A New Species of *Attiliosa* (Muricidae: Neogastropoda) from the Upper Eocene/Lower Oligocene Suwannee Limestone of Florida

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Abstract. Attiliosa aenigma, sp. nov., a muricine muricid, is described from the shallow water, carbonate paleoenvironment of the uppermost Eocene/lowermost Oligocene Suwannee Limestone of Florida. This new species predates all other New World species of Attiliosa Emerson, 1969, by roughly 15 ma and is contemporaneous with, or slightly older than, the oldest known fossil species of Attiliosa from the Old World. This new occurrence indicates that phylogenetic diversification and geographic range expansion in Attiliosa took place much earlier than previously thought. Attiliosa aenigma, sp. nov. is most similar in morphology to the Recent A. bozzettii Houart, 1993, from Somalia. Both have up to four nodules on the anterior portion of the columella, a posterior channel along the outer lip of the aperture, and fine, closely spaced and paired cords on the upper portion of the body whorl. This latter feature has not been described in muricine muricids until now, although it may have significance for muricine phylogeny.

INTRODUCTION

In a series of papers revising the systematics and fossil history of the muricid genus Attiliosa Emerson, 1968, E. Vokes proposed that Attiliosa likely originated in the Old World from within the Poirieria clan of the muricid subfamily Muricinae (Vokes, 1971, 1976, 1988, 1989, 1992, 1999; Vokes & D'Attilio, 1982). In support of this hypothesis, Vokes noted potential synapomorphies in the shells of both fossil and Recent Poirieria (Panamurex) Woodring, 1959, and Attiliosa, such as the presence of columellar nodules and labral lirations in the aperture, and general similarities between the radulae of living species of Attiliosa and Poirieria (Vokes, 1976, 1992, 1999). Vokes' revision of the Attiliosa fossil record has also shown that the earliest geological occurrence of the genus is an undescribed species from the early Oligocene of France. The oldest Attiliosa in the fossil record of the Americas reported by Vokes is from the late early Miocene Chipola Formation of Florida (Vokes, 1989, 1992, 1999).

In the present study, we describe an enigmatic new species of muricid gastropod from the latest Eocene/earliest Oligocene of Florida, which we refer tentatively to the genus *Attiliosa*. This new fossil species predates all other New World *Attiliosa* by at least 15 ma, and it is roughly contemporaneous with, or possibly even slightly older than, the oldest known species of *Attiliosa* in the fossil record from France. In addition, we discuss the paleoecology of the Suwannee Limestone in order to provide general information on the ecology and habitats present. Finally, we report a previously undocumented shell character found in certain members of the *Poirieria* clan, which may offer further insight into the phylogeny and evolutionary history of this problematic group.

GEOLOGY AND PALEOECOLOGY

The most diverse Paleogene molluscan fauna known from Florida (Mansfield, 1937, 1939; Vokes, 1992; Petuch, 1997) occurs at a now disused limestone quarry informally named Terramar 01 (= University of Florida [UF] locality PO017). The quarry is located approximately 9.7 km northwest of Socrum, S 1/4, sec. 10, T. 26 S, R. 22 E, Socrum Quadrangle USGS 7.5' series (1987), Polk County, Florida (Figure 1). Intensive collecting of spoil piles near the water-filled quarry by staff and volunteers of the Florida Museum of Natural History (FLMNH) from 1988 until 1992 yielded numerous silicified invertebrate taxa as well as remains of sirenians and fishes (primarily sharks). During de-watering of the pit in 1990, R.W.P. observed in situ, a fine-grained, white limestone underlying an upper silicified zone containing numerous completely or incompletely silicified pseudomorphs of Foraminifera, Cnidaria, Bryozoa, Mollusca, and Echinodermata. Based on lithology and the abundant presence



Figure 1. Map of Florida showing location of Terramar 01 (= University of Florida [UF] locality PO017). The quarry is located 9.7 km northwest of Socrum, Polk County, Florida.

of the irregular echinoid *Rhyncholampas gouldii* (Bouvé) throughout the white limestone and silicified zone and the strombid gastropod *Orthaulax hernandoensis* Mansfield, in the silicified zone, the unit was referred to the Suwannee Limestone.

Cooke & Mansfield (1936) originally defined the Suwannee Limestone as a hard, crystalline, yellowish limestone exposed along the Suwannee River near Ellaville, Florida with fossils of *Cassidulus gouldii* (= *Rhyncholampas gouldii*). Typically, the formation is a white to pale orange, soft, and porous wackestone, packstone, or grainstone with loosely cemented foraminifera, common echinoids, and rare to locally abundant mollusks. Moderate variation in lithology exists in the formation throughout its areal distribution, and induration varies from incompletely cemented to highly cemented to silicified. The Suwannee Limestone is exposed intermittently at the surface from central peninsular Florida to the eastern panhandle region and has been recorded in the subsurface as far south as Key West (Bryan, 1991).

Brewster-Wingard et al. (1997) provided an age estimate for the deposition of the Suwannee Limestone of peninsular Florida using an integrated approach of lithostratigraphic, biostratigraphic (primarily mollusks and dinocysts), and chronostratigraphic (Strontium isotopes) analyses. They determined the Suwannee Limestone to have a depositional age of 36.9 to 30.9 ma (± 1 –3 ma), which they considered early Oligocene based on the time scale of Berggren et al. (1985). A revised Cenozoic geochronology presented by Berggren et al. (1995) now places the Eocene/Oligocene boundary at 33.7 ma; thus, deposition of the Suwannee Limestone may have begun during the late Eocene. Although the Brewster-Wingard et al. (1997) study did not analyze Terramar 01 material, Jones et al. (1993) determined an ⁸⁷Sr/⁸⁶Sr isotope age for the Suwannee Limestone at Terramar to be 33.6 to 34.1 ma (± 0.5 –1.0 ma) based on analysis of asteroid (cf. *Goniodiscaster* sp.) marginal ossicles. Following the time scale of Berggren et al. (1995), the Jones et al. (1993) strontium dates indicate the Suwannee Limestone at Terramar 01 straddles the Eocene/Oligocene boundary.

The environment of deposition of the Suwannee Limestone was essentially like that found today off the Florida keys with a shallow water, marine environment floored with carbonate sands and mud and inhabited by a wide range of invertebrates, including corals (Cooke, 1945; Randazzo, 1972; Bryan, 1991; Petuch, 1997). This is generally consistent with what is known of habitat occurrences for modern species of Attiliosa, which are commonly collected from 20-30 m depth under coral rubble (Vokes, 1989, 1992, 1999). Several Suwannee Limestone localities contain coral-dominated buildups; and abundant branches of Stylophora sp., massive colonies of Siderastrea sp., and large heads of Astrocoenia sp. have been reported from Terramar 01 (Bryan, 1991). However, based on the common remains of dugongs (sea cows) and the low diversity of branching and massive colonial corals at Terramar 01, the paleoenvironment probably comprised a patch reef and/or coral thickets with sea grass beds, not true reef tracts (Bryan, 1991). Petuch (1997) reported four main substrate types at Terramar 01: bioherms of Stylophora; deeper lagoonal open bottom areas; sea grass beds; and very shallow water oyster beds and intertidal mud flats. While Petuch's interpretation of the paleoecology represented by this fauna generally agrees with prior interpretations, it must be pointed out that nearly all the material obtained from Terramar 01 was collected as spoil and that material collected in situ during de-watering in 1990 indicated transport. No paired valves of bivalves were found, no preferred orientations were observed, and invertebrate taxa representing different habitats were jumbled together. Clearly, either relatively high wave or current action, as indicated by the presence of small-scale cross beds (Huddlestun, 1993), played a role in the formation of this deposit. Furthermore, Petuch's report of an unmapped and still-unstudied Oligocene coral reef tract that developed farther to the west of Terramar 01 is unsubstantiated.

SYSTEMATIC PALEONTOLOGY

The following locality number and catalogued specimens are those of the Invertebrate Paleontology Division, Florida Museum of Natural History (FLMNH), University of Florida, Gainesville (collection acronym UF), and the Institut royal des Sciences naturelles de Belgique (IRSNB).

Class GASTROPODA

Order NEOGASTROPODA

Superfamily MURICACEA

Family MURICIDAE Rafinesque, 1815

Subfamily MURICINAE Rafinesque, 1815

Genus Attiliosa Emerson, 1968

Type species: *Coralliophila incompta* Berry, 1960 (= *Peristernia nodulosa* A. Adams, 1855), by original designation.

Attiliosa aenigma Herbert & Portell, sp. nov.

(Figures 2a-d)

Material examined: Holotype (UF 103371). Height 17.1 mm; maximum diameter 10.3 mm.

Type locality: UF locality PO017, Terramar 01 (West Coast Mine), 9.7 km northwest of Socrum, Socrum Quadrangle USGS 7.5' Series (1987), S 1/4, sec. 10, T. 26 S, R. 22 E, Polk County, Florida. Collected from spoil by Roger Portell and Kevin Schindler, November 1989.

Stratigraphic distribution: Known only from the type locality.

Etymology: aenigma (L.) = a mystery or puzzle. A reference to our tentative assignment of the new species to the genus *Attiliosa*.

Description: Shell of average size for genus, body whorl inflated. Protoconch and early teleoconch whorls eroded. Spire low, with six visible teleoconch whorls. Spire, last body whorl, and canal (incomplete) each approximately one-third of total shell height. Axial ornamentation comprising nine, thick, rounded ribs on earliest teleoconch whorls, reduced to seven on final whorl. Ribs strong over entire last body whorl, arch-shaped, adherent to previous whorl, and converging with other ribs at suture and tip of siphonal canal. Spiral ornamentation on early whorls not visible due to worm nature of holotype. Final whorl with 15 primary cords of approximately equal strength. Cords paired on adapical portion of penultimate and last whorls. Aperture broad posteriorly, constricted anteriorly. Abapical portion of columella with three or four nodules, the adapical-most nodule being strongest and slightly separated from remaining ones. Low parietal ridge formed by protuberance of rib from previous whorl. Parietal shield broad, adherent to whorl, and flattened ventrally over its abapical half. Adaxial margin of outer lip with eight strong lirae becoming obsolete within. Lirae visible again farther back inside aperture ($\sim 5 \text{ mm}$ from edge of



Figure 2. Attiliosa aenigma Herbert & Portell, sp. nov. UF 103371 (Holotype); height 17.1 mm, maximum diameter 10.3 mm. Locality: Terramar 01 (PO017), Suwannee Limestone, Polk County, Florida. a. Apertural view. b. Abapertural view. c. View of fine, closely spaced, paired cords on the upper portion of the body whorl. d. Apertural view showing presence of columellar nodules.

aperture) corresponding to resting point at previous lip. Adapical-most lira within aperture separated from anterior seven, delineating a shallow posterior canal. Lower tip and abaxial lip of canal missing. Pre-terminal canals visible over last whorl indicating canal constricted, short, and recurved distally, forming a shallow pseudoumbilicus.

Discussion: We assign the new species, *Attiliosa aenig-ma*, to the Muricinae based on conchological similarities between the holotype and members of the *Poirieria* clan, particularly *Poirieria* (*Panamurex*) Woodring, 1959; *Cal-otrophon* Hertlein & Strong, 1951; *Dermomurex* (*Takia*) Kuroda, 1953; and *Attiliosa* Emerson, 1968. As in the new species, members of these genera tend to be small (10–30 mm) with inflated body whorls; a broad aperture with a broad parietal shield; lirae on the adaxial margin of the outer apertural lip; six to nine archlike axial elements of equal strength, which extend from the suture to

the tip of the siphonal canal; and an open and slightly recurved siphonal canal.

The combined presence of three additional morphological features of the teleoconch whorls, however, is consistent only with an assignment of the new species to the genus Attiliosa. The fine, closely spaced, and paired cords on the upper portion of the body whorl of the new species (Figure 2c), for example, are found in a number of species of Attiliosa (Vokes, 1999: figs. 1, 41) and Takia (Vokes, 1975: pl. 5, fig. 4; Vokes, 1992: pl. 18, figs. 8, 9) but not Panamurex or Calotrophon (Vokes, 1992). The presence of columellar nodules in the new species (Figure 2d) is also characteristic of Attiliosa, as well as Panamurex and Calotrophon, but no columellar nodules of this type are found in any species of Takia (Vokes, 1992). Lastly, a posterior channel formed along the posterior portion of the aperture in the new species (Figure 2d) is found in several species of Attiliosa (Vokes, 1999: figs.



Figure 3. Attiliosa bozzettii Houart, 1993. IRSNB IG27.873/ 454 (Holotype); height 17.0 mm, maximum diameter 10.1 mm. Locality: Ras Hafun, Somalia, 150–200 m. a. Apertural view. b. Abapertural view. (Photographs courtesy of R. Houart)

2, 5, 7) and at least in one species of *Calotrophon* (Vokes, 1992: pl. 19, fig. 11), but no clearly delineated posterior channels are formed in species of *Panamurex* or *Takia*.

Despite this consistency, we regard our generic placement as tentative due to the low number of potentially informative characters in the type material. This problem is attributable, in part, to poor preservation, since the protoconch and early teleoconch whorls are missing in the holotype. More problematic, however, is the relatively simple morphology of the new species, a condition that characterizes a number of sub-lineages within the Poirieria clan and has been a prime source of systematic confusion in the Muricinae (Vokes, 1992, 1999). Strengthening our position somewhat is the close morphological resemblance of A. aenigma to the living Attiliosa bozzettii Houart, 1993 (Figure 3) from deep waters off the coast of Somalia. Both A. aenigma and A. bozzettii exhibit paired (or bisected) cords, a rounded rather than a shouldered body whorl, and up to four rather than only three columellar nodules, although these characters vary somewhat in A. bozzettii (Roland Houart, 2001, personal communication). These species differ in the more pronounced posterior channel in A. aenigma.

Similarities to other species of Attiliosa, however, even

to the early fossil taxa, are generic only. *Attiliosa aenigma* differs from the undescribed early Oligocene species from France in having a less angulate and sloped body whorl, a broader parietal shield, heavier spiral ornamentation, and a stronger posterior channel. *Attiliosa aenigma* differs from the next earliest New World species, *Attiliosa gretae* Vokes, 1999, of the late early Miocene of Florida, in having a less angulate body whorl, a broader parietal shield, heavier spiral ornamentation, spiral cords of equal rather than unequal strength, a weaker anal channel, and a less recurved siphonal canal.

The new species superficially resembles *Panamurex rutschi* Vokes, 1992 (Vokes, 1992: pl. 11, figs. 1–4) from the Pliocene Punta Gavilán Formation of Venezuela, particularly in the morphology of the axial ribs, apertural lirae, and columellar nodules; however, *P. rutschi* differs in lacking the prominent anal channel and in having thicker, unpaired, and more widely spaced cords on the body whorl. Older species of *Panamurex*, particularly the Paleogene and early Neogene species, all have open spines on the body whorl and siphonal canal, and thus are very different from *A. aenigma*, which lacks spines altogether.

The paired condition of the spiral cords in *A. aenigma* and *A. bozzettii* is noteworthy because the occurrence of similar spiral ornamentation in a number of species of *Takia* (see above), including one of its geologically oldest species, *Dermomurex* (*Takia*) cookei MacNeil MS in Vokes, 1975, may indicate a closer phylogenetic relationship between *Attiliosa* and *Takia* than previously recognized. Until now, *Attiliosa* has been compared only to *Panamurex* or *Calotrophon* (Vokes, 1971, 1976, 1992, 1999). Detailed studies of the ontogeny of this character and cladistic methods are necessary to determine whether the paired condition is homologous in these different groups. We draw attention to this condition primarily because it has been ignored in past species descriptions and systematic reviews in the literature.

A second fossil muricid (Figure 4) collected from Terramar 01 could be referable to *A. aenigma* because of its nearly identical shell shape, size, and paired spiral cords. However, the axial ribs of this second specimen are narrower, and the columellar nodules are more prominent than in the holotype of *A. aenigma*. Additional material is needed to determine whether this specimen should be included in *A. aenigma* or whether it represents yet another undescribed species.

The discovery of *A. aenigma* has significance for our understanding of the biogeographic history of the genus. Although Vokes (1989, 1992, 1999) proposed that the genus originated in the Old World during the Paleogene and migrated westward in post-Paleogene times, the latest Eocene/earliest Oligocene age of *A. aenigma* and its occurrence in the New World questions this interpretation. Although age resolution of the European material and sampling resolution of the Paleogene fossil record are too



Figure 4. *Attiliosa* sp. cf. *A. aenigma* Herbert & Portell. UF 104450; height 19.0 mm, maximum diameter 11.3 mm. Locality: Terramar 01 (PO017), Suwannee Limestone, Polk County, Florida. a. Apertural view. b. Abapertural view.

poor to determine when and where *Attiliosa* first evolved, the timing and geographic position of the new species indicates, at the very least, that diversification and geographic range expansion in *Attiliosa* were occurring much earlier than previously thought. Future studies should concentrate on refining the systematics of Paleogene Muricidae from the Old World. Are there additional undescribed or "lost" taxa referable to *Attiliosa* and/or closely related groups, and, if so, what do they tell us about character evolution and biogeographic patterns within the Muricinae?

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