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PHYLOGENY AND SYSTEMATICS OF FOSSIL AND RECENT *VERMICULARIA* (CAENOGASTROPODA: TURRITELLIDAE)

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ABSTRACT

Vermicularia Lamarck, 1799 is a clade of Miocene–Recent gastropods with an unusual uncoiled shell morphology. Like other “worm-snails,” they are taxonomically troublesome, and although earlier work affirmed the turritellid affinity of one species, their systematic relationships have not otherwise been previously examined. Here, we present a molecular phylogeny of turritellids, including members of other previously named genera [*Mesalia* Gray, 1847; *Zaria* Gray, 1847; *Torcula* Gray, 1847; *Protomella* Thiele, 1929; *Maoricolpus* Finlay, 1926; and the recently named *Turritellinella* Harzhauser & Landau, 2019, represented by *Turritellinella tricarinata* (Brocchi, 1814) = “*Turritella communis*” Risso, 1826], to establish the monophyly of *Vermicularia* and determine higher level relationships. We provide a revised taxonomy with detailed diagnoses for all known living and fossil species of *Vermicularia*, including the synonymy of *Vermicularia lumbricalis* (Linnaeus, 1758) and the commonly used junior synonym *Vermicularia knorrii* (Deshayes, 1843). The new Miocene–Pliocene species ***Vermicularia katiae* n. sp.** is described from the Dominican Republic. The phylogenetic relationships within living and fossil *Vermicularia* are also established based on morphological characters and with close outgroup turritelliform species chosen based on the molecular phylogeny. *Callostracum gracile* (Maltzan, 1883) was found to be well nested among the other species and is reassigned to *Vermicularia* herein as *Vermicularia gracilis* (Maltzan, 1883). The reconstructed phylogeny indicates that new species arose via cladogenesis much more frequently than by anagenesis, with most lineages originating in the Pliocene, but prior to the complete closure of the Central American Seaway ~ 3.5 million years ago.

Key words: wormsnails, molecular phylogeny, Vermiculariinae, Neotropics, *Turritella*, punctuated equilibrium

INTRODUCTION

“Worm-snails,” the polyphyletic term applied to uncoiled or openly coiled gastropods with an elongated (i.e., vermiform) morphology, are systematically problematical (Bieler, 1993, 1996). Vermiform morphology evolved independently several times in Gastropoda (Morton, 1953, 1955; Bieler, 1996; Bandel & Kowalke, 1997; Bieler & Petit, 2011): in Vermetidae (Caenogastropoda: Littorinimorpha), Siliquariidae (Caenogastropoda: Cerithioidea), and *Vermicularia* Lamarck, 1799 within the family Turritellidae (Caenogastropoda: Cerithioidea), as well as extinct forms, e.g., the campaniloid *Trypatrochus conicus* (Lamarck, 1804) (Caenogastropoda: Campaniloidea; Lozouet, 2012), *Loxoplocus* Fischer, 1885 (Vetigastropoda: Murchisonioidea; Peel, 1975), and *Helminthozyga* Knight, 1930 (Caenogastropoda: Pseudozygopleuridae; Peel, 1975). Of these taxa, only Siliquariidae and Turritellidae could have a close phylogenetic relationship (Strong et al., 2011), but the overwhelming majority of turritellid taxa are regularly coiled and the family Turritellidae has a long geologic history prior to the first appearance of the *Vermicularia* in the fossil record (Allmon, 2011; Das et al., 2018) making it most likely that *Vermicularia* independently evolved uncoiled morphology. Vermiform gastropods have been the subject of extensive taxonomic confusion; for example, Gould & Robinson (1994: 374) referred to vermetid taxonomy as “a nightmare.” Taxonomic issues have occurred at all levels, including the initial assumption that all uncoiled or openly coiled gastropods were a single taxonomic group, confusion of nominal gastropod

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and polychaete taxa, and the naming of species and subspecies based on ecophenotypic characteristics of uncoiling (Keen, 1961; Bieler & Petit, 2011). Mörch (1861) named over 150 varieties of worm snails intended to be descriptive rather than taxonomic and that Bieler & Petit (2011: 6) considered to be primarily infrasubspecific. Fully treating all of these varieties, most of which are not members of Turritellidae, is beyond the scope of our investigation, but where we have examined specimens of these taxa, they are noted in the Remarks.

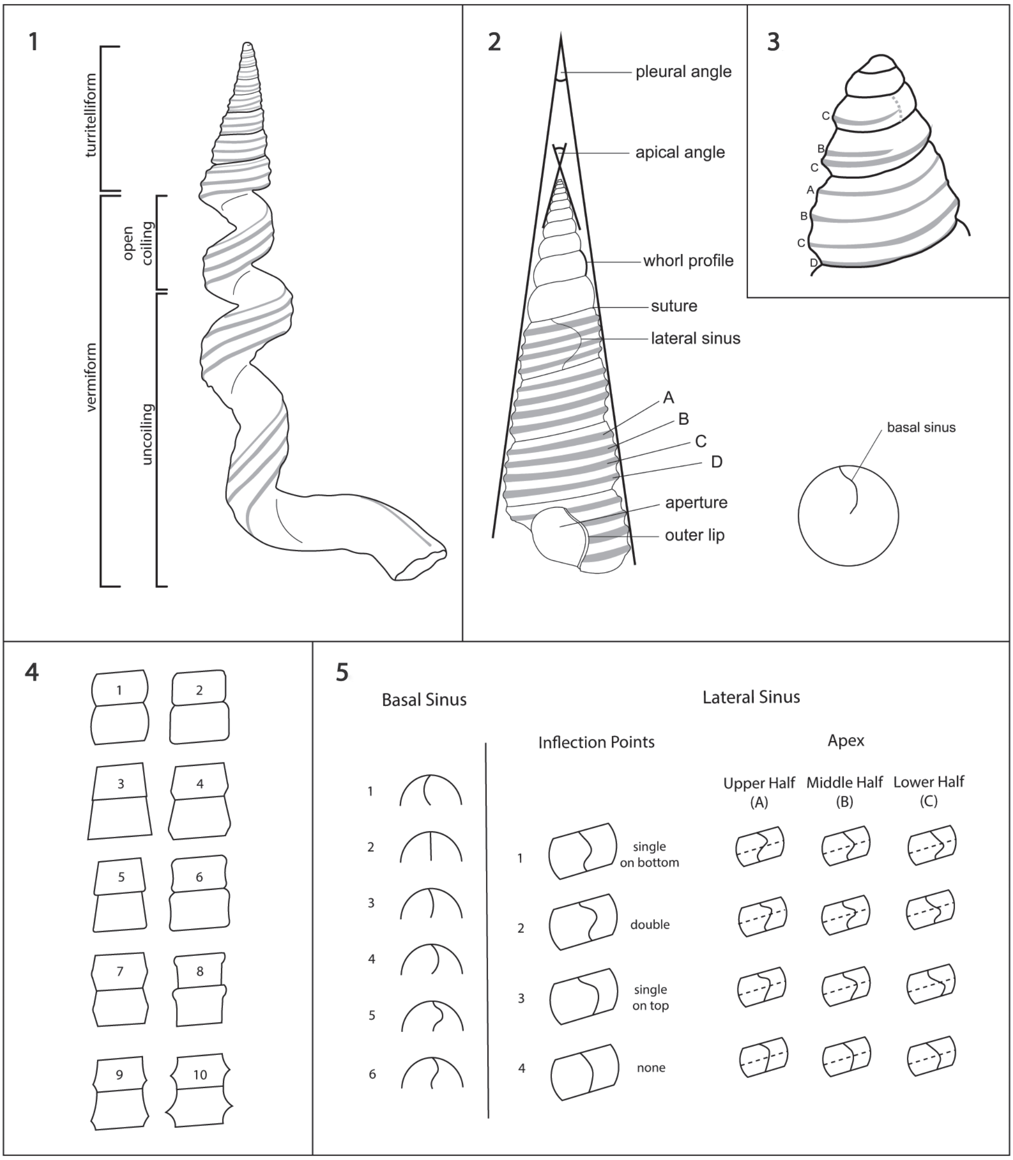
Vermiculariinae (Morton, 1953) is a Miocene–Recent clade of turritellid gastropods consisting of the genera *Vermicularia* Lamarck, 1799, and *Callostracum* E. A. Smith, 1909 (MolluscaBase, 2018), which share an initial turritelliform morphology followed by an openly coiled or uncoiled shell (Fig. 1). We follow Yochelson (1971) in distinguishing *open coiling* (in which whorls are not in contact with previous whorls but might or might not maintain the same coiling axis) from *uncoiling* (in which the coiling axis itself becomes irregular). In *Vermicularia* and other high-spired vermiform gastropods, these frequently occur simultaneously or close in ontogeny, and so the distinction can be more readily conceptualized when considering open-coiled Paleozoic gastropods that are planispiral or near planispiral, e.g., *Macluritella* E. Kirk, 1927; *Nevadaspira* Yochelson, 1971; *Straparollus* Montfort, 1810; and *Ecculiomphalus* Portlock, 1843, in which the whorls are not in contact but the direction of coiling is stable, leading to a nonvermiform morphology (Yochelson, 1971; Yochelson & Stinchcomb, 1987). The turritelliform portion can be examined with reference to morphological characters that have been described in other turritellids (Allmon, 1996; Harzhauser & Landau, 2019; Friend et al., 2023), including apical and pleural angles (Fig. 2), spiral-sculpture ontogeny (Fig. 3), whorl profile (Fig. 4), and growth-line trace (Figs. 2, 5). Following Allmon (2011), herein we subsume Vermiculariinae in Turritellinae *sensu* Marwick, 1957.

Living *Vermicularia* are of ecological interest, because they can be significant or numerically dominant components of their local molluscan communities (e.g., Gould, 1968a, b; Barrientos-Lujan et al., 2017). Several species of *Vermicularia* are known to intercoil with other conspecifics, forming bioherms that can be of ecological and stratigraphic significance (Figs. 6–9; Philippi, 1836; Pearse & Williams, 1951; Olsson & Harbison, 1953; Allmon, 1992a, 1993). They are also of evolutionary interest as, compared with other uncoiled/openly-coiled gastropods, evolved relatively recently (Miocene) and remain the most similar to their regularly coiled turritellid relatives (Morton, 1953, 1955; Bieler & Petit, 2011). They might also be the only group of "worm-snails" in which regular coiling was lost and then re-evolved in a population (Gould, 1969; Gould & Robinson, 1994), and the uncoiled portion of the shell also appears to have been secondarily reduced in *Vermicularia fargoi owensi* Petuch & R. F. Myers, 2014 (Petuch & Myers, 2014).

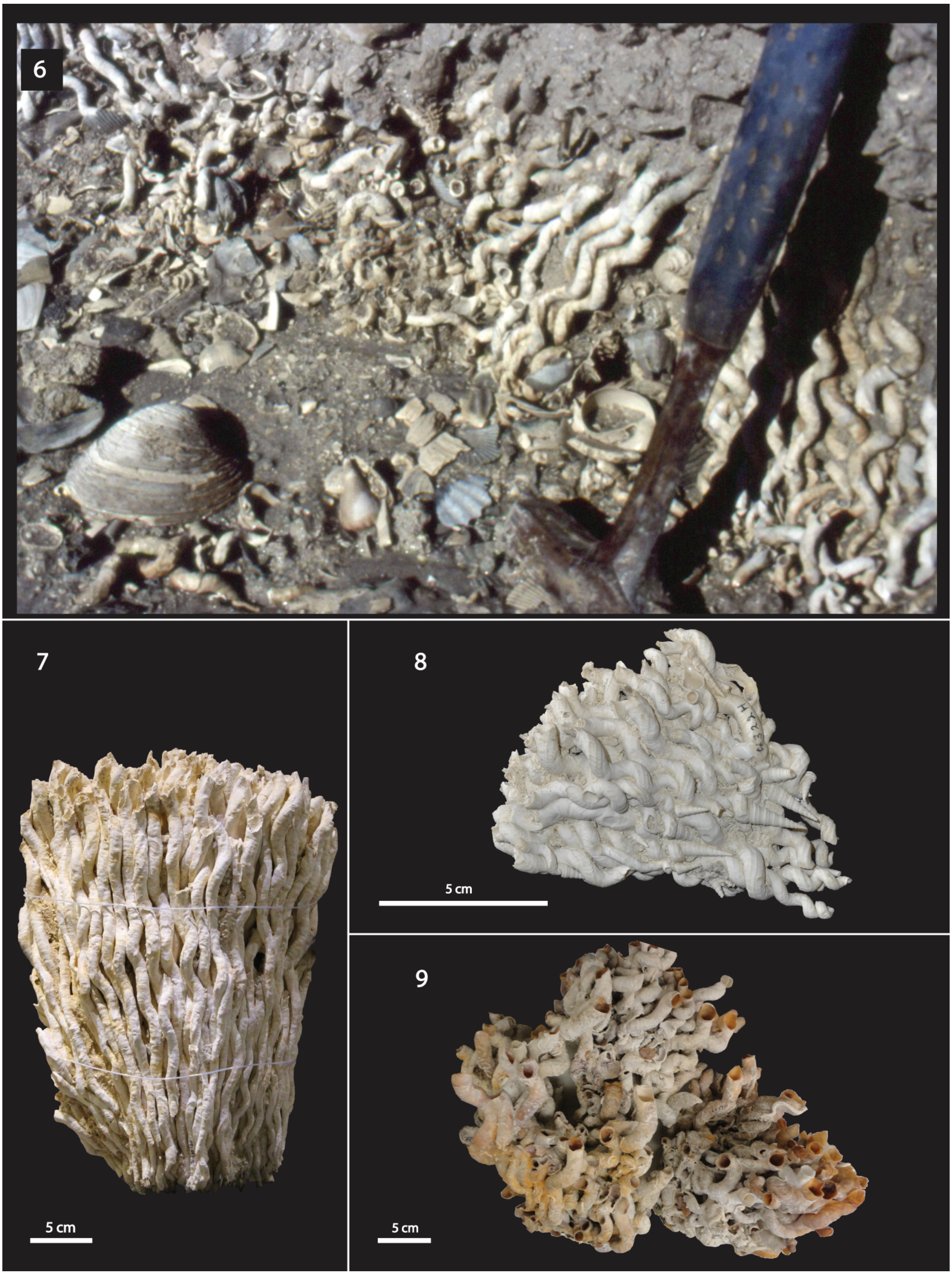
Unlike other "worm-snails," *Vermicularia* spp. always have early teleoconch sections that are regularly coiled (tightly coiled with whorls in contact with previous whorls), resembling other turritellids in all respects prior to uncoiling (or open coiling if coiling direction does not initially deviate from the earlier coiling axis), and have apertures of similar shapes to other turritellids even after uncoiling (e.g., not always round, sometimes quadrate, subquadrate, or teardrop-shaped). A tightly coiled early teleoconch, coupled with strong spiral, but not axial, sculpture on the whorls is highly suggestive of turritellid affinity, as opposed to other vermiform snails. After initiating open coiling, *Vermicularia* also do not completely lack consistent helical coiling direction (chirality), with most typically adopting a new coiling axis as they attach to a substratum and maintaining that axis until further changes are dictated by the substratum (i.e., they show the plasticity to change the direction of the aperture as needed while generally maintaining the same spiral coiling direction).

Vermicularia soft anatomy closely resembles that of other turritellids (Morton, 1953, 1955; Bieler & Hadfield, 1990; Allmon, 2011), with a small foot, an elongated mantle cavity facilitating suspension feeding (H. E. Andrews, 1974; Allmon, 2011), and the apical part of the visceral mass occupied by digestive gland and reproductive organs. They possess pallial tentacles at the mantle edge, which in semi-infaunal turritellids help to keep debris from entering the mantle cavity (Hughes, 1985; Allmon, 2011) and distinguish them from siliquariids (Tunnel et al., 2010). See the Systematics section below for further discussion of the turritelline affinity of *Vermicularia.*

The goals of this study were threefold: (1) to evaluate and determine appropriate taxonomic nomenclature for all fossil and Recent species formerly placed in Vermiculariinae, (2) to de-



FIGS. 1–5. Morphological characters of *Vermicularia* referred to in this study. (1) Generalized *Vermicularia* shell showing the transition from the tightly coiled, turritelliform portion to the open-coiled (where whorls no longer touch) and uncoiled (where the coiling axis has deviated from that of previous whorls) vermiform portion. (2) Generalized turritelline shell morphological characters, modified from Friend et al. (2023: fig. 3). (3) Initiation of primary spiral cords at the protoconch-teleoconch boundary (dashed line), modified from Friend et al. (2023). In this example, the order of appearance is C1B2A3. (4) Whorl profile classification system used herein, redrawn from Allmon (1996): 1 = convex; 2 = subquadrate; 3 = flat-sided; 4 = frustrate; 5 = imbricate; 6 = concave; 7 = keeled; 8 = telescoped; 9 = campanulate; 10 = hypercampanulate. (5) Classification of basal and lateral growth line traces, following and redrawn from Allmon (1996).



FIGS. 6–9. *Vermicularia* species known to form reef structures. 6. Field photo of *Vermicularia recta* Olsson & Harbison, 1953, Sarasota, Florida, Pliocene. Hammer is 28 cm long. 7. *Vermicularia recta*, PRI 49895, Lee County, Florida, Pliocene. 8. *Vermicularia woodringi* Olsson & Harbison, 1953, PRI 84853, Palm Beach County, Florida, Pleistocene. 9. *Vermicularia spirata* (R. A. Philippi, 1836), USNM 122207, Bermuda, Recent.

termine the phylogenetic history of the group, and (3) to clarify for researchers and collections managers the characters used to properly identify species of this troublesome clade. To accomplish these goals, we examined specimens of *Vermicularia* present in major museum collections, including all specimens assigned to *Vermicularia* in the collections of PRI, LACM, UF, and USNM, as well as specimens assigned to Vermetidae in the collections of PRI and UF (Table 1). We examined specimen morphology including existing type specimens (or photographs) regardless of institution; and we explored the relevant literature. Clarifying characters for identifying specimens is a nontrivial point, because collections data are increasingly available for analyses through systems such as the Paleobiology Database (www.paleodb.org) and misidentifications can affect analyses of biodiversity and biogeography (Allmon et al., 2018). Many specimens were reidentified during collections visits associated with this research, indicating that even collections familiar with these taxa commonly record errors. To that end, all biogeographic information presented herein has been confirmed with specimen data (either personally observed in museum collections, or figured in publications) by us, or the authors who named the species in question, and so represents a conservative estimate of

TABLE 1. Institutional abbreviations used.

Acronym	Institution
ANSP	Academy of Natural Sciences of Drexel University, Philadelphia, Pennsylvania, U. S. A.
CAS IZ	California Academy of Sciences, San Francisco, California, U. S. A.
FMNH	Field Museum of Natural History, Chicago, Illinois, U. S. A.
LACM	Malacology Collection, Natural History Museum of Los Angeles County, Los Angeles, California, U. S. A.
LACMIP	Invertebrate Paleontology Collection, Natural History Museum of Los Angeles County, Los Angeles, California, U. S. A.
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U. S. A.
MHNG	Muséum d’Histoire Naturelle, Geneva, Switzerland
MNHN	Muséum National d’Histoire Naturelle, Paris, France
NHMUK	The Natural History Museum, London, U. K.
NHMW	Naturhistorisches Museum Wien, Vienna, Austria
PRI	Paleontological Research Institution, Ithaca, New York, U. S. A.
SMF	Naturmuseum Senckenberg, Frankfurt, Germany
TAMU	Texas A & M University, Marine Invertebrates, College Station, Texas, U. S. A.
TMAG	Tasmanian Museum and Art Gallery, Hobart, Tasmania, Australia
TU	Tulane University, New Orleans, Louisiana, U. S. A.
UCBL	Universite Claude Bernard, Lyon, France
UF	Florida Museum of Natural History, University of Florida, Gainesville, Florida, U. S. A.
USNM	National Museum of Natural History, Smithsonian Institution, Washington, D. C., U. S. A.
UUZM	Uppsala University Zoological Museum, Linnésamlingen (Linnean Collection), Uppsala, Sweden
ZMB	Zoologisches Museum, Humboldt Universitat, Berlin, Germany

species stratigraphic and geographic ranges. This study redescribes and provides synonymies for species within *Vermicularia* and is also the first to demonstrate the relationship of all of these species to other turritellid gastropods using a molecular phylogeny with multiple *Vermicularia* species, as well as the first to provide a morphological phylogeny including all valid Recent and fossil species.

NATURAL HISTORY

Most *Vermicularia* are typically found in shallow (< 30 m) subtidal marine environments, attached (cemented) to a hard substratum, e.g., coral, rocks, or conspecifics, but can also be found living within sponges (Reed & Mikkelsen, 1987; Gould & Robinson, 1994; Bandel & Kowalke, 1997; Petuch & Myers, 2014; Sept, 2016; Barrientos-Lujan et al., 2017) and sometimes in greater depths (Kobluk & Lysenko, 1986; Petuch, 2002; Reyes et al., 2005; Tunnell et al., 2010; Oleinik et al., 2012; Redfern, 2013). Like all turritellids, *Vermicularia* spp. are primarily suspension feeders (Bieler & Hadfield, 1990; Allmon, 2011). The reproductive biology of *Vermicularia spirata* (Philippi, 1836) was thoroughly treated by Bieler & Hadfield (1990). *Vermicularia spirata* is a protandrous hermaphrodite, in which juvenile males are free-living, but they become attached and uncoiled when they undergo sex change. The paraspermatozoa of *Vermicularia spirata* are multiflagellate (Bieler & Hadfield, 1990). Stimpson (1851) noted that eggs of *Vermicularia radicula* (W. Stimpson, 1851) (*Vermicularia spirata radicula* herein) near Buzzard's Bay, Massachusetts, were deposited in July in a mass shaped like an elongated cone bent into a half circle.

Uncoiling and open coiling would seem to be a disadvantage in two ways. Firstly, they should result in limited mobility. In *Vermicularia*, the foot remains functional even after the turriteliform phase of shell growth ends, and even if they spend most of their lives lightly cemented in place, the adults can and do move (Gould, 1969; Hughes, 1985; contra Morton, 1953). Although the animals can retain the ability to move into adulthood, Bandel & Kowalke (1997) reported that after attachment, the foot becomes reduced and functions primarily to manipulate the operculum. Despite the unusual form of the shell, dead uncemented shells of *Vermicularia spirata* and *Vermicularia lumbricalis* (Linnaeus, 1758) in Bermuda are frequently inhabited by hermit crabs (Rodrigues et al., 2002).

Secondly, irregular coiling also might be expected to increase susceptibility to predation (cf. Yochelson, 1971; Vermeij, 1987). Little appears to be known about predators on *Vermicularia* (e.g., Witzell & Schmid, 2005, reported that they are consumed by sea turtles). This presumed susceptibility is mitigated in *Vermicularia* by a combination of living in association with sponges and/or corals, cementation to hard substratum, and a frequently gregarious habit. Several species of *Vermicularia* have achieved the extreme expression of the ancestral turritellid habit of high abundance and sessile suspension feeding by intercoiling their shells in large numbers, which allows them to grow vertically and reach new food sources (Gould, 1969) (Figs. 6–9). *Vermicularia recta* Olsson & Harbison, 1953, *Vermicularia spirata*, and *Vermicularia woodringi* Olsson & Harbison, 1953 are known to form bioherms that can extend laterally for several meters. These masses provide refuge from both predation and physical disturbance (Gibson et al., 2011; Barrientos-Lujan et al., 2017), provide habitat for other species, and can be of local stratigraphic significance in the fossil record (Philippi, 1836; Pearse & Williams, 1951; Olsson & Harbison, 1953; Petuch, 1982; Allmon, 1993). The timing of uncoiling or open coiling appears to be ecophenotypic in some species, with *Vermicularia spirata* uncoiling earliest in ontogeny in the presence of their preferred host, the branching coral *Oculina*, uncoiling later on massive coral substrata and uncoiling only rarely in the coral-free environment of Walsingham Pond, Bermuda (Gould, 1968a, b, 1969; Gould & Robinson, 1994). Other species, e.g., *Vermicularia fargoi* Olsson, 1951, uncoil without any attachment. Nevertheless, typical uncoiling widths (midwhorl diameter of the last whorl prior to the loss of contact between whorls, i.e., the last whorl in complete contact with the previous whorl) or the numbers of regularly coiled whorls help to discriminate species, so long as these are not the sole criteria employed.

MATERIALS AND METHODS

Nominal species and potential subspecies that have previously been considered to be members of Vermiculariinae include: the Recent species *Callostracum gracile* (Maltzan, 1883) [= *Vermicularia gracilis* (Maltzan, 1883)]; *Vermicularia bathyalis* Petuch, 2002; *Vermicularia fargoi fargoi*; *Vermicularia fargoi owensi*; *Vermicularia fewkesi* (Yates, 1890); *Vermicu-*

laria frisbeyae McLean, 1970; *Vermicularia lumbricalis*; *Vermicularia knorrii* (Deshayes, 1843); *Vermicularia pellucida* (Broderip & G. B. Sowerby I, 1829); *Vermicularia radicula*; *Vermicularia spirata*; the Miocene–Pliocene species †*Vermicularia milleti* (Deshayes, 1850); and the Plio–Pleistocene species †*Vermicularia recta*, †*Vermicularia trilineata* (Guppy, 1867), †*Vermicularia weberi* Olsson & Harbison, 1953, and †*Vermicularia woodringi*. Examination of specimens also resulted in the identification of the Miocene–Pliocene species **†*Vermicularia katiae* n. sp.**

Examination of collections material was essential for determining biogeographic and stratigraphic ranges of species, because a large number of specimens in many collections are misidentified (or stored among vermetids, rather than turritellids). Abbreviations for repository institutions visited or consulted during this project are given in Table 1. In total, > 5,000 specimens were examined. This included all specimens identified as *Vermicularia* in both modern and fossil collections at PRI (70 fossil and 60 Recent lots), UF (392 fossil and 380 Recent lots), LACM (3 fossil and 60 Recent lots), and USNM (720 Recent lots), as well as examination of specimens in these collections identified as vermetids for forms that might have been misidentified turritellids. Common identification errors include fossil species misassigned to the geographically widespread Recent species *Vermicularia spirata*, lots containing multiple species, and general confusion among *Vermicularia fargoi, Vermicularia lumbricalis* (= *Vermicularia knorrii*), and *Vermicularia spirata.* Some of this confusion might be related to the substantial ambiguity in the use of common names (e.g., the name "West Indian Wormsnail (or worm-snail)" applied variably to any of the Recent western Atlantic species, and the common name "Florida wormsnail (or worm-snail)" used to refer either to *Vermicularia fargoi* or *Vermicularia lumbricalis* (= *Vermicularia knorrii*) depending on the author (e.g., compare Rehder, 1981 with Witherington & Witherington, 2017). Specimens have apparently frequently been assigned uncritically to the most common species from the region or geologic formation. Some authors have directly expressed doubts that there are multiple species, and have synonymized any western Atlantic turritellid worm snails under *Vermicularia spirata* (e.g., J. Andrews, 1977: 100), making definite identification of literature-reported, unfigured examples impossible. Nomenclatural issues have also been exacerbated by a history of naming *Vermicularia* spp. without properly examining specimens of other named species, or with apparent reference to misidentified examples of the previously named species. Further confusion has resulted from the mislabeling of locality information for *Vermicularia lumbricalis* as "habitat in indiis" (Linnaeus, 1758: 787), interpreted by authors as the East Indies or Indian Ocean, whereas all known species belonging to *Vermicularia* are Atlantic or eastern Pacific (Bieler & Petit, 2011).

Several type specimens of species discussed here have apparently been lost or destroyed. The type of *Vermetus radicula* W. Stimpson, 1851 was destroyed in the 1871 Chicago fire, along with Stimpson's Smithsonian specimens of American invertebrates, his private collection, and all of his manuscripts in preparation (Warner, 2015). The type of *Vermicularia pellucida* is no longer in the collections of The Natural History Museum, London, and is presumed lost (A. Salvador, pers. comm.). *Smithia gracilis* Maltzan, 1883 was not found with the Maltzan collection, which is now divided between The Natural History Museum, London and National Museum of Wales, Cardiff (A. Salvador & H. Wood, pers. comm., respectively). The original specimen of *Callostracum gracile* (Maltzan, 1883) accessioned by Smith and leading to the erection of the genus *Callostracum*, was located (NHMUK 1909.7.27.1) and is used here as the exemplar of this species. *Vermicularia knorrii* Deshayes was named based on Knorr's figure (Knorr, 1757: pl. 17, fig. 2) from the Sommer collection, the fate of which is unresolved (Dijkstra, 2010); we did not here designate a neotype for *Vermicularia knorrii* because we conclude it to be a junior synonym of *Vermicularia lumbricalis*. Additionally, many older species have been ascribed to the genus *Vermicularia* in error (i.e., they are not members of Turritellidae; see Bieler & Petit, 2011). Many of these ascriptions were without accompanying illustration or referred to illustrations that do not sufficiently replicate detail to confirm they are of turritellid affinity (e.g., illustrations or specimens that lack the apical portion of the shell or for which type material could not be located). These names and our determinations are listed in Table 2 but are otherwise beyond the scope of this investigation. Further treatment of species that appear to be properly assigned to *Vermicularia*, but for which available illustrations and/or materials are insufficient to determine synonymy are listed as *taxa inquirenda* at the end of the systematics section. Additionally, a

TABLE 2. Species that have sometimes been assigned to *Vermicularia* in error or of unknown affinity. Authorities not otherwise referenced in the manuscript are not included in the literature cited.

Species	**Proper Assignment**	**References**
Vermicularia africana Cox, 1930	Gastropod, *incertae sedis*	Bieler & Petit, 2011
Vermicularia alternans Böhm, 1895	Not *Vermicularia* or Vermetidae; *incertae sedis*	Bieler & Petit, 2011
Vermicularia anguillina Deshayes, 1861	Silliquariidae? Deshayes, 1861 pl. 9, figs. 16, 17, pl. 10, figs. 5, 6, show morphology and sculpture inconsistent with turritellids	Herein; Bieler & Petit, 2011, refer it to Siliquariidae?
Vermicularia bezanconi Cossmann, in Cossmann & Pissarro, 1910	Not *Vermicularia*; Vermetidae?	Bieler & Petit, 2011
Vermicularia bognoriensis Mantell, 1822	Polychaete	Bieler & Petit, 2011
Vermicularia calyculata Fischer von Waldheim, 1807	*Nomen inquirendum*; type appears lost, but the original description as stacked funnels suggests that it could be a polychaete	Bieler & Petit, 2011; herein
Vermicularia carinata Schumacher, 1817	Polychaete	Bieler & Petit, 2011
Vermicularia concava J. Sowerby, 1814	Polychaete	Wrigley, 1951; Bieler & Petit, 2011
Vermicularia conica Lamarck, 1804	*Trypatrochus conica*; campaniloid gastropod	Lozouet, 2012
Vermicularia deposita Hedley, 1909	Vermetidae	Bieler & Petit, 2011
Vermicularia flava Verco, 1907	Polychaete	Bieler & Petit, 2011
Vermicularia funicalis Crespin, 1926	Vermetidae?	Bieler & Petit, 2011
Vermicularia fuscata Humphrey, in Jackson, 1937	*Serpula fuscata* is unavailable; Humphrey's binomial names in the letter published by Jackson (1937) were not accompanied by descriptions. These names referred to da Costa (1771: pl. 10, figs. 5, 6), and are suggestive of *Vermicularia lumbricalis* and *Vermicularia spirata*, respectively, but which do not accurately show apices for these species.	Bieler & Petit, 2011; herein
Vermicularia gorensis Bosc, 1801	= *Serpula goreensis* Gmelin, 1791; Vermetidae	Bieler & Petit, 2011
Vermicularia granulata Gravenhorst, 1831	Vermetidae	Bieler & Petit, 2011
Vermicularia intestinalis Bosc, 1801	*Incertae sedis*	Bieler & Petit, 2011

(continues)

TABLE 2 (continued).

Vermicularia lineolata Gravenhorst, 1831	Vermetidae	Bieler & Petit, 2011
Vermicularia manzourensis Abbass, 1963	Cassiopidae	Herein; see Discussion of "*Pseudomesalia*"
Vermicularia maoriana Powell, 1937	Not *Vermicularia*; Vermetidae*?*	Herein; examination of holotype, NHMUK 19621042, and paratype, NHMUK 19621043.
Vermicularia montensis Briart & Cornet, 1877	*Incertae sedis*, not *Vermicularia*, not Vermetidae	Bieler & Petit, 2011
Vermicularia murayi Hedley, 1911	Polychaete	Bieler & Petit, 2011
Vermicularia nodosa Hedley, 1907 (incorrectly renamed *Vermicularia hedleyi*)	Polychaete	Bieler & Petit, 2011; examination of *Vermicularia nodosa* syntypes, NHMUK 1907.9.10.172-173.
Vermicularia nodus Phillips, 1829	Polychaete	Bieler & Petit, 2011
Vermicularia omphalocolpus Cossmann & Pissarro, 1902	Gastropoda; not vermetid or *Vermicularia*	Bieler & Petit, 2011
Vermicularia ophiodes Marshall & Murdoch, 1921	Vermetidae	Bieler & Petit, 2011
Vermicularia ovata J. Sowerby, 1814	Polychaete	Bieler & Petit, 2011
Vermicularia porrectus Deshayes, 1861	Vermetidae	Bieler & Petit, 2011
Vermicularia rouyanus d'Orbigny, 1844 (sometimes misspelled as "*Vermicularia royanus*")	Turritellidae; not *Vermicularia*	Bieler & Petit, 2011; herein
Vermicularia solariiformis Cossmann, 1899	Liotiidae	Bieler & Petit, 2011
Vermicularia sowerbii Mantell, 1822	Polychaete	Bieler & Petit, 2011
Vermicularia staadti Cossmann, 1907	Gastropoda; not Vermetidae, not *Vermicularia*	Bieler & Petit, 2011; herein
Vermicularia striatus Reis, 1897	Gastropoda; not *Vermicularia*	Bieler & Petit, 2011
Vermicularia torsa Böhm, 1895	Gastropoda; not *Vermicularia*	Bieler & Petit, 2011
Vermicularia tricarinatus Pethö, 1906	Gastropoda; not *Vermicularia*	Bieler & Petit, 2011
Vermicularia umbonata J. Sowerby, 1814	Polychaete	Bieler & Petit, 2011
Vermicularia vermetus Bosc, 1801	Vermetidae	Bieler & Petit, 2011; herein
"*Vermicularia* species A" of Ladd, 1972;, USNM 648498, USNM 648499	Turritellidae; not *Vermicularia*	Herein

(continues)

TABLE 2 (continued).

Genus *Laxispira* Wenz, 1939	Siliquariidae	Bandel & Kowalke, 1997; Bieler & Petit, 2011
Genus “*Provermicularia*” Stoppani, 1857; Kittl, 1899 (including *Provermicularia circumcarinata)*	Gastropod, not Vermiculariinae; *taxon inquirendum*	Bieler & Petit, 2011
Genus “*Pseuomesalia*” Douvillé, 1916	Cassiopidae	Pereira et al., 2016
Subgenus *Anguillospira* Cossmann, 1912	Siliquariidae?	Bieler & Petit, 2011

TABLE 3. Molecular data included the sequence data used by Sang et al. (2019) and new sequence data as detailed below. ES = sequence data provided by Ellen Strong (USNM).

Species	**Analysis ID**	**Locality**	**Specimen or Voucher shell ID**	**Genbank IDs**
Maoricolpus roseus (Quoy & Gaimard, 1834)	BA22	Green Island, Tasmania	TMAG E35226	OQ996147 OQ996116 OQ998364
Mesalia brevialis (Lamarck, 1822)	BA7	Portugal	NHMUK 20030319	OQ996143 OQ996112 OQ998361
	BA35	Spain, Mediterranean	UF 380804	OQ996148 OQ998365
Mesalia mesal (Deshayes, 1843)	BA40	Senegal	MNHN IM-2013-63037	OQ996150 OQ996118 OQ998366
	BA42	Senegal	MNHN IM-2013-63039	OQ996151 *H3 sequence identical to OQ998366 OR022084
Protomella capensis (Krauss, 1848)	BA16	South Africa	KwaZulu-Natal Museum PO490	OQ996144 OQ996113
Turritellinella tricarinata (Brocchi, 1814) (= *Turritella communis* Risso, 1826)	NSBA20	North Sea (Scotland)	NHMUK 20170009	OQ996146 OQ996115 OQ998363
Turritella conspersa A. Adams & Reeve, 1849	BA43	Senegal	MNHN IM-2013-63040	OQ996152 OQ996119 OQ998367
	BA46	Senegal	MNHN IM-2013-63043	OQ996153 OQ996120 OQ998368

(continues)

TABLE 3 (continued).

Turritella maculata Reeve, 1849	BA17	Red Sea	PRI 104846	OQ996145 OQ996114 OQ998362
Turritella nivea Anton, 1838	BA38	Senegal	MNHN IM-2013-63035	OR016143 OR022085
	BA41	Senegal	MNHN IM-2013-63038	OQ996149 OQ996117
Vermicularia lumbricalis (Linnaeus, 1758)	BA10	Florida	UF 446833	OQ996140 OQ996109 OQ998359
Vermicularia pellucida (Broderip & G. B. Sowerby I, 1829)	BA9	Gulf of Panama	UF 372362	OQ996141 OQ996110
Vermicularia spirata (R. A. Philippi, 1836)	ESC	Florida	ES1_C04	OQ996154 OQ996121 OQ998369
	ESD	Florida	ES1_D04	OQ996155 OQ996122 OQ998370
	ESE	Florida	ES1_E04	OQ996156 OQ996123 OQ998371
Zaria duplicata (Linnaeus, 1758)	BA1	Bangladesh	PRI 104845	OQ996142 OQ996111 OQ998360

presently undescribed species that has been previously figured (Redfern, 2013: 39) and referred to *Vermicularia*, but which we do not believe belongs within the clade, is addressed among *taxa inquirenda*.

A significant effort was made to locate living specimens of the unusual population of *Vermicularia spirata* from Walsingham Pond, Bermuda described by Gould (1968a, b, 1969), in which it was observed that the majority of individuals maintain turritelliform coiling throughout ontogeny (i.e., they have secondarily lost their uncoiled form). Walsingham Pond is a relatively small anchihaline pond in Bermuda, where two days of surveying and hand dredging in 2016 by BMA and field assistant Emily Waldman resulted in thousands of dead shells of *Vermicularia spirata* being examined, but no living individuals being found. Given that a previous survey conducted in 1991 of the biotas of Bermudan anchialine ponds also noted the absence of living *Vermicularia spirata* (see Thomas et al., 1991), it is likely that this unusual population has been extirpated. Gould (1968a, b) described ~ 95–99% of specimens as retaining coiled morphology at the largest attained sizes, which was consistent with our own observations of dredged material.

Molecular Methods

Molecular analyses were based on the western Atlantic and tropical eastern Pacific turritellid phylogeny of Sang et al. (2019), with additional sequence data (Table 3) obtained for eastern Atlantic species and species from other named turritellid genera (*Maoricolpus*; *Mesalia* Gray, 1847; *Protomella* Thiele, 1929; *Zaria* Gray, 1847). Following Sang et al. (2019), *Batillaria zonalis* (Bruguière, 1792) and *Lampania cumingi* Crosse, 1862 (Batillariidae) were chosen as the outgroups based on their

TABLE 4. Morphological character matrix. For character and character state definitions, see Appendix. *T. perexilis* = *T. acropora* (see Friend et al., 2023).

	T. perexilis	*Torcula altilira*	*Torcula exoleta*	*T. nodulosa*	*V. bathyalis*	*V. fargoi*	*V. frisbeyae*	*V.gracilis*	***V. katiae* n. sp.**	*V. lumbricalis*	*V. milleti*	*V. pellucida*	*V. recta*	*V. spirata*	*V. spirata radicula*	*V. weberi*	*V. woodringi*
(1) Protoconch diameter	2	1	2	1	?	?	?	2	0	2	2	1	?	?	?	?	1
(2) Protoconch number of whorls	1	1	0	1	?	?	?	0	?	1	?	1	?	?	?	?	1
(3) Apical angle (protoconch)	1	1	1	1	1	?	?	0	1	1	0	0	?	?	?	?	?
(4) Pleural angle	1	0	0	1	2	2	1	2	2	1	2	0	2	2	2	1	1
(5) Whorl profile	0	5	5	9	3	3	2	0	9	8	8	8	3	8	8	1	2
(6) Size class	0	2	1	0	0	1	1	0	0	0	0	1	1	1	1	1	1
(7) Suture depth	1	2	1	1	1	1	0	2	1	0	0	0	1	0	0	2	0
(8) Umbilicate	0	0	0	0	0	1	1	0	1	0	0	1	0	0	0	1	1
(9) Early whorls coloration	1	?	0	0	0	1	1	0	?	0	?	0	?	1	1	?	?
(10) Late whorls coloration	0	?	0	1	1	1	1	1	?	1	?	0	?	1	1	?	?
(11) Coloration pattern	1	?	1	1	0	1	1	2	?	0	?	0	?	0	1	?	?
(12) Raised Growth lines	0	1	1	0	0	1	0	0	0	0	0	0	0	1	1	0	0
(13) Basal Sinus Shape	3	3	4	2	0	1	4	?	0	0	0	0	0	1	1	0	1
(14) Lateral sinus depth	0	1	2	0	1	1	2	1	2	2	0	1	1	0	0	1	2
(15) Lateral sinus angle	1	0	1	0	1	0	2	2	2	2	2	1	0	1	1	1	2
(16) Lateral type (Inflection points)	3	3	1	3	3	3	2	3	0	3	2	0	3	3	3	3	2
(17) Lateral sinus apex location	1	1	1	1	1	1	1	0	0	1	0	1	1	1	1	1	0
(18) Aperture shape	2	1	2	1	2	0	?	3	1	2	2	2	0	2	2	1	1
(19) Anterior body whorl shape	1	0	0	0	?	?	2	0	?	?	?	?	?	?	?	?	?
(20) Strongest cord, early	2	3	2	2	2	3	3	2	2	3	2	3	3	3	3	3	3
(21) Strongest cord, late	2	3	0	2	0	4	3	0	2	4	2	3	3	3	3	3	0
(22) Number of primary spirals, early	3	4	2	4	1	3	2	2	3	2	3	3	4	3	3	3	3
(23) Number of primary spirals, late	3	2	2	4	4	4	?	0	4	1	1	3	4	4	4	4	3
(24) Minor spiral sculpture, early	4	4	3	4	0	4	4	4	1	0	0	4	0	0	0	1	4
(25) Minor spiral sculpture, late	4	4	3	4	4	4	4	4	4	0	0	4	0	4	4	4	4
(26) Beading	1	1	0	1	0	1	0	0	0	0	0	0	0	0	1	0	0
(27) Lineated adapertural surface	?	?	?	?	0	1	1	0	1	0	0	1	1	1	1	1	1
(28) Uncoiling typical of ontogeny	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1
(29) Uncoiling diameter	?	?	?	?	0	3	?	0	1	0	0	1	0	0	2	2	1

(continues)

TABLE 4 (continued).

(30) Average number of coiled whorls	0	0	0	0	3	1	1	3	2	3	2	2	2	2	2	1	2
(31) Uncoiled length	?	?	?	?	2	2	2	0	0	1	0	3	3	3	?	?	3
(32) Coiling axis typically changes	0	0	0	0	1	1	1	0	0	1	1	1	1	1	1	1	1
(33) Lateral of uncoiled portion wrinkled	0	0	0	0	1	1	1	0	0	0	1	0	1	1	?	0	1
(34) Frequently cements to other *Vermicularia*	0	0	0	0	0	0	0	0	0	0	0	0	1	1	?	0	1

close relationship to Turritellidae in combined morphological and molecular analysis (Strong et al., 2011: fig. 8). No material amenable to sequencing could be located for the Recent species *Vermicularia fargoi, Vermicularia frisbeyae,* or *Vermicularia gracilis* (= *Callostracum gracile*).

DNA was extracted using a Qiagen DNeasy kit, following the manufacturer's protocol. The mitochondrial 12S (456 bp), 16S (527 bp), and nuclear H3 (376 bp) regions were chosen as gastropod-specific primers available for these genes (Simon et al., 1991; Colgan et al., 1998; Zou et al., 2011; see Sang et al., 2019 for primer sequences used). The polymerase chain reaction (PCR) protocols used by Sang et al. (2019) were followed for additional species, including 0.002 µg/µL bovine serum albumen to improve PCR yields (Woide et al., 2010; Farell & Alexandre, 2012). Sanger sequencing was performed at the Cornell University Biotechnology Resource Center. Sequence data was added to the alignment of Sang et al. (2019), aligned with MUSCLE (Edgar, 2004), and visually checked using Mesquite v. 3.40 (Maddison & Maddison, 2018).

Morphological Characters

Turritellids are generally acknowledged to have a paucity of shell characters, despite having moderately high modern (~ 150 spp.) and fossil (~ 800 spp.) diversity (Allmon, 1996, 2011; Friend et al., 2023). By combining a morphological analysis with outgroup choices derived from the molecular analysis, we hoped to improve our ability to resolve species relationships within *Vermicularia*. The outgroups consisted of *Turritella nodulosa* King, 1832 and *Turritella perexilis* Conrad, 1873 (the latter is the senior synonym for *Turritella acropora* Dall, 1889; see Friend et al., 2023; *Turritella acropora* is used throughout the phylogenetic analyses herein because molecular sequences are those used for *Turritella acropora* by Sang et al., 2019). The regularly coiled species *Torcula exoleta* (Linnaeus, 1758) (Recent) and *Torcula altilira* Conrad, 1857 (Miocene) were included in the analysis as representatives of the lineage recovered as sister to *Vermicularia* in the molecular phylogeny. Morphological characters used include protoconch size, teleoconch whorl profile, growth lines, sculpture, size, growth form, shell coloration, and hermatypic life mode (Figs. 1–5; Appendix). Several characters were evaluated twice, treated separately early and late in ontogeny, with adult apertural whorls of regularly coiled turritellids compared to the late (i.e., uncoiled) whorls of *Vermicularia* spp. Previous researchers have distinguished the apical, coiled portion of the shell from the uncoiled/openly-coiled portion by referring to the "*Turritella* stage or turritellid stage," but we find this use clumsy (because by any monophyletic definition, *Vermicularia* are *always* turritellids) and here distinguish the apical "turritelliform" (regularly coiled) portion from the "vermiform" (uncoiled) portion (Fig. 1).

A total of 34 morphological characters were identified and coded (Table 4, Appendix). Characters were based on those traditionally used in diagnosing turritellid species and determining taxonomic relationships (Marwick, 1957; Allmon, 1996; Harzhauser & Landau, 2019; Friend et al., 2023). Some characters were discretized into categories to encompass observed infraspecific variation (e.g., protoconch size, width at uncoiling) while recognizing discontinuities among species, following general practices (Forey, 2006) that have been applied

TABLE 5. Reports in the literature of *Vermicularia* spp. Occurrences of potential biogeographic, stratigraphic, or other significance that could not be confirmed through associated figures or materials. This table excludes appearances in occurrence lists/checklists where the species is already known from the specified stratigraphic and geographic location. Radula figure by Morton (1953) is given in the synonymy of *Vermicularia spirata* below, but because the shell was unfigured, we include it in this table as well.

Name used	Location	Age	Citation	Notes
Vermicularia fargoi Olsson, 1951	Rio de Janeiro, Brazil	Recent	Barroso et al., 2016	Potential significant range expansion. This is the southernmost report of *Vermicularia,* however, it appears only in a biogeographic table and is unfigured.
	Yucatan Peninsula, Mexico	Recent	H. Vokes & E. Vokes, 1983	Potential significant geographic range expansion. Text indicates that photographs supplied might have been from other regions in the Gulf of Mexico, hampering identification of the Yucatan specimens. The species identification of the photographed specimen appears correct.
Vermicularia knorrii (Deshayes, 1843)	500 m Deep waters off of the Texas-Louisiana coast, U.S.A.	Recent	Tunnell et al., 1978	Potentially *Vermicularia bathyalis*, a significant range expansion for that species, but likely the deepest occurrence of *Vermicularia lumbricalis*.
	Yucatan Peninsula, Mexico	Recent	H. Vokes & E. Vokes, 1983	Potential geographic report of *Vermicularia lumbricalis*. Text indicates that photographs supplied might have been from other regions in the Gulf of Mexico, hampering identification of the Yucatan specimens. The species identifications of the photographed specimens appear correct.
	Campeche Bank, Mexico	Recent	Hicks et al., 2001	Potential geographic report of *Vermicularia lumbricalis*.
Vermicularia sp. “resembling *V. eburneus*” Reeve, 1842	Trinidad	Miocene	Mansfield, 1925	Mansfield noted that *Vermicularia* are present in Springvale Formation (upper Miocene). However, Mansfield stated that the material is not adequate for species identification. Because specimens from this locality could be among the earliest occurrence of western Atlantic *Vermicularia*, proper identification of additional specimens from this locality would be very significant.
Vermicularia cf. *radicula* (W. Stimpson, 1851)	Trinidad	Recent, Pliocene, upper Miocene	Maury, 1925	Specimen not well preserved, said to resemble “*lumbricalis*.”

(continues)

TABLE 5 (continued).

Vermicularia spirata (R. A. Philippi, 1836)	Trinidad	Upper Pliocene	Maury, 1925	Figured specimen is from Florida and belongs to *Vermicularia fargoi*. The Trinidad specimen was not figured.
	Jamaica	Pliocene	Woodring, 1928	*Vermicularia spirata* listed as late Miocene, Bowden, Jamaica. Specimens could not be located. Olsson & Harbison (1953) speculated that this was *Vermicularia woodringi*, but the text indicates that specimens were not examined. The Bowden Formation is now considered to be Pliocene, not late Miocene.
	Yucatan Peninsula, Mexico	Recent	H. Vokes & E. Vokes, 1983	Text indicates that photographs supplied might have been from other regions in the Gulf of Mexico, hampering identification of the Yucatan specimens. The species identification of the photographed specimen appears correct.
	Dry Tortugas, Florida, U.S.A.	Recent	Morton, 1953	Radula of “*Vermicularia spirata*”; very probable that this is correctly *Vermicularia spirata*, but only the dissected soft tissues are drawn and it was common for all extant western Atlantic species to be assigned to *Vermicularia spirata*.
	Trinidad	Unassigned	Jung, 1969 (with ?)	“Matura region” specimen is figured (pl. 44, fig. 11) but is too worn to be definitively identified. Because it co-occurs with *Vermicularia trilineata*, it might be a more severely eroded form of this species with a slightly earlier uncoiling onset. The aperture, however, does not appear broken and appears close to circular, and the coiled portion of the shell is much smaller than specimens assigned to *Vermicularia trilineata*. It could represent an additional species, but without preservation of sculpture or growth line characters, the definition and placement of the species in the phylogeny remains unclear.
	Campeche Bank, Mexico	Recent	Hicks et al., 2001	If species identity were confirmed, this would represent additional geographic occurrence data.
	Brazil	Recent	Barroso et al., 2016	Record of this species in Brazil would be a significant range expansion, however, it is not figured and appears only in a biogeographic table.
Vermicularia cf. *woodringi* Olsson & Harbison, 1953	Cubagua, Venezuela	Pliocene	Landau et al., 2008	Listed only. If species identity were confirmed, this would represent additional geographic information.

previously to turritellids (Allmon, 1996; Friend et al., 2023) and a variety of taxa beyond Turritellidae (e.g., Lamsdell et al., 2010; Wright & Stigall, 2013; Selden et al., 2015; Lamsdell, 2020). Koch et al. (2015) suggested implied weighting as a means of adjusting for the nature of continuous or discretized continuous characters, but Congreve & Lamsdell (2016) suggested that implied weighting has a higher error rate than equal weighting when examined against simulated datasets. Characters were discretized into categories that minimized multiple-state occupations within operational taxonomic units based on observation of specimens in collections, and to have roughly equal occupation of the total range of observed variation within Turritellidae. See individual character descriptions in the Appendix for additional details.

Characters specifically related to uncoiling were coded as unknown character states for regularly coiled turritellid species, except that the number of whorls before uncoiling was considered an ordered character with species that remain coiled coded as state 0 and species with six or fewer regularly coiled whorls coded as state 3. This ordering of character states allowed for *Vermicularia* with the longest period of coiling to be coded as most similar to regularly coiled turritellids.

Coloration of the shell appears to be important for discrimination of species and potential species relationships in *Vermicularia* [e.g., one of the characters by which *Vermicularia lumbricalis* (= *Vermicularia knorrii*) can be distinguished from *Vermicularia spirata* is the distinct white tip of the turritelliform portion of *Vermicularia lumbricalis*]. Several species have an early unpigmented turritelliform stage that becomes pigmented as the specimen becomes larger or begins to uncoil. This character was coded both for early and late whorls of extant specimens to capture this transition, but because individuals that otherwise appear to be conspecifics showed some variation from horn-colored to dark brown to reddish or (rarely) blue-gray in the color of the pigmented portion of the shell, coloration was only coded as translucent/white or pigmented. Additionally, some species have color patterning that is more complex (e.g., the dashed or mottled pattern of *Vermicularia gracilis*), and so the complexity of coloration pattern was also used as a character (unpatterned, striped, or complex). This character was left as unknown for all fossil forms in the morphological phylogenetic analysis.

Description of shell sizes within species descriptions are relative to the other species included in this study. Character state descriptions are given in the Appendix and the character matrix is presented in Table 4.

In this study, we used the conception of fossil species advocated by Allmon (1996, 2016c): fossil species are groups of morphologically distinct populations within which variation is of the magnitude displayed by closely related living species and their local populations, and between which the differences are of the kind and degree expected to result from reproductive isolation of populations in such related or analogous species. Fossil species are indicated by a dagger (†) symbol.

Scanning electron microscopy (SEM) imaging was performed with a JEOL JCM-5000 Neoscope at the Paleontological Research Institution. For a putative *Vermicularia pellucida* fossil that was completely encrusted in epibionts, computed tomography (CT) imaging was acquired through the imaging facility at the Cornell University Institute of Biotechnology using a Zeiss-Xradia Versa 520 X-ray microscope.

Phylogenetic Methods

Parsimony analysis of both molecular and morphological characters was performed in PAUP v. 4.0 build 168 (Swofford, 2003). For the molecular dataset, likelihood analysis was performed using RAxML (Stamatakis, 2006) under a GTRGAMMA model to calculate the ML best tree and 100 bootstrap replicates. Trees were visualized using FigTree v. 1.4.3 (Rambaut, 2016). Bayesian analysis of the molecular dataset was performed using BEAST v. 1.8.0 (Drummond & Rambaut, 2007) with Batillariidae designated as a monophyletic outgroup, using ten million generations, with the first 10% of results discarded as burn-in. Terminals with identical sequence data were removed prior to analyses of molecular data. All other settings were left as default. For the morphological analysis including both fossil and extant species of *Vermicularia* and *Torcula* Gray, 1847 (the clade found to be sister to *Vermicularia* in the molecular analysis), *Turritella nodulosa* + *Turritella perexilis* Conrad, 1875 (= *Turritella acropora*) was designated as the monophyletic outgroup. Equal weighting was used, because simulation data suggest that equally weighted analyses are more conservative in their estimation of tree topologies than parsimony analyses using implied weighting (Congreve & Lamsdell, 2016). All analyses were run on an HP ENVY 17 with an Intel Core i7-4710HQ CPU.

SYSTEMATICS

Current Status of Taxonomy

Previous molecular analysis by Lieberman et al. (1993) confirmed *Vermicularia knorrii* as a member of Turritellidae, as had long been suspected based on morphology (Morton, 1955), nested among species usually assigned to *Turritella s.l.* Here we expand on this finding by incorporating evidence from multiple genes and multiple *Vermicularia* spp. with new data from tropical eastern Pacific and Atlantic turritellids to establish monophyly of the group and determine its closest relatives. We also have analyzed morphological characters for all valid Recent and fossil species within Vermiculariinae to construct a phylogenetic tree documenting the clade's history.

A large number of species have been assigned to the genus *Vermicularia* or the subfamily Vermiculariinae in error (see Bieler & Petit, 2011 for an assessment of the majority of these names) and we have provided a reference table of these names (Table 2). Of particular relevance to the evolutionary history of the group are the taxa *Laxispira* Gabb, 1877 and "*Pseudomesalia*" Douvillé, 1916. Vermiculariinae is occasionally reported as originating in the Cretaceous, based primarily on the misassignment of the uncoiled genus *Laxispira* to the Vermiculariinae. This genus, however, does not belong to Turritellidae, based on its nonturritellid protoconch morphology (Bandel & Kowalke, 1997) and should be assigned either to Vermetidae (Bandel & Kowalke, 1997) or as a slit-less siliquariid (Bieler & Petit, 2011). "*Vermicularia concava*" J. Sowerby, 1814, is another example of a Cretaceous species occasionally named as a pre-Cenozoic *Vermicularia* (e.g., Fordham, 1876), but is a polychaete (Wrigley, 1951; Bieler & Petit, 2011). "*Pseudomesalia*" is preoccupied by *Pseudomesalia* Ganglbauer in Bodemeyer, 1900 in Coleoptera, but no new name is presently in use for the gastropods assigned to this genus. The group has been mentioned as a relative of either *Vermicularia* or Vermetidae (Cossmann, 1925; Wenz, 1939; Bieler & Petit, 2011), but has been more recently assigned to Cassiopidae (Bieler & Petit, 2011; Pereira et al., 2016).

Due to widespread confusion regarding the application of species names, synonymy lists herein are limited to instances in which identifications could be properly evaluated (i.e., cases in which species were illustrated, or where corresponding specimens were examined). We ignored mentions of species in numerous published lists that could not be explicitly connected to published illustrations or specimens. Examples of additional uses of these names that could not be confirmed but are potentially significant occurrences are listed in Table 5. The admixture of multiple species in photographs or lots of *Vermicularia* spp., particularly those described as "*Vermicularia spirata*" or "*Vermicularia knorrii*," also complicates synonymy lists. [In at least one case, for example, "poor quality material" from a novel locality was identified to species-level and the figured specimens, although correctly identified, were noted to be (or to potentially have come) from museum specimens obtained from other localities (H. Vokes & E. Vokes, 1983).] Distribution information presented here was derived from observed specimens in the collections of PRI, LACM, USNM, and UF, combined with information from original descriptions, and from literature in which specimens were illustrated or described in sufficient detail to confirm species identities. Distribution information provided herein should therefore be treated as a conservative estimate for all species [Rosenberg et al. (2009) had more inclusive estimates of geographic ranges of the extant western Atlantic species *Vermicularia fargoi*, *Vermicularia knorrii* (= *Vermicularia lumbricalis*) and *Vermicularia spirata*).] Reports of *Vermicularia* spp. in the literature that could not be confirmed through figures, descriptions, or associated collections materials but which represent potentially important occurrences are listed in Table 5. Of particular interest were published reports of *Vermicularia* from Brazil, with both *Vermicularia fargoi* and *Vermicularia spirata* reported as far south as Rio de Janeiro (Barroso et al., 2016), but no figured specimens or material were available for our identification.

Family Turritellidae Lovén, 1847

Subfamily Turritellinae Woodward, 1851

Remarks: Dall (1913b) removed *Vermicularia* Lamarck, 1799 from Vermetidae, erecting Vermiculariidae. The subfamily is occasionally incorrectly reported as being first proposed by Dall (1913a); the correct reference is Dall (1913b: 546), in which he listed several non-turritellids in his Vermiculariidae, including *Thylacodes* Guettard, 1770, *Siliquaria* Bruguière, 1789, and *Petaloconchus* H. C. Lea, 1843. Morton (1953) subsequently recognized Vermiculariinae as a subfamily within Turritellidae. A monophyletic Turritellinae (*sensu* Marwick, 1957) includes *Vermicularia*; molecular evidence (Lieberman et al., 1993, and herein) indicates that *Vermicularia* is nested well within the clade of species belonging to Turritellinae *sensu* Marwick (1957) and Allmon (2011). The soft anatomy (including presence of pallial tentacles, form of the foot, food groove, and reproductive anatomy), feeding mode, and larval shell morphology of *Vermicularia* are also all consistent with other turritelline taxa (Morton, 1953; Hughes, 1985; Bieler & Hadfield, 1990; Allmon, 2011). If all members of Vermiculariinae are assigned to the single genus *Vermicularia*, as advocated herein, retaining the subfamily would be uninformative as well as make Turritellinae paraphyletic. Therefore, we do not support the use of the separate subfamily Vermiculariinae.

Genus *Vermicularia* Lamarck, 1799

Type species (by monotypy): *Serpula lumbricalis* Linnaeus, 1758: 787.

Original species diagnosis (translated from Linnaeus, 1758): “Smooth and flexible shell. Apex in a pointed spiral. Habitat in Indiis” [in error].

Original generic diagnosis (translated from Lamarck, 1799: 78): “Shell tubular, regularly twisted in a spiral at its origin, and entire in all its length; suborbicular aperture,”

Diagnosis: Early teleoconch regularly coiled followed by an open, typically uncoiled adult morphology. Early spiral ontogeny is B1A2 (known confidently in *Vermicularia lumbricalis*, *Vermicularia milleti*, ***Vermicularia katiae* n. sp.**, *Vermicularia pellucida*, *Vermicularia spirata*, *Vermicularia weberi*, and *Vermicularia woodringi*) (Fig. 3; Appendix: Sculpture, for additional information on naming conventions for turritellid spiral sculpture).

Description (shell only): Protoconch is similar to other Turritellinae, with the turbinate form and slightly depressed nucleus common among turritellids. No axial sculpture is present. Onset of spiral sculpture begins with B (medial) followed by A (adapical of B); C and D do not appear in close proximity to A and B, if they are present. Teleoconch maintains regular coiling in early whorls, but then becomes openly coiled, and usually uncoiled (Fig. 1). Shells maintain a spiral direction even after uncoiling (i.e., although the direction in which the vermiform portion grows is irregular, the shell continues to grow helically). Larger shells commonly have a high number of internal septa. Although the presence of septa is neither unusual for turritellids nor for other vermiform snails, some *Vermicularia* have a noticeably high frequency of septation (see Anderson & Allmon, 2018).

Generic stratigraphic and geographic ranges: Miocene (Burdigalian)–Recent; Europe (fossil only), subtropical and tropical Atlantic (western Africa, North and South America), and subtropical and tropical eastern Pacific (North and South America).

Remarks: Bieler & Petit (2011; 70) noted that *Serpula lumbricalis* was based on four illustrations, all assignable to modern *Vermicularia*, and that the locality given as “habitat in Indiis” is in error, because *Vermicularia* are an exclusively Atlantic and tropical eastern Pacific group. See discussion of *Vermicularia lumbricalis* below.

There have been previous suggestions of pre-Miocene *Vermicularia,* either due to usage prior to the name being restricted to Turritellidae (e.g., Norman, 1882) or the misassignment of other uncoiled taxa (e.g., *Laxispira*) to Vermiculariinae (see discussion above). These reports cannot, however, be confidently assigned to Turritellidae (e.g., they display non-turritellid protoconch characteristics or uncoil immediately after the protoconch-teleoconch transition; Bandel & Kowalke, 1997; Bieler & Petit, 2011).

The combination of highly unusual morphology and distinctive spiral-ornament ontogeny justifies uniting these species within a single genus (see Friend et al., 2023, for further discussion of turritellid genera).

Vermicularia bathyalis Petuch, 2002
Figs. 10–13

Vermicularia bathyalis Petuch, 2002: 63, fig. 1C–F; Aley, 2005: 73–75, pl. 3, figs. 5, 6; Oleinik et al., 2012: 25, 26, fig. 3F, G.

Types: Holotype, UF 277097; paratype, UF 279230.

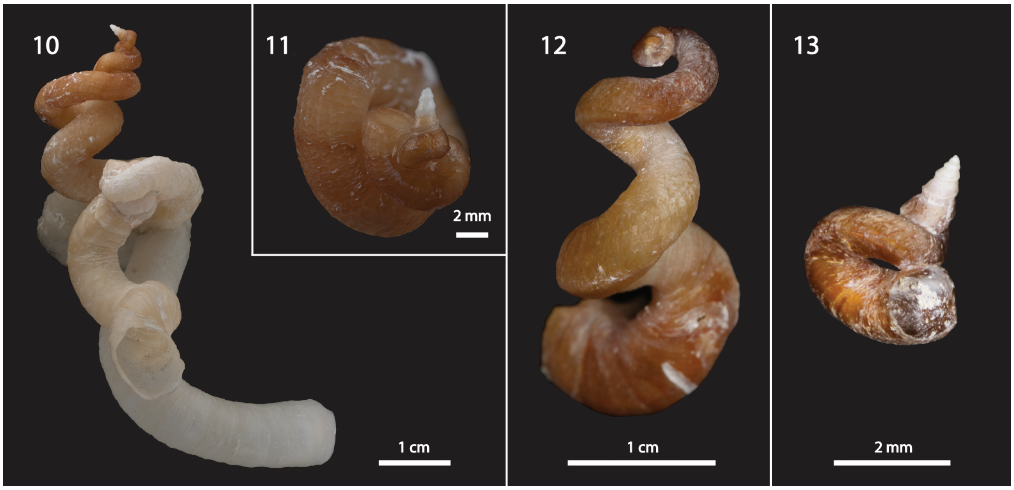
Other Material Examined: USNM 1138077 (2 specimens).

Diagnosis: Differs from most other *Vermicularia* in having a small, light-colored, keeled turritelliform portion with many fine spiral cords. Most similar to *Vermicularia lumbricalis*, but the turritelliform portion has fewer whorls and the uncoiled portion has more, finer, spiral cords whereas *Vermicularia lumbricalis* has two stronger cords that weaken as the shell lengthens and better defined sutures. Differs from *Vermicularia gracilis* in having a frustate whorl profile rather than convex.

Description: Protoconch unknown but inferred to be large based on broken apex on types (Petuch, 2002). Average size for the genus; coiling loosens at last turritelliform whorl before becoming uncoiled after approximately four whorls. Apex light-colored, beginning to darken in last turritelliform whorl. Uncoiled portion has reduced spiral sculpture but has a scaly/wrinkled appearance. Aperture of uncoiled portion rounded. Whorl profile frustate. Turritelliform portion keeled. Sculpture consists of 12 faint, evenly spaced spiral cords on uncoiled portion. Basal sinus type 1 (Fig. 5). Lateral sinus of medium depth, straight inclination, no major inflection points, with apex located on upper third of shell.

Distribution: Recent. Deep water (400–600 m), presently known only from the Bahamas, east of the Straits of Florida.

Remarks: *Vermicularia bathyalis* is presently only known from a very small number of specimens, and is only known definitively to occur in the Bahamas. The deepest-dwelling species of *Vermicularia* are *Vermicularia bathyalis* and *Vermicularia lumbricalis* (= *Vermicularia knorrii*), the latter recorded at ~ 600 and ~ 500 m on the Texas continental slope (Oleinik et al., 2012; Tunnell et al., 2010). Because *Vermicularia bathyalis* is most similar to *Vermicularia lumbricalis* among all other *Vermicularia* spp., and has a broader depth range, it is possible that reports of *Vermicularia lumbricalis* (= *Vermicularia knorrii*) in Texas could be examples of *Vermicularia bathyalis*, greatly expanding the range of this species. Unfortunately, we have not been able to examine any deepwater Texas specimens because no specimens meeting these criteria (locality and depth) were present in the collections that we visited (Table 1). The constriction, deflection, and merger of currents in the Straits of Florida also provides downwelling of warm surface waters and plankton (Oleinik et al., 2012). Strong (to 50 cm/sec) bottom currents provide *Vermicularia bathyalis* with an unusual hardground environment, with a moving veneer of soft sediments (Oleinik et al., 2012). This might therefore represent a uniquely suitable deepwater environment for the species.



FIGS. 10–13. *Vermicularia bathyalis* Petuch, 2002. (10, 11) Holotype, UF 277097 (with detail of apex Fig. 11), Bimini Chain, south and west of Victory Cay, Bahamas, Recent. Note that the specimen of *Vermicularia bathyalis* (top) is entangled with the holotype of *Thylacodes squamolineatus* (Petuch, 2002). Photos by R. Bieler. (12, 13) USNM 1138077 (2 specimens), south and west of Victory Cay, Bahamas, Recent.

FIGS. 14–17. *Vermicularia fargoi* Olsson, 1951. (14) UF 277956, St. Petersburg, Pinellas County, Florida, Recent. (15) Holotype, ANSP 187640, Tampa Bay, near Pass-a-Grille, Florida, Recent. Photo by P. Callomon. (16) PRI 108648, Tampa Bay, Florida, Recent. (17) Holotype of *Vermicularia fargoi owensi* Petuch & R. F. Myers, 2014, USNM 1231410, Ten Thousand Islands, Florida, Recent.

Vermicularia fargoi Olsson, 1951
Figs. 14–17

Vermicularia spirata Philippi. Maury, 1925: 227, 228 (in part; figured specimen on pl. 41, fig. 13 is *Vermicularia fargoi*, but the plate indicates that this specimen is from Florida, and so the Trinidad specimen might not be *Vermicularia fargoi*; see Table 5); Salvador, 2022: 90, f.n. (corresponding text on p. 91 contains information about *Vermicularia spirata* not *Vermicularia fargoi*).

Vermicularia cf. *spirata*. J. Andrews, 1977: 100.

Vermicularia fargoi. Olsson, 1951: 7, 8, pl. 1, figs. 7, 8; Morris, 1973: 141, pl. 41, fig. 16; Abbott, 1974: 96, fig. 920; Tunnell et al., 2010: 135, 397; Witherington & Witherington, 2017: 10.

Vermicularia fargoi owensi Petuch & Myers 2014: 157, 238, 239, pl. 7.14, figs. F, G.

Types: Holotype of *Vermicularia fargoi*, ANSP 187640; holotype of *Vermicularia fargoi owensi*, USNM 1231410.

Other Material Examined: UF 277956, PRI 108648; plus numerous specimens in the collections of PRI, UF, and LACM.

Diagnosis: Large turritelliform stage. Similar to Pacific *Vermicularia frisbeyae*, but *Vermicularia fargoi* has three prominent spiral cords whereas *Vermicularia frisbeyae* has only two. Differs from *Vermicularia weberi* in having a higher pleural angle, beading, and position of spiral sculpture.

Description: Protoconch unknown. Largest turritelliform portion among *Vermicularia*. Whorl profile frustate. Two prominent spiral cords above and below midpoint of the whorl, with a third slightly weaker, but still prominent cord near the top of the whorl. Sculpture commonly beaded. Umbilicate. Basal sinus type 2. Lateral sinus of medium depth, prosocline, no significant inflection points, with apex at midpoint on whorl. Aperture quadrate.

Distribution: Recent. Depth 0–10 m; Cuba, Florida to Texas. Typically found unattached on sand or mud (Olsson, 1951; Petuch & Myers, 2014).

Remarks: Three subspecies might exist: *Vermicularia fargoi fargoi* Olsson, 1951 (western Florida), *Vermicularia fargoi owensi* Petuch & Myers, 2014 (Florida Keys and southern Florida), and an unnamed subspecies in Texas identified by Petuch & Myers (2014) and illustrated by Tunnell et al. (2010). Subspecies are variable in pleural angle. *Vermicularia fargoi owensi* appears to only have two uncoiled whorls, whereas *Vermicularia fargoi fargoi* typically undergoes a gradual separation of whorls and takes on a more vermiform appearance late in ontogeny. Specimens can change their coiling axis, but it is notable that they often do not, or remain close to the coiling axis of the turritelliform portion. Although the species was listed as common by Olsson (1951), we were unable to locate material appropriate for molecular analysis.

Vermicularia frisbeyae McLean, 1970

Figs. 18–20

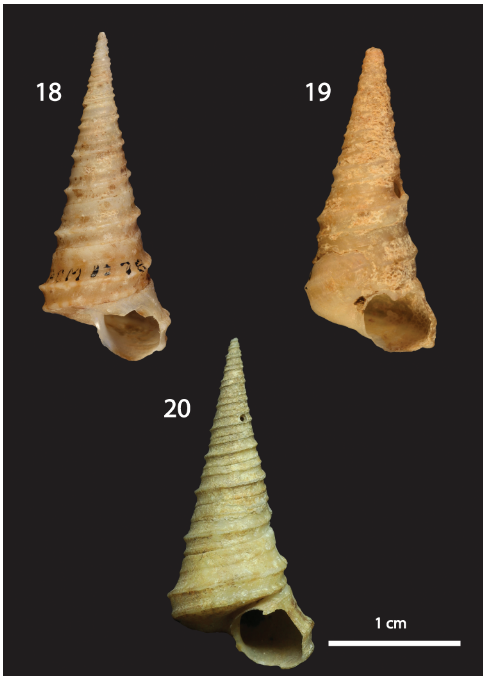
Vermicularia frisbeyae McLean, 1970: 311, pl. 46, figs. 5, 6; Abbott, 1974: 96; Keen, 1971: 396, fig. 447; Vega & González, 2002: 8; Bastida-Zavala et al., 2013: 360; Galván-Villa & Ríos-Jara, 2018: 4; Hendrickx et al., 2019: 65, 66, pl. 5, fig 54.

Types: Holotype, LACM 1278; paratypes, LACM 1279, CAS IZ 64719, USNM 679555.

Other Material Examined: LACM 27434; USNM 67955.

Diagnosis: Only two modern species of *Vermicularia* occur in the eastern Pacific, *Vermicularia pellucida* and *Vermicularia frisbeyae*, with *Vermicularia frisbeyae* possessing a substantial turritelliform stage that *Vermicularia pellucida* does not. Compared to *Vermicularia fargoi*, which also has an extended turritelliform stage, *Vermicularia frisbeyae* possesses only two prominent spiral cords whereas *Vermicularia fargoi* has three. The flat-sided whorl profile also distinguishes the species from the fossil *Vermicularia weberi*.

Description: Protoconch unknown. Large turritelliform stage, ~12 teleoconch whorls. Earliest teleoconch cream-colored. Darker patches give the later whorls a roughly striped appearance, which can make sculpture appear lightly beaded, but it is smooth on the holotype and paratype LACM 1279. Whorl profile flat-sided. Sculpture consists of two strong cords initially equal in strength with the top (posterior) cord reducing in strength later in ontogeny, but the D (sutural) cord becomes more prominent. Turritelliform portion umbilicate before uncoiling. Vermiform portion not present in the holotype, but described by McLean (1970) as opening for a complete volution, and then producing two more whorls at a 45°angle to the initial coiling axis. McLean described the uncoiled specimen as 61.2 mm in total length, approximately half of that length belonging to the uncoiled portion. Basal sinus type 5. Lateral sinus deep, opisthocline, single inflection on top, with apex in middle third of whorl.



FIGS. 18–20. *Vermicularia frisbeyae* McLean, 1970. (18) Holotype, LACM 1278, Manzanillo, Colima, Mexico, Recent. Photo by L. Groves. (19) Paratype, LACM 1279, Manzanillo, Colima, Mexico, Recent. Photo by L. Groves. (20) LACM 27434, south of Navidad Head, Tenacatita Bay, Jalisco, Mexico, Recent.

Distribution: Recent. Eastern Pacific: southern Mexico to western Panama.

Vermicularia gracilis (Maltzan, 1883), new combination

Figs. 21–23

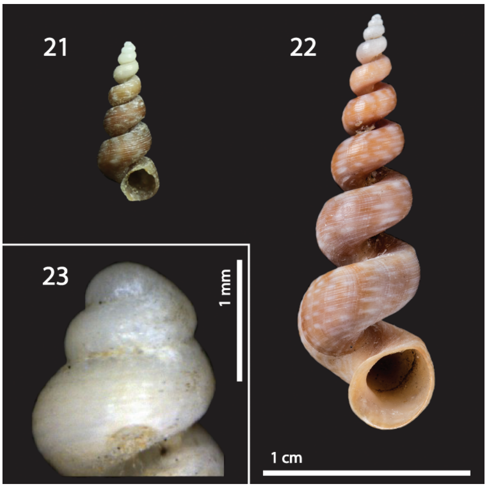
Smithia gracilis Maltzan, 1883: 98.

Callostracum gracile E. A. Smith, 1909: 229; 1915: 365.

Types: Holotype of *Smithia gracilis* lost; neotype (designated herein), NHMUK 1909.7.27.1.

Other Material Examined: PRI 77070; TU 3192, figured specimen of C. Vos (http://www.marinespecies.org/aphia.php?p=image&pic=84172).

Diagnosis: Small for the genus. Retains the same coiling axis despite whorls becoming detached. Whorl profile rounded. Coloration pattern complex, beginning as white fol-



FIGS. 21–23. *Vermicularia gracilis* (Maltzan, 1883). (21) PRI 77070, Senegal, Recent. (22) Neotype, NHMUK 1909.7.27, Isle of Goree, Senegal, Recent. Photo by K. Webb, © The Natural History Museum, London. (23) Vos personal collection specimen, C. Vos specimen number TU 3192, Senegal, Recent. Photograph © C. Vos.

lowed by darker reddish brown, with regularly spaced light-colored dashes or ellipses. Only *Vermicularia fargoi* also frequently maintains an open-coiled portion close to retaining the original coiling axis, and *Vermicularia fargoi* has a much larger coiled stage along with pronounced spiral sculpture with three primary spiral cords. The rounded whorl profile also readily distinguishes *Vermicularia gracilis* from *Vermicularia lumbricalis* (= *Vermicularia knorrii*), which has a strongly campanulate whorl profile with strong sculpture.

Description: Protoconch paucispiral, nucleus slightly submerged, ~ 600 μm in diameter. Whorls become detached (openly coiled) after two or three volutions, but shell maintains coiling axis. Early whorls white to cream-colored, later whorls dark, with light maculations. Aperture teardrop-shaped. Whorl profile convex. Sculpture consists of many fine spiral lineations of approximately equal strength. Lateral sinus of medium depth, opisthocline, no significant inflection points, with apex on upper third of whorl.

Distribution: Recent. West Africa, often reported from Senegal; reported occurrence in Mediterranean considered spurious by Gofas & Zenetos (2003).

Remarks: Maltzan named *Smithia gracilis*, but Smith noted that the genus "*Smithia*" was preoccupied and erected the genus *Callostracum*. The Maltzan type specimen was lost (A. Salvador & H. Wood, pers. comm.), but the specimen used by Smith is designated as a neotype herein. This is the only eastern Atlantic *Vermicularia* species presently known. The species has been referred to Turritellidae because it has a typical turritellid protoconch and spiral sculpture pattern (Marwick, 1957; Allmon, 2011). Marwick (1957) noted that Wenz (1939) classified *Callostracum* as a subgenus of *Mesalia*, but Marwick (1957) considered it to be turritelline, because *Vermicularia gracilis* lacks the truncated columella and basal spout of *Mesalia*, and the operculum is more similar to *Turritella* than *Mesalia*. The species has the typical *Vermicularia* growth form with a coiled turritelliform portion followed by later uncoiling, and similar growth-line characters to other *Vermicularia.* The taxon nests well within the *Vermicularia* morphological phylogeny presented below (Fig. 87), and in the absence of molecular evidence to the contrary, it seems most parsimonious to place the species within *Vermicularia*.

†***Vermicularia katiae*** **Anderson n. sp.**

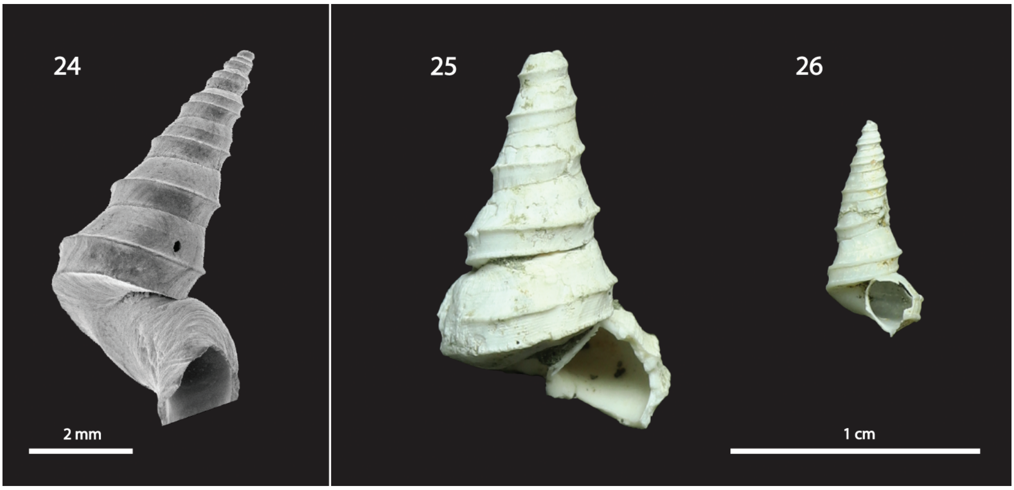
Figs. 24–26

Types: Holotype, PRI 76997; 2 paratypes, PRI 68759; UF 75668.

Etymology: "Katie's worm-snail," named for Katherine Mary Anderson, the spouse of BMA.

Diagnosis: Small for the genus. Unlike *Vermicularia woodringi*, the species has only one truly prominent spiral cord, just below the midpoint of the whorl, with a secondary noticeable but much weaker cord above and a moderate D cord evident on the latest whorls. Whorls are hypercampanulate, distinguishing the species from *Vermicularia lumbricalis*, which also has a more prominent D cord than ***Vermicularia katiae*** **n. sp.** It does not resemble *Vermicularia milleti* in uncoiling habit and has a much weaker A cord on early whorls than *Vermicularia milleti*.

Description: Protoconch unknown, diameter < 350 μm. Small, uncoiling early in ontogeny (~ 5–6 whorls). B and A cords appear nearly equal in strength on earliest teleoconch whorls, with A cord rapidly decreasing in strength and B cord migrating away from the aperture. Whorls hypercampanulate. Later turritelliform

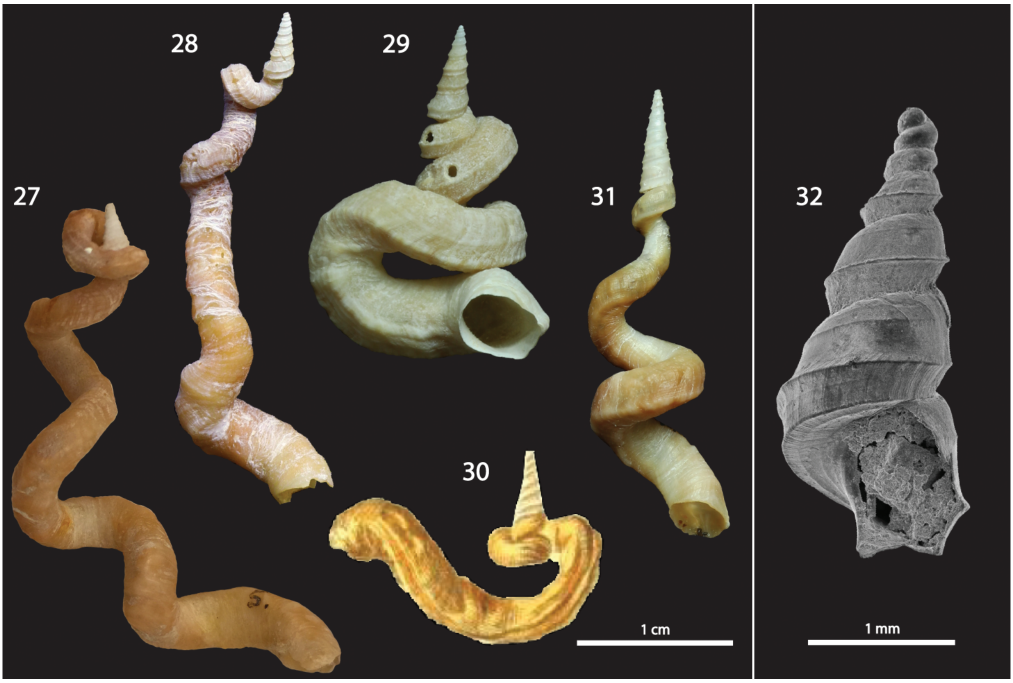


FIGS. 24–26. ***Vermicularia katiae* n. sp.** (24) UF 75668 (SEM), Rio Bueno Harbour East, Jamaica, Pliocene. (25) Holotype, PRI 76997, Santiago, Rodriguez Province, Dominican Republic, Miocene. (26) Paratype, PRI 68759, Valverde Province, Dominican Republic, Pliocene.

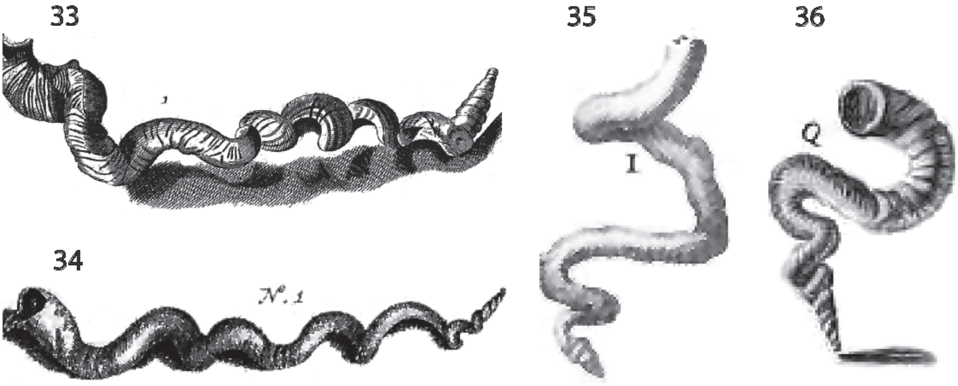
whorls develop a strong D cord prior to uncoiling, showing two strong spiral cords (B and D), with the B cord forming a prominent keel. Turritelliform portion umbilicate. Aperture appears subquadrate, but all known specimens are broken shortly after uncoiling. Basal sinus type 1. Lateral sinus deep, opisthocline, single inflection on bottom, with apex on upper third of whorl.

Distribution: Upper Miocene (Messinian)–Pliocene, Dominican Republic and Jamaica. Type locality is the banks of the Rio Gurabo, Gurabo Formation (upper Miocene–Pliocene), Dominican Republic, Vokes (TU) locality 1277. Paratype from Vokes (TU) 1210. Saunders et al. (1986) considered the Gurabo Formation to be primarily Pliocene, however McNeill et al. (2012) dated the Gurabo Formation to include both the latest Miocene (Messinian) and early Pliocene, between 5.6 and 4.2 Ma, using a combination of Sr isotope and paleomagnetic data and previously published U-Pb age data (Denniston et al., 2008) and foraminiferal biostratigraphy (Lutz et al., 2008). The locality TU 1277 is ~ 2–2.5 km above the ford on Los Quemados–Sabaneta road (1976–1977), at ~ 222–226 m in stratigraphic height (approximate height from Waller, 2011, following the convention of Saunders et al., 1986) at latitude 19.485105, longitude -71.179. The locality TU 1210 is on the eastern bank, the first bluff downstream from the ford on Los Quemados–Sabaneta road (1976–1977), 394–396 m in stratigraphic height (approximate height from Waller, 2011) at latitude 19.51243, longitude -71.18571. Following the age-depth model of McNeill et al. (2012), these stratigraphic levels correspond to latest Miocene and early Pliocene ages for TU 1277 and TU 1210, respectively. An additional specimen of ***Vermicularia katiae* n. sp.** (UF 75668) is from the St. Thomas Parish, Layton Formation, Bowden member (Pliocene), Jamaica, at latitude 17.8896, longitude 76.3146.

Remarks: This species is presently known from only three specimens. However, ***Vermicularia katiae* n. sp.** is likely the source of much confusion regarding the distribution of *Vermicularia woodringi* in space and *Vermicularia lumbricalis* (= *Vermicularia knorrii*) in time, because it is only known from small specimens and the strong medial cord and early development of the D cord could be mistaken for the two stronger A and B cords of *Vermicularia woodringi*. This species represents the oldest Western Hemisphere *Vermicularia* for which both age and specimen identity are confidently known.



FIGS. 27–32. *Vermicularia lumbricalis* (Linnaeus, 1758). (27) Neotype, UUZM 802, locality unrecorded, Recent. (28) PRI 108643, off Sanibel Ferry, near the end of Ferry Road, Lee County, Florida, Recent. (29) TAMU 4-5045, off the coast of Gulf Shores, Alabama, Recent. (30) Illustration from Knorr (1757) referenced as the type of *Vermicularia knorrii* (Deshayes, 1843), locality unknown. (31) LACM 91751, Sanibel, Lee County, Florida, Recent. (32) UF 132812 (SEM), Jamaica, Pleistocene.



FIGS. 33–36. Published illustrations referenced by Linnaeus (1758) in his original description of *Vermicularia lumbricalis*. (33) Lister (1688). (34) Rumphius (1705). (35) Argenville (1742). (36) Gualtieri (1742).

Vermicularia lumbricalis (Linnaeus, 1758)
Figs. 27–36

Serpula lumbricalis Linnaeus, 1758: 787; 1764: 699; 1767: 1266.

Vermicularia lumbricalis Lamarck, 1799: 78; Friend et al., 2023: text-fig. 35, no. 4, text-fig. 37.

Not *Vermetus lumbricalis* Lamarck, 1822: 225 (based on examination of referenced figure: Adanson, 1757, pl. 11, fig. 1).

Vermetus knorrii Deshayes in Deshayes & Milne-Edwards, 1843: 68.

Vermiculus lumbricalis Mörch, 1861: 171.

Vermicularia knorri (Deshayes). Perry & Schwengel, 1955: 136, 137, pl. 26, fig. 183; Warmke & Abbott, 1961: 64, pl. 12, fig. C; Rice & Kornicker, 1962: 370: 2, figs. 16, 17; Morris, 1973: 141, pl. 41, fig. 15; Humfrey, 1975: 77, pl. 5, fig. 10; Emerson & Jacobson, 1976: 73, 74, pl. 20, fig. 6; Petuch, 2002: 63.

Vermicularia knorrii (Deshayes). Abbott, 1974: 96, fig. 918; Tunnell et al., 2010: 136, 397, fig. 3.30, no. 17, fig. 3.38, nos. 25, 25a; Sept, 2016: 66, 67; Witherington & Witherington, 2017: 10; Sang et al., 2019: 5311, 5312, 5316.

Types: Neotype (designated herein), UUZM 802; four illustrations were given by Linnaeus (1758) as syntypes, but the illustrations are insufficient for definite species determination and the original material corresponding to these illustrations could not be located. See discussion below. *Vermicularia knorrii* was named based on Knorr's figure (1757: pl. 17, fig. 2) from the Sommer collection, the fate of which is unresolved (Dijkstra, 2010), but we have reproduced the figure herein (Fig. 30). As noted by Bieler (1996: 28), Mermod & Binder (1963: 159, 160) cited three specimens in Lamarck's collection in Geneva (MHNG) as type material of "*Vermetus lumbricalis* Lamarck, 1822," but this was in error "because Lamarck had clearly referred to Linne's species." It is also noteworthy that these specimens (figured by Mermod & Binder, 1963) all lack apices.

Other Material Examined: specimens previously identified as *Vermicularia knorrii:* LACM 25985, 91751; PRI 73787, 108643; TAMU 4-5045; UF 446833, 132812; plus many additional specimens at UF, USNM, and PRI.

Diagnosis: Small for genus, both in length and maximal width. Color shifts from light to dark from early to later whorls, although the pigmented portion can range from tan to dark brown. Distinguished from *Vermicularia spirata* by its smaller size and two spiral keels that decrease in strength on the vermiform portion. Vermiform portion less strongly ornamented than is typical for *Vermicularia spirata*. Lacks the numerous fine spiral cords present in *Vermicularia bathyalis.* Larger than *Vermicularia gracilis*, which also has a round whorl profile*,* whereas the early whorls of *Vermicularia lumbricalis* are campanulate with strong sculpture*.*

Description: Protoconch maximal diameter 350–400 µm. Turritelliform portion white, becoming much darker (tan to brown or reddish brown) at uncoiling. Whorl profile campanulate. Typically uncoils from 4–6 whorls, but can have up to eight whorls. One prominent spiral cord on turritelliform portion accentuating the keel, with a second more reduced cord also present. Vermiform portion has spiral cords that can be greatly reduced, and can appear smooth or wrinkled. Basal sinus type 1. Lateral sinus deep, opisthocline, no inflection points, with apex located medially. Aperture circular.

Distribution: Pleistocene–Recent. Typically 2–50 m depth, but reported to 500 m (Tunnell et al., 2010), although it is possible that these specimens are in fact *Vermicularia bathyalis (*see discussion in the Remarks under *Vermicularia bathyalis*). Gulf of Mexico: Texas to Florida, Antigua, Barbuda, Cuba, Jamaica, Campeche Bank, Mexico, and Belize; Atlantic coast from Florida to North Carolina, Bermuda.

Remarks: Four previously published illustrations were referenced by Linnaeus (1758), with an additional specimen referenced in the 12th edition of *Systema Naturae* (Linnaeus, 1767), that same specimen listed in a published catalog by Linnaeus (1764) and now UUZM 802 designated herein as neotype. The four pre-Linnean illustrations (Figs. 33–36) that have served as syntypes all appear to belong to *Vermicularia*, but include forms that would likely be placed in synonymy either with *Vermicularia spirata* (illustration by Lister, 1688; date of publication of book IV *fide* Woodley, 1994) or *Vermicularia knorrii* (illustration by Gualtieri, 1742)*,* or which cannot be definitively distinguished based on the illustrations alone (illustrations by Argenville, 1742, and Rumphius, 1705). The specimen attributed to Rumphius does not have a clear depiction of the turritelliform stage. If it is a turritellid, it might have been an addition by Dutch artist Simon Schynvoet (1652–1727), who added images of specimens to the publication of Rumphius' *D'Amboinsche Rariteitkamer* which did not belong to Rumphius and some of which were not from Ambona (Indonesia) (Beekman, 1999: xc). The specimen is presumed lost (C. Vos, pers. comm. with BMA, especially because no reference to another collection was given by Rumphius). The specimen of Lister could not be located at NHMUK (A. Salvador, pers. comm. with BMA) and was also not located in the collection of the Linnean Society of London (Dance, 1967). The specimen of Argenville could not be located because much of his personal collection was distributed at auction after his death. Coomans (1985: 284) noted that at least some molluscan specimens of Argenville (e.g., *Conus cedonulli* Linnaeus, 1767) were "in the cabinet of the Rev. C. Chais (1701–1788) at the Hague, Netherlands," cataloged by Meuschen (1766), but the subsequent fate of these specimens is unresolved. Gualtieri's specimen could not be located among the collections at the University of Pisa Museo di Storia Naturale e del Territorio of Pisa (M. Dellacasa, pers. comm. with BMA, 2023), which houses the surviving 700 specimens from Gualtieri's collection purchased by Stefano Lorena (Manganelli & Benocci, 2011).

In the 12th edition of the *Systema Naturae* (Linnaeus, 1767: 1266), Linnaeus added a reference to an additional specimen, now designated UUZM 802 (Wallin, 2001), which he had cataloged in the 1764 catalog (p. 699, no. 431). Because none of the original type material appears available, and this surviving specimen of *Vermicularia lumbricalis* is known to have been handled, classified as *Vermicularia lumbricalis*, and provided as a reference for the species by Linnaeus (1767), we therefore select this specimen as the neotype of the species.

Vermicularia "*knorrii*" is among the most common *Vermicularia* present in collections, but it appears to be a junior synonym of *Vermicularia lumbricalis*. The illustration referenced for the name *Vermicularia knorrii* (see Deshayes & Milne-Edwards, 1843: 68, referencing Knorr, 1757: pl. 17, fig. 2) is consistent with the neotype of *Vermicularia lumbricalis*. The specimen illustrated by Knorr (1757) is lost, with the fate of the Sommer collection being unresolved (Dijkstra, 2010). There are numerous specimens in collections listed as *Vermicularia* "*knorrii*," many of which we examined closely for comparison to the Linnean type. Both species have a similar whorl profile in the turritelliform portion, light-colored early teleoconchs that transition to darker shell material, and similar spiral sculpture on the uncoiled portion of the shell (with the existing illustration of the type of *Vermicularia knorrii* not sufficient for proper characterization of sculpture on the early teleoconch). Additionally, the overwhelming majority of material examined assigned to *Vermicularia knorrii* is consistent with the neotype of *Vermicularia lumbricalis*, whereas the remainder of specimens are properly assigned to other species. *Vermicularia knorrii* was originally described as being easily distinguished from *Vermicularia* "*lumbricalis*," however the description by Deshayes (1843) implies that it is in fact being distinguished from *Vermicularia spirata*. It is likely that a specimen of *Vermicularia spirata*, which had itself been misidentified as *Vermicularia lumbricalis*, led to this original conclusion. The species is often found in sponges (e.g., Abbott, 1974). Given the widespread confusion of common names and identifications among *Vermicularia fargoi, Vermicularia lumbricalis* (= *Vermicularia knorrii*), and *Vermicularia spirata,* it is worth noting that *Vermicularia lumbricalis* is more common in Florida than the other extant species. It has been frequently mislabelled as *Vermicularia spirata*, although both *Vermicularia lumbricalis* and *Vermicularia spirata* are widespread in the western Atlantic (in agreement with the cautionary note given by Abbott, 1974: 96).

†*Vermicularia milleti* (Deshayes, 1850)
Figs. 37–39

Vermetus milleti Deshayes, 1850: 43, pl. 70, figs. 9, 10.

Vermetus carinatus Hörnes, 1856: 486, pl. 46, fig. 17.

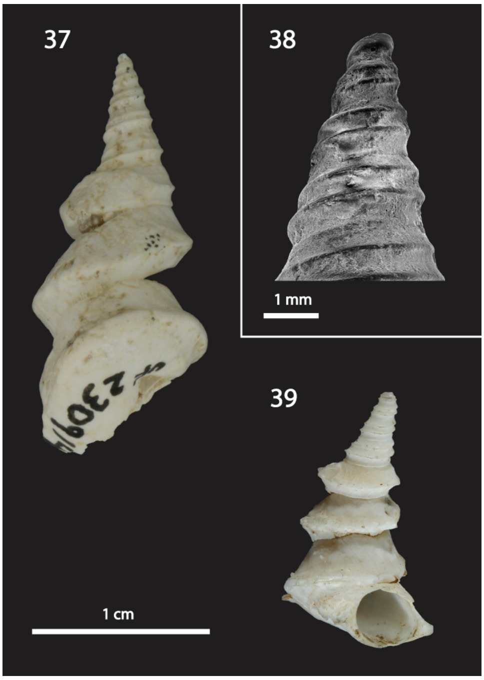
Turritella cf. *terebralis* Lamarck. Boettger, 1901: 153, no. 471.

Vermetus (*Vermicularia*) *pseudoturritella* Boettger, 1906: 171; Zilch, 1934: 220, pl. 7, fig. 25a, b; Strausz, 1966: 121, pl. 3, figs. 22, 23; Atanacković, 1985: 99, pl. 24, figs. 1, 2.

Vermetus (*Vermicularia*) *milleti* Deshayes. Glibert, 1949: 128, pl. 7, fig. 10.

Vermicularia milleti (Deshayes). Cossman & Peyrot, 1922: 86, 87, pl. 3, figs. 14, 32; Bałuk, 1975: 123, 124, pl. 14, figs. 6, 7; 2006: 194, pl. 6, figs. 5, 6; Landau et al., 2004: 26, pl. 3, fig. 18; 2018: 195, pl. 18, figs. 1–4; Vaessen, 2013: 42, 43, figs. 4–7; Harzhauser & Landau, 2019: 105, 106, fig. 29A, B, C; Friend et al., 2023: text-fig. 35, no. 5, text-fig. 37.

Types: syntype of *Vermetus milleti*, UCBL-EM 32115; syntype of *Vermetus carinatus*, NHMW 1876/0011/0077; lectotype (Zilch, 1934) of



FIGS. 37–39. *Vermicularia milleti* (Deshayes, 1850). (37, 38) UF 230914, Loire-Atlantique, France, Miocene (with SEM of early whorls in Fig. 38). (39) Lectotype of *Vermetus* (*Vermicularia*) *milleti pseudoturritella* Boettger, 1906, SMF 12.2496a, Romania. Miocene.

Vermetus (Vermicularia) pseudoturritella, SMF 12.2496a.

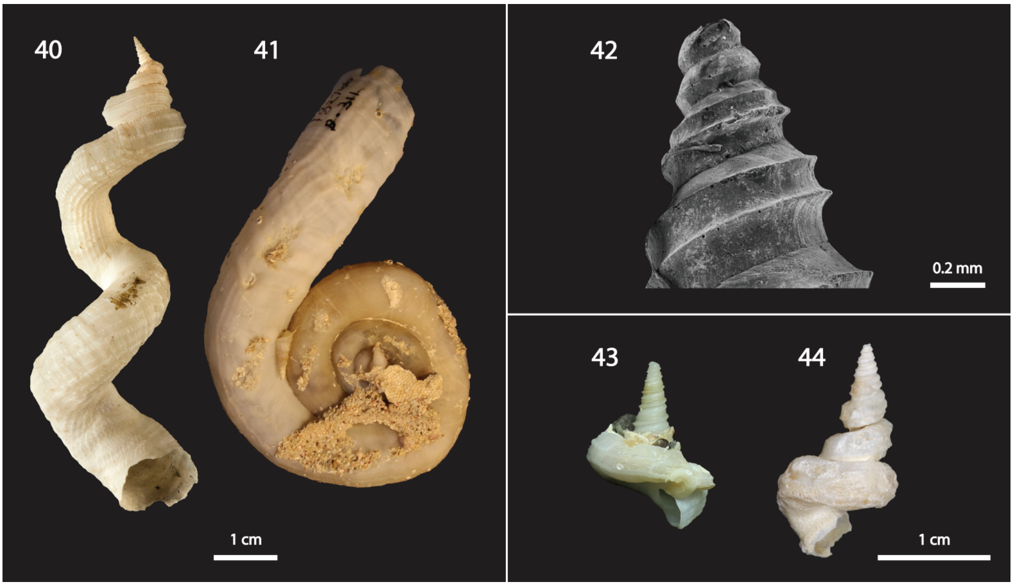
Other Material Examined: UF 230914.

Diagnosis: Average size for the genus. Uncoiled portion maintains a strong campanulate whorl profile rather than becoming highly tubular as in other *Vermicularia*. Unlike the co-occurring uncoiled gastropod *Trypatrochus conicus* (synonyms *Vermicularia conica, Delphinula conica*), which has a campanilioid protoconch and growth lines lacking a lateral sinus, *Vermicularia milleti* appears to have genuine turritellid affinities. No other *Vermicularia* spp. are presently known from the Miocene–Pliocene of Europe.

Description: Small, 2–3 cm long, open coiling beginning after seven whorls. Whorl profile campanulate. Two spiral cords (B and A) on the earliest teleoconch, with B appearing first, followed by A, and then D cord forming the three spiral cords present on later turritelliform whorls. The strongest is B cord, which accents a keel that is maintained on the openly coiled whorls. D cord (just above the suture) is minor on earliest teleoconch whorls, increasing in strength on the turritelliform whorls but weakening and migrating toward the portion of the shell that would previously have been the abapical portion at uncoiling. A cord begins nearly as prominent as B cord, but then fades in relative strength. Basal sinus type 1. Lateral sinus shallow, uninclined, single inflection point on top, with apex on upper third of whorl. Rarely found attached to other conspecifics, but does not form large masses (Landau et al., 2018).

Distribution: The type is from the Middle Miocene Faluns de Touraine Formation, Paris Basin (Deshayes, 1839). First appearance is in the Burdigalian (20.44–15.97 Ma) of the Aquitaine Basin (Cossmann & Peyrot, 1922; Landau et al., 2018). Middle Miocene (Langhian and Serravallian) of Austria (Hörnes, 1856), Hungary, Romania (Saint Martin et al., 2000), Poland (Bałuk, 2006), and Turkey (Landau et al., 2013). Langhian, Tortonian, and Messinian of France (Vaessen, 2013). Reported in the Pliocene of Spain by La Perna et al. (2001) but was unfigured. These reports were confirmed by Landau et al. (2004), with the species persisting in the late Pliocene (Piacenzian, 2.58–3.6 Ma) Estepona Basin of Spain, but is unknown from other localities in the Pliocene (Landau et al., 2004, 2018).

Remarks: This species was recently treated by Landau et al. (2018) and Harzhauser & Landau (2019), in which three syntypes of *Vermetus carinatus* (Hörnes, 1856) were figured. The species is not generally associated with reef environments but rather clayey to sandy environments (Harzhauser & Landau, 2019). There is an occurrence reported in a Badenian coral microbialite reef in Hungary (Saint Martin et al., 2000), but specimens were unfigured. This is the earliest known *Vermicularia* species, with an extremely long stratigraphic range. Its assignment to the *Vermicularia* is well supported by overall morphological similarity and spiral ontogeny, and its precise relationship to other members of the clade is extensively examined in the discussion, below. The locality for the lectotype of *Vermetus* (*Vermicularia*) *pseudoturritella* was given by Zilch (1934: 220) as “Kostej, Parau ungurului,” now known in English as Costeiu de Sus (Kostej), Timis County, Banat Region, Transylvanian Basin, Romania.



FIGS. 40–44. *Vermicularia pellucida* (Broderip & G. B. Sowerby I, 1829). (40) Holotype of *Vermetus eburneus* Reeve, 1842, NHMUK 1950.11.28.31, western Colombia, Recent. Photo by H. Taylor, NHMUK © The Natural History Museum, London. (41) LACM 182766, Playa Venado, Panama, Recent. (42) LACM 1933-170.8, SEM of early whorls, Galápagos, Ecuador, Recent. (43) PRI 43296, Tenacatita Bay, Jalisca, Mexico, Recent. (44) *Vermicularia fewkesi* (Yates, 1890), USNM 682150, dredged from 61.5 m, off of Santa Barbara Islands, California, Recent.

Vermicularia pellucida (Broderip & G. B. Sowerby I, 1829)
Figs. 40–44

Vermetus pellucidus Broderip & G. B. Sowerby I, 1829: 369.

Vermetus eburneus Reeve, 1842: 46, pl. 152, fig. 2.

Vermiculus pellucidus. Mörch, 1861: 177, pl. 25, figs. 18, 19.

Vermetus fewkesi Yates, 1890: 42, 48, pl. 2, figs. 8, 9; Abbott, 1974: 96.

Vermicularia fewkesi (Yates). Berry, 1956: 151; Coan & Scott, 1990: 404, fig. 2.

Vermicularia pellucida pellucida (Broderip & Sowerby). Keen, 1971: 396, fig. 448; Vega & González, 2002: 28.

Vermicularia pellucida eburnea (Reeve). Keen, 1971: 396, fig. 449; Hughes, 1985: 320–324, fig. 1; Vega & González, 2002: 28; Bastida-Zavala et al., 2013: 360; Brusca, 2020: 275, 284.

Vermicularia pellucida (Broderip & Sowerby, 1829). Keen, 1971: 396; Abbott, 1974: 96; Hendrickx et al., 2019: 66, pl. 5, fig. 55; Friend et al., 2023: text-fig. 35, fig. 6, text-fig. 37.

Vermicularia spirata Allmon, 2011: 164, 183, figs. 7–10; not Philippi, 1836.

Types: Type material of Broderip & Sowerby (1829) could not be located, and is presumed lost (A. Salvador, pers. comm.). Holotype of *Vermetus eburneus*, NHMUK 1950.11.28.31. Holotype of *Vermetus fewkesi* is lost, but a photograph of the type was reproduced by Coan & Scott (1990). “Syntypes” of *Vermiculus lumbricalis var. rugulosa* Mörch, 1861, NHMUK 20210292.

Other Material Examined: LACM 1966-188.3, 1972-85.37, 1938-52.8, 1933-170, 164252, 182766; PRI 43296; UF 372362. “*Vermicularia fewkesi*” USNM 682150. Plus additional specimens at LACM, PRI, and USNM. Fossil specimens LACMIP 66.809, 66.1598, and 1210.185 were examined but were found not to be turritellids (see Remarks, below).

Diagnosis: Large for the genus. Smaller turritelliform stage than in *Vermicularia frisbeyae*, the only other Recent eastern Pacific

Vermicularia, and maintains two strong spiral cords throughout turritelliform stage, whereas the upper cord diminishes in strength in *Vermicularia frisbeyae*. Vermiform portion typically has numerous spiral cords that persist at similar strength for a large portion of the uncoiled shell length. Vermiform portion increases in width much more rapidly than in *Vermicularia spirata*, the only other modern species that can have a small turritelliform portion and strongly ornamented vermiform portion.

Description: Protoconch 300–350 µm in maximum diameter; uncoiled portion often nearly planispiral, which is unusual for the group, but can take on other forms. Can be large for the group, with apertural widths reaching ~ 1 cm. Whorl profile campanulate with two prominent spiral cords. The first teleoconch whorl appears medially keeled, but the posterior (more apical) spiral cord increases in prominence by the second teleoconch whorl and remains strong on the remainder of the turritelliform portion. Typically uncoils after 7–9 whorls, but can reach 9–10 whorls. Three spiral cords present on vermiform portion of the shell. Basal sinus type 1. Lateral sinus of medium depth, uninclined, single inflection point at bottom of whorl, with apex located medially. Shape of uncoiled portion highly variable.

Distribution: Recent. Depth 10–80 m; eastern Pacific: southern California (Channel Islands) to Peru and the Galápagos Islands.

Remarks: Degree of pigmentation varies substantially from translucent to solid cream or tan, with brown maculations commonly occurring on any background or not at all. Two subspecies names are in common use: *Vermicularia pellucida pellucida and Vermicularia pellucida eburnea* Reeve, 1842. It is unclear whether these subspecies are geographically distinct in microhabitat, because they do overlap in range in Central America, with *Vermicularia pellucida pellucida* occupying California through Panama and *Vermicularia pellucida eburnea* occupying the southern portion from Mexico to Peru. Both were reported from the same locality by Vega & González (2002). Absent additional information on population structure, the use of the subspecific names does not seem warranted. We concur with Keen (1971) that *Vermetus fewkesi* is a junior synonym of *Vermicularia pellucida*. Specimen USNM 682150, discussed but unfigured by Berry (1956: 151), was examined and is figured herein (Fig. 44). *Serpula panamensis* Chenu, 1845, is likely a junior synonym based on the sculptural pattern of the vermiform portion of the shell and geographic implications of its name, but the illustration given lacks both an apex and geographic information, and this species is therefore addressed below as a *taxon inquirendum*.

Several bryozoan-encrusted specimens in the Invertebrate Paleontology collection of the LACM (LACMIP 66.809, 66.1598, 1210.185) from the Palos Verdes Sand (Pleistocene) of Newport Beach and Los Angeles, California were considered potential examples of fossil *Vermicularia pellucida* based on the size and general shape of the encrusted apices, but CT imaging of LACMIP 1210.185 showed that the encrusted shells are not turritellid. Although there is therefore presently no confirmed fossil record of this eastern Pacific species, it must have dispersed to the eastern Pacific prior to the closure of the Central American Seaway (see Discussion below).

Syntypes of *Vermiculus lumbricalis* var. *rugulosa* Mörch, 1861 (NHMUK 20210292, but an unavailable name *fide* Bieler & Petit, 2011) appear to be *Vermicularia pellucida*, however the locality information given is the Philippines, which we consider in error because there are no other specimens discovered in our examinations of collections or literature reports of genuine *Vermicularia* from the western Pacific.

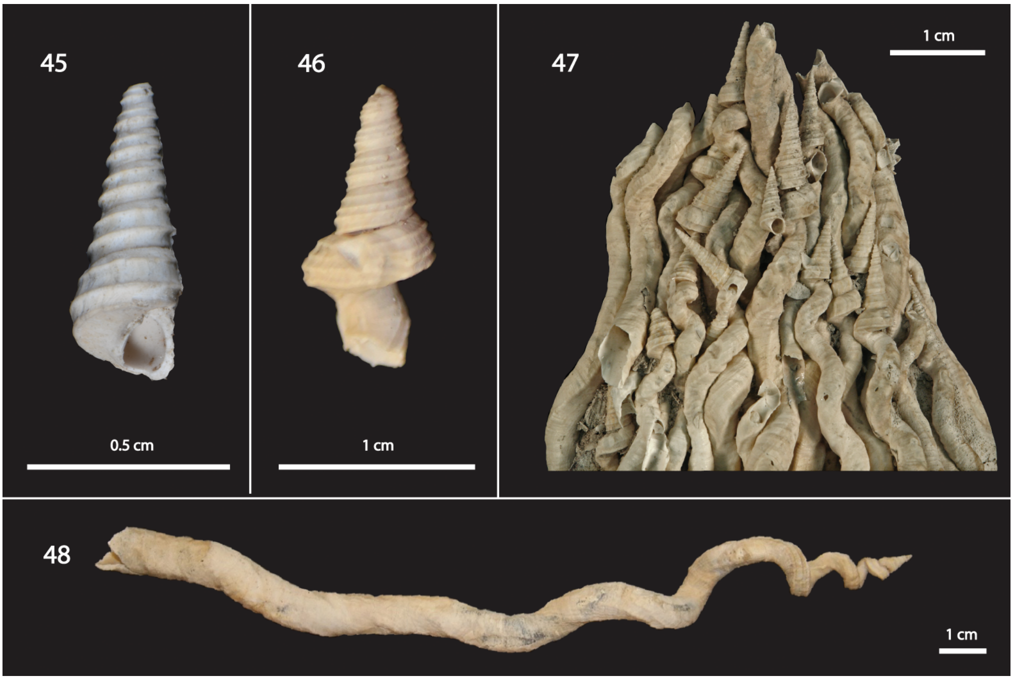
†*Vermicularia recta* Olsson & Harbison, 1953
Figs. 6, 7, 45–48

Vermicularia recta Olsson & Harbison, 1953: 307; Petuch, 1982: 14, 18; Geary & Allmon, 1990: 261, fig. 3; Allmon, 1992b: p. 134, fig. 5B; Petuch & Roberts, 2007: 85, figs. 4.11G, 4.13; 2019: 88, 90, figs. 4.11G, 4.13; Anderson & Allmon, 2018: 445, fig. 1B; Ossó et al., 2018: 550; Petuch & Berschauer, 2021: 82, unnumbered fig. on p. 86, fig. 5.20.

Types: Holotype, ANSP 18974 (specimen is a mass of shells), 18384 (apex taken from ANSP 18974).

Other Material Examined: PRI 73952, 76998, 49895, 108644; UF 123499; plus many other UF and PRI specimens.

Diagnosis: Large for the genus. Individual specimens are very similar to the Recent *Vermicularia spirata*; *Vermicularia recta* has a more rectilinear aperture and cross section, whereas *Vermicularia spirata* is nearly circular in cross section. When the turritelliform apex is not severely worn, it displays much stronger spiral sculpture than in *Vermicularia spirata*,



FIGS. 45–48. *Vermicularia recta* Olsson & Harbison, 1953. (45) Holotype, ANSP 18974 (a tip taken from ANSP 18974, not the same tip removed from ANSP 18974 and figured by Olsson & Harbison, 1953 as ANSP 18384), Ortona Locks, Glades County, Florida, Pleistocene. (46, 48) PRI 108644 (removed from bioherm PRI 76998), APAC Pit, Sarasota County, Florida, Plio–Pleistocene (with apex in Fig. 46). (47) UF 123499, Macasphalt Shell Pit, Sarasota County, Florida, Plio–Pleistocene.

with A, B, and C cords distinct on earliest whorls and D cord becoming more prominent in the last turritelliform whorls.

Description: Can reach the greatest lengths of known fossil *Vermicularia*. Occurs free, but often in lightly cemented intercoiled masses. Turritelliform portion ~ 8 whorls. Whorl profile frustate. Vermiform portion 200–300 mm long. Turritelliform portion with three (rarely two) spiral cords, with a fourth (D) cord becoming stronger as the suture deepens before coiling opens. Two strong medial spiral cords on vermiform portion that can fade toward the aperture but are detectible throughout ontogeny. Many minor spiral cords are present throughout ontogeny. Flattened on inner side of the whorl giving a more rectangular appearance to the aperture than in *Vermicularia spirata*, which is circular in cross section. Basal sinus type 1. Lateral sinus of medium depth, prosocline, uninflected, with apex medially placed.

Distribution: Plio–Pleistocene of Florida: Bermont Formation, Caloosahatchee Formation, Tamiami Formation (Pinecrest Sand), Jackson Bluff Formation.

Remarks: *Vermicularia recta* forms prominent masses or reefs that can be of stratigraphic significance, especially in the Pliocene Pinecrest Beds (Tamiami Formation) of Florida (DuBar, 1958; Petuch, 1982; Geary & Allmon, 1990; Allmon, 1993). Often any substantial fossil mass of intercoiled/cemented *Vermicularia* tubes is assigned to *Vermicularia recta*, but *Vermicularia woodringi* and *Vermicularia spirata* also form such associations. *Vermicularia recta* maintains a flattened inner coiling surface as opposed to a rounded one and is generally larger in diameter at a given length than *Vermicularia woodringi*, which frequently co-occurs with *Vermicularia recta* and is misidentified as such. *Vermicularia recta* reef masses that have been washed to remove sediment frequently have finer spiral sculpture abraded off of the apices.

Vermicularia spirata (Philippi, 1836)
Figs. 9, 49–63

Vermetus spiratus Philippi, 1836: 224, 225, pl. 7, fig. 1; Rogers, 1908: 167, 180, fig. 8.

Vermetus bicarinatus Deshayes in Deshayes & Milne-Edwards, 1843: 67 [a typographical error initially listed the name as "*bricarinatus*" but with the common name given as "Vermet bicaréné" (ICZN 1999: Art. 32.5), E. Coan, pers. comm.].

Vermetus indicus Chenu, 1844a, pl. 3, fig. 2; not Daudin, 1800.

Vermetus bicaréné Chenu, 1847: 262, fig. 979.

Vermetus quadrangulus Philippi, 1848b: 17; Coan & Kabat, 2017: 146 (listed as a probable synonym of *Vermicularia spirata*).

Vermetus radicula W. Stimpson, 1851: 37–39; Abbott, 1974: 96.

Not *Vermetus* cf. *radicula* Stimpson. Maury, 1925: 228, 229, pl. 41, fig. 1.

Vermetus lumbricalis. Reeve, 1842: 46, pl. 152, fig. 1; Chenu, 1859: 319, fig. 2294; not Linnaeus, 1758.

Vermicularia spirata (Philippi). Perry, 1940: 127, pl. 26, fig. 184; Pearse & Williams, 1951: 141, 146, figs. 3, 4; Morton, 1953: 80–82, 84–86, figs. 1, 3a; Olsson & Harbison, 1953: 306, 307; Parker & Curray, 1956: 2434, pl. 1, fig. 10; Gould, 1968a: fig. 1 (in part); 1968b: 804, fig. 1; 1969: figs. 1, 2; Warmke & Abbott, 1961: 64; Humfrey, 1975: 78, pl. 5, fig. 9; Morris, 1973: 142, pl. 41, fig. 17; Emerson & Jacobson, 1976: 73, pl. 6, fig. 2; Thomas et al., 1991: 133–135; Gould & Robinson, 1994: fig. 2; Bieler & Hadfield, 1990; Bandel & Kowalke, 1997: pl. 2, figs. 7, 8; Tunnell et al., 2010: 136, 397, fig. 3.41, no. 5; Allmon, 2011: 164, 170–173, 175–178, 181–183, 187, figs. 11, 16, 33, 46, 54, 55; Redfern, 2013: 39, fig. 110; Tunnell et al., 2014: 45; Sept, 2016: 65h; Coan & Kabat, 2017: p. 147; Selly et al., 2018: 249, fig. 3.2; Salvador, 2022: 91 (text only; figured specimen on p. 90 is *Vermicularia fargoi*).

Vermicularia fargoi Olsson. Perry & Schwengel, 1955: 137, pl. 26, fig. 184.

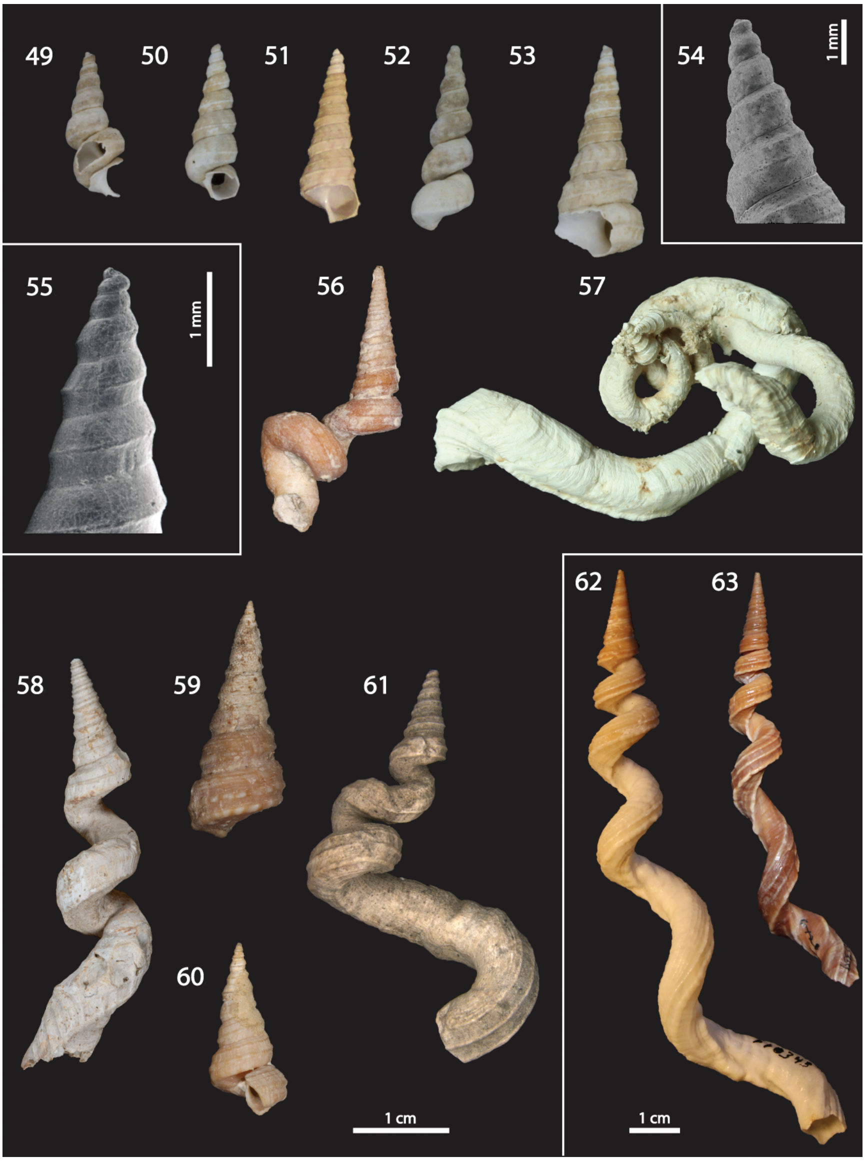
Types: Syntypes of (*Vermicularia*) *spirata*, ZMB 17294; Coan & Kabat (2017) noted that six additional possible syntypes are located at MNHN. Holotype of *Vermetus radicula* destroyed in the 1871 Chicago fire (*fide* Warner, 2015). Type material of *Vermetus bicarinatus* lost (E. Coan, pers. comm.). Type material of *Vermiculus lumbricalis* var. *cornea* Mörch, 1861, NHMUK 20210293; *Vermiculus lumbricalis* var. *ampliata* Mörch, 1861, NHMUK 20210294; and *Vermiculus lumbricalis* var. *diaphana* Mörch, 1861, NHMUK 20210295.

Other Material Examined: LACM 110343, 164243; MCZ 113208; TAMU 4-2730; USNM 122207, 435015, 463252, 776784; MCZ 382941, specimens collected from Walsingham Pond, presently housed at PRI. USNM 74788 (two specimens) of *Vermicularia spirata radicula* from Massachusetts was examined as representative of *Vermetus radicula.* ANSP 31383 was examined as a representative of "*Vermicularia carolinensis*" (Conrad, 1863).

Diagnosis: Reaches the greatest length of any modern *Vermicularia* species, and is substantially larger in width at a given length than *Vermicularia lumbricalis*, the other wide-ranging Atlantic species. Possesses a less carinate whorl profile than in *Vermicularia lumbricalis,* and maintains distinct spiral cords well into the uncoiled portion of the shell. Shell has similar coloration throughout ontogeny unlike *Vermicularia lumbricalis* or *Vermicularia bathyalis*. Vermiform portion has both fine and strong spiral sculpture unlike *Vermicularia pellucida*, which has cords of similar strength. Turritelliform portion smaller than in *Vermicularia fargoi*, *Vermicularia weberi*, and *Vermicularia frisbeyae*.

Description: Protoconch of ~ 1.5 unsculptured whorls. Longest Recent species, ~ 22 cm. Typically has a brief turritelliform stage of 7–9 whorls that is pigmented like the rest of the shell, but uncoiling whorl number is variable and can be ecophenotypic, proceeding once viable substratum is found. Whorl profile campanulate to frustate. Sculpture dominated by two strong medial cords, with a minor A cord the D cord increasing in prominence as coiling loosens. Color is most commonly tan but ranges to reddish brown. Vermiform portion has many fine lineations. Basal sinus type 2. Lateral sinus shallow, uninclined, uninflected, with apex medially placed. Aperture circular. Sculpture is typically smooth, but beading is known to occur in specimens from throughout the range, especially in individuals of *Vermicularia spirata radicula* and some specimens from the Walsingham Pond, Bermuda population.

Distribution: Recent. Type locality Cuba. Atlantic coast from Texas to Massachusetts and Bermuda. Also known from Belize and the Yucatán Peninsula. Found throughout the



FIGS. 49–63. *Vermicularia spirata* (R. A. Philippi, 1836). (49–54) Specimens from Walsingham Pond, Bermuda, collected under Bermuda Department of Environment and Natural Resources Permit #160401, presently housed at PRI, Recent (SEM in Fig. 54). (55) MCZ 113208, protoconch (SEM), Dick's Point, Nassau, New Providence, Bahamas, Recent. (56) USNM 776784, Carrie Bow Cay, Belize, Recent. (57) TAMU 4-2730, southern Florida, Recent. (58) "*Vermicularia carolinensis*" (Conrad, 1863), ANSP 31383, North Carolina, Recent (listed as fossil but this is unlikely, see text discussion of *Vermicularia carolinensis*). (59, 60) *Vermicularia radicula* (W. Stimpson, 1851), USNM 74788 (2 specimens), Vinyard Sound, Massachusetts, Recent. (61) Holotype of *Vermicularia spirata*, ZMBH 17294, Havana, Cuba, Recent. (62) LACM 110343, Gulfport, Pinellas County, Florida, Recent. (63) LACM 164243, Florida (not further specified), Recent.

Caribbean including Barbuda, the Dominican Republic, Trinidad, and confirmed as far south and east as Guyana.

Remarks: A significant reef former on the coast of the Carolinas, *Vermicularia spirata* is more typically found among corals, especially branching corals, although it can also be found associated with sponges, or in masses of conspecifics. This is the most widespread modern species, and we concur with Olsson & Harbison (1953) that it is exclusively modern. *Vermicularia radicula* type material has been destroyed, but material collected at the type locality, Vineyard Sound, Massachusetts (USNM 74788) falls within the typical range of variation of *Vermicularia spirata*. *Vermicularia spirata radicula* might be more likely to have beaded spiral cords, a feature shared by the extirpated Walsingham Pond (Bermuda) population of *Vermicularia spirata*, *Vermicularia spirata radicula* more frequently exhibits pinkish to dark reddish-brown coloration, and no large (> 5 cm length) specimens from Massachusetts were encountered, so retention of this name as a subspecies (*Vermicularia spirata radicula*) restricted to waters north of Long Island is justified.

The affinities of the specimen given as *Vermetus lumbricalis* by Chenu (1859: 319, fig. 2294) are unclear because the apices depicted do not agree with *Vermicularia spirata* and lack sculptural definition; however, the bioherm habit, sculpture on the uncoiled portion, and general size of the regularly coiled portion suggest *Vermicularia spirata*.

Vermetus indicus Daudin, 1800, figured by Chenu (1859: fig. 2297), belongs to Vermetidae, and does not agree with *Vermetus indicus* Chenu (1844a: pl. 3), which is *Vermicularia spirata*.

We note that at least three of Mörch's (1861) varieties of "*Vermiculus lumbricalis*"—*Vermiculus lumbricalis* var. *cornea, Vermiculus lumbricalis* var. *ampliata*, and *Vermiculus lumbricalis* var. *diaphana* based on photographs of type specimens, NHMUK 20210293, 20210294, and 20210295, respectively— appear to refer to *Vermicularia spirata*, but these names are unavailable (Bieler & Petit, 2011).

†*Vermicularia weberi*
Olsson & Harbison, 1953
Figs. 64–69

Vermicularia weberi Olsson & Harbison, 1953: 308, pl. 47, figs. 1, 1a, b; Portell et al., 1995: 141, 153.

Types: Holotype, ANSP 17370; lectotype of *Vermicularia trilineata*, USNM 115455.

Other Material Examined: USNM 64364; PRI 45417, 68758, 104844; UF 45471, 127327. *Vermicularia trilineata* USNM 645364, 645365.

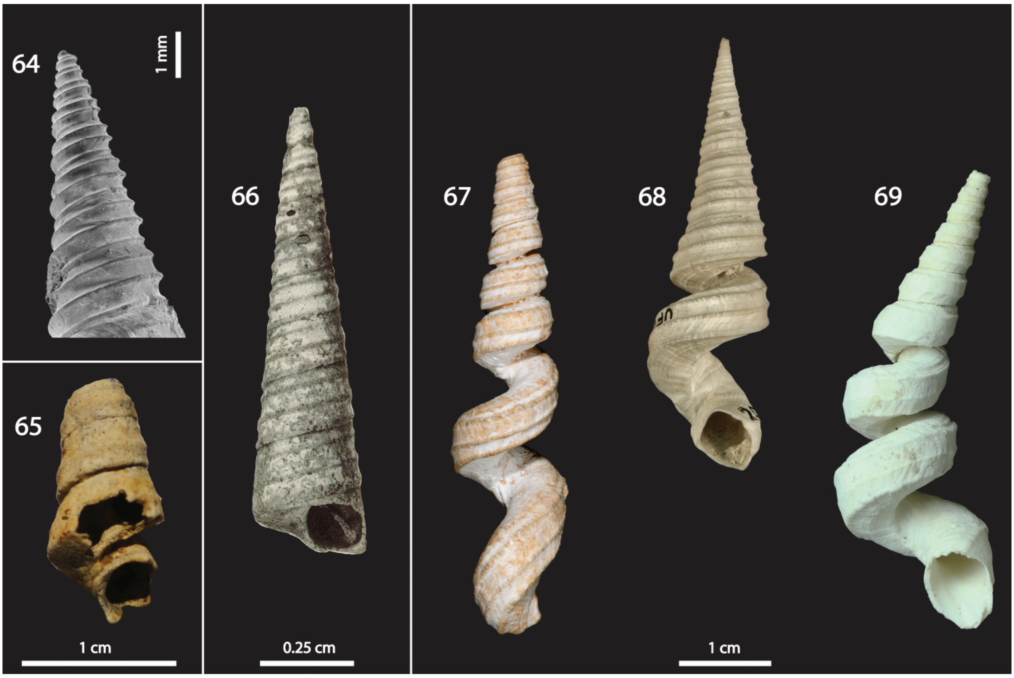
Diagnosis: Large turritelliform portion. Shell divided by three major spiral cords into roughly equal flattened areas. Subquadrate whorl profile distinguishes this species from other *Vermicularia* spp.

Description: Protoconch known only incompletely. Turritelliform portion of shell large, 8–12 whorls. Whorl profile subquadrate. A and B cords strong on upper and lower thirds of whorl with a smaller medial cord. D cord present on first teleoconch whorl but is very weak and remains the least prominent cord. Numerous very fine lineations in addition to the major spiral cords. Turritelliform portion umbilicate. Basal sinus type 1. Lateral sinus of medium depth, uninclined, uninflected, with apex medially placed. Aperture rounded square.

Distribution: Plio–Pleistocene (Jackson Bluff Formation) of Florida. *Vermicularia trilineata* (Guppy, 1867), a potential senior synonym, is present in the Matura region of Trinidad, from the Pliocene Matura Formation (Jung, 1969: 442, 443). A single specimen of *Vermicularia weberi*, UF 45471, is labelled as occurring in the Miocene Chipola Member of the Alum Bluff Formation, a stratigraphic assignment that is almost certainly an error for the overlying Pliocene Jackson Bluff member, in which *Vermicularia weberi* frequently occurs.

Remarks: The large turritelliform portion of early whorls could easily be mistaken for a normally coiled turritellid.

Existing material referred to *Vermicularia trilineata* (Guppy, 1867: 156, 170), USNM 115455, 645364, and 645365, appears consistent with *Vermicularia weberi* in characters that can be determined (whorl profile, dominant sculpture spacing, and size of regularly coiled section). The lectotype and additional material for *Vermicularia trilineata,* however, are in poor condition, lacking either the apex or vermiform portion, and with visible erosion of the spiral sculpture, and characters such as growth lines cannot be confirmed as definitively identical.



FIGS. 64–69. *Vermicularia weberi* Olsson & Harbison, 1953. (64) UF 45471 (SEM), Alum Bluff, Liberty County, Florida, likely Pliocene (Jackson Bluff Formation) but reported as Miocene (Chipola Formation), see text discussion of this specimen. (65) *Vermicularia trilineata* (Guppy, 1867), USNM 645364, Matura, Trinidad, likely Pliocene (Matura Formation). (66) Lectotype of *Vermicularia trilineata*, USNM 115455, Matura, Trinidad, likely Pliocene (Matura Formation), modified from Jung (1969: pl. 54, fig. 10). (67) Holotype of *Vermicularia weberi*, ANSP 645365, Ortona Locks, Glades County, Florida, Pleistocene. Photo by P. Callomon. (68) UF 127327, Palm Beach County, Florida, Pleistocene. (69) PRI 104844, Florida Shell and Fill, Charlotte County, Florida, Pleistocene.

If better material of *Vermicularia trilineata* becomes available and can be demonstrated to definitively be synonymous with *Vermicularia weberi,* the name *Vermicularia trilineata* would have priority for this species. *Vermicularia trilineata* is sometimes listed as attributed to Guppy 1864, but the name and description are from Guppy (1867), who stated that it was listed as "*Vermetus royanus*" in the list published in 1864. Guppy's species was also used as "*Vermicularia* ? *trilineata* (Guppy)" by Jung, 1969 (442, 443, pl. 44, figs. 6–10). Jung (1969: 443) noted that if it is a "*Turritella*" and not a *Vermicularia*, the species is preoccupied by *Turritella trilineata* W. Smith, 1817.

†*Vermicularia woodringi*
Olsson & Harbison, 1953
Figs. 8, 70–73

Vermicularia spirata var. *trilineata* Maury, 1925: 228, pl. 41, fig. 6; not *Vermicularia trilineata* (Guppy, 1867).

Vermicularia woodringi Olsson & Harbison, 1953: 307, 308, pl. 47, fig. 2.

Types: Holotype, ANSP 19321.

Other Material Examined: UF 174475, 115913; PRI 68757, 84853, 108645; plus additional material at UF and PRI.

Diagnosis: Average size for the genus. *Vermicularia recta* maintains a flattened inner coiling surface as opposed to a rounded one, and is generally larger in diameter at a given length than *Vermicularia woodringi*, which frequently co-occurs with *Vermicularia recta* and is often misidentified as such. *Vermicularia woodringi* has a more strongly sculptured vermiform portion than *Vermicularia recta*, with two prominent cords more adapical than at midline rather than evenly spaced or bracketing the whorl. The D cord is also more prominent in *Vermicularia woodringi* than in *Vermicularia recta.*

Description: Protoconch 250–350 μm. Turritelliform portion approximately seven whorls. Whorl profile subquadrate. Vermiform portion often irregularly coiled but can form masses in association with conspecifics. Typically has multiple loosely coiled or offset whorls before complete separation. Two strong spiral cords straddling the middle of the shell, moving posterior (adapically) as the shell becomes uncoiled, and the D cord strengthens. Medial cord becomes the strongest of the three. Many fine lineations on the vermiform portion, especially the basal part. Basal sinus type 2. Lateral sinus deep, opisthocline, single inflection on top, with apex on upper third of shell. Aperture rounded-square to circular, becoming more circular in the vermiform portion than the turritelliform portion.

Distribution: Plio–Pleistocene. Florida: Caloosahatchee Formation, Bermont Formation, Pinecrest Sand of the Tamiami Formation. South Carolina: "Bear Bluff" Formation. North Carolina: Waccamaw Formation. Trinidad: Matura.

Remarks: Experience in collections suggests that frequently any substantial mass of intercoiled/cemented *Vermicularia* tubes is assigned to *Vermicularia recta,* but *Vermicularia woodringi* and *Vermicularia spirata* also form such associations (Fig. 2). Conversely, isolated individuals of *Vermicularia recta* are often mistakenly referred to *Vermicularia woodringi. Vermicularia woodringi* appears to be much less common in collections than *Vermicularia recta* or *Vermicularia weberi,* which all co-occur in Florida.

TAXA INQUIRENDA—DUBIOUS FORMS THAT COULD BELONG TO *VERMICULARIA*

Serpula tortuosa Lightfoot, 1786

Remarks: Lightfoot (1786) named this species with no description but with a reference to "Humph. Conch. Pl. 11, figure 4," which likely

FIGS. 70–73. *Vermicularia woodringi* Olsson & Harbison, 1953. (70) Holotype, ANSP 19321, St. Petersburg, Florida, Pleistocene. Photo by P. Callomon. (71) UF 115913, Davis Pit, Okeechobee County, Florida, Pleistocene. (72) UF 174475 (SEM), Florida Shell and Fill 02, Charlotte County, Florida, Pleistocene. (73) PRI 108645, Cross-State Marl Pits, 6 mi west of West Palm Beach, Florida, Pleistocene.

refers to *Humphrey's Conchology*, an anonymous unfinished work published in 1770–1771, which has more recently been considered to have been authored by da Costa not Humphrey (Iredale, 1915; Whitehead, 1977). Locality unknown. One of the figures labelled "4" is a siliquariid (reproduced here; Fig. 74). The other referenced figure (reproduced here; Fig. 75) lacks an apex or clear depiction of perforations, making definitive assignment uncertain. It could represent an example of *Vermicularia spirata*, which sometimes maintains strong sculpture along the edges of the vermiform portion of the shell, however none of the fine sculpture or other distinct characteristics of the species are depicted. Unfortunately, the descriptions corresponding to plates 10 and 11 were apparently unpublished. R. Bieler (pers. comm., 2019) reported that the type specimen is located at NHMUK, but the specimen could not be located by collections staff (K. Collins, pers. comm., 2020).

Vermetus carolinensis Conrad, 1863 (*nomen nudum*)

Remarks: Reported from the Pliocene of North Carolina. Conrad's (1863) description refers to the description of a *Vermetus* species by Conrad (1862), which had no name assigned. No figure or reference specimen was given. The description reads "Neuse River below Newbern," (Conrad, 1862: 288) with the area around New Bern containing rocks dating from the Cretaceous–Pliocene, and more recent deposits closer to the coast. Although appearing in "Miocene shells" (Conrad, 1863), there is no lithologic information in the description and fossiliferous rock from the area includes the Yorktown Formation (late Miocene to early Pliocene; Gibson, 1983) and the Pliocene Duplin Formation, as well as Recent shell deposits farther downriver along the coast. A Conrad specimen from North Carolina, ANSP 31383 (Fig. 58), which we examined appears to be a modern *Vermicularia spirata,* which occurs today in North Carolina coastal waters.

Vermetus tenuis Rousseau in Chenu, 1843

Remarks: The illustrations (Chenu, 1843: pl. 1, figs. 6, 7; reproduced here as Figs. 76, 77) are not of sufficient quality to confirm their identity, but they are unlikely to be turritellids. The irregular form of the early uncoiling section and possible annular or vertical sculpture on the shell are not typical of *Vermicularia* and therefore the species might properly belong in a different family. In sculpture of the vermiform section, it is most similar to *Vermicularia spirata* and, if it does represent this species, it would be a junior synonym. The illustration does not indicate any sculptural properties of the regularly coiled portion of the shell that could aid in interpretation.

Vermetus costalis Rousseau in Chenu, 1844

Remarks: The illustrations available [Chenu, 1844a: pl. 3, fig. 1 (reproduced herein; Figs. 78, 79); 1859: 319, fig. 2295 (reproduced herein; Fig. 80)] are not of sufficient quality to determine whether the referred images are conspecifics or if they are definitively *Vermicularia*. It is unclear whether this is a synonym of *Serpula costalis* Lamarck, 1818 (see below), which was not illustrated and for which type material could not be located, but Bieler & Petit (2011) considered both uses of "*costalis*" to potentially be different species within *Vermicularia*. At least one specimen of Chenu (1844a: pl. 3, fig. 1) appears to be *Vermicularia spirata,* in which case it would be a junior synonym of *Vermicularia spirata,* but the illustration of Chenu (1859) shows a species with a much more rounded coiled portion near the apex.

Serpula costalis Lamarck, 1818

Remarks: No illustration or reference specimen was provided by Lamarck. The description (Lamarck, 1818: 367; translated) reads: "shell angular, loosely contorted, base finely spiralled, ribs and longitudinal striations uneven, mucilaginous ... solitary tubes." This is, however, insufficient to determine affinity. If "ribs and longitudinal stripes" indicates axial sculpture in addition to spiral sculpture present on the shell, then this is unlikely to be *Vermicularia*. It is unclear whether this is a synonym of *Vermetus costalis* Rousseau in Chenu, 1844, but Bieler & Petit (2011) considered both uses of "*costalis*" to potentially be different species within *Vermicularia*.

Vermetus hindsii J. E. Gray in M. E. Gray, 1850 (*nomen nudum*; *incertae sedis*)

Remarks: Bieler & Petit (2011) listed *Vermetus hindsii* Gray, 1850, as *Vermicularia,* but we are unsure of its proper synonymy. The entirety of the description given is "irregularly

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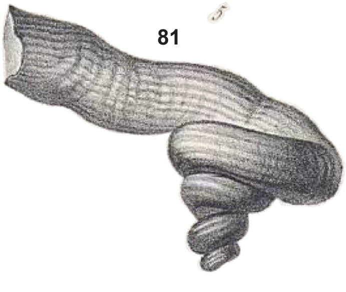


FIGS. 74–81. *Taxa inquirenda*: dubious names that could belong to *Vermicularia*. (74, 75) Illustrations referenced by Lightfoot (1786) for *Serpula tortuosa* Lightfoot, 1786, reproduced from da Costa (1771; "Humphrey's Conchology"), locality unknown. (76, 77) Illustrations given for *Vermetus tenuis* Rousseau in Chenu, 1843, locality unknown. (78, 79) Illustrations given for *Vermetus costalis* Rousseau in Chenu, 1844, locality unknown. (80) Illustration given for *Vermetus costalis* by Chenu, 1859. (81) Illustration given for *Serpula panamensis* Chenu, 1846: pl. 10, fig. 5, locality unknown.

twisted," without accompanying illustration or referenced specimen or illustration and we therefore consider it to be a *nomen nudum*. The name occurs not in the list of plates, but rather in the systematics portion accompanying the index of plates. Gray (1850) noted that synonymous names that were not listed by Gray (1847) were added after the corresponding entry in the systematics section. "*Vermicularia hindsii*" appears in this manner (Gray, 1850: 82) under *Vermetus*, after a reference to *Vermicularia lumbricalis.* However, this reference is to *Vermicularia lumbricalis* Lamarck, which might or might not have been intended to refer to *Vermicularia lumbricalis* Linnaeus (see Bieler & Petit, 2011: 70 for further discussion). The corresponding entry by Gray (1847: 156) for *Vermetus* is not exclusively a reference to *Vermicularia,* but includes *Vermicularia,* polychaetes (*Serpula maxima* G. B. Sowerby I, 1825), and vermetids (*Siphonium* Gray, 1850). Two specimens were encountered originally labelled as *Vermetus hindsii* (Gray), from the Cornell University collection now housed at PRI (PRI 99198 and 99197), both of which are *Vermicularia pellucida* from Panama.

Serpula panamensis Chenu, 1845 (Chenu, 1846: pl 10, fig. 5)

Remarks: This species was named without description or locality (although Panama is implied by the name, *Vermicularia* and other worm snails occur on both coasts). The figure by Chenu (1846) is reproduced herein as Figure 81. If it is a Pacific shell, it is most likely a junior synonym of *Vermicularia pellucida*, which it most closely resembles among the *Vermicularia*, however the figured specimen lacks an apex and therefore even definitively identifying it as a turritellid is uncertain.

Vermicularia sp. (Redfern, 2013: 39, fig. 111)

Remarks: Redfern (2013) illustrated a shell, protoconch, and living individual of a species listed as "*Vermicularia* sp.," with a living specimen collected from 7.5 m water depth from Abaco, Bahamas. We cautiously do not consider this species to belong to *Vermicularia*. Redfern stated that only immature shells were collected (meaning all shells depicted are regularly coiled). The protoconch does not resemble any other *Vermicularia* for which protoconchs have been observed in that it is distinctly pointed apically ("thumb-like"). This is not a common morphology for turritelline protoconchs, which generally have nuclei depressed to varying degrees (Marwick, 1957; examples by Friend et al., 2023). The only protoconch that is emergent shown in Marwick's (1957) treatment of turritellid genera was *Kimberia* Cotton & N. H. Woods, 1935 (Marwick, 1957: fig. 53), which is now considered to be a member of Vanikoroidea (e.g., Goulding et al., 2023). The specimen also does not appear to follow the B1A2 apical formula, because the spiral sculpture does begin medially, however, no A cord appears on the early whorls (or any whorls depicted), although a possible D cord does appear to be present. The first full volution of the protoconch also appears to have fine striations and be granulose, whereas other *Vermicularia* and turritelline protoconchs generally are untextured. A second protoconch volution with numerous fine striae and granular texture does occur in Siliquariidae (e.g., Gould, 1966; Bieler, 2004), but the protoconch and teleoconch morphology do not otherwise agree with placement in Siliquariidae either. Given the lack of similarity in protoconch gross morphology, texture, and spiral sculpture ontogeny (which are considered especially important in determining affinities within Turritellidae; see Friend et al., 2023), we do not at present consider this taxon to be a member of *Vermicularia*. Because the species is extant and living specimens have previously been examined, we are hopeful that in the future molecular evidence could determine whether these species have turritelline or other affinities.

RESULTS

All molecular analyses recovered a monophyletic *Vermicularia* sister to a clade of *Torcula exoleta* + *Torcula radula* (Kiener, 1843) (Figs. 82–86). This *Torcula* + *Vermicularia* clade was more closely related to the western and southern African clade of *Protomella capensis* (Krauss, 1848) + *Turritella nivea* Anton, 1838 than to other western Atlantic or tropical eastern Pacific turritellids with high bootstrap support values or posterior probabilities for each of these clades. Parsimony analysis found 390 molecular characters to be parsimony-informative, resulting in two most parsimonious trees (tree length 1328, CI 0.508, RI 0.751, RC 0.381), differing only in the placement of *Turritella banksii* Reeve, 1849. Parsimony analyses including these most parsimonious trees and a 70% majority rule consensus of the

100 best trees placed *Vermicularia lumbricalis* (= *Vermicularia knorrii*) as sister to *Vermicularia spirata* (Figs. 82, 83). The tree with the single best-likelihood score placed *Vermicularia pellucida* as sister to *Vermicularia lumbricalis* (Fig. 84), but a 70% majority-rule consensus tree under maximum likelihood was unable to resolve a polytomy among *Vermicularia* spp. (Fig. 85). *Vermicularia spirata* was recovered as sister to *Vermicularia lumbricalis* with 0.99 posterior probability in the Bayesian analysis, consistent with the parsimony analysis (Fig. 86). Consistent with Lieberman et al. (1993), Turritellinae *sensu* Marwick (1957) is paraphyletic with respect to *Vermicularia*. Consistent with Sang et al. (2019), a monophyletic *Torcula* was recovered that is not closely related to other regularly coiled western Atlantic turritellids (with even the southwestern Pacific species *Maoricolpus roseus* (Quoy & Gaimard, 1834) being more closely related than other western Atlantic/eastern Pacific species).

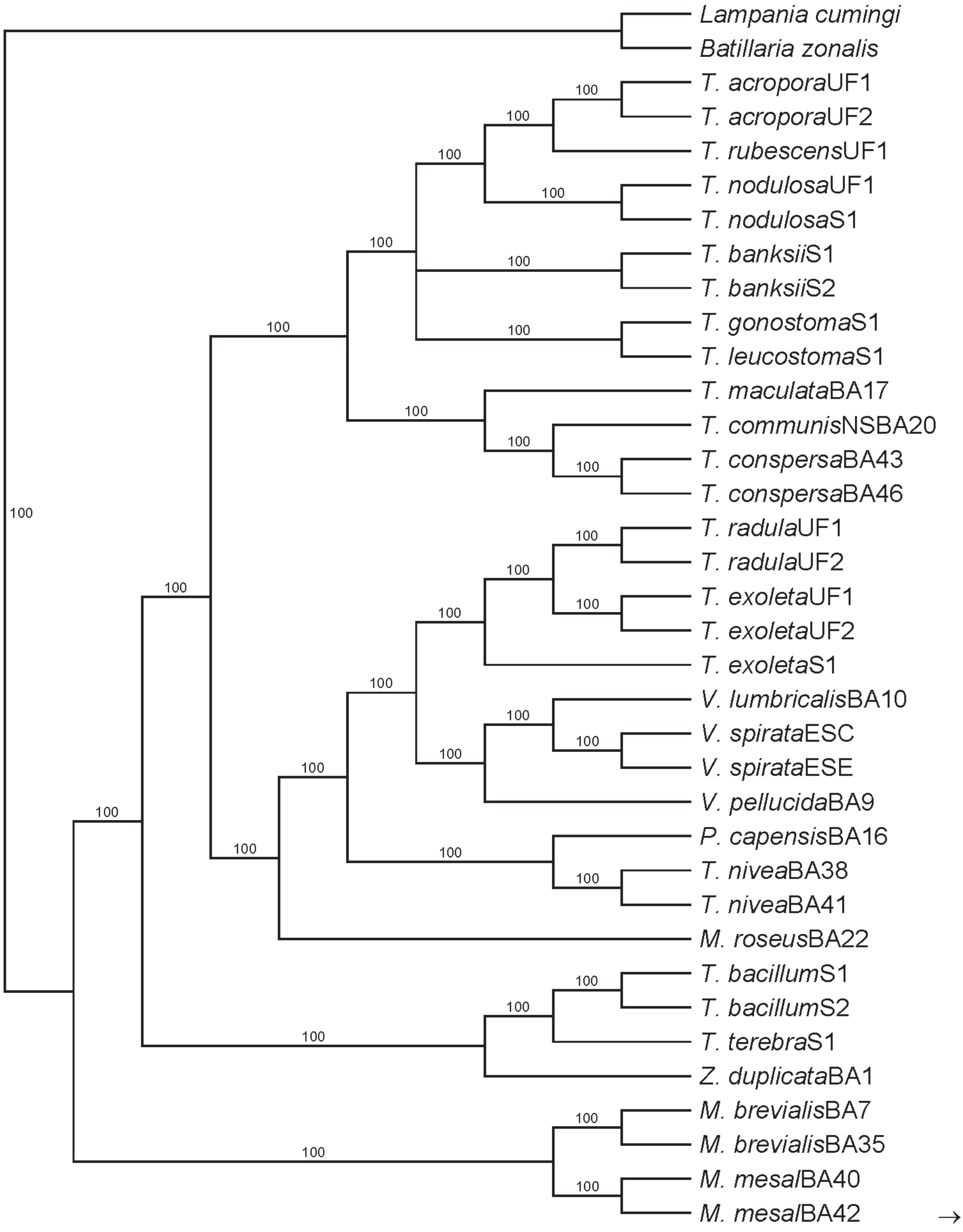
Additional results of the molecular analyses include identification of *Mesalia* as a well supported clade, as is *Turritella s.s.* [*Turritella terebra* (Linnaeus, 1758) + *Turritella bacillum* Kiener, 1843]. *Zaria duplicata* (Linnaeus, 1758), *Maoricolpus roseus*, and *Protomella capensis* all show considerable molecular distance from their sister taxa, supporting the potential for these genera to carry meaningful phylogenetic information; however, non-*Vermicularia* Turritellidae clearly require a revision beyond the scope of this study based on additional molecular data.

Parsimony analysis of morphological characters recovered a single most-parsimonious tree (Fig. 87; tree length 173, CI 0.422, RI 0.531, RC 0.224). This tree was consistent with the molecular analysis for species with molecular data (*Vermicularia lumbricalis* as sister to *Vermicularia spirata*, in a monophyletic *Vermicularia* with *Vermicularia pellucida*, with *Vermicularia* sister to the clade including *Torcula exoleta* and *Torcula altilira* (Miocene). Tree topology was robust to the removal of *Vermicularia milleti*, *Vermicularia spirata radicula,* or both (*Vermicularia spirata radicula* being considered a subspecies and therefore duplication of *Vermicularia spirata* for most characters, and *Vermicularia milleti*'s stratigraphic occurrence making this highly derived phylogenetic position unlikely; see discussion below).

Morphological analysis recovered a monophyletic *Vermicularia*, with *Vermicularia gracilis* (= *Callostracum gracile*) and *Vermicularia milleti* nested well within the clade. Considering the known stratigraphic ranges of these species, an alternative topology with an early divergence of *Vermicularia milleti* is more likely to be correct (discussed below). For the purposes of tree construction, we treated *Vermicularia trilineata* to be synonymous with *Vermicularia weberi,* because it is identical in all characters that could be confirmed; however, if better material becomes available and this species does differ from *Vermicularia weberi*, it would be worthwhile to reanalyze the tree topology. Reports of *Vermicularia woodringi* in Jamaica (e.g., Olsson & Harbison, 1953) could not be confirmed. There is a single specimen of *Vermicularia weberi*, UF 45471, labelled as occurring in the Miocene Chipola Member of the Alum Bluff Formation, but this is likely an error (see Remarks on *Vermicularia weberi* above).

Vermicularia milleti originates in the Burdigalian, and an apical placement in the phylogeny would imply 15 Myr of unrecorded history for all western Atlantic *Vermicularia* spp., whereas other turritellid fossils are abundant (e.g., Friend et al., 2023; note that excluding *Vermicularia milleti* from the analysis did not otherwise alter the topology of the tree). If this phylogenetic placement is correct, nearly all species would have extremely long ghost ranges during a time period that is richly fossiliferous in the American Neotropics. Given the generally excellent fossil record of marine gastropods at this time and the high incidence of convergence in whorl profile and sculpture known to occur in Turritellidae among basins (e.g., Allmon, 1994, 1996), it seems most likely that *Vermicularia milleti* gave rise to a monophyletic western Atlantic clade once, with *Vermicularia lumbricalis* evolving a similar early teleoconch morphology secondarily (see a similar treatment of cheilostome bryozoans by Jackson & Cheetham, 1994). This interpretation, integrating stratigraphic and cladistic information, is presented in Figure 88.

The sister relationship between the western Atlantic *Vermicularia woodringi* and eastern Pacific *Vermicularia frisbeyae* implies a cladogenetic event prior to the closure of the Central American Seaway in the mid–late Pliocene (Fig. 88) and suggests the possibility of an unnoticed tropical eastern Pacific fossil record for *Vermicularia*, a conclusion also supported by the long ghost range in the morphological tree and substantial molecular divergence of *Vermicularia pellucida* from the clade of *Vermicularia lumbricalis* + *Vermicularia spirata*.



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DISCUSSION

Grabau (1907) hypothesized the paraphyly of the genus *Turritella* with respect to *Vermicularia*, but also that *Vermicularia* itself was paraphyletic. Previous anatomical work (Morton, 1953, 1955; Bieler & Hadfield, 1990), and the molecular and morphological cladistic analyses herein support the monophyly of *Vermicularia*. Lieberman et al. (1993) used a partial sequence of 16S to study turritelline relationships and determined that the genus

FIG. 82 (at left). Parsimony analysis performed in PAUP4 of concatenated molecular dataset of H3, 12S, and 16S showing the strict consensus of the two most-parsimonious trees. *Turritella communis* Risso, 1826 was recently synonymized with the senior synonym *Turritellinella tricarinata* (Brocchi, 1814), but because *Turritella communis* is widely used to refer to the extant representatives, we employed this name in the phylogeny. *Turritella acropora* Dall, 1889 was also recently synonymized with *Turritella perexilis* Conrad, 1873 (Friend et al., 2023), and *Turritella gonostoma* Valenciennes, 1832 and *Turritella leucostoma* were moved to the genus *Caviturritella* (Friend et al., 2023), but these sequence data were previously published as *Turritella acropora*, *Turritella gonostoma*, and *Turritella leucostoma* (see Sang et al. 2019). and the name is widely used for extant representatives of this species. This phylogeny presents both species identifications and individual specimen identification numbers; see Table 3 for information on individual specimen identification numbers for newly published sequence data (BA and ES specimens); sequence data from specimens previously published by Sang et al. (2019) are listed with the identification numbers with which they were previously published (UF or S numbers). Taxa on the tree not otherwise discussed in the text are: *Torcula exoleta* (Linnaeus, 1758); *Turritella gonostoma* Valenciennes, 1832; *Turritella leucostoma* Valenciennes, 1832; and *Turritella rubescens* Reeve, 1849.

Turritella is paraphyletic with respect to both *Vermicularia* and *Maoricolpus*. The latter two genera were, however, identified by Lieberman et al. (1993) as sister taxa, with this clade sister to a clade consisting of *Turritella anactor* S. S. Berry, 1957 and "*Turritella communis*" (= *Turritellinella tricarinata*). Our analysis of H3, 12S, and 16S for three *Vermicularia* spp. and a much-expanded turritellid dataset confirms the monophyly of *Vermicularia* and Turritellinae (*sensu* Marwick, 1957) as paraphyletic if not inclusive of *Vermicularia*. The generic concept employed herein for a monophyletic *Vermicularia* is cautious, as advocated by Friend et al. (2023) for applying generic names to turritellids, encompassing only those species that both typically have uncoiled, vermiform morphology, a turritelline protoconch, and spiral sculpture that begins B1A2. We note, however, that Friend et al. (2023) intriguingly documented a single nonvermiform turritellid from the Plio–Pleistocene of Florida and the U.S. Atlantic Coastal Plain, *Turritella alticostata* (Conrad, 1834), that also has this spiral ontogeny, which could indicate either a close relative of *Vermicularia* or an example of complete loss of uncoiling.

Vermicularia lumbricalis appears to be the senior synonym of *Vermicularia knorrii,* a very common Recent species (also known from the Pleistocene). *Vermicularia trilineata* might be the senior synonym of *Vermicularia weberi*, but the lectotype material of *Vermicularia trilineata* is of poor quality, as are other figured specimens from the type region. Although consistent with *Vermicularia weberi*, not all characteristics of *Vermicularia weberi* can be confirmed as present in Guppy's material of *Vermicularia trilineata*. The specimens do appear to be *Vermicularia* (initiating uncoiling as a normal part of ontogeny) rather than *Turritella* (as suggested by Olsson & Harbison, 1953).

It is notable that hermatypy is hypothesized to have evolved twice in *Vermicularia,* in the *Vermicularia recta*-*Vermicularia spirata* lineage and in *Vermicularia woodringi*, a case of parallelism within *Vermicularia* (gregariousness and cementation to hard substratum likely predisposed the group to this habit) and convergence with reef-forming vermetids (see, e.g., Shier, 1969).

An unexpected result was the recovery of the eastern Atlantic species *Vermicularia gracilis* (= *Callostracum gracile)* and *Vermicularia milleti* in a clade with *Vermicularia lumbricalis*. Although both *Vermicularia lumbricalis* and *Vermicularia gracilis* are modern species, with *Vermicularia lumbricalis* being broad-ranging (confirmed as far east as Bermuda) making this placement reasonable for *Vermicularia gracilis*, we urge caution regarding the interpretation of *Vermicularia milleti*, the oldest *Vermicularia* species (originating 16–20 Ma), because this implies substantial ghost ranges across the tree (Fig. 22). In the absence of molecular evidence definitively assigning *Vermicularia gracilis* to a group other than *Vermicularia*, the placement of *Vermicularia gracilis (= C. gracile)* within the phylogeny and general similarity to other *Vermicularia* suggests that it should be moved to *Vermicularia*, regardless of whether it is more likely sister to *Vermicularia milleti* or *Vermicularia lumbricalis*. Molecular data from *Vermicularia gracilis (= C. gracile)* could help to resolve this issue, with a position sister to all living *Vermicularia* favoring the interpretation that it is sister to European *Vermicularia milleti*, or placement in a clade with *Vermicularia lumbricalis (= Vermicularia knorrii)* resolving the issue unambiguously.

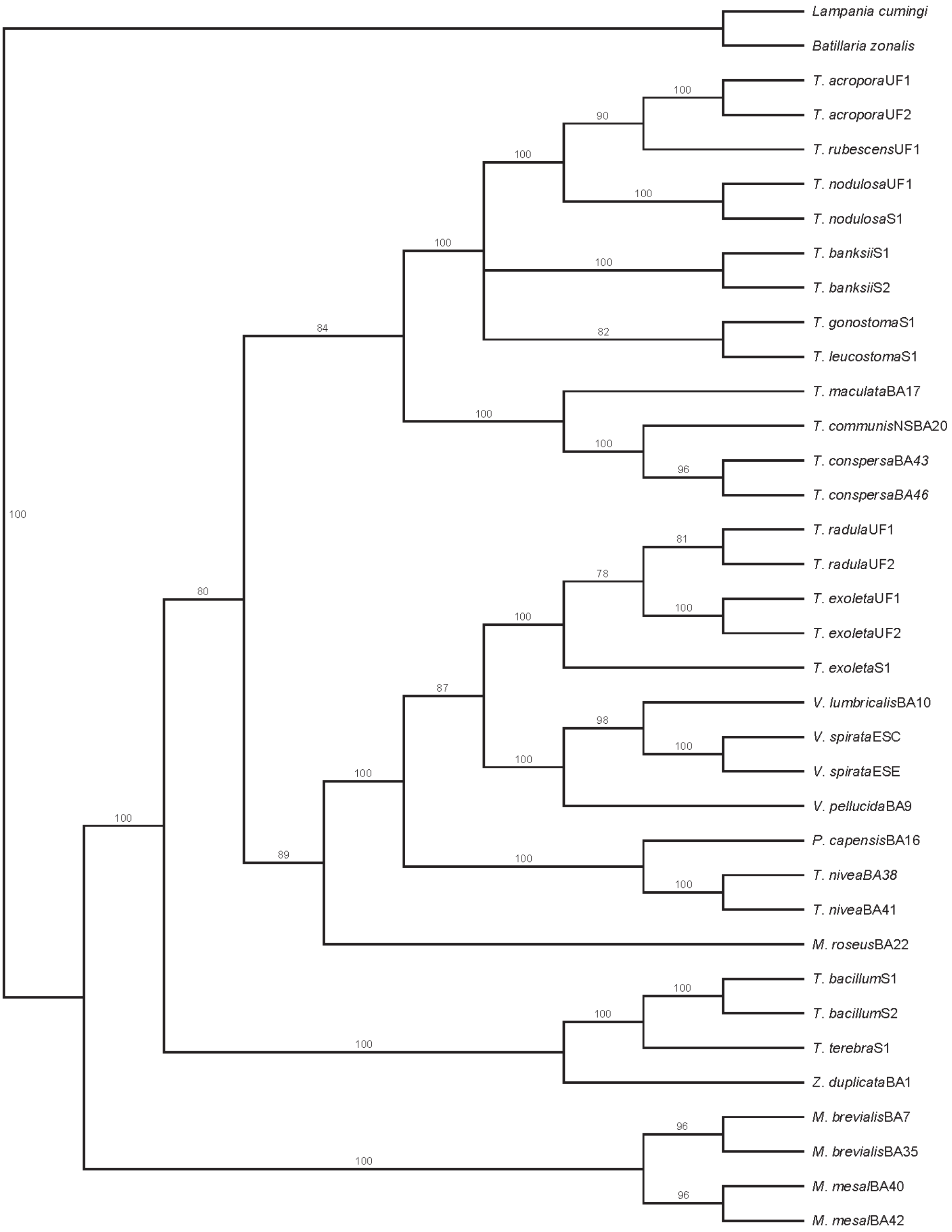

FIG. 83. Parsimony analysis performed in PAUP4 of concatenated molecular dataset of H3, 12S, and 16S showing the 70% majority rule consensus tree of 100 trees, with numbers on nodes indicating bootstrap support. See Fig. 82 for naming conventions used.

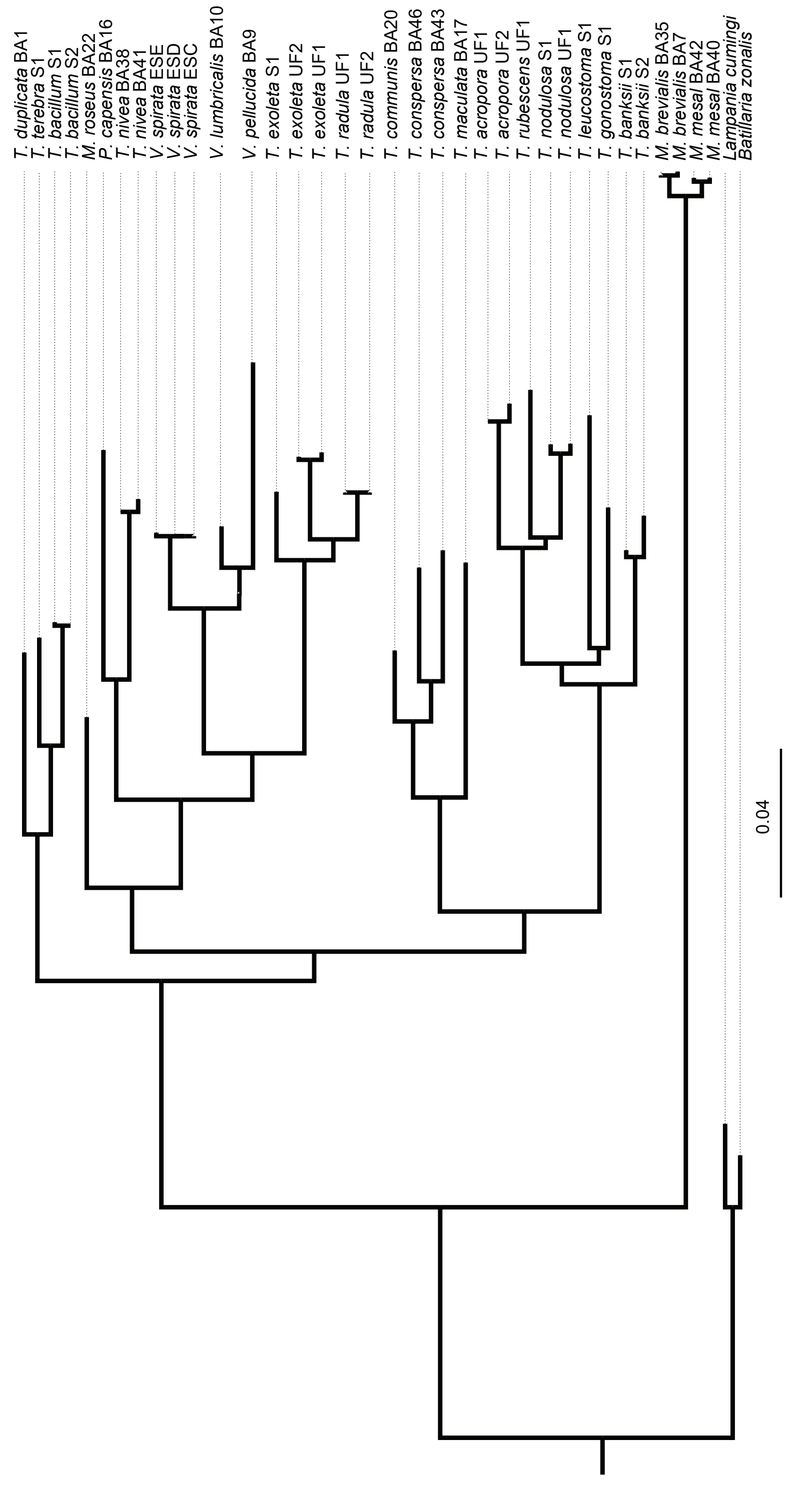

FIG. 84. Single best ML tree reconstruction based on analysis of concatenated molecular dataset of H3, 12S, and 16S in RAxML. See Fig. 82 for naming conventions used.

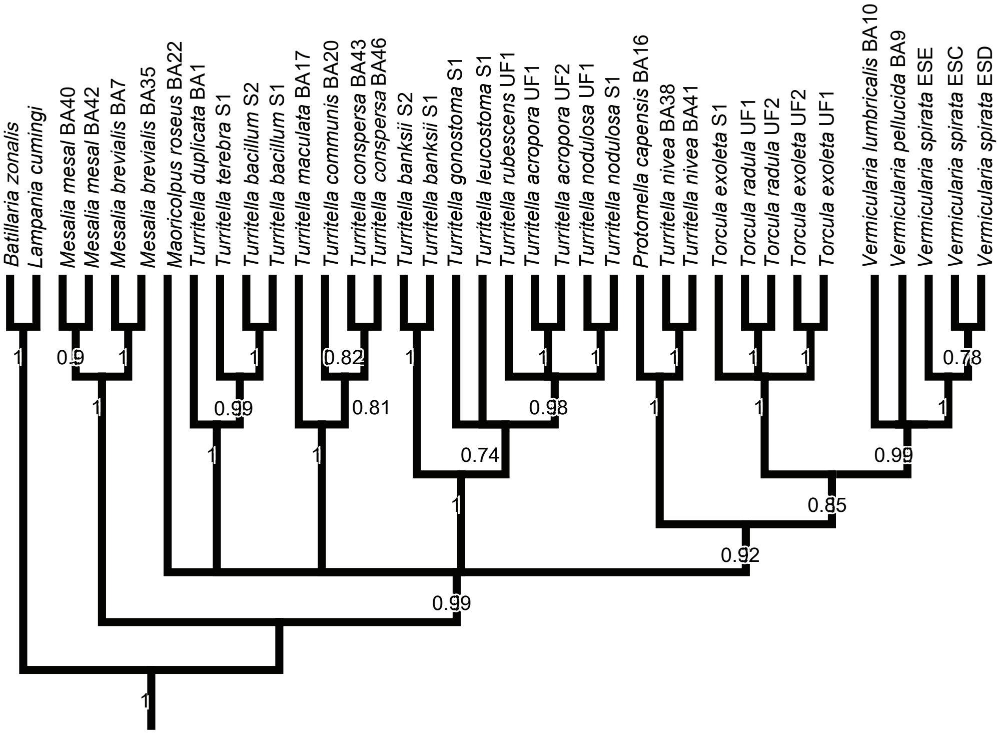

FIG. 85. Maximum liklihood analysis, 70% majority rule RAxML tree of 100 trees. Node values indicate bootstrap support. See Fig. 82 for naming conventions used.

Vermicularia milleti represents an interesting morphological experiment, with a very long stratigraphic range for a turritellid. Given the phylogeny, three hypotheses are possible for *Vermicularia milleti*'s relationship to the other *Vermicularia*:

(1) *Vermicularia milleti* truly is sister to the *Vermicularia lumbricalis* lineage, implying that all major *Vermicularia* lineages originated in the Miocene.

(2) *Vermicularia milleti* properly belongs to *Vermicularia* but diverged from the western Atlantic clade prior to the Pliocene expansion of the latter and *Vermicularia lumbricalis* converged on a similar whorl profile and sculptural morphology.

(3*) Vermicularia milleti* independently converged on uncoiled morphology and either belongs to the clade consisting of *Vermicularia* and the stem group of normally coiled turritellids in the *Vermicularia* lineage or developed uncoiled morphology completely independently and is derived from a different branch of Turritellidae than the *Vermicularia* clade.

Hypothesis 1 seems unlikely given the exceptionally good record of Miocene Turritellidae of the western Atlantic. Hypothesis 2 is tentatively supported over hypothesis 3 by the monophyly of *Vermicularia* for which molecular data were available, the consistency of characters such as apical spiral ontogeny, basal sinus and lateral sinus with other *Vermicularia*, the reasonably deep divergence time indicated by the ML and Bayesian trees, and the long fossil record (at least Eocene) of the sister group leading to *Torcula exoleta* [*Torcula martinensis* (Dall, 1892); PaleoDB collection 92785, authorized/entered by Austin Hendy; see Allmon, 1996].

Because *Vermicularia milleti* persisted through the Pliocene, as reported by La Perna et al. (2001) and Landau et al. (2004), the most likely scenario according to stratigraphic

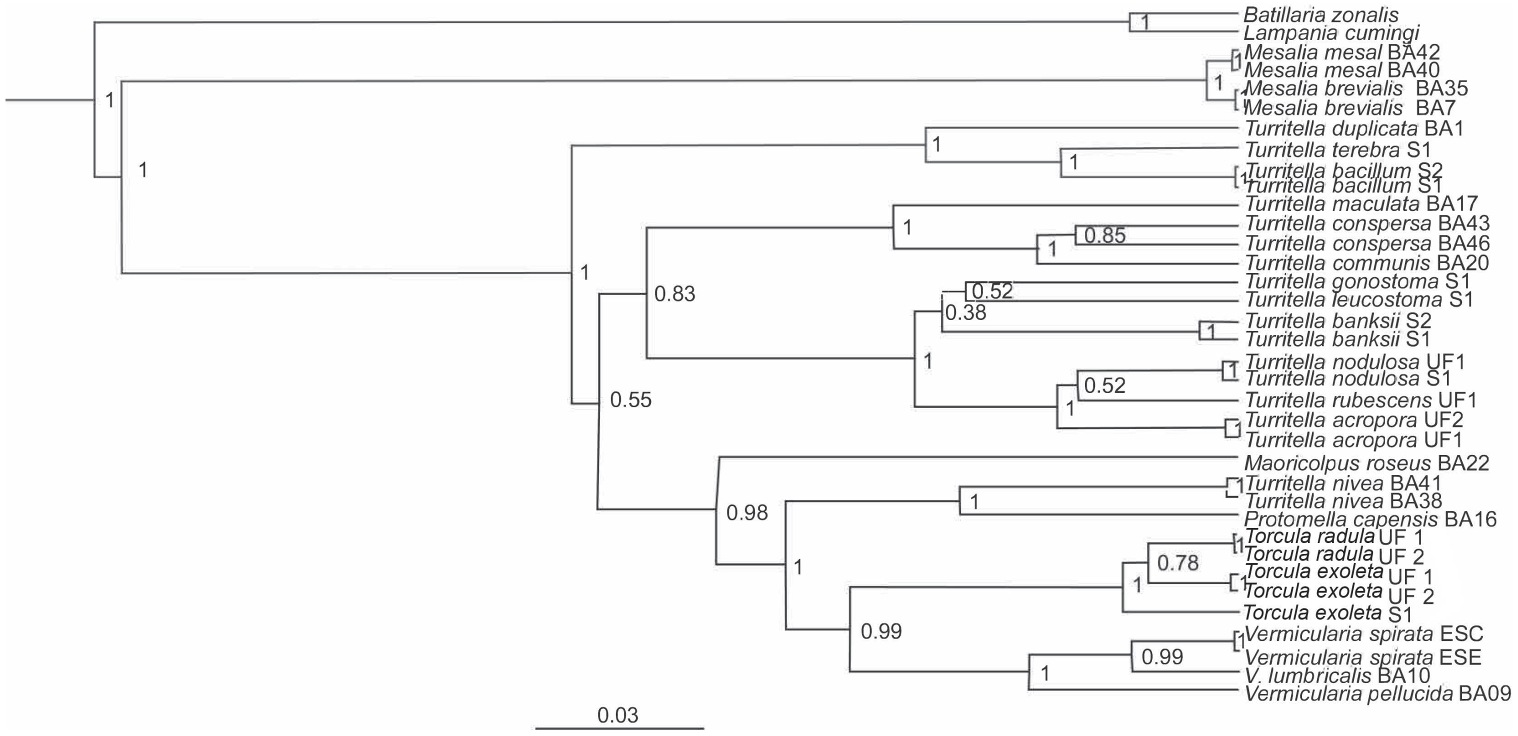

FIG. 86. Bayesian phylogenetic reconstruction generated using BEAST v. 1.8.0 based on the concatenated molecular dataset. Node values indicate posterior probabilities. See Fig. 82 for naming conventions used.

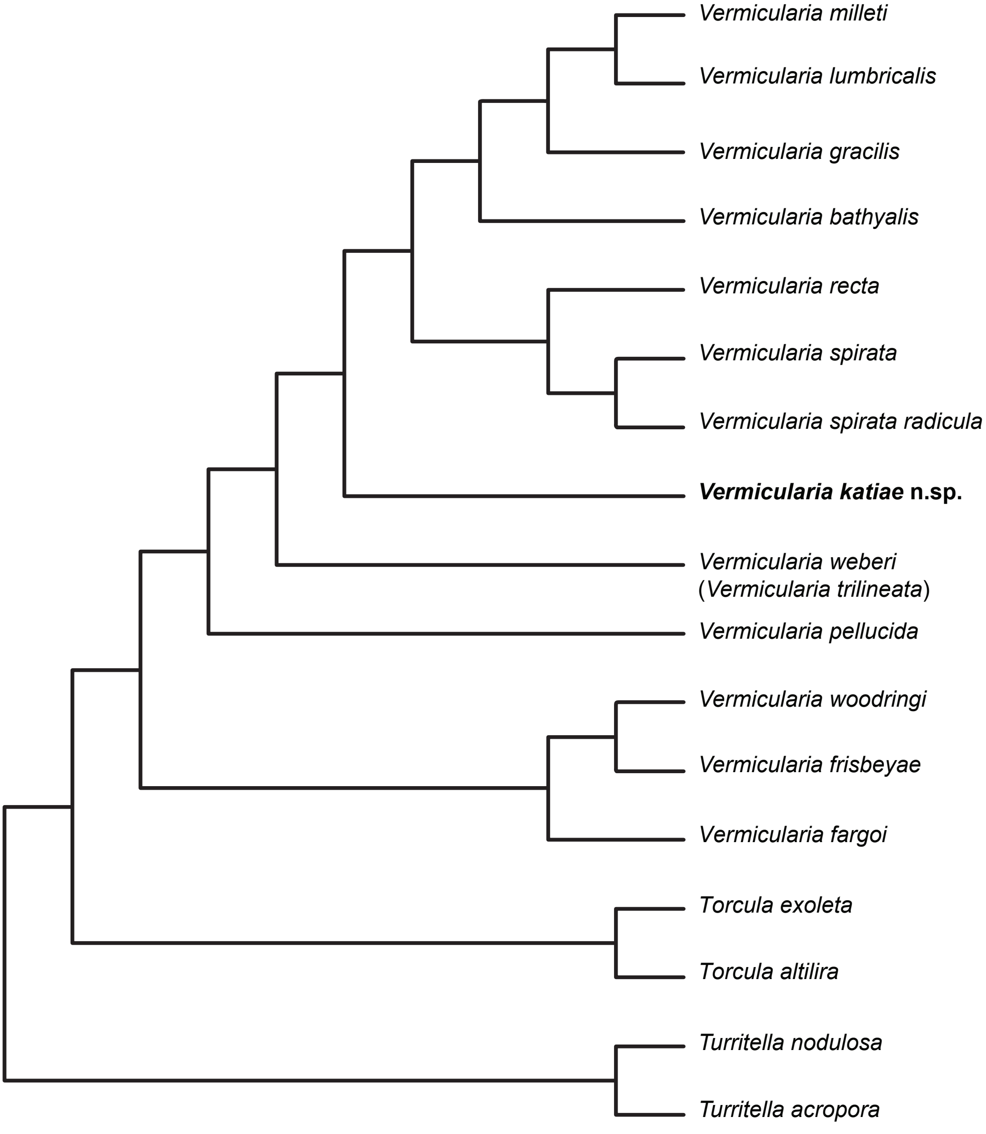

FIG. 87. Maximum parsimony tree of *Vermicularia* species + the modern and fossil species that have been assigned to the genus *Torcula* [*Turritella* (*Torcula*) *exoleta* and *Turritella* (*Torcula*) *altilira* (Miocene)] generated in PAUP based on morphological characters, using *Turritella nodulosa* + *Turritella acropora* (= *Turritella perexilis*) as a monophyletic outgroup. The two *Torcula* species were included to represent variation in this genus, because molecular data (Figs. 82–86) indicated *Vermicularia* as sister to *Torcula exoleta* and its relatives.

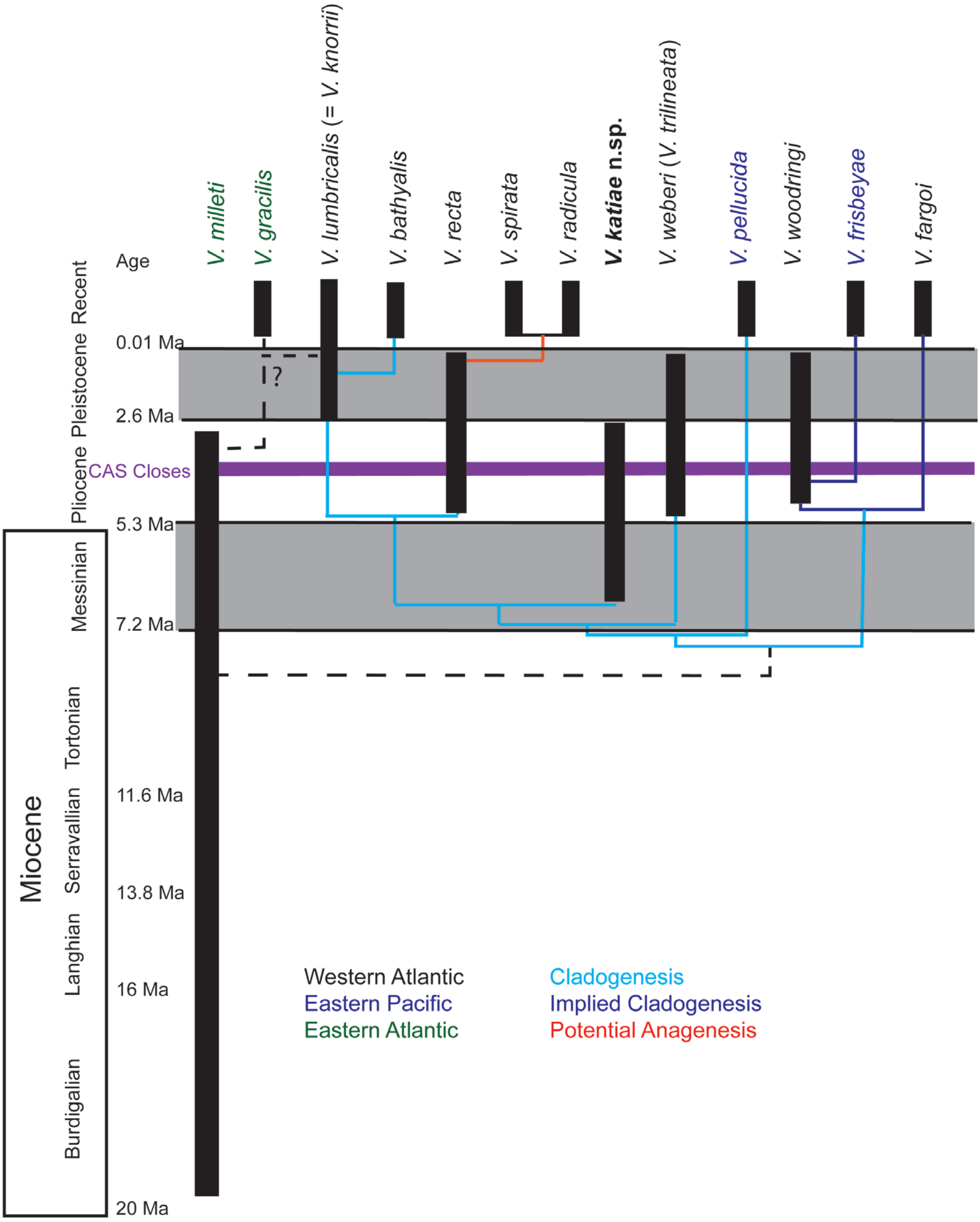

FIG. 88. Phylogeny of fossil and extant *Vermicularia* showing the fossil record of each species (solid bars) minimizing ghost ranges in the richly fossiliferous Plio–Pleistocene of the western Atlantic. Because eastern Pacific species could not have originated from western Atlantic species after closure of the Central American Seaway (CAS), *Vermicularia frisbeyae* and *Vermicularia fargoi* must have ghost ranges extending prior to 3.5 Ma. It is equally parsimonious for *Vermicularia gracilis* to be sister to *Vermicularia milleti* or *Vermicularia knorrii*, with both possibilities geographically plausible.

and geographic occurrences is a late Miocene dispersal event to the western Atlantic from an eastern Atlantic population of *Vermicularia milleti*. It is also reasonable to consider that the Recent West African species *Vermicularia gracilis* could be equally likely a descendant of the Pliocene Iberian population of *Vermicularia milleti* as it is to be the result of west-to-east dispersal by the *Vermicualria lumbricalis* lineage. Further analysis of turritellid molecular data is needed to determine both the frequency of transoceanic dispersal and evaluate the frequency of convergence in various types of shell characters, including changes in coiling parameters.

CONCLUSIONS

The taxonomic and geographic expansion of *Vermicularia* spp. in the Pliocene and Recent of the Americas is an interesting evolutionary event, especially because non-*Vermicularia* turritellids exhibited a significant reduction in species diversity after the Pliocene closure of the Central American Seaway (Allmon, 1992a, 2001). Because *Vermicularia* is properly assigned to the turritellids, the decline in turritellid species number (although still dramatic) is typically overestimated. Most Recent western Atlantic turritellids (4 of 7 species) are *Vermicularia*. *Vermicularia*, like tetrapods within the sarcopterygians (Greene, 2001), represent diversity that is not generally appreciated because a component of the clade is so highly derived that it is readily apprehended as different. Such highly derived taxa are not only interesting to evolutionary biologists, but also represent opportunities for educating students or the public about how evolutionary relationships are hypothesized and tested, and how apparently dramatic evolutionary changes have been accomplished.

Because we have conducted a complete review of all species in a clade, we are also able to test the relative frequency of evolutionary mode (anagenesis vs. cladogenesis; see Allmon, 2016a, b, c; Allmon et al., 2022) associated with morphological change (Jackson & Cheeham, 1999). The phylogeny (Fig. 88) indicates that 9 of 10 species originated by cladogenesis (as determined by ancestral persistence; Gould, 2001), with only *Vermicularia spirata* possibly derived from *Vermicularia recta* by anagenesis. An alternate placement of *Vermicularia gracilis* as sister to *Vermicularia milleti* would potentially represent an additional anagenetic origination. Biogeography suggests that *Vermicularia bathyalis* and *Vermicularia gracilis* might both have originated separately by allopatry from *Vermicularia lumbricalis*, resulting in a true (hard) polytomy even though resolution is achieved in the maximum parsimony analysis (Hoelzer & Meinick, 1994). Reports of *Vermicularia spirata* in the Plio–Pleistocene do not appear to be accurate (consistent with the observations of Olsson & Harbison, 1953), but suggest a completely cladogenetic history for *Vermicularia* spp., if confirmed. The history of this clade thus supports the hypothesis of punctuated equilibria (Eldredge & Gould, 1972; Gould & Eldridge, 1977), contradicting Erwin & Anstey (1995), but consistent with Prothero (1992), Jackson & Cheetham (1999), and Gould (2002). This diversification and the ontogenetic mechanisms that resulted in the unusual morphology of this group are also worthy of further examination.

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APPENDIX: DESCRIPTION OF MORPHOLOGICAL CHARACTERS AND MORPHOLOGICAL CHARACTER STATE DETERMINATIONS

Protoconch Characters

Protoconch data are limited, especially for fossil taxa, because protoconchs are typically lost prior to collection, even for live-collected individuals (Johnson et al., 2017). Where present, protoconchs were classified according to maximal diameter (including for partial protoconchs) and whorl number.

(1) Protoconch diameter: 0 = < 250 μm; 1 = 250–350 μm; 2 = > 350 μm.
(2) Number of whorls: 0 = 1.25 volutions or fewer; 1 = > 1.26 volutions.

General Teleoconch Characters

(3) Apical angle (Fig. 1B): 0 = < 30°; 1 = 30° or greater.
(4) Pleural angle (Fig. 1B): 0 = 10–15°; 1 = 15–20°; 2 = > 20°.
(5) Whorl profile (Fig. 1D; following the definitions of Allmon et al., 1996): 0 = convex; 1 = subquadrate; 2 = flat-sided; 3 = frustrate; 4 = imbricate; 5 = concave; 6 = keeled; 7 = telescoped; 8 = campanulate; 9 = hypercampanulate; 10 = straight-sided; 11 = telescoped acute. These are unordered, and this numbering system encompasses forms not here observed for ease of incorporating additional species in more expansive turritellid matrices.
(6) Size (overall size defined as the maximum length of the shell for turritellids, and the length of the turritelliform portion plus the sum of whorl widths for each complete volution in the *Vermicularia*, effectively compressing them to their size if they had been coiled): 0 = < 5 cm; 1 = 5–13 cm; 2 = 13–20 cm; 3 = > 20 cm.
(7) Suture depth: 0 = shallow; 1 = medium; 2 = deep.
(8) Umbilicus (on the turritelliform portion of the shell before uncoiling): 0 = absent; 1 = present.

Coloration

Coloration of modern species was characterized as clear/white/very light or tan/dark. Although several species varied in shell coloration from tan to reddish to very dark brown among individuals, the characteristic of an adult shell that is either very light (translucent or white) as opposed to pigmented was generally stable in all species. Coloration was recorded both for the apical/coiled portion of the shell and the later whorls, because early whorl color was identified separately from later coloration; this pattern is diagnostic for some species. All fossil species were coded as unknown for all coloration characters.

(9) Coloration, early whorls: 0 = unpigmented, 1 = pigmented.
(10) Coloration, late whorls: 0 = unpigmented, 1 = pigmented.
(11) Pattern of coloration: 0 = solid; 1 = vertically striped; 2 = spotted or otherwise complex.

Growth Line Characters

(12) Growth lines: 0 = smooth; 1 = raised.
(13) Basal sinus (Fig. 1E; defined according to Allmon, 1996): 0 = type 1; 1 = type 2; 2 = type 3; 3 = type 4; 4 = type 5; 5 = type 6.
(14) Lateral sinus depth: 0 = shallow; 1 = medium; 2 = deep.
(15) Lateral angle: 0 = prosocline; 1 = uninclined (straight); 2 = opisthocline.
(16) Lateral type (inflection points): 0 = single on bottom; 1 = double; 2 = single on top; 3 = none.
(17) Lateral sinus apex location (Fig. 1E): 0 = upper third; 1 = middle third; 2 = lower third.

Aperture Shape

Gould & Robinson (1994; also Gould, 1969) noted that free-growing gastropod tubes are typically circular, but turritellid aperture shape ranges from quadrate to fully circular or teardrop-shaped and *Vermicularia* species do exhibit variation in aperture shape.

(18) Aperture shape (ordered): 0 = square; 1 = subquadrate; 2 = circular; 3 = teardrop-shaped.
(19) Angle between aperture and anterior of previous body whorl: 0 = smooth; 1 = prominent; 2 = near 90°; 3 = obtuse. Some species of *Vermicularia* did not have exemplars observed in the preuncoiling stage for which this feature could be characterized.

Sculpture

Sculpture was characterized separately for early teleoconch whorls and the uncoiled (or late ontogeny for coiled species) portion of the shell. The number of major (primary) spiral cords and minor (secondary) spiral cords was determined for both early whorls and the equivalent side of the uncoiled portion in later ontogeny. Spiral cords were divided into two types: primaries and secondaries (Allmon, 1996). To be designated as a primary spiral cord (A, B, C, D), the cord must appear within 3 or 4 whorls of all other primaries (Fig. 1C). These primary cords must also be the most prominent cords and begin within several whorls of the protoconch-teleoconch boundary. Spiral cords are identified by relative position on the whorl. We used scanning electron micrographs whenever possible to examine juvenile sculpture, because the position of each cord is often not constant throughout ontogeny. In alignment with Marwick (1957), Landau et al. (2018), and Friend et al. (2023), we identified the cord in the medial portion of the whorl as B. Cords A and C were identified based on their relative position to cord B. Cord D forms along the abapical suture of the whorl. In the event that there is no primary cord near midwhorl, we treated cord B as absent, and the space at the midwhorl as where B should have been; we then continued identifying the other cords. Secondaries appear later than primaries and can be identified by their relative positions to the primaries. They must begin as relatively weaker than the primaries. Secondary cords, however, are allowed to increase in relative strength compared to all other cords throughout ontogeny.

(20) Strongest cord, early: 0 = no strong primaries or cords present of equal strength; 1 = A; 2 = B; 3 = C; 4 = D.
(21) Strongest cord, late: 0 = no strong primaries or cords present of equal strength; 1 = A; 2 = B; 3 = C; 4 = D.
(22) Number of primary spiral cords, early (regardless of cord identity): 0 = 0; 1 = 1; 2 = 2; 3 = 3; 4 = 4.
(23) Number of primary spiral cords, late in ontogeny (regardless of cord identity): 0 = 0; 1 = 1; 2 = 2; 3 = 3; 4 = 4.
(24) Number of secondary spiral cords, early: 0 = 0; 1 = 1; 2 = 2; 3 = 3; 4 = 4 or more secondary lateral cords.
(25) Number of secondary spiral cords, late in ontogeny: 0 = 0; 1 = 1; 2 = 2; 3 = 3; 4 = 4 or more secondary lateral cords.
(26) Spiral sculpture: 0 = smooth; 1 = beaded.
(27) Lineations on the exposed, formerly adapical, surface of the shell (in uncoiled forms): 0 = absent; 1 = present. Coiled forms were coded as unknown.

Characters Related to Uncoiling

The uncoiled portion of the shell was characterized according to typical range of whorl number at onset, typical width of the final coiled whorl, and whether the uncoiled portion had a wrinkled or smooth appearance. Exact whorl number/size at uncoiling appears to be partially ecophenotypic (Gould, 1968b) and therefore ranges were used rather than specifying particular whorl numbers, however species do not typically exceed the ranges to which they have been classified here.

(28) Uncoiling during ontogeny: 0 = atypical; 1 = typical.
(29) Typical uncoiling diameter (ordered, in uncoiled forms): 0 = ≤ 0.5 cm; 1 = 0.5–0.75 cm; 2 = 0.75–1 cm; 3 = > 1 cm. This was measured at the whorl prior to the first separation, even if the first separation was open coiling without axis alteration. Coiled forms were coded as unknown.
(30) Number of whorls at uncoiling (ordered): 0 = never uncoiling; 1 = uncoiling at > 10 whorls; 2 = uncoiling between seven and nine whorls; 3 = uncoiling at six or fewer whorls. This is also a variable trait infraspecifically, therefore average numbers were used and divisions reflect apparently consistent groups. Character state 3 was kept intentionally broad because early-uncoiling species were also observed to be more highly variable.
(31) Maximum observed length of the uncoiled portion: 0 = < 3 cm; 1 = 3–6 cm; 2 = 6–9 cm; 3 = > 9 cm.
(32) Coiling axis through ontogeny: 0 = uncoiled portion retaining similar coiling axis to rest of the shell; 1 = changing through ontogeny.
(33) Surface of uncoiled portion: 0 = smooth; 1 = wrinkled.

Hermatypic Behavior

(34) Frequent formation of bioherms with conspecifics: 0 = not characteristic; 1 = her-

matypic. The frequent formation of bioherms with conspecifics was noted as characteristic of the species or not, and when any species known to form such structures frequently was coded as hermatypic even if it is often found isolated or associated with other reef-forming taxa as well. Many species have been observed in collections to occasionally cement to one or two other individuals, but this characterization was reserved for species that frequently form large aggregations.