

Paleocene pareorine turritellid gastropods from the Pacific slope of North America

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ABSTRACT

This paper presents the first detailed study of *Mesalia martinenezensis* (Gabb, 1869) and *Mesalia clarki* (Dickerson, 1914a), the only two known pareorine (spout-bearing) turritellid gastropods from the Pacific slope of North America. Both species are redescribed, in light of new morphologic information that also confirms their assignment to genus *Mesalia* Gray, 1847, which we believe to be congeneric with *Sigmesalia* Finlay and Marwick, 1937. New stratigraphic information allows for refinement of the chronologic range of each species. *Mesalia martinenezensis* is of early late Paleocene (late Danian) to early late Paleocene (early Thanetian) age and ranges from northern California to northern Baja California. *Mesalia clarki* is of late middle to early late Paleocene age (late Selandian to early Thanetian) age and is known only from California; in southern California it is restricted to a coralline-algal facies. Both species have considerable variability in their spiral sculpture.

Mesalia originated during either the Late Cretaceous (Maastrichtian) in northern Africa or the early Paleocene (Danian) in northern Africa and western Iran. It became widespread during the warm (greenhouse) conditions of the Paleocene and Eocene but became geographically restricted during subsequent cooler global conditions. *Mesalia* is an extant genus with possibly six species, and whose total geographic range is in coastal waters in southern Portugal, southern Spain, Mediterranean Sea (primarily the western part), Canary Islands, and the west coast of northern Africa.

INTRODUCTION

The object of this study was to rectify the identification uncertainties concerning the only two known pareorine (spout-bearing) turritellid gastropod species from shallow-marine rocks on the Pacific slope of North America. They are *Mesalia martinenezensis* (Gabb, 1869) and *Mesalia clarki* (Dickerson, 1914a). Most modern workers

(e.g., Zinsmeister, 1983) have generally placed both species in *Mesalia* Gray, 1847, but some workers (e.g., Saul, 1983a: fig. 2; Squires, 2003: table 2.4) have been hesitant to unequivocally use the genus name because of inadequate morphologic information about these species. The shape of the aperture of the latter one was unknown until now, and apertural information is critical in distinguishing pareorine gastropods from similar looking turritellids (see "Systematic Paleontology" for morphological comparisons). There has also been the possibility that *Mesalia macreadyi* Waring, 1914, which has commonly been put into synonymy with *M. martinenezensis*, could be a distinct species.

We conclude that there are only two species, both belonging to *Mesalia*, which we believe to be congeneric with *Sigmesalia* Finlay and Marwick, 1937. In addition to providing new morphologic information about the study area *Mesalia*, we refine their geographical (Figure 1) and chronologic ranges (Figure 2). Both *M. martinenezensis* and *M. clarki* have considerable variability in their spiral sculpture.

Mesalia has long been reported (e.g., Cossmann, 1912) as originating during the Late Cretaceous in the region between northern Africa and western Iran. Our review of the literature shows that the genus most likely originated during either the Late Cretaceous (Maastrichtian) or the early Paleocene (Danian) in this Old World region.

Modern systematic studies of *Mesalia* are sorely lacking as are detailed ecologic studies of the few extant species. The classification scheme used here follows that of Bouchet et al. (2005: 249), and morphological terms are taken from Cox (1960). Pacific slope of North America *Turritella* zones are taken from Saul (1983b).

Institutional abbreviations used in the text are: ANSP: Academy of Natural Sciences of Philadelphia; LACM: Natural History Museum of Los Angeles County, Malacology Section; LACMIP: Natural History Museum of Los Angeles County, Invertebrate Paleontology Section; UCMP: University of California, Berkeley, Museum of Paleontology.

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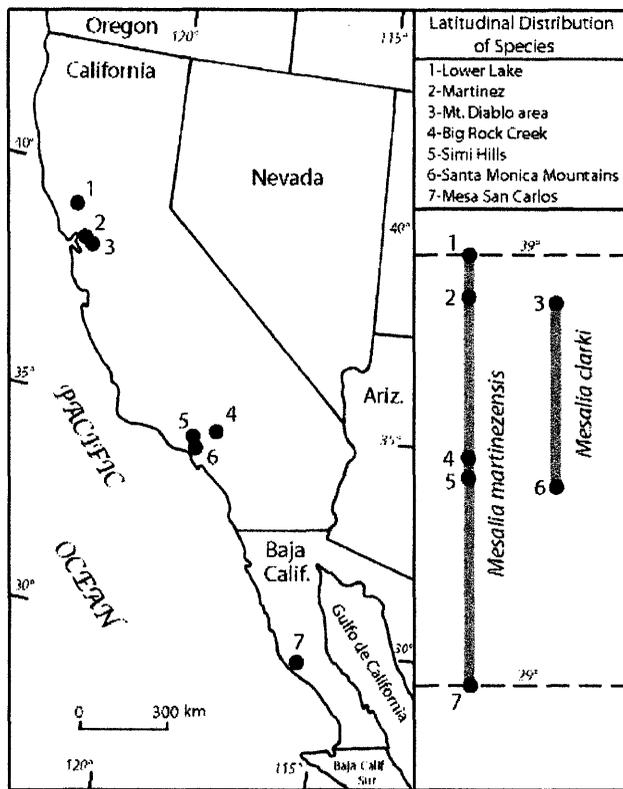


Figure 1. Locales and latitudinal distribution of the study area gastropods.

STRATIGRAPHY AND DEPOSITIONAL ENVIRONMENTS

The geologic ages of the formations and most of the depositional environments of the formations containing the two studied species are mentioned in Squires (1997).

Mesalia martinezensis is widespread in the study area (Figure 1) and always found in siltstone or sandstone beds that formed either as storm accumulations of mollusk-rich assemblages in shelfal-marine depths or as localized displaced shallow-marine mollusks in deeper

depths. These mollusks commonly include shallow-marine mollusks such as naticid and buccinid gastropods, as well as glycymerid and crassatellid bivalves. All are indicative of normal marine salinities.

The type locality of *Mesalia martinezensis* has been generally assigned (e.g., Keen and Bentson, 1944) to the "Martinez Formation" in the vicinity of the city of Martinez, Contra Costa County, northern California (Figure 1). The history of how early workers referred to this originally poorly defined "formation" has been summarized by Mallory (1959). In this present study, we follow the work of Weaver (1953), who refined the stratigraphy of the Paleocene and Eocene formations in the vicinity of the area where the "Martinez group" was first established. He established new stratigraphic names, and the rocks that pertain to the type locality of *M. martinezensis* belong in his Paleocene Vine Hill Sandstone.

Mesalia clarki is only known from two locales: 1) its type locality (UCMP loc. 1540, see "Appendix") on the north flank of Mount Diablo, Contra Costa County, northern California, and 2) from the Santa Monica Mountains, Los Angeles County, southern California (Figure 1). Its type locality is near the site of Stewartville, and according to Dickerson (1914a: 74), this locality is "300 to 400 ft. above the base of the Martinez in hard, gray-green glauconitic sandstone." Numerous mollusks have been found at this locality (Dickerson, 1914a: 75). They consist of turritellid and buccinid gastropods, crassatellid bivalves, and other shallow-marine species, all indicative of normal marine salinities. *Turritella infragranulata pacheocensis* Stanton, 1896, which is found at this locality, is indicative of the upper middle Paleocene (upper Selandian) (Figure 2). On the geologic map of Brabb et al. (1971), the locality plots within the glauconitic sandstone lower member of the "Martinez" Formation. Megafossils are generally scarce in the "Martinez" Formation in the vicinity of this type locality (E. Brabb, personal commun.), thus, it seems plausible that the fossils probably occur in storm-derived, isolated lenses.

Mesalia clarki in the Santa Susana Formation in the Palisades Highlands area of the Santa Monica Mountains, southern California, is always found near outcrops of coralline-algal limestone. Hoots (1931: 91-92, 133-134, pl. 19B) reported that these limestones are resistant, can be cliff forming, weather white, are nodular and irregularly bedded, up to 35 m thick, up to 1200 m in lateral extent, and commonly terminate in an abrupt wall. Additional geologic and/or paleontologic details concerning these limestones are mentioned in Strathearn et al. (1988), Colburn (1996), Squires and Saul (1998), Squires and Kennedy (1998), and Squires and Saul (2001).

At LACMIP loc. 10508, in the Palisades Highlands area, abundant specimens of *M. clarki* are found in a thin coralline-algal-rich micaceous muddy siltstone bed about 1 m stratigraphically below a blocky, coralline-algal-limestone interval approximately 24 m thick. Also found

Age (Ma)	System/Series	European Stages	<i>Mesalia martinezensis</i>	<i>Mesalia clarki</i>	<i>Turritella</i> zones
55	Lower Eocene	Ypresian			
		Thanetian			<i>T. infragranulata</i>
60	Middle Paleocene	Selandian	█	█	<i>T. l. pacheocensis</i>
		Danian			<i>T. peninsularis</i> <i>T. peninsularis quateyi</i>
65	Lower Paleocene				
	Upper Cret.	Maastr.			

Figure 2. Chronostratigraphic position of the study area taxa. Ages of stage boundaries from Gradstein et al. (2004). *Turritella* zones from Saul (1983b).

in this bed is the large neritid gastropod *Corsania (Januncia) rhoga* Saul and Squires, 1997, as well as the bivalves *Plicatula lapidicina* Squires and Saul, 1998, and *Plicatula trailerensis* Squires and Saul, 1998. Occurring in nearby beds in close association with the coralline-algal deposits are the gastropods *Terebralia susana* Squires and Kennedy, 1998, and *Campanile greenellum* Hanna and Hertlein, 1939. All of these aforementioned mollusks indicate very nearshore, tropical to subtropical conditions (Squires and Saul, 1997; Squires and Kennedy, 1998). The latter workers concluded that the coralline-algal limestones, like those at locality 10508, were deposited in a protected bay (no deeper than 40 to 70 m) with warm-algal-limestone buildups associated with shoals on the bay floor. These limestone buildups are very similar in lithology and sedimentologic/tectonic setting to limestones in the Paleocene Sepultura and Bahia Ballenas formations in northern Baja California (Abbott et al., 1995), as well as similar to limestones in the upper Paleocene to lower middle Eocene Sierra Blanca Limestone in Santa Barbara County, southern California. These limestones were deposited when tectonic plate-edge strain in the fore-arc basin caused local basement highs to form within the otherwise deeper marine environment (Whidden et al., 1995; Abbott et al., 1995). It is likely that the Santa Susana Formation coralline-algal limestones formed under similar conditions.

Although *Mesalia clarki* and *Mesalia martinezensis* both occur in the Santa Susana Formation in the Santa Monica Mountains, southern California, they never occur together in the same beds. *Mesalia martinezensis* is not associated with the coralline-algal facies there or anywhere else in the study area.

PALEOBIOGEOGRAPHIC IMPLICATIONS

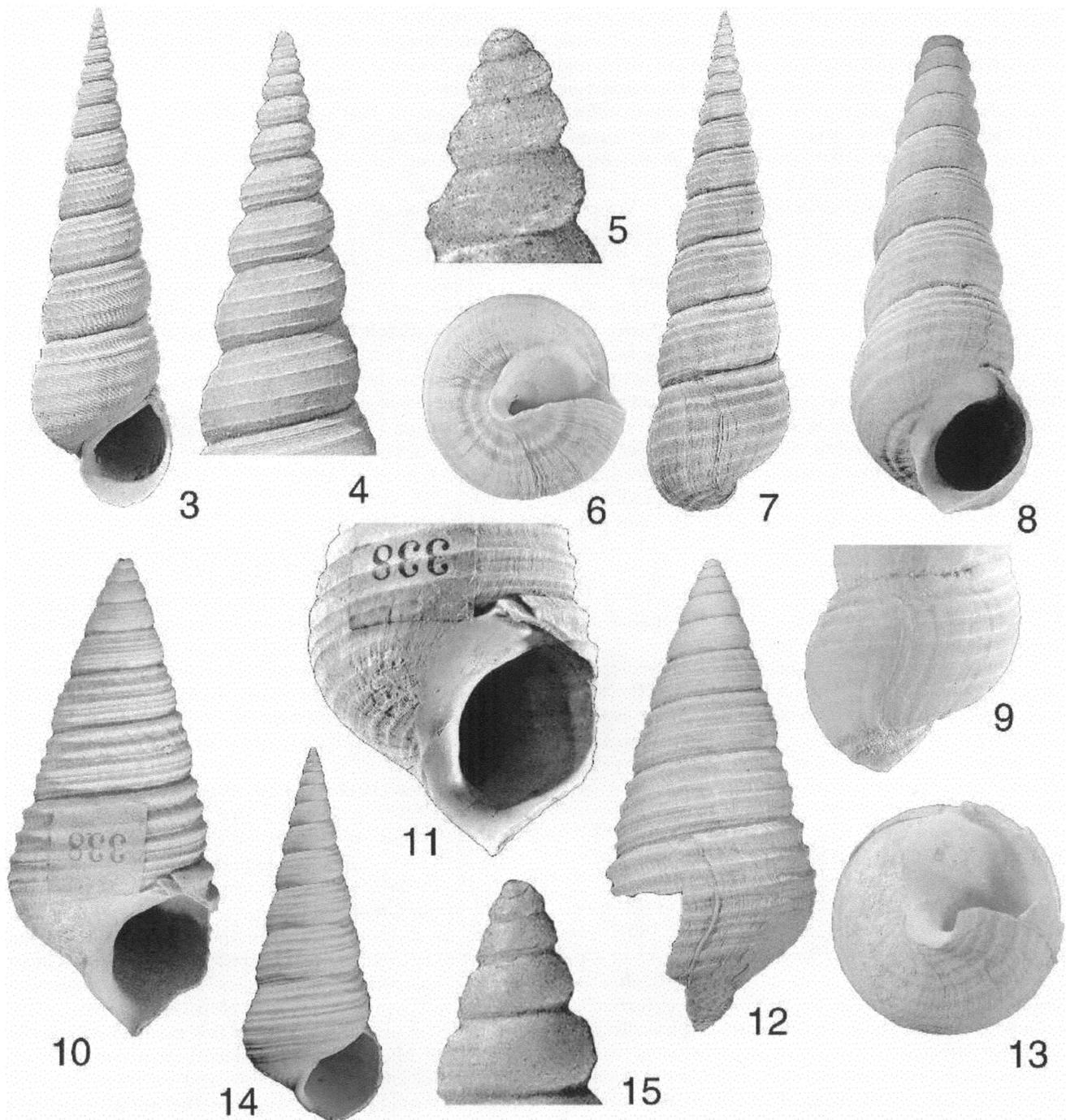
Kiel and Bandel (2004: 120, fig. 71) reported two specimens of *Mesalia* cf. *multilineata* (J. Müller, 1851) from Cenomanian strata at the Kassenberg quarry in Germany. If these specimens actually belong to *Mesalia*, they would be the geologically oldest. The conical-turriculate shell with convex whorls bearing strong spiral ribs does resemble *Mesalia*, but there are no specimens with an intact aperture nor with a protoconch. *Turritella multilineata* J. Müller (1851: 29, pl. 4, figs. 4, 6) was originally reported from the lower Campanian Aachen strata of Germany, thus, it is considerably younger than the Kassenberg quarry material. *Turritella multilineata* was also figured by G. Müller (1898: 97, pl. 13, figs. 4, 5), who reported it from middle Santonian to lower Campanian strata at Braunschweig/Ilse, Germany. There is also a mention of *T. multilineata* in Kollmann and Odin (2001: 441), and they also consider this Campanian species to belong to genus *Turritella*. The pleural angle of J. Müller's figure is much narrower than that of Kiel and Bandel (2004), and in our opinion, Kiel and Bandel's *M.* cf. *M. multilineata* (J. Müller) does not look like J. Müller's species. Kiel and Bandel (2004) tentatively syn-

onymized J. Müller's specimens and G. Müller's specimens with their Kassenberg quarry specimens. We believe, however, that Kiel and Bandel's Cenomanian specimens have nothing to do with *T. multilineata* and represent, at best, a very questionable *Mesalia*. More specimens of this possible *Mesalia* from the Cenomanian of Germany are needed in order to determine its generic assignment.

Cossmann (1912: 126) reported the chronologic range of *Mesalia* to be Late Cretaceous (Turonian) to Recent, as did Wenz (1939), who apparently simply reiterated Cossmann's findings. We were unable, however, to corroborate any of Cossmann's Cretaceous occurrences. He reported *Mesalia gazellensis* Whitfield (1891: 424, pl. 9, fig. 10) as being from the Turonian of Syria, but the aperture of this species is unknown. In addition, the sculpture is obsolete, which is unlike *Mesalia*.

Cossmann (1912: 126) listed five *Mesalia* species of Late Cretaceous (Senonian) age, and these are discussed in the following sentences. *Arcotia indica* Stoliczka (1868: 215, 469, pl. 16, figs. 12, 12a; pl. 19, fig. 6) from southern India is not a *Mesalia*. This species is also discussed later under "Systematic Paleontology." Specimens of *Turritella ventricosa* Forbes (1846: 123, pl. 13, fig. 3; Stoliczka, 1868: 227, pl. 17, fig. 15) from southern India are missing the aperture. *Turritella martinezensis* Gabb (1869: 159, pl. 28, fig. 51) from California is not of Cretaceous age. *Mesalia nettoana* White (1887: 164–165, p. 18, figs. 3, 4) from the Maria Farinha beds in Brazil is Paleocene age. *Mesalia hebe* White (1887: 165, pl. 18, fig. 5), also from Brazil, looks like a juvenile specimen of *M. nettoana*.

Cossmann (1912: 126) also listed two Late Cretaceous (Maastrichtian) species. The first one is *Mesalia jovisammonis* (Quaas, 1902: 256, pl. 26, figs. 18–20), which Quaas reported, in a very generalized way, to be associated with the *Exogyra overwegi* biozone at Ammonite Hill in the Great Sand Sea in western Egypt. This biozone can also be recognized in the Maastrichtian (but not latest Maastrichtian) part of the Ammonite Hill Member of the Campanian to Paleocene Dakhla Formation in western Egypt (Barthel and Herrmann-Degen, 1981). Tantawy et al. (2001) assigned this member an early to early late Maastrichtian age, based on planktic foraminifera, calcareous nannofossils, and macrofossils. They also determined, however, that the entire formation ranges in age from early Maastrichtian to early Danian. Immediately above the widespread K/T disconformity in the region, a sedimentologically complex sequence marks the lower Danian Bir Abu Minqar horizon, which contains a mixture of Maastrichtian (reworked) and Danian fossils, including both microfossil and macrofossil species (e.g., including some ammonites.). Unfortunately, Quaas did not provide any information as to where exactly in the stratigraphic section he collected the specimens of *M. jovisammonis*. His specimens were lost, so it is not possible to match their rock matrix to actual outcrops. Recollecting of this gastropod is necessary to decipher its exact geologic age.



Figures 3–15. Type species of *Mesalia* and *Sigmesalia*, plus comparative pictures of *Mesalia solida* (Deshayes, 1861). Specimens coated with ammonium chloride. **3–9.** *Mesalia mesal* (Adanson, 1757), Baie de Hann, Senegal, West Africa (Recent). **3–7.** Hypotype LACM 173163. **3.** Apertural view, height 45 mm, diameter 15 mm. **4.** Tip of specimen shown in previous figure, height 14 mm, diameter 5.5 mm. **5.** Protoconch and earliest spire whorls, apertural/ right-lateral view, height 1 mm, diameter 0.7 mm. **6.** Base, diameter 15.6 mm. **7.** Abapertural view, height 45 mm, diameter 15 mm. **8–9.** Hypotype LACM 173164. **8.** Oblique apertural view, height 51 mm, diameter 16.3 mm. **9.** Close-up of abapertural view of last whorl, diameter 17.2 mm. **10–13.** *Mesalia koeneni* (Le Renard, 1994), LACMIP hypotype 13397, Grignon, Paris Basin, France (middle Eocene, Lutetian Stage), height 45.8 mm, diameter 20.3 mm. **10.** Apertural view. **11.** Close-up of aperture. **12.** Right-lateral view (outer lip broken). **13.** Base. **14–15.** *Mesalia solida* (Deshayes, 1861), hypotype LACMIP 13398, Le Guépelle, Paris Basin, France (late Eocene). **14.** Apertural view, height 21.6 mm, diameter 8.1 mm. **15.** Protoconch and earliest spire whorls, apertural to slightly right-lateral view, height 1 mm, diameter 0.7 mm.

Abbass (1963: 39–40, pl. 2, figs. 20–22) illustrated *M. jovisammonis* from eastern Egypt and referred to it as *Mesalia* (*Woodsalia*) *jovisammonis* of Maastrichtian age. He did not provide, however, any discussion as to how this age was determined.

Mesalia cf. *M. multisulcata* (Lamarck 1804), reported by Serra (1937: 313–315, pl. 16, figs. 12, 12a, 13) from near Tripoli, Libya, looks like it might be conspecific with *Mesalia jovisammonis*. Serra provided no detailed stratigraphic or geologic age information.

The second species that Cossmann (1912) listed from the Maastrichtian is *Mesalia fasciata* (Lamarck, 1804) from Iran. Cossmann based this occurrence on work by Douvillé (1904: 329–330, pl. 47, figs. 23–27), who reported *M. fasciata* from the “Couches à Cérithes” beds in the Luristan region in west-central Iran. Douvillé (1904) believed that these Iranian specimens of *M. fasciata*, whose type locality is in middle Eocene (Lutetian Stage) strata at Grignon in Paris Basin, France (Eames, 1952: 34), are of Maastrichtian age, but the “Couches à Cérithes” beds contain the bivalve “*Cardita*” *beaumonti* d’Archiac and Haime, 1854, which is diagnostic of earliest Danian age in Iran and Pakistan (Douvillé, 1928; Eames, 1952; Davies, 1975). *Mesalia fasciata* is long-ranged geologically (early Paleocene to late Eocene) and widespread geographically (western Europe to Pakistan) (Eames, 1952).

Another *Mesalia* that needs investigation as to its precise stratigraphic position and geologic age is *Mesalia foucheri* Pervinquier (1912: 44, pl. 3, figs. 6–15), from the Ghadames (Garat Temblili) region in Tunisia, northern Africa. Pervinquier (1912: 336) reported the species as being of Maastrichtian age, but no critical geologic details are provided. He did differentiate between Maastrichtian and Danian fossils; thus, like in nearby Egypt and Libya, the stratigraphic section containing *M. foucheri* and other macrofossils in Tunisia, also spans the K/T boundary.

Two species of so-called *Woodsalia* Olsson, 1929, from Upper Cretaceous (Campanian?) strata in northwestern Peru (Olsson, 1944) might eventually be placed in *Mesalia*, once their apertures become known. They are: *Woodsalia paitana* Olsson (1944: 69–70, pl. 11, fig. 5) and *Woodsalia paitana robusta* Olsson (1944: 70, pl. 11, figs. 3, 9).

The so-called *Mesalia* (*Mesalia*) *mauryae* Allison (1955: 414–415, pl. 41, fig. 3; Perrilliat, 1989: 149, fig. 51h) from the upper Aptian upper member of the Alisitos Formation, Punta China region, Baja California, Mexico, is, according to Squires and Saul (2006), *Turritella seriatimgranulata* Roemer, 1849.

In addition to the above-mentioned Old World Danian species of *Mesalia*, three New World Danian species are known from the Gulf Coast of the southeastern United States. They are from the Clayton Formation (Palmer and Brann, 1966), which is of earliest Danian age (Dockery, 1986). The three species are: *Mesalia allentonensis* (Aldrich, 1894: 246–247, pl. 13, figs. 4a, 4b, 6; Stenzel

and Turner, 1942: card 110); *Mesalia hardemanensis* (Cabb, 1860: 392, pl. 68, fig. 15; Stenzel and Turner, 1942: card 116); and *Mesalia pumila* (Cabb, 1860: 392, pl. 68, fig. 14; Stenzel and Turner, 1942: card 118).

In summary, our search of the literature revealed that *Mesalia* most likely originated during either the Maastrichtian in northern Africa or the early Paleocene (Danian) in northern Africa and western Iran. During the Danian it spread quickly to the Gulf Coast of the United States by means of westward-flowing ocean currents emanating from the western Tethyan region. These currents, which existed during the Late Cretaceous (Gordon, 1973; Johnson, 1999) and continued into the Paleocene and Eocene (Saul, 1986; Squires, 1987), were part of a circumglobal-tropical current that contributed to a widespread dispersal of marine biota (Haq, 1981). By the late Danian, it reached California and northern Baja California, Mexico, as well as Belgium (Cox, 1930; Glibert, 1973). By middle Paleocene, it reached Greenland (Kollmann and Peel, 1983), and by the late Paleocene, it reached Nigeria (Adegoke, 1977). During the Paleocene and Eocene, *Mesalia* reached its peak diversity and became most widespread, with occurrences mainly in the Old World western Tethys Sea region. We did not detect, however, any reported occurrences in Australia, New Zealand, Japan, or Antarctica. The Paris Basin of France (see Cossmann and Pissarro, 1910–1913), southwestern Nigeria (Adegoke, 1977), and the Gulf Coast of the United States (Stenzel and Turner, 1940, 1942; Palmer and Brann, 1966) are the principal areas in which numerous species of *Mesalia* have been recognized. Some species became very widespread. For example, as mentioned earlier, *Mesalia fasciata* ranged from the Paris Basin, France to Pakistan (Eames, 1952). After the warm greenhouse conditions that existed during the Eocene, *Mesalia* was much reduced in its distribution and mainly occurred in what is now the Mediterranean Sea region (Cossmann, 1912).

MODERN MESALIA

Mesalia is extant and review of the scant literature, as well as use of the internet (note: <<http://www.alboranshells.com/turritellidae>> was particularly helpful), revealed as many as possibly six species. They are the following: *M. mesal* (Adanson, 1757), *M. brevisalis* Lamarck, 1822; *M. varia* Kiener, 1843; *M. opalina* Adams and Reeve, 1850; *M. freytagi* von Maltzan, 1884; and *M. flammifera* Locard, 1897, which includes the subspecies *M. flammifera flammifera* Locard, 1897 and *M. flammifera simplex* Locard, 1897. There is much confusion as to exactly how many species there are, and potential synonyms need to be resolved. For example, some workers (e.g., Smith, 1915; Bowles, 1939) equated *M. mesal* with *M. brevisalis*, but other workers (e.g., Advovini and Cossignani, 2004) separated them. Bowles (1939) gave a thorough review of the nomenclatural history of *Mesalia brevisalis*.

A comprehensive malacological study of the modern species of *Mesalia* is greatly needed. Because of the uncertainties stemming from the poorly known systematics, it is confusing to try to determine which species is found where. We were able to establish with certainty (see references below), however, that modern *Mesalia* is only found in the Atlantic coastal areas of southern Portugal, southwestern Spain, Morocco, Canary Islands, Western Sahara, Mauritania, Senegal, and Guinea, as well as in the westernmost Mediterranean Sea, particularly in the Alboran Sea (i.e., Strait of Gibraltar to southern Spain on the north and Morocco on the south) and the Aegean Sea region of western Turkey.

Mesalia mesal and *M. brevisialis* have the widest distribution. *Mesalia mesal* has been reported from the Algarve region of southern Portugal, the Algeiras region of southwestern Spain, and the Alboran Sea (Poppe and Goto, 1991), the Canary Islands (Macedo and Borges, 1999), Senegal (Bouchet, 1977; Ardochini and Cossignani, 2004), and western Turkey (Demir, 2003). *Mesalia brevisialis* has been reported from the Algarve region of southern Portugal (Afonso et al., 2000; Alves et al., 2003), southwestern Spain and the Alboran Sea (Hidalgo, 1917), Senegal (Ardochini and Cossignani, 2004), and Guinea (Pasteur-Humbert, 1962). *Mesalia opalina* has been reported from the Canary Islands and Morocco (Poppe and Goto, 1991), as well as from Mauritania (Ardochini and Cossignani, 2004). The other modern species/subspecies of *Mesalia* are apparently restricted to the northwestern coast of Africa (Ardochini and Cossignani, 2004).

Mesalia melanioides Reeve, 1849, was reported (Smith, 1915) to be from West Australia, but this species is now the type species of *Neodiastoma* Cotton, 1932, which differs from *Mesalia* by having axial sculpture on the early spire. Marwick (1957) summarized the systematics of *Neodiastoma* and classified it as a pareorine.

Mesalia is found today on both muddy and sandy bottoms in coastal waters ranging in depth from lower intertidal to 20 m (Hidalgo, 1917; Pasteur-Humbert, 1962; Poppe and Goto, 1991; Afonso et al., 2000; Demir, 2003; Alves et al., 2003). Bouchet (1977) reported that *M. mesal*, although not common there, can be found in the seaward part of mangrove-swamp systems along the coast of Senegal. Specimen LACM 17316 (Figures 3–7) of *M. mesal* was collected in approximately 5 m depth, on sand and rubble in Senegal.

Large numbers of *M. mesal* have been reported (Afonso et al., 2000) as almost always being partially infaunal (with their apices pointed upward) when found on exposed low-tide mud flats on the inner lagoon sides of islands within the Rio Formosa coastal-lagoon system of southern Portugal.

The modern ecological parameters mentioned above are not totally reliable for fossil *Mesalia* because preferences for substrate and depth of water might have possibly changed over time. In addition, the fossil occurrences of *Mesalia* had a pan-Tethyan distribution,

whereas the modern occurrences have contracted primarily to the Iberian Peninsula, Alboran Sea, and northwestern Africa.

SYSTEMATIC PALEONTOLOGY

Superfamily Cerithioidea Fleming, 1822
Family Turritellidae Lovén, 1847

Discussion: Allmon (1996: 9–12, table 1) thoroughly reviewed the history of the classification of turritellid gastropods and listed the five subfamilies and all the genera/subgenera within each subfamily. These subfamilies are: Turritellinae Löven, 1847; Protominae Marwick, 1957; Pareorinae Finlay and Marwick, 1937; Vermiculariinae Lamarck, 1799; and Turritellopsinae Marwick, 1957. Bouchet et al. (2005) included the first four of these subfamilies, but removed Turritellopsinae. Instead, they included subfamily Orectospirinae Habe, 1955.

Subfamily Pareorinae Finlay and Marwick, 1937

Discussion: Pareorine turritellids are characterized from the other subfamilies of family Turritellidae by having an aperture obliquely effuse over the anterior end of the columella and forming a sinus (short spout), with the adapical margin of the sinus usually making a spiral ridge on the columella (Marwick, 1957).

Mesalia can be readily identified if its aperture is intact, but when it is missing, workers have commonly misassigned it to the similar looking genus "*Turritella*" Lamarck, 1799, *sensu lato*, a group comprising at least 35 genera and subgenera names (Allmon, 1996), all of which are turritellines whose apertures do not have a sinus (short spout) at the anterior end of the aperture nor have a spiral ridge on the columella. In addition, according to Smith (1915), the corneous operculum of *Mesalia* is paucispiral and not multispiral, as in "*Turritella*," but this later distinction is not useful when studying fossil species.

Ten pareorine genera were listed by Marwick (1957), who also provided illustrations of the growth-line traces of some of these genera. Comparative information about the stratigraphic range, growth-line details, whorl profile, and protoconch shape of most of these genera was given by Allmon (1996: table 1).

Genus *Mesalia* Gray (*nomen nudum*, 1840), 1847

Type Species: *Cerithium mesal* Adanson, 1757 [= *Turritella mesal* Deshayes, 1843], by original designation; Recent, southern Portugal, southwestern Spain, Alboran Sea, Canary Islands, Senegal, and western Turkey.

Description: Small to large (up to approximately 95 mm shell height), turritelliform, slender to conical rotund. Pleural angle ranges from 15° to 41°. Protoconch conical, small, smooth, and approximately two whorls. Protoconch to teleoconch transition gradual. Teleoconch whorls up to 16, whorl sides convex to flattish/concave. Sculpture on early juvenile teleoconch whorls variable, ranging from nearly smooth or with very fine, unicostate, bicostate, or tricostate spiral lirae; sculpture on adult

whorls highly variable, ranging from smooth to numerous, weak to moderately strong closely spaced spiral ribs, but less commonly with fewer and more prominent spiral ribs. Growth lines parasigmoidal on last whorl (including base); lateral sinus variable in amount of concavity (flexure). Aperture with shallow effuse spout, ranging from somewhat constrained to broad. Adapical edge of spout usually forms weak spiral ridge that continues onto columella.

Discussion: *Mesaliopsis* Thiele, 1929 [type species: *Mesalia opalina* (Adams and Reeve, 1850)], recent, was reported by Wenz (1939) to be a subgenus of *Mesalia*, but future work might show it to be synonymous with *Mesalia*.

Mesalia somewhat resembles *Lithotrochus* Conrad, 1855, of Jurassic age from Chile, South America. Cossmann (1912: 125) reported *Lithotrochus* to be a junior synonym of *Mesalia*, but Wenz (1938: 280, fig. 596) and Cox (1960: 1248–1249, fig. 159, 11) believed *Lithotrochus* to be a trochid. It is an extraordinarily large gastropod (height 125 mm) with a wide pleural angle, domed upper spire, turritelliform shape, anteriorly carinate whorls, and relatively few spiral ribs. Details of its aperture are unknown.

Cossmann (1912: 125) also reported *Lithotrochus* to be a junior synonym of *Arcotia* Stoliczka, 1868, whose type species, *Arcotia indica* Stoliczka (1868: 215, 469, pl. 16, figs. 12, 12a; pl. 19, fig. 6) is from Upper Cretaceous (Trichinopoly Group) strata near the town of Alundanapooram, southern India. According to Sundaram et al. (2001: fig. 3), this town's name is also referred to as Alundalippur and, from information in their map, this town is underlain by the Kulakkalnattam Formation of Turonian age. Wenz (1939) synonymized *Arcotia* with *Mesalia*. Finlay and Marwick (1937) reviewed the morphology of *Arcotia* and reported that, based on its straight growth lines and open umbilicus, this genus is not a synonym of *Mesalia*. They reported, furthermore, that *Arcotia* appears to be a mathildid. Bandel (2000) came to the same conclusion.

Mesalia is similar to the pareorine *Woodsalia* Olsson 1929, whose type species, *Woodsalia negritosensis* Olsson (1929: 13–15, pl. 4, figs. 5, 6) is from lower Eocene rocks in northwestern Peru. Woods (1922: 78–79, pl. 7, figs. 5–7; pl. 8, figs. 1–3) and Wenz (1939: 651, fig. 1852, two views) also illustrated this species. The full shape of the aperture of this Peruvian gastropod, however, is not known.

Genus *Sigmesalia* Finlay and Marwick, 1937, was originally erected to accommodate a group of Eocene gastropods from the Paris Basin, France that were previously identified as *Mesalia*. There has been no consensus as to whether or not *Sigmesalia* is a distinct genus. Marwick (1957) reported it to be a separate genus, as did Le Renard (1994). Eames (1952) reported it to be a subgenus of *Mesalia*, and Palmer and Brann (1966) reported *Sigmesalia* to be synonymous with *Mesalia*.

Various views of representative specimens of the type

species of *Mesalia* are illustrated in Figures 3–9, and various views of a representative specimen of the type species of *Sigmesalia* are illustrated in Figures 10–13. Its type species, *Sigmesalia koeneni* Le Renard, 1994 [new name for *Turritella sulcata* Lamarck, 1804 (original designation), *non* Bosc, 1801], is of middle Eocene (Lutetian) age and from Paris Basin, France. Finlay and Marwick (1937) stated that the aperture and growth lines of the type species of *Mesalia* seem to be generically different than those of the Paris Basin shells, but they did not provide any details. Davies (1971: 312, figs. 677a, 677b) mentioned that the growth lines of *Sigmesalia* have a more flexed outer lip sinus than does *Mesalia*. According to Marwick (1957: 163), *Sigmesalia* differs from *Mesalia* by usually having a wider pleural angle. The following paragraphs deal with our observations concerning these proposed diagnostic features of *Sigmesalia*.

Inspection of representative specimens of several of the Eocene Paris Basin species, including the type species of *Sigmesalia*, stored in the LACMIP collection, as well as inspection of photographs of 17 Paris Basin species (see Cossmann and Pissarro, 1910–1913: pl. 21, figs. 126–1 to 126–15), revealed variability in the shape of the aperture of *Sigmesalia*. For example, the aperture of *Sigmesalia incerta* (Deshayes, 1832; Cossmann and Pissarro, 1910–1913: pl. 21: fig. 126–4, two views) is similar to that of *M. mesal*, in that the spout is broad and not well constrained. The aperture of *Sigmesalia koeneni* however, is better developed (Cossmann and Pissarro, 1910–1913: pl. 21, fig. 126–15).

The amount of flexure of the outer lip sinus is basically similar in all the Eocene Paris Basin species, although *Mesalia solida* (Deshayes, 1861) does show some variability. The amount of flexure of this feature is variable in *M. mesal* and can be similar to the amount seen on Eocene Paris Basin species. Variability in the amount of flexure for both the Eocene and modern *Mesalia* shells can also occur in proximity of growth checks and breakages of the outer lip incurred during the life of the gastropod.

The pleural angle of the Eocene Paris Basin shells is quite variable, ranging from 21° to 41°, but the low end of this range [e.g., *Mesalia ecki* (Laubrière, 1881; Cossmann and Pissarro, 1910–1913: pl. 21, fig. 126–2)] is very close to the value (16° to 18°) on *M. mesal*. *Sigmesalia koeneni* has one of widest pleural angles (41°; see Figures 10 and 12). For comparative purposes, an illustration (Figure 14) is provided for *Sigmesalia solida*. It has a relatively narrow pleural angle of 25°, more like that found on *M. mesal* (Figures 3, 4, and 7).

Other morphologic features that are variable on the Eocene Paris Basin shells are strength and number of spiral ribs, pattern of development of sculpture on the early juvenile teleoconch whorls, and degree of indentation of the suture. Even the strength of the spiral ridge (Figure 10) on the columella is variable. *Mesalia mesal* possesses a spiral ridge on the columella, as do most specimens of *Sigmesalia koeneni* (compare Figures 8 and 11).

A few species of *Sigmesalia* are similar to *Mesalia* in having a relatively narrow pleural angle and bicostate sculpture on the early juvenile whorls but not on the adult whorls. They are the following: *Sigmesalia instabilis* (Briart and Cornet, 1873: 86, pl. 12, figs. 9a–9b) of early Paleocene (Danian) age from Belgium; *Sigmesalia salvani* (Adegoke, 1977: 86–88, pl. 14, figs. 10–16) of Paleocene age from Nigeria; and *Sigmesalia fasciata* (Lamarck, 1804: 217) from Eocene strata in France, Belgium, and Pakistan (Cossmann and Pisarro, 1910–1913; Cox, 1930; Eames, 1952); *Sigmesalia pagoda* (Cox, 1930: 160–161, pl. 18, figs. 6a–b, 7a–b) from Eocene strata in Pakistan; *Sigmesalia biplicata* (Bowles, 1939: 328, pl. 34, figs. 6, 8) from Paleocene strata in Alabama; and *Sigmesalia gomün* (Bowles, 1939: 326–327, pl. 33, fig. 9) from Paleocene strata in South Carolina.

The protoconchs of *Mesalia mesal* and *Sigmesalia solida* are very similar (compare Figures 5 and 15); both are small, smooth, have essentially the same shape, and the transition to the teleoconch is gradual.

In summary, we found that the morphologic features of the Eocene Paris Basin shells are variable. We could find no reliable, constant morphologic characters to distinguish *Mesalia* from *Sigmesalia*; hence, we regard them as congeneric.

Mesalia martinezensis (Gabb, 1869)
(Figures 16–23)

Turritella martinezensis Gabb, 1869: 169–170, 228, pl. 28, fig. 51; Dickerson, 1914a: pl. 13, fig. 10; Waring, 1917: 100, pl. 14, fig. 5.

Turritella maccreeadyi Waring, 1914: 783; Waring, 1915: fig. 15 [not fig. 14]; Waring 1917: 87–88, pl. 12, fig. 10.

Mesalia maccreeadyi (Waring).—Paredes-Mejia, 1989: 176–177, pl. 3, figs. 3–6.

Mesalia martinezensis (Gabb).—Cossmann, 1912: 126; Stewart, 1927: 353–354, pl. 25, fig. 1; Schenck and Keen, 1940: pl. 20, fig. 5; Merriam, 1941: 127–128, pl. 39, figs. 1–5, 7; Zinsmeister, 1974: 118–119, pl. 12, figs. 5, 9; Zinsmeister, 1983: pl. 2, fig. 14; Paredes-Mejia, 1989: 173–176, pl. 3, figs. 7–10; Saul, 1983a: text-fig. 2, pl. 1, fig. 2.

Mesalia clarki (Dickerson).—Zinsmeister, 1983: pl. 2, fig. 13.

Description: Large (up to approximately 95 mm height). Turritelliform. Pleural angle approximately 20°. Protoconch unknown. Teleoconch up to 12 whorls, increasing rapidly in size from the apex. Suture slightly impressed. Sculpture consisting only of spiral ribs of differing strength but dominated by carina located anteriorly; ribs generally becoming stronger with growth; spiral threads on interspaces and on carina surface. Carina usually strongly angulate but can be rounded or even subdued. Posterior to carina, several widely spaced spiral ribs of variable strength occur, ranging from tertiaries to primaries: two ribs on uppermost spire, three to four on upper spire, and one to three on lower spire. Anterior to carina, several spiral ribs of variable strength occur, ranging from tertiaries to primaries: approximately five ribs on upper spire and one to two ribs (both occasionally

quite prominent) on lower spire. Last whorl with three primaries, both posterior and anterior to carina. Base with three secondaries, anteriormost one weak; ribs obsolete on short neck. Aperture relatively small, D-shaped; columella relatively broad, smooth; spout effuse and short with anterior end projecting slightly; growth-line trace of last whorl (including base) parasigmoidal, with lateral sinus flexure strongest in vicinity of carina.

Holotype: ANSP 4344, height 57 mm, diameter 23 mm.

Type Locality: Martinez, northern California (details not given).

Geologic Range: Late early Paleocene to early late Paleocene (near the Danian-Selandian boundary to early Thanetian).

Distribution: DANIAN = *Turritella peninsularis qualey* Zone: lower San Francisquito Formation, Warm Springs Mountain, Los Angeles County, southern California (new stratigraphic occurrence, LACMIP loc. 21581). NEAR THE DANIAN-SELANDIAN BOUNDARY = *Turritella peninsularis qualey* Zone transitional with *Turritella peninsularis* Zone: Martinez Formation, Herndon Creek east of Lower Lake, Lake County, northern California (Stanton, 1896 [faunal list]; Dickerson, 1914a; Merriam, 1941); upper Las Virgenes Sandstone, Simi Hills, Ventura County, southern California (Waring, 1917; Nelson, 1925 [faunal list]; Merriam, 1941; Zinsmeister, 1983; Saul, 1983a). PROBABLY NEAR THE DANIAN-SELANDIAN BOUNDARY: Reworked specimens in Santa Susana Formation, Poison Oak Canyon, north side Simi Valley, Los Angeles County, southern California (new stratigraphic occurrence, LACMIP loc. 21554); Reworked specimens in Stokes Canyon Breccia Member of the middle Miocene Calabasas Formation, Stokes Canyon, Santa Monica Mountains, Ventura County (new stratigraphic occurrence, LACMIP loc. 25281). SELANDIAN = *Turritella peninsularis* Zone: Lower Vine Hill Sandstone, Martinez area, Contra Costa County, northern California (Weaver, 1953 [faunal list]); lower San Francisquito Formation, Pinyon Ridge east of Big Rock Creek, Valymero area, Antelope Valley, Los Angeles County, southern California (Dickerson, 1914b [faunal list]; Merriam, 1941; Kooser, 1980 [faunal list]); lower Santa Susana Formation (= "Martinez marine member" of Nelson, 1925 [faunal list]), Simi Hills, Ventura County, southern California (Kew, 1923 [faunal list]; Nelson, 1925 [faunal list]; Zinsmeister, 1983; Saul, 1983a). LOWER THANETIAN = *Turritella infragranulata* Zone: Upper Vine Hill Sandstone, Martinez area, Contra Costa County, northern California (Weaver, 1953 [faunal list]); upper Santa Susana Formation, Palisades Highlands, Santa Monica Mountains, Los Angeles County, southern California (new stratigraphic occurrence, LACMIP locs. 7060 and 11717); Sepultura Formation, Mesa San Carlos, northern Baja California, Mexico (Paredes-Mejia, 1989).