55 (UF collection).

Louisiana.—Twelve localities.

LA-BI-1.—Bienville Parish. "Holstein's well, 5 miles southeast of Gibbsland" (Palmer, 1937, p. 298).

LA-BI-2.—Bienville Parish. Hammetts Branch, ~2 miles NW of Mt. Lebanon (PRI 730).

LA-GR-1.—Grant Parish. Montgomery Landing, Moodys Branch Formation (PRI 11).

LA-NA-1.—Natchitoches Parish. "Cultivated hill on L.E. Place's farm in the NE¼ NW¼ of sec. 22, T9N, R10W" (Barry and LeBlanc, 1942, p. 34).

LA-NA-2.—"Hillside at end of an old road in the NW¼ SE¼ NW¼ of sec. 36, T9N, R9W" (Barry and LeBlanc, 1942, p. 39).

LA-NA-3.—"Road cut along local road ion NE¼ SW¼ NE¼ of sec. 19, T9N, R8W" (Barry and LeBlanc, 1942, p. 39)

LA-OU-1.—Ouachita Parish. Monroe (PRI 735).

LA-OU-2.—Ouachita Parish. East bank, Ouashita River, Lapiniere Landing (PRI 756).

LA-OU-3.—Ouachita Parish. Brewer's, 1200 ft., Monroe (PRI 735).

LA-SA-1.—Sabine Parish. "About ¼ of a mile upstream from the bridge over the Sabine River on Louisiana Highway 6" (Barry and LeBlanc, 1942, p. 37).

LA-SA-2.—Sabine Parish. South bank of Slaughter Creek. In approximately the NW¼ SE¼ of sec 34, T6N, R13W (Barry and LeBlanc, 1942, p. 37).

LA-SA-3.—Sabine Parish. Sabine River bank (PRI 724, 725?).

Mississippi.—Fifteen localities.

MS-CL-1.—Clarke County. Doby's Bluff. East side of Chickasawhay River (MGS 26).

MS-CL-2.—Clarke County. Garland Creek. Moodys Branch Formation (MGS 9).

MS-LA-1.—Lauderdale County. Low bluff behind Red Hot Truck Stop parking lot, on Interstate 10, east of Meridian; Bashi Marl (MGS 19).

MS-LA-2.—Lauderdale County. Large concretions placed along 31st Street exit, south of I-20, Meridian; Bashi Marl (MGS 20).

MS-HI-1.—Hinds County. Town Creek, Jackson (MGS 1).

MS-HI-2.—Hinds County. Riverside Park, Jackson (MGS 2).

MS-HI-3.—Hinds County. Moodys Branch, Jackson (MGS 3).

MS-HI-4.—Hinds County. Sewer excavation across Town Creek, Jackson (MGS 7).

MS-NE-1.—Newton County. "Hill on south side of county road paralleling Interstate 20 along north side, 0.3 mile west of Mississippi Highway 15, just north of Newton" (TU 923; MGS 68).

MS-NE-2.—Newton County. Hickory (PRI 728).

MS-NE-3.—Newton County. Two miles N of Newton, on Rt. 15 (PRI 803).

MS-TI-1.—Tippah County. Roadcuts on north-facing slope of a tributary of Fourth Creek, 0.9 mile north of Providence School. Owl Creek Formation (USGS 25422).

MS-TI-2.—Tippah County. Bluffs on right bank of Owl Creek, 2.5 miles northeast of Ripley. Owl Creek Formation (USGS 541, 546, 594, 707, 6464, 6876, 25423).

MS-WA-23.—Warren County. "Kings Crossing. Four miles N of Kings Crossing, Vicksburg, MS. Road cut ~3 miles N of Mint Spring Bayou entrance to National Cemetery" (PRI 887).

MS-YA-1.—Yazoo County. Techeva Creek (MGS 11).

South Carolina.—One locality

SC-OR-1.—Near Orangeburg (PRI 707, 708).

Tennessee.—One locality.

TN-HA-1.—Hardeman County. Roadcut on Tennessee State Route 57, on west-facing slope of Muddy Creek valley, near Trimm's old mill site, 3.3 miles east of the road junction that is 1.5 miles south of Middleton. Clayton Formation, basal beds containing reworked Late Cretaceous fossils (Sohl, 1964, p. 325) (USGS 25420).

Texas.—Sixteen localities.

TX-BA-1.—Bastrop County. Bluff on right bank of Colorado River, ~200 m downstream from Highway 71 bridge at Smithville, Viesca Member, Weches Formation (PRI 733, 767; TBEG loc 11-T-2; USGS 6088, 10386).

TX-BA-2.—Bastrop County. Dry creek at mouth of Colorado River (Loc. 11-T-101 of Garvie, 2013).

TX-BA-3.—Bastrop County. Solomon's Farm (Locs. 11-T-3, 11-T-13 of Garvie, 2013).

TX-BA-4.—Bastrop County. East bank of mouth of Gazley Creek, south side of Colorado River, Smithville, Queen City Formation (PRI 776; Price and Palmer, 1928; Molineux et al., 2013).

TX-BA-5.—Bastrop County. Colorado River, 4 ± miles below Webberville, bed No. 3, Kincaid Formation (USGS 11696?, 11914, 12112) (Gardner, 1935, p. 231).

TX-BE-1.—Bexar County. Smith Tract, Somerset field, 659–680 feet and 769–782 feet (USGS 8656) (Gardner, 1935, p. 231).

TX-BR-1.—Brazos County. Little Brazos River, 2.5 miles above Stone City (PRI 727).

TX-BU-1.—Burleson County. Moseleys Ferry, Brazos River (PRI 723).

TX-FA-1.—Falls County. Quarry of Frost Crushed Stone Company, 1 km (0.62 mile) south of Highway 7 and ~17 km (10.6 miles) east of Marlin. Kincaid Formation, Tehuacana Limestone Member (Loc. FQ of Garvie, 2021).

TX-KA-1.—Kaufman County. Water Hill, 5 miles northeast of Kemp. Kincaid Formation (USGS 11665?) (Gardner, 1935, p. 231).

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TX-MI-1.—Milam County. Joe Taylor Branch (Locality 20 of Garvie, 1996).

TX-MI-2.—Milam County. U.S.G.S. Station 11921, Brazos River, 1 mile below the Falls County line, Kincaid Formation (USGS 11921) (Gardner, 1935, p. 231).

TX-RO-1.—Robertson County. “Big Branch of Cedar Creek, east of Mr. Pollard’s (deceased) farm, 3 miles N.W. of Stone City”; Stone City Beds (Palmer, 1937, p. 11) (PRI 766). (Palmer’s listing of this location as in Burleson County was in error. She corrected it to Robertson County in Palmer and Brann [1966, p. 779], citing Stenzel et al. [1957, p. 11]).

TX-SA-1.—Sabine County. Pendleton Bluff, Pendleton Formation (Locality 40 of Barry and LeBlanc, 1942).

TX-TR-1.—Travis County. Webberville, Kemp Clay (USGS 7601).

TX-WI-1.—Williamson County. Lower bed, Dry Brushy Creek, 6 miles south of Thrall on Taylor-Beaukiss road Wills Point Formation (USGS 10420) (Gardner, 1935, p. 231).

France.—One locality.

FR-1.—Ducy, near Montepilloy (PRI collection).

Mexico.—Two localities.

MX-NL-1.—Nuevo Leon. “On southeast slope of low hill 1 km east of triangulation point Palma, Carlos Cantu, General Bravo” (USGS 13554).

MX-TA-1.—Tamaulipas. 15.9 km SE of Ciudad Camargo (USGS 13504).

United Kingdom.—One locality.

UK-WS-1.—West Sussex. Selsey Peninsula. Bracklesham Beds, Selsey Formation (Tracey et al., 1996; Squires, 1997).

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