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hypotheses on origins and affinities

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Expanded concept of the milliped family Spirobolidae (Diplopoda: Spirobolida: Spirobolidea): Proposals of Aztecolini n. tribe and Floridobolinae/ini and Tylobolini n. stats.; (re)descriptions of *Floridobolus* and *F. penneri*, both Causey, 1957, and *F. orini* n. sp.; hypotheses on origins and affinities

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Abstract. The endemic Floridian milliped genus, *Floridobolus* Causey, 1957, more closely related to tylobolinines in the western United States (US), Mexico, and Guatemala than syntopic spirobolines, is incorporated into Spirobolidae (Spirobolida: Spirobolidea). With taxonomic priority by one year, its monotypic family is reduced to Floridobolinae, n. stat., comprising Floridobolini and Tylobolini, n. stats., the counterpart to Spirobolinae, comprising Spirobolini and **Aztecolini, n. tribe**; relationships are Floridobolini + (Tylobolini + (Aztecolini + Spirobolini)). Like *F. penneri* Causey, 1957, 208 km (130 mi) to the south in the Lake Wales Ridge, Polk and Highlands counties (cos.), ***F. orini* n. sp.**, inhabits “Big Scrub” environments in the Ocala National Forest, Marion Co. Biogeographic reconstructions, compatible with broader hypotheses on the class’ evolutionary history, indicate that, from a presumptive source area in northern Mexico where the subfamilies overlap, spirobolid stock penetrated the “proto-US” four times, once per tribe, **before** the Western Interior Seaway developed in the Cretaceous Period, Mesozoic Era. Three expansions headed northeastward into future “Appalachia,” from which taxa spread southward as the Seaway receded. Floridobolini, the first invader, had to be in “proto-Georgia” and positioned to penetrate Florida when the sand dunes that comprise the “Central Highlands” emerged from the sea in the Oligocene (Cenozoic), ~25 mya. As sea levels rose and fell, the dunes fragmented into islands and the subcontinuous *Floridobolus* population was partitioned. The southernmost became *F. penneri*; ***F. orini*** inhabited a northern island; and a graduate student is investigating other insular remnants for additional species. Shortly after Floridobolini began spreading, *Hiltonius*/Tylobolini arose and expanded both southward to Guatemala and northwestward to California; *Tylobolus* Cook, 1904, diverged in the latter area and dispersed northward to Washington and eastward to Utah/Arizona. The third invader, and the second to disperse northeastward, was **Aztecolini**, which probably eradicated Floridobolini from some of its established range and was partitioned into Mexican (*Aztecolus* Chamberlin, 1943) and US (*Chicobolus* Chamberlin, 1947) taxa by the Seaway. The final invader, Spirobolini, dispersed northwestward and northeastward to both the Pacific and Atlantic coasts; instead of Trans-Beringia, we prefer penetration of the Asian part of “Asiamerica,” when it temporarily formed during the Cretaceous, to explain the Mongolian fossil genus, *Gobiulus* Dzik, 1975, herein assigned to Tylobolini, and the occurrence of *Spirobolus* Brandt, 1833, in China and Taiwan today. In the east, *Narceus* Rafinesque, 1820, spread across Appalachia, eradicated most remaining populations of *Floridobolus* and *Chicobolus*, and expanded to Maine and Québec after retreat of the Wisconsin glaciation. *Chicobolus* and *Narceus* also penetrated earliest Florida; the former established itself in the Central Highlands, spread through the widening peninsula as sea levels fell, and remained on insular refugia when waters rose. Apparently fueled by the different Floridian environments, *Narceus* underwent time-consuming speciation; consequently, *Floridobolus* and *Chicobolus* still survive on the peninsula, and an allopatric population of the latter inhabits coastal South Carolina. However, *N. gordanus* (Chamberlin, 1943) occurs syntopically with both in peninsular Florida and may be actively eradicating them from their last stronghold. *Trigoniulus niger*, *takahasii*, and *segmentatus*, all by Takakuwa, 1940, are removed from Spirobolidae and returned to Trigoniulidae (Trigoniulidea). New records in the Appendix include the first of *Aztecolus* from Durango and Jalisco, Mexico.

Key Words. Appalachia; *Aztecobolus*; Central Florida Highlands; *Chicobolus*; Cretaceous; Floridobolidae; *Hiltonius*; Lake Wales Ridge; Laramidia; Mexican Highlands; *Narceus*; Ocala National Forest; Spirobolinae/ini/*Spirobolus*; Tylobolini/*Tylobolus*; Western Interior Seaway.

Introduction

Two strikingly analogous geographical enigmas have long perplexed North American diplopodologists – *Floridobolus* Causey, 1957 (Spirobolida: Spirobolidea: Floridobolidae) and *Choctella* Chamberlin, 1918 (Spirostreptida: Epinannolenidea: Choctellidae). Both are juliformians, occupy limited ranges in the southeastern United States (US/USA), comprise monotypic families, contain two known species, and are mysterious as to their origins and affinities. Presently monotypic for *F. penneri* Causey, 1957, in the Lake Wales Ridge, Polk and Highlands counties (cos.), Florida, *Floridobolus* also includes *F. orini* n. sp., described herein from the Ocala National Forest, Marion Co., and hence is known from a 208 km (130 mi) stretch of the arid, sandy Central Florida Highlands. It therefore equates with *Choctella*, which inhabits a 320 km (200 mi) stretch of the Cumberland Plateau in central Tennessee and northern Alabama and includes *C. cumminsi* Chamberlin, 1918, and *C. hubrichti* Hoffman, 1965 (Chamberlin 1918a; Loomis 1938, 1943; Chamberlin and Hoffman 1950, 1958; Causey 1957; Hoffman 1965, 1969, 1980a, 1999; Jeekel 1985; Mauriès 1987; Shelley and Golovatch 2011). Observing that partitioning coupled with extinctions isolated atypical southern forms in the eastern North American *Sigmaria* mosaic (Polydesmida: Xystodesmidae), Shelley (1990) reasoned that this process might explain the origins of other geographical oddities. He suggested that *Choctella* may be the former northern component of an ancient epinannolenidean mosaic that is so anatomically dissimilar as to require a monotypic family and now so isolated as to be the only remaining North American representative. In the New World, however, Epinannolenidea otherwise inhabit the West Indies (except Jamaica), southern Central America, and South America, populations deriving from Gondwana. Thus, while Shelley's (1990) hypothesis may explain the origins of some oddities, it is biogeographically inoperative for *Choctella*, which is unrelated to any remotely proximate taxon. We can only suggest that it may be a remnant of the ancestral diplopod radiation onto Laurentia in the early Silurian, ~440 million years ago (mya) (Shelley and Golovatch 2011). *Choctella* therefore remains a mystery, but we herein address *Floridobolus* and remove it from the enigmatic roster.

Consisting primarily of vagile, large-bodied juliformians, Spirobolida is a prominent, indigenous order in the former “Gondwanan” region of the world (Shelley and Golovatch 2011). Though absent from Europe and central Asia, the nominate suborder represents it in former Laurasian east-Asia and North/Central America, accessing the latter in the late-Carboniferous Period, Paleozoic Era, ~306 mya, when the “proto-Mexico” part of “Euramerica” collided with the “proto-South America” part of the existing Gondwana, which derived from breakup of the supercontinent Pannotia in the early-Cambrian (ca. 540 mya). Shelley and Golovatch (2011) referenced Pannotia Gondwana as “Gondwana I” because it preceded Pangaeon “Gondwana II” that began forming in the late-Jurassic (Mesozoic), ~152 mya. When Euramerica and “Gondwana I” merged, taxa in “proto-South America” penetrated vacant niches in “proto-Mexico,” from which they spread in all directions including northward into the “proto-US.” Five ordinal taxa that were absent from Euramerica entered then – Glomeridesmida, Siphonophorida, Spirobolidea (Spirobolida), Spirostreptidea (Spirostreptida), and Stemmiulida – as did Gondwanan representatives of the polydesmidan suborder Leptodesmidea. Siphonophorida and Spirostreptidea spread into the “proto-US” seemingly without diversifying (Chamberlin and Hoffman 1958; Loomis 1968a; Causey 1975; Shelley 1996a, b; Hoffman 1999; Shelley and Golovatch 2011), but apparently fueled by newly encountered niches, Spirobolidea and Leptodesmidea underwent familial divergences, and progeny taxa inhabit the southeastern/central/western US, northern Mexico, and/or northern Central America today. In the western and eastern US, respectively, Spirobolidae have spread northward to southern Washington state and Québec, Canada, traversing the Mississippi River for the latter. *Narceus* Rafinesque, 1820, is ubiquitous east of the Central Plains, and encountering an individual on every field trip is virtually guaranteed. Non-specialists, picknickers, hikers, and children are equally likely to see an individual walking on pavement or paths on any outdoor excursion. Its vast distribution (Shelley et al. 2006) and adaptability to most environments make *Narceus* the most successful milliped genus in eastern North America.

Three spirobolidean families occupy the southcentral/western US – Allopocockiidae, in southernmost Texas; Atopetholidae, from southern Texas to Monterey Co., California; and Spirobolidae, covering the rest of the indigenous range (Chamberlin and Hoffman 1958; Keeton 1960a, 1966; Hoffman and Orcutt 1960; Buckett 1964; Loomis 1968a; Hoffman 1980a, 1999; Shelley 1988, 2001a, 2002a; Shelley and Hoffman 1995; Shelley and Golovatch 2011). The southernmost counties in peninsular Florida – Broward, Collier, Miami-Dade, and Monroe – harbor the introduced families, Rhinocricidae and Trigonulidae (Shelley and Edwards 2002, Shelley et al. 2005), and native spirobolids blanket the peninsula. *Narceus* is represented by three species – *americanus* Beauvois, 1817; *gordanus* (Chamberlin, 1943); and *woodruffi* Causey, 1959 – and the lone component of *Chicobolus* Chamberlin, 1947, *C. spinigerus* (Wood, 1864), also inhabits the Keys (Hoffman 1951, 1980a, 1999; Causey 1955a, 1959; Chamberlin and Hoffman 1958; Keeton 1960a; Shelley 1988, 2001a, 2002b, c). One other spirobolidean genus occurs there, *Floridobolus* Causey, 1957, presently assigned to the monotypic Floridobolidae and itself monotypic for *F. penneri* Causey, 1957, inhabiting arid “Big Scrub” environments in the Lake Wales Ridge, Polk and Highlands cos. (Causey 1957; Keeton 1959; Hoffman 1980a, 1999; Deyrup 1994, 2012; Shelley 2001a). In August 2012, SDF discovered a male spirobolidean in scrub habitat in the Ocala National Forest, Marion Co., 208 km (130 mi) to the north, and sent it to Orin McMonigle in Ohio. Recognizing *Floridobolus* from its color, transversely ovoid body form, rounded epiproct (Fig. 1–5), and its ability to rapidly uncoil from a helical resting position, he transferred the specimen to RMS. A gonopodal examination confirmed the allopatric species described herein along with updated accounts of the genus and *F. penneri*. Hoffman (1982) redescribed Floridobolidae, and simultaneously also *Floridobolus* and *F. penneri*, and Pitz and Sierwald (2010) affirmed the family’s validity molecularly, though noting affinity with Spirobolidae.

In the 57 years since *Floridobolus* was proposed, the overriding and still unanswered questions have been what is it related to, does it warrant separate familial status, and how did it become isolated in the central sand dunes of southern peninsular Florida, which only began emerging from the sea ~25 mya? Anatomically-based phylogenetic and phylogeographic assessments reveal its origin and affinities, which require encapsulating Florida’s geological history plus a review of Spirobolidae based on gonopodal illustrations and RMS’ observations over 42 years. Terminology primarily follows Keeton (1960a); datings follow Shelley and Golovatch (2011); and unpublished localities are cited in the Appendix. In reconstructing biogeographic dispersals, we arbitrarily place all taxa in Cretaceous land masses by the middle of this geological time period, ~104 mya. Separate familial status for *Floridobolus* is not warranted despite its considerable gonopodal and somatic apomorphies, so we provide a new taxonomy to accommodate the genus and reflect its true position as the plesiomorphic sister-group to the rest of Spirobolidae. We therefore reduce Floridobolidae, with priority by one year over Tylobolinae, to subfamilial status, the latter to a tribe, and for consistency, erect **Aztecolini, n. tribe**, for the unnamed lineage comprising *Aztecobolus* and *Chicobolus*; we also address the Mongolian fossil genus, *Gobiulus* Dzik, 1975. During the final stage of manuscript preparation, O. McMonigle contributed a photo of *Floridobolus* and *Narceus* rings that clearly contrasts the transversely ovoid and rounded/cylindrical profiles; it constitutes fig. 33 and is necessarily out of sequence. We cannot infer the former generic composition of Floridobolini nor when *Floridobolus* actually evolved; we only know that they invaded Florida ~25 mya. Consequently, when associating these spirobolids with Florida and south Georgia, we use the generic name, and when associating them with earlier time periods and other geographic areas, we use the tribal. Aspects of spirobolid biogeography were addressed by Shelley and Golovatch (2011), but we specifically reference the Cretaceous Western Interior Seaway and its impact, by inundating central North America, on the segregated eastern and western faunas of today. Repository acronyms are **ABS**, Archbold Biological Station, Lake Placid, Florida; **AMNH**, American Museum of Natural History, New York, New York; **CAS**, California Academy of Sciences, San Francisco; **FSCA**, Florida State Collection of Arthropods, Gainesville; **KMNH**, University of Kansas Museum of Natural History, Lawrence; **MCZ**, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; **NCSM**, North Carolina State Museum of Natural Sciences, Raleigh; and **UMMZ**, University of Michigan Museum of Zoology, Ann Arbor.



Figures 1–5. *Floridobolus orini* holotype. **1)** Head, collum, and anterior pleurotergites, dorsal view. **2)** The same, right sublateral view. **3)** Entire body, dorsal view. **4)** The same, dorsolateral view. **5)** Paraprocts, epiproct, and caudal pleurotergites, caudolateral view.

Gonopodal Characters

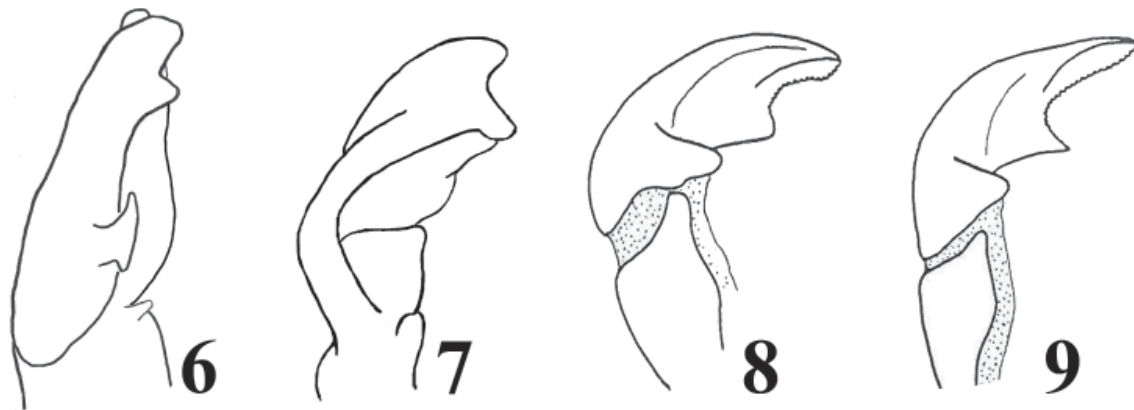
We address taxonomic features of spirobolid gonopods based on comparative observations by RMS and published statements by Keeton (1959, 1960a, b) and Hoffman (1957, 1982). We do not conduct a true revision, whose time-consuming lengthiness might exceed RMS' remaining life-expectancy, so admittedly, this is an imperfect contribution. To us, however, imperfect new insight always bests the *status quo*, so we provide a compromise treatment focusing on basic questions surrounding *Floridobolus*. Consequently, diplopodologists who dislike our approach, favor the *status quo* over new but imperfect insight, disapprove of anatomically-based taxonomy, or to paraphrase Hoffman (1999), regard insights derived from broad geographical patterns with “disdain as mere hackwork,” because they are neither Bayesian nor molecularly based, should stop reading now.

Anterior gonopods

Sternum and apodeme. In contrast to the large, dominant, subtriangular structure in Rhinocricidae, the only native spirobolidean family in South America, southern Central America, and the Antilles (Hoffman 1980b, fig. 1, 1998a, fig. 1, 3; Hoffman and Golovatch 2012, fig. 3, 8, 13), the anterior gonopod sternum in Spirobolidae is a comparatively narrow, arched band that expands moderately mediad and may or may not possess a lobe protruding between the coxal endites. It lies dorsal to the gonopods and connects with short, lateral apodemes that are oriented dorsoventrally in the body. The primary taxonomic feature of the sternum is the size (both length and width) of the medial lobe, if one exists, and the degree to which it protrudes between and separates the coxal endites. A few forms lack the lobe but the arch itself protrudes ventrad between, and slightly separates, the endites (Fig. 11, 15; Keeton 1960a, fig. 23, 32, 105, 111, 122, 127, 136, 142, 166, 172, 178, 184, 189, 253, 264).

Coxal endites. Broad, flattened, plate-like structures that arise from the coxae, they extend mediad and overlie the ventral margin of the sternum. Opposing ones approach each other, may touch or nearly touch in the midline (Fig. 14, 18; Keeton 1960a, fig. 166, 171, 185, 228, 234–235, 242, 284), or be separated to varying degrees by the sternal arch or medial lobe (Keeton 1960a, fig. 23, 32, 105, 111, 122, 127, 138, 141, 142; Shelley 2002c, fig. 2, 5, 8). In many species, the medial corners of the endites are variably extended or prolonged into lobes that can be rather long (Keeton 1960a, fig. 166, 171, 174, 178, 184, 188, 264).

Telopodites. Fused to the coxae with only a faint suture line in Floridobolini, the anterior gonopod telopodites are separate, distinct, and articulate with them in other tribes. As gonopods are modified ambulatory appendages in which telopodites, specifically prefemora, articulate with coxae, we interpret



Figures 6–9. Comparison of Floridobolinae posterior gonopods. **6)** *Floridobolus penneri* (Floridobolini), caudal view of caudal acropodital surface of holotype left posterior gonopod. **7)** *Hiltonius carpinus* (Tylobolini), anterior view of right posterior gonopod of male from Cochise Co., Arizona. **8)** *H. pulchrus* (Tylobolini), caudal view of right posterior gonopod of male from Riverside Co., California. **9)** The same, caudal view of right posterior gonopod of male from Los Angeles Co., California. Fig. 7 is reproduced from Shelley (2010) with permission from the Center for Systematic Entomology; Fig. 8–9 are reproduced from Keeton (1960a) with permission from the American Entomological Society.

Table 1. Potential defining apomorphies in Spirobolidae.

Apomorphy	Clade
1. Narrow coxal endites	Spirobolidae
2. Curved, spatulate posterior gonopod coxal apodemes	Spirobolidae
3. Transversely ovoid body profile	Floridobolini
4. Gnathochilarial mentum with knob-like convexity	Floridobolini
5. Epiproct apically rounded	Floridobolini
6. Anterior gonopod telopodite fused to coxa	Floridobolini
7. Anterior surface of posterior gonopod acropodite with bifurcate projection	Floridobolini
8. Loss of posterior gonopod sternum	Tylobolini + Spirobolinae
9. Posterior gonopod acropodite without extension of caudal surface	Tylobolini
10. Lengthening of prefemoral process into discrete structure	Spirobolinae
11. Thinning, elongations, and expansions of anterior and caudal extensions of posterior gonopod acropodites	Spirobolinae
12. Spiniform projections on acropodital margins	Aztecolini
13. Acropodite expanded into deeply concave, hood-like cover overhanging and enveloping prefemoral process	Spirobolini

the fusion in Floridobolini as apomorphic. Whether separate or fused, the condition is primarily visible in lateral and caudal views but may be obscured by torn, dissected muscles and membranes.

The apical telopodital configuration ranges from slightly elevated and unadorned to strongly and conspicuously uncinat. All Spirobolinae are uncinat and both species of Floridobolini are non-uncinat (Fig. 14, 18); anatomically intermediate Tylobolini demonstrate both conditions in both component genera. *Hiltonius mexicanus/carpinus* and *Tylobolus claremontus/ergus/monachus/castaneus* possess apically uncinat telopodites (Keeton 1960a, fig. 166, 171, 174, 224, 228, 234–235, 242), and *H. pulchrus/mimus* and *T. uncigerus/utahensis* are non-uncinat (Keeton 1960a, fig. 178, 184, 253–254, 264–265). This trait stabilizes in Spirobolinae, and the non-uncinat condition in Floridobolini is the same as that in the mentioned tylobolinines, which also occupy intermediate geographic positions.

Posterior gonopods

Sternum. Absence of the posterior gonopod sternum is synapomorphic among Tylobolini, Aztecolini, and Spirobolini; it is a non-functional vestige in Floridobolini.

Coxa and apodeme. Keeton (1960a) considered the presence of the posterior gonopod coxa to be an important diagnostic feature of Spirobolidae, but it has little taxonomic value otherwise. The apodeme varies from long and extending lengthwise internally to ring 10, in *F. penneri* (Keeton 1959, fig. 14), to short and oriented dorsoventrally, in Spirobolinae (Keeton 1960a, fig. 26–27, 113, 128–129; Shelley 2002c, fig. 3, 6, 9). Of the tylobolinines whose apodemes have been illustrated, those of *H. mexicanus/pulchrus* and *T. deses* are moderately long and intermediate in length (Keeton 1960a, fig. 168, 179, 239). Consequently, Keeton's statement (1959, 1960b) that long apodemes characterize Floridobolini is at best misleading because the ones of *H. mexicanus* (Keeton 1960a, fig. 168), for example, are considerably longer than those in Spirobolinae.

Telopodite. The posterior gonopod telopodite spans an array of configurations with Floridobolini exemplifying the plesiomorphic state. The structure that Keeton (1960a) and subsequent authors termed, “prefemoral endite,” in Spirobolini, and “mesal apodeme of the posterior telopodite,” in Tylobolini, was labeled “prefemoral process” by Hoffman (1957). Muscles attach to it (Hoffman 1957, fig. 1–3; Keeton 1960a, fig. 26–27, 139–140, 143, 167–169, 172–173, 225–226, 229–230, 236–237, 239–240, 244–246, 255–256, 263, 268), which are also shown by Causey (1955b, fig. 5) and Buckett and Gardner (1966, fig. 1). We believe they constitute the same structure that has three different names and employ “prefemoral process,” which holds priority and reflects a fundamental telopodital component rather than an extraneous projection as implied by “endite.” It appears to be absent from Floridobolini, but we believe the lightly sclerotized, nubbin-like structure (Fig. 6, 15–16, 20) is homologous as it is in the same relative position on the telopodital stem and has been attached to muscles in our dissections. We

Table 2. Comparisons of anatomical attributes of Floridobolini with conditions in Spirobolinae and Tylobolini.

Condition in Floridobolini	Condition in Spirobolinae	Condition in Tylobolini
Gnathochilarial mentum swollen into knob-like boss or convexity.	Gnathochilarial mentum flat.	Gnathochilarial mentum flat.
Segmental profile transversely ovoid (Fig. 33).	Segmental profile rounded (Fig. 33).	Segmental profile rounded (Fig. 33).
Legs invisible in dorsal view (Fig. 3).	Legs slightly visible in dorsal view.	Legs slightly visible in dorsal view.
Epiproct broadly rounded apically (Fig. 5).	Epiproct narrowly rounded apically.	Epiproct narrowly rounded apically.
Paraprocts slightly re-entrant, without marginal rims (Fig. 5).	Paraprocts with marginal rims, not re-entrant (Fig. 5).	Paraprocts usually without, occasionally with marginal rims, usually slightly re-entrant.
Anterior gonopod (AG) sternum without medial lobe, arch not projecting ventrad between coxal endites.	AG sternum with medial lobe extending ventrad between coxal endites.	AG sternum usually without medial lobe, arch or lobe extending ventrad between coxal endites.
Coxal endites contiguous in midline or at most only narrowly segregated (Fig. 14, 18).	Coxal endites widely separated by medial sternal lobe.	Coxal endites usually only slightly separated by sternal arch or medial lobe.
AG coxa and telopodite fused with only faint suture line as evidence of former articulation.	AG coxa and telopodite articulating as clearly separate and distinct podomeres.	AG coxa and telopodite articulating as clearly separate and distinct podomeres.
AG telopodite not uncinat distad (Fig. 14, 18).	AG telopodite uncinat distad.	AG telopodite usually uncinat distad, occasionally not uncinat.
Posterior gonopod (PG) sternum present as a short, lightly sclerotized, detached remnant	PG sternum absent.	PG sternum absent.
PG sternal apodeme long, oriented lengthwise internally and extending to pleurotergite 10.	PG sternal apodeme short and oriented subdorsoventrad.	PG sternal apodeme variable, moderately long to long.
PG acropodite thickened and distinctly lobate, both surfaces prolonged (Fig. 15-16, 19-20).	PG acropodite thin and laminate, both surfaces prolonged, forming cupulate hood enveloping prefemoral process.	Pg acropodite thickened and lobate, only anterior surface prolonged (Fig. 7-9).
PG prefemoral process nubbin-like, inconspicuous (Fig. 15-16, 20).	PG prefemoral process distinct, with basal lobe and variable distal part, either lying entirely outside, or strongly overhung and enveloped by acropodite.	PG prefemoral process larger, moderately distinct and conspicuous.

therefore consider the prefemoral process in Spirobolinae and Tylobolini to be an enlargement of the nubbin-like structure in Floridobolini.

Floridobolini's acropodite is an essentially upright, elongated, post-like structure whose anterior and caudal surfaces are thickened, lobate, and prolonged mediad (Fig. 6, 15–16, 19–20; Keeton 1959, Fig. 14), thereby creating a central cavity or depression of varying breadths. The most noticeable aspect of spirobolid gonopods and most indicative of tribe, the acropodite has essentially metamorphosed into configurations and conditions that bear no resemblance to the plesiomorphic state, the main source of confusion regarding *Floridobolus*' familial assignment. Its telopodite appears almost "alien" compared to the familiar structures of *Narceus* and *Chicobolus*, in which they are so modified as to obscure the basic pattern. The upright alignment in Floridobolini is transformed into bent, leaning, or curved (Fig. 7–9; Keeton 1960a, fig. 26–27, 30, 33–34, 106–107, 112–113, 123–124, 128–129, 143–144, 167–168, 172–173, 179, 186, 190, 225–226, 229–230; Shelley 2002c, fig. 3, 6, 9), and structural features are so enlarged and modified that they do not resemble the plesiomorphic conditions. In Tylobolini, only the anterior acropodital surface is prolonged; the caudal elongation is absent, so there is no central depression. Acropodites in *Hiltonius* (or rather the anterior surfaces) are lobed distally as are both surfaces of *Floridobolus*, and the configurations in *H. carpinus* Chamberlin, 1943, and *H. pulchrus* Chamberlin, 1918, resemble those on both surfaces in *Floridobolus* (Fig. 6–9). The lobes differ proportionally in other species of *Hiltonius*, and in *Tylobolus*, the proximal one is absent and the distal one is prolonged and decurved, thus imparting an uncinat configuration to the appendage. In Spirobolinae, the acropodite is thin and laminate, both the anterior and caudal surfaces are extended, and the prefemoral process is bulbous basally, elongate, and broad distad (Keeton 1960a, fig. 26–27, 30, 33–34; Shelley 2002c, fig. 3, 5, 9). The acropodital lobes in Floridobolinae merge such that Aztecolini constitutes an incomplete version of Spirobolini. In the latter, lobes/projections are eliminated and extensions are greater with

smoothly linear margins; in *Narceus*, the distal part of the prefemoral process is extended and broadened, and the entire projection is recessed into the acropodital cavity, which overhangs and envelops it as a cupulate “hood.” The effect is of an endomere overhanging a telopodite, as in *Scytonotus* Koch, 1848 (Shelley 1994, fig. 5–8, 11–18, 21–28) and other representatives of Polydesmidae (Polydesmida). Aztecolini represents an early developmental stage of both the acropodite and prefemoral process – the acropodital cavity is shallow, its surfaces are less extended, and the margins are incomplete with spines and incisions. The prefemoral process lies outside the cavity, and the distal part is variably short and slender.

The posterior gonopods of *Floridobolus* therefore possess the same structures as Spirobolinae but in different positions, configurations, and proportions, and they are similar to those in Tylobolini (Fig. 6–9) except for the absence of the extension of the caudal acropodital surface. We therefore conclude that *Floridobolus* is a plesiomorphic spirobolid reflecting an early stage in the evolution of the condition that reaches its zenith in Spirobolini, and separate familial status is not warranted.

Relationships

We present (Fig. 10) a cladogram of spirobolid tribes with the base line representing Spirobolidea; numbered apomorphies are cited in Table 1. From illustrations of other subordinal families, two potentially apomorphic conditions for Spirobolidae are the relatively narrow coxal endites, which are broader in other families, and the curved, strongly spatulate posterior gonopod apodemes that otherwise tend to be straight and less spatulate.

We list in Table 2 features of *Floridobolus* and their conditions in the two spirobolid subfamilies per Keeton (1960a). Few similarities exist with sympatric Spirobolinae, in contrast to Tylobolinae, whose most geographically proximate species, *H. carpinus*, occurs some 2,816 km (1,760 mi) to the

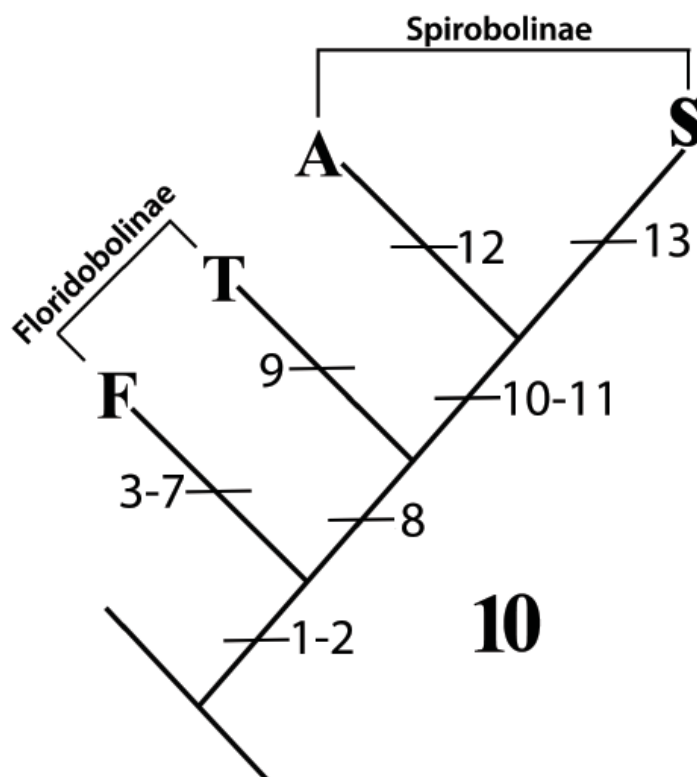


Figure 10. Relationships among spirobolid tribes, apomorphies are listed in table 1. F, Floridobolini. T, Tylobolini. A, Aztecolini. S, Spirobolini.

Table 3. Distances between proximate spirobolid range areas.

Area 1	Area 2	Approximate Distance in km (mi)
Eastern North America	Continuous area in western North America	1,226 km (766 mi) to Arizona “finger”; 1,635 km (1,022 mi) to continuous North/South area in California
Eastern North America	Southeastern Arizona	992 km (620 mi)
Eastern North America	“Mainland” Mexico	234 km (146 mi)
“Mainland” Mexico	Guatemala	992 km (620 mi)
“Mainland” Mexico	Southeastern Arizona	1,285 km (803 mi)
Continuous area in western North America	Southeastern Arizona	392 km (245 mi) to Arizona “finger”; 582 km (364 mi) to continuous North/South area in California
Continuous area in western North America	Eastern Asia	13,683 km (8,522 mi)

west-northwest in Cochise Co., Arizona (Shelley 2010). The following points seem particularly relevant and constitute evidence of affinity between *Floridobolus* and Tylobolini.

- The anterior gonopod sterna in *Floridobolus* and Tylobolini usually lack medial lobes protruding between the coxal endites, which are close together and may be (sub)contiguous (Fig. 14, 18; Keeton 1960a, fig. 166, 170, 174, 176, 224, 242, 253), whereas lobes are present on spiroboline sterna and their coxal endites are distinctly separate (Keeton 1960a, fig. 23, 32, 105, 111, 122, 127, 136, 142; Shelley 2002c, fig. 2, 5, 8).
- Posterior gonopod coxal apodemes in Tylobolini are longer than in spiroboline taxa (Keeton 1960a, fig. 26–27, 113, 128–129, 168, 179, 239; Shelley 2002c, fig. 3, 6, 9), a contrast missed by Keeton (1960a), and hence resemble the condition in *Floridobolus*.
- Tylobolinine posterior gonopod acropodites terminate in one or two lobes, and the lobed configurations in *H. carpinus/pulchrus* resemble those in *Floridobolus* (Fig. 6–9, 16, 20; Keeton 1960a, fig. 172–173, 179–182; Shelley 2010, fig. 2).
- Though prolonged, the anterior gonopod telopodites in *Tylobolus uncigerus* (Wood, 1864) and *T. utahensis* Chamberlin, 1925, as in *Floridobolus*, are apically unadorned (Fig. 14, 18; Keeton 1960a, 178, 184, 189, 253, 264), as opposed to uncinately in other tylobolinines and all spirobolines (Keeton 1960a, 23, 32, 105, 111, 122, 127, 141–142, 166, 171, 174, 224, 228, 242; Shelley 2002c, fig. 2, 5, 8).

Taxonomy

Keeton (1959, 1960a, b) interpreted *Floridobolus*' numerous somatic and gonopodal apomorphies as meriting familial distinction, so Floridobolidae was established on a sound basis. However, our review of spirobolid gonopods shows that his taxonomy, subsequently accepted by Hoffman (1980a, 1982, 1999), Shelley (2003), and Shear (2011), requires alteration. Hoffman (1980a) and Pitz and Sierwald (2010) **suggested** returning *Floridobolus* to Spirobolidae, its original assignment (Causey 1957), but did not actually do so. We believe that Floridobolini, Tylobolini, and Spirobolini constitute clades of Spirobolidae, the oldest family-group name (Fig. 10), and that *Floridobolus*' affinities lie with geographically distant Tylobolini, in Mexico, Guatemala, and the southwestern US (Keeton 1960a; Hoffman 1980, 1999; Shelley 2010), rather than syntopic Spirobolinae. Additionally, the lineage comprising *Aztecobolus* and

Chicobolus warrants a name, and Floridobolidae holds priority by one year over Tylobolinae (Keeton 1959, 1960a). Arguments can be advanced for four resolutions:

- three families – Spirobolidae, Floridobolidae, and Tylobolidae;
 - two families, one divided into two subfamilies – Spirobolidae and Floridobolidae, the latter with subfamilies Floridobolinae and Tylobolinae;
 - one family, Spirobolidae, with two subfamilies, each divided into two tribes – Spirobolinae (with **Aztecolini n. tribe** and Spirobolini) and Floridobolinae (with Floridobolini and Tylobolini); and
- the present arrangement of two families, with Spirobolidae divided into Spirobolinae and Tylobolinae.

From an anatomical standpoint, option 3, one family, best reflects true affinities. That concept of Spirobolidae encompasses forms both with and without the posterior gonopod sternal remnant, but precedent exists for families traversing this spectrum. In Xystodesmidae (Polydesmida: Leptodesmidea), for example, Sismocheirini possess a strong sternum, Rhysodesmini have a small, lightly sclerotized remnant, and Apheloriini lack the structure (Hoffman 1960, Shelley and Whitehead 1986, Shelley 1995).

Order Spirobolida Cook, 1895

Suborder Spirobolidea Cook, 1895

Family Spirobolidae Bollman, 1893

Spirobolinae Bollman, 1893:156. Jeekel, 1971:210 (list). Kevan, 1983:2962.

Spirobolidae: Verhoeff, 1893:481; 1931:1680 (key), 1683–1684. Pocock, 1894a:484 (Key); 1894b:388.

Cook, 1895:7; 1904:64. Brölemann, 1913:476; 1914:29. Attems, 1926:194, 225. Blake, 1931:16. Chamberlin, 1941:253; 1943a:5; 1947:44; 1949:163; 1951:30; 1953:148. Loomis, 1944:169; 1968a:92; 1968b:391; 1971:53. Hoffman, 1950:31; 1969:233–234; 1980a:76; 1998b:64; 1999:36. Loomis and Hoffman, 1951:51. Causey, 1954:224; 1955ba:87; 1963:78. Johnson, 1954:248 (list). Chamberlin and Hoffman, 1958:159. Keeton, 1960a:28–31. Buckett, 1964:23. Reddell, 1965:164. Stewart, 1969: 384. Filka and Shelley, 1980:16. Kevan, 1983:2962. Shelley, 1978:52; 1988:1642; 2000a:184; 2001a:244; 2002a:98; 2002b:1868. Snider, 1991:179. Wang and Zhang, 1993:845. Watermolen, 1995:2. Wang and Mauriès, 1996:84. Zhang et al, 1997:509. Korsós, 2004:17. Bueno-Villegas et al., 2004:586. Snyder, 2008:18–19.

Euspirobolidae Attems, 1909:25; 1910:89–90.

Type-genus. *Spirobolus* Brandt, 1833.

Diagnosis. Small- to large-bodied (primarily moderately large), rounded/cylindrical or transversely ovoid Spirobolidea with the following gonopodal features. Sternum of anterior gonopods relatively narrow and arched mediad, with or without medial lobe protruding ventrad between coxal endites. Latter large and prominent, overlying and closely appressed to sternum, either separated by medial sternal lobe or (sub)contiguous. Telopodites moderately long, curving mediad, either fused to coxa with only faint suture line or separate from and articulating with latter; apex usually slightly prolonged and variably configured, either linear, rounded, or subacuminate, uncinuate or not. Posterior gonopod sternum usually absent, a vestigial remnant in one tribe. Coxa short; apodeme spatulate, varying from short and oriented dorsoventrad to long and extending caudad inside body up to 10th ring. Telopodite with variable prefemoral process, either an inconspicuous, nubbin-like enlargement on telopodital stem or a variably long, lobate, conspicuous projection subequal in length to acropodite. Latter long and prominent, overall appearance varying from thick, upright, and post-like to a thin, laminate, endomere-like hood leaning strongly mediad and overhanging and enveloping prefemoral process to varying degrees, caudal and/or anterior surfaces extending submediad for short but varying lengths, margins thickened and lobate with or without additional projections, or thin, laminate, sublinear and with or without indentations, marginal lobes, and spiniform projections.

Components. Two subfamilies: Floridobolinae Keeton, 1959, and Spirobolinae Bollman, 1893.

Distribution (Fig. 11). Occupying seven variably disjunct areas, six in North and Central America and one in eastern Asia. In eastern North America, Spirobolidae range from southern Québec, Canada, and Maine and the Upper Michigan Peninsula, USA, to the south Florida Keys and the Gulf Coast to the latitude of Nueces Bay/Corpus Christi, Texas; east-west, they extend from the Atlantic Ocean from Maine through Florida to the Plains of eastern Nebraska and central Texas, with an apparently allopatric population some 80 km (50 mi) to the northwest in southwestern Minnesota. In western North America, Spirobolidae occur continuously between the Pacific Ocean and the crest of the Sierra Nevada and Cascade Mountains from north of the Columbia River in Klickitat and Sakamania cos.,

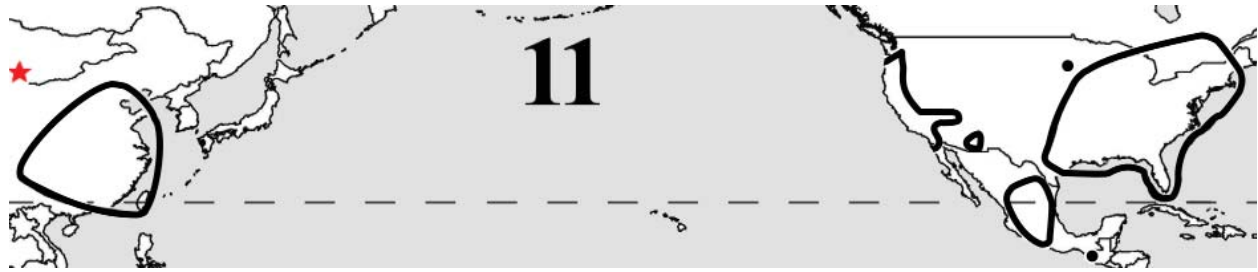


Figure 11. Distribution of Spirobolidae. The red star marks the approximate location of the Mongolian, Cretaceous fossils assigned to *Gobiulus* (Floridobolinae: Tylobolini).

Washington, USA, to northern Baja California Norte, Mexico, with a dactyliform eastward expansion from the southern Sierra Nevada through the Mohave and Great Basin deserts, Nevada, to southwestern Utah and northwestern Arizona. The fourth US area is a small, isolated, subtriangular region in the Pinaleno, Dragoon, and Chiricahua Mountains of southeastern Arizona. In “mainland” Mexico, Spirobolidae occupy a broad, central area that extends, north-south, from northern Nuevo León and central Durango to Guerrero, with an isolated point locality on Volcán Tajumulco, San Marcos Dept., Guatemala (Chamberlin and Hoffman 1958; Keeton 1960a, 1966; Loomis 1968a; Hoffman 1980a, 1999; Shelley 1988, 2001a, 2002a, c, 2010; Shelley and Hoffman 1995; Shelley and Bauer 1997; Shelley and Stevens 2003; Bueno-Villegas et al. 2004; Shelley et al. 2006; Shelley and Golovatch 2011; plus unpublished records cited in the Appendix). The east Asian area covers Taiwan and eastern China from the East China Sea to Sichuan Province (Prov.) and from north of Beijing to Guizhou Prov. (Wang and Mauriès 1996, Korsós 2004), with a disjunct fossil record in southern Mongolia. Distances between presently occupied areas are listed in Table 3.

Origin. Represented by Floridobolini, Spirobolidae arose in northern “proto-Mexico” (“northern Mexican Highlands” [Keeton 1960a]), after Euramerica merged with the “proto-South America” part of “Gondwana I” around 306 mya. Their geographically restricted distributions suggest that Allopocockiidae, Atopetholidae, Hoffmanobolidae, Messicobolidae, and Typhlobolellidae also originated there after this geologically dated event. We submit that this source area is plausibly the mountainous region of northern Mexico where Floridobolinae (Tylobolini) and Spirobolinae (Aztecolini) overlap (Fig. 12, 28, 32), which includes all of Aguascalientes and parts of Coahuila, Guanajuato, Jalisco, Nuevo León, San Luis Potosí, Tamaulipas, and Zacatecas states. Allowing a modicum of time for Floridobolini to evolve from ancestral spirobolidean stock, we arbitrarily estimate the age of the family and Floridobolinae/ini at ≤ 303 my.

Remarks. Though specialized in some ways, spirobolid posterior gonopod telopodites are simpler than those in other spirobolidean families, involving only a prefemoral process and a dominant acropodite, both varying in size, position, proportions, and configuration. Noting the family’s discontinuous distribution and restriction to temperate latitudes in a primarily tropical (sub)order, Keeton (1960a) concluded that it held relictual status and was unable to withstand competition from more advanced tropical families. This, however, is not the case; Spirobolidae and the families in the previous paragraph arose in the general northern Mexican source area where elements of each remain today.

Subfamily Floridobolinae Keeton, 1959, new status

Floridobolidae Keeton, 1959:1–2; 1960a:31(key); 1960b:137. Hoffman, 1980a:77; 1982:695; 1999:48. Deyrup, 1994:254. Shelley et al., 2000:20. Shelley, 2001a:243.

Type-genus. *Floridobolus* Causey, 1957.

Diagnosis. Body profile rounded/cylindrical or transversely ovoid (Fig. 33). Gnathochilarial mentum with or without apical, knob-like convexity. Paraprocts slightly re-entrant or not, without marginal rims, not overhung by epiproct. Anterior gonopod telopodites fused or articulating with coxae, apically uncinuate or not. Membrane caudal to appendages with or without sclerotized remnant of posterior gonopod sternum. Posterior gonopod coxal apodeme long/moderately long, oriented lengthwise in body. Telopodites with rounded apical lobes on short, thickened, expansions of caudal and/or anterior surfaces, with or without additional projections.

Description. Robust, rounded cylindrical/transversely ovoid, and glabrous/glossy Spirobolidae, narrowing and tapering caudad or on both ends. Apex of gnathochilarial mentum with or without elevated, knob-like convexity between lingual lamellae. Collum terminating above caudolateral corners of 2nd pleurotergite. 7th pleurotergites of males lengthened and expanded or not. Epiproct apically rounded, shorter than and not overhanging paraprocts; latter slightly re-entrant, with or without low marginal rims. Males with pregonopodal lobes on 2nd–5th or 3rd and 4th coxae. Anterior gonopod sternum narrow, expanding medially, with or without lobe, only slightly protruding between, and at most only barely separating, coxal endites (Fig. 6, 10). Membrane caudal to sternum with or without narrow, transverse, unattached sternal remnant. Coxal endites with or without distinct, prolonged medial lobes; telopodites fused with or articulating with coxae, with faint suture lines in former condition, distal extremities narrow, uncinuate or not, demarcated from midlengths to varying degrees. Posterior gonopod coxa curved caudad, apodeme moderately long to long, oriented generally lengthwise inside body; telopodite upright and sublinear or curved varyingly mediad/dorsomedial; prefemoral process varying from small, nubbin-like vestige to larger but inconspicuous structure; acropodite with either anterior or both anterior and caudal margins extending variably mediad, demarcating central depression or cavity in latter condition, distal surfaces of extended margins thickened and variably lobed, distal lobe prolonged and curved downward/dorsad in one genus.

Components. Two tribes: Floridobolini Keeton, 1959, and Tylobolini, Keeton, 1960.

Distribution (Fig. 12). Floridobolinae occupy six areas, two each in Florida, the western US and adjacent Mexico, and one each in central Mexico and Guatemala. Floridobolini occupy Florida, and areas in western North America, inhabited by Tylobolini, include the continuous familial region along the Pacific Coast with the eastward expansion into Utah/Arizona, the triangular region in southeastern Arizona, and the Guatemalan point locality. The subfamilial area in central Mexico differs from that of the family in being farther southward, extending from southern Durango, Coahuila, and Nuevo León to Guerrero (Chamberlin and Hoffman 1958; Keeton 1960a, 1966; Loomis 1968a; Hoffman 1980a, 1999; Shelley and Bauer 1997; Shelley 2002a, 2010; Shelley and Stevens 2003; Bueno-Villegas et al. 2004; Shelley and Golovatch 2011; plus additional localities in the Appendix).

Origin. As it contains the most plesiomorphic component, Floridobolinae originated simultaneously with the family, which we arbitrarily date at ≤ 303 mya.

Tribe Floridobolini Keeton, 1959, new status

Figures 1–5, 14–21, 33

Type- and only component genus. *Floridobolus* Causey, 1957.

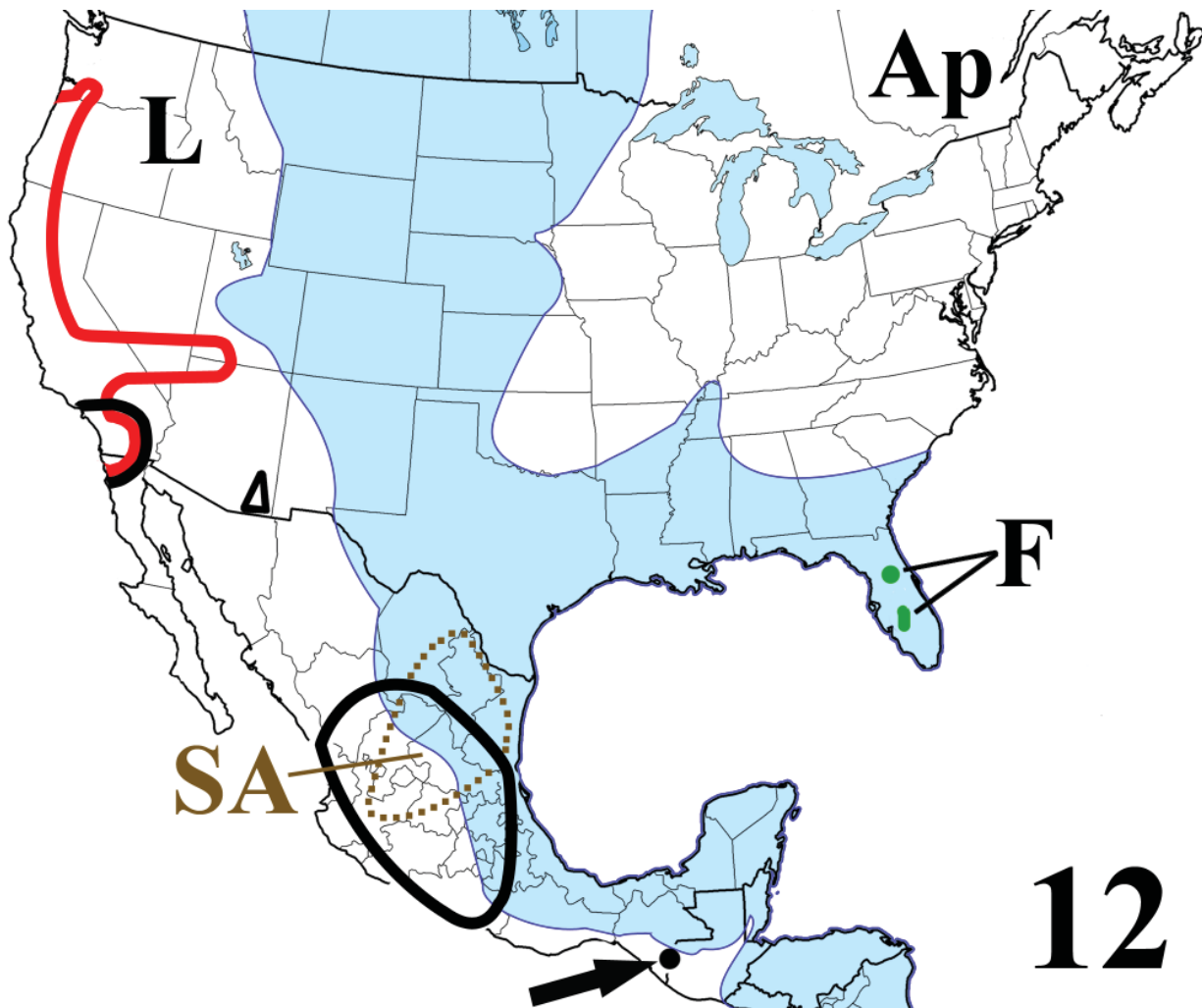


Figure 12. Distribution of Floridobolinae plotted against Cretaceous land patterns; submerged, marine Florida terrane and approximate maximal dimensions of the Western Interior Seaway in light blue. Ap, Appalachia. F, *Floridobolus/Floridobolini*. L, Laramidia. SA, Presumptive Source Area in the “northern Mexican Highlands.” Black lines and dot (delineated by the arrow), *Hiltonius/Tylobolini*. Red line, *Tylobolus/Tylobolini*. Green line and dot (in Florida), *Floridobolus/Floridobolini*. The area where Tylobolini/*Hiltonius* and *Aztecocolus* overlap constitutes the presumptive source area.

Diagnosis. With the characters of the subfamily.

Description. Robust, transversely ovoid (Fig. 33), and glabrous/glossy Spirobolidae with 47–50 pleurotergal rings, broadest around rings 12–13, narrowing and tapering at both ends, more so caudad. Apex of gnathochilarial mentum elevated into knob-like convexity between lingual lamellae. Mandibular stipes concave, rounded, and greatly expanded, with strong, elevated marginal rims forming shelves for antennae in resting positions. Collum terminating above caudolateral corners of 2nd pleurotergite, anterior margin slightly excavated below levels of ocelli, ridge pronounced (Fig. 1–2). 7th pleurotergites of males not lengthened or expanded, subsimilar to adjoining rings (Fig. 3–4). Epiproct broadly rounded apically, shorter than and not overhanging paraprocts; latter slightly re-entrant, without marginal rims (Fig. 5). Legs not extending beyond lateral pleuroteral margins, invisible in dorsal view (Fig. 3). Males with pregonopodal lobes on 3rd and 4th coxae only, former elongate dorsoventrally and with two closely appressed distal lobes extending to midlengths of 2nd podomeres and directed caudad, triangular in ventral aspect and situated *in situ* between 4th lobes, latter short, subtriangular in ventral aspect. Anterior gonopod sternum expanding mediad but without lobe and not protruding between coxal en-

Table 4. Anatomical comparisons of the species of *Floridobolus*.

<i>F. penneri</i> Causey, 1957	<i>F. orini</i> Shelley, 2014
2 nd pleurotergite extending slightly below ends of collum, margins lightly scalloped.	2 nd pleurotergite extending distinctly below ends of collum, margins lobe-like anteriorly with thickened rims.
Pro-, meso-, and metazona separated by depigmented lines.	Pro-, meso-, and metazona separated by faint grooves or sulci.
Pleurotergal striae strong and distinct, elevated and subcarinate ventrolaterad.	Pleurotergal striae faint, less elevated and carinate ventrolaterad.
Paraprocts marginally rugulose.	Paraprocts marginally smooth (Fig. 5).
Coxal endites of anterior gonopods distinctly separated (Fig. 14).	Coxal endites of anterior gonopods narrowly separated, virtually touching (Fig. 18).
Anterior gonopod telopodites directed ventromedial (Fig. 14).	Anterior gonopod telopodites directed ventrad (Fig. 18).
Telopodital apices flattened, blunt (Fig. 14).	Telopodital apices narrowly rounded (Fig. 18).
Telopodital apices shallowly and indistinctly demarcated from midlengths (Fig. 14).	Telopodital apices clearly and deeply demarcated from midlengths (Fig. 18).
Posterior gonopod leaning ventromedial <i>in situ</i> .	Posterior gonopod leaning medial <i>in situ</i> .
Bifurcate projection of anterior surface of posterior gonopod acropodite directed mediad, profile visible in caudal view (Fig. 15).	Bifurcate projection of anterior surface of posterior gonopod acropodite directed subcaudad, profile not visible in caudal view (Fig. 19).
Ventral branch of bifurcate projection rounded (Figs. 15, 17).	Ventral branch of bifurcate projection tapering distad, subtriangular (Fig. 21).
Dorsal branch of bifurcate projection apically prolonged (Fig. 17).	Dorsal branch of bifurcate projection rounded, with narrow marginal rim (Fig. 21).
Caudal surface of posterior gonopod acropodite with basal process on caudal surface (Fig. 16).	Caudal surface of posterior gonopod acropodite without basal process (Fig. 20).
Apical lobe of caudal surface of posterior gonopod acropodite directed ventromedial, obscuring distal extremity of anterior surface in caudal view (Fig. 15).	Apical lobe of caudal surface of posterior gonopod acropodite directed submedial, distal extremity of anterior surface visible in caudal view (Fig. 19).

dites, at most only barely separating latter (Fig. 14, 18); membrane caudal to sternum with narrow, unattached, transverse sternal remnant; coxal endites broad, margins lightly scalloped or curvilinear, medial corners not or only slightly extended; telopodites fused with coxae and with faint suture lines, distal extremities narrow, not uncinat, demarcated from midlengths to varying degrees (Fig. 14, 18). Posterior gonopod coxal apodeme long, oriented lengthwise and extending caudad internally up to level of 10th ring; telopodite subupright and post-like; prefemoral process small and inconspicuous, either a pyramidal, nubbin-like structure or minute enlargement of telopodital stem; anterior and caudal acropodital surfaces thickened and expanding mediad thereby demarcating narrow cavity or depressed area between them, apically lobed and rounded (Fig. 16, 20); strong bifurcate projection, with rounded ventral and stronger, more variable dorsal branches (Fig. 15, 17, 19, 21), arising distad from anterior surface; caudal surface with or without short, inconspicuous, closely appressed basal process with rounded apical and subapical lobes, latter directed submedial.

Distribution (Fig. 13). Endemic to a latitudinal distance of approximately 248 km (155 mi) in central peninsular Florida, where it is known from Marion and Polk/Highlands cos.

Origin. The oldest and most plesiomorphic clade, Floridobolini constitutes the original lineage of both Spirobolidae and Floridobolinae and its arbitrary date of origin is the same, ≤ 303 mya.

Remarks. Noting the lack of a clear articulation, Keeton (1959) originally thought that the anterior gonopod coxa and telopodite were fused without a remnant of their boundaries, but with a cleared gonopod, he later (Keeton 1960b) reported a faint suture line. Hoffman (1982) also observed that the podomeres are fused.

Genus *Floridobolus* Causey, 1957

Floridobolus Causey, 1957:206. Hoffman and Keeton, 1960:14. Jeekel, 1971:198. Hoffman, 1980a:77; 1999:48. Shelley et al., 2000:20. Shelley, 2001a:243.

Type-species. *F. penneri* Causey, 1957, by original designation.

Diagnosis. With the characters of the tribe (Fig. 1–5, 14–21, 33).

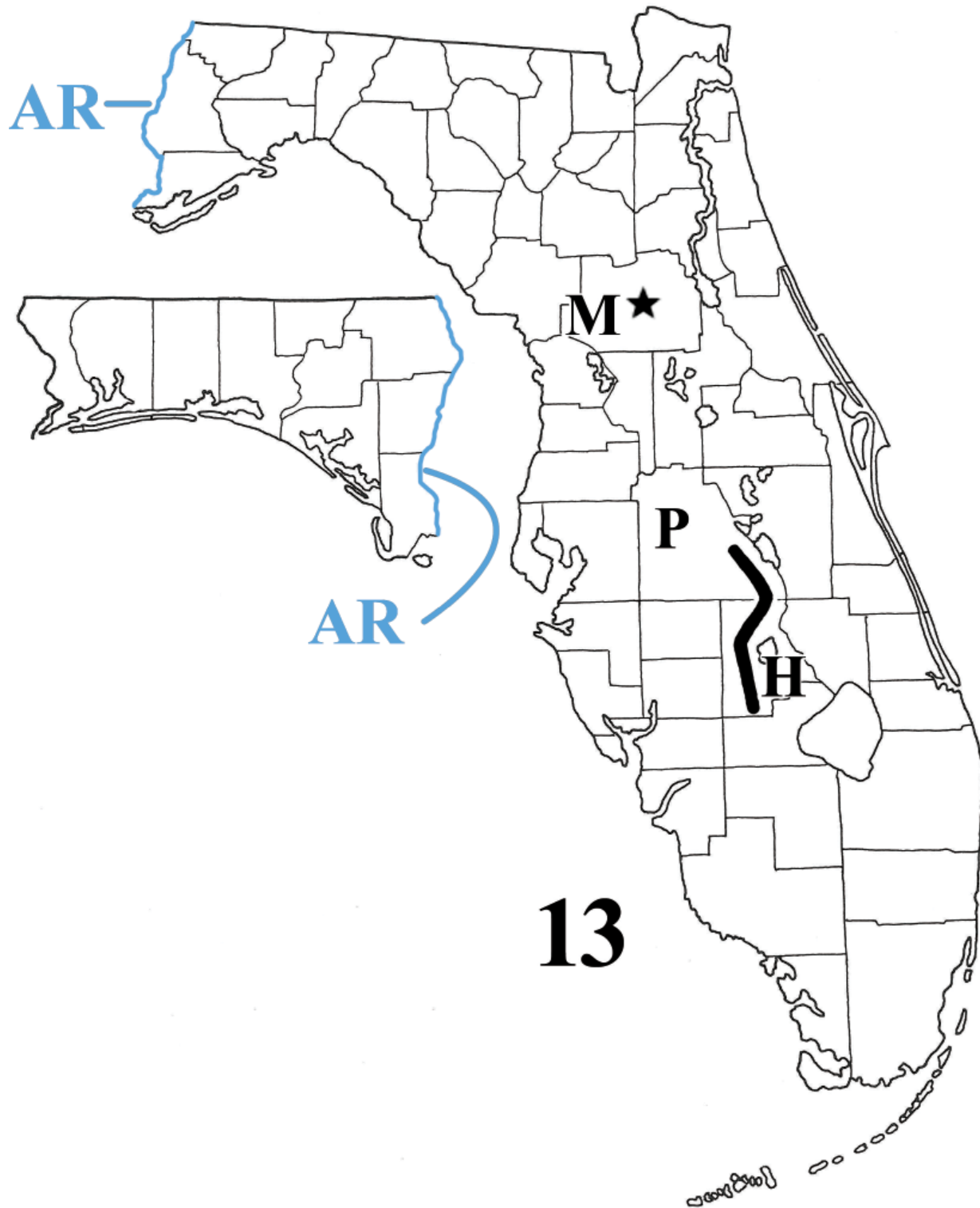


Figure 13. Distributions of Floridobolini and *Floridobolus*. Star, type locality of *F. orini*. Black line, known and projected distributions of *F. penneri* on the Lake Wales Ridge. AR, course of the Apalachicola River in Florida. H, Highlands Co. M, Marion Co. P, Polk Co.

Components. Two species, *F. penneri* Causey, 1957, and *F. orini*, n. sp., are known; undiscovered populations and undescribed species likely inhabit other sandy ridges and “Big Scrub” habitats in Florida.

Distribution (Fig. 13). Apparently restricted to the arid, sandy Central Highlands of Florida, *Floridobolus* is known only from the Lake Wales Ridge, Highlands and Polk cos., and the Ocala National Forest, some 208 km (130 mi) to the north in Marion Co.

Origin. As it exists today, *Floridobolus* could have evolved ~303 mya or anytime later up until 25 mya, the earliest date that Floridobolini could have invaded peninsular Florida. There is no reason to believe that this geographically restricted genus arose simultaneously with the family/subfamily/tribe or that no other floridobolinine genera ever existed, but no evidence exists suggesting otherwise. Therefore, we can only assume that *Floridobolus* arose simultaneously with the tribe/(sub)family and arbitrarily set its age at ≤ 303 my.

Remarks. *Narceus gordanus* and *Floridobolus* spp. are the only eastern spirobolids whose male 7th pleurotergites are not enlarged and whose bodies are not distorted in this region. Individuals of *Floridobolus* are also the only spirobolids whose bodies taper at both ends, are wider than high, and whose profiles are transversely ovoid (Fig. 33). All southeastern spirobolids coil rapidly, but *Floridobolus* is unusual in that individuals **rapidly uncoil**, particularly in comparison to sympatric *N. gordanus* and *C. spinigerus*. Perhaps this unusual ability is facilitated, or even enabled, by the somewhat “flattened” body form.

Floridobolus penneri and *F. orini* are similar anatomically, but only the former has the extraneous basal process, termed “lateral process” by Keeton (1960b), on the caudal surface of the posterior gonopod telopodite. This plus allopatry and the totality of small differences (Table 4) mandate specific recognition of the form in the Ocala National Forest.

Floridobolus penneri is commonly known as the “Florida Scrub Milliped” (Deyrup 1994) because it inhabits environments with low growing, shrubby plants in dry, sandy soil. With a second species now known, this environmental characteristic is properly attributable to the genus, and we recommend that *Floridobolus* be labeled the “Genus of Florida Scrub, Spirobolidan Millipeds.” More species likely occur in other patches of scrub habitat, the research topic of an RMS graduate student, but a chance discovery as with the holotype of *F. orini* seems unlikely. Nocturnal investigations and long-term pitfall trapping seem the best techniques for finding *Floridobolus*; the holotype and only specimen of *Arvechamboides ocala* Shelley, 2007 (Julida: Parajulidae), also endemic to scrub habitat in the Ocala National Forest, was discovered in a pitfall trap (Shelley 2007a, b).

***Floridobolus penneri* Causey, 1957**

Fig. 14–17, 33.

Floridobolus penneri Causey, 1957:206–207, fig. 1–3. Keeton, 1959:2–7, pl. 1, fig. 1–9, pl. 2, fig. 10–16; 1960b:137–139, fig. 8. Deyrup, 1994:254–256, unnumbered fig. Hoffman, 1999:48. Shelley, 2001a:243–244.

Type specimens. M Holotype (AMNH) collected by L.R. Penner, 8 August 1956, at the junction of Florida highway 70 and US highway 17 in Arcadia (16 km (10 mi) W of ABS and Lake Placid), Highlands Co., Florida; M Paratype (FSCA) taken by same collector at same locality on 19 July 1957. The reputed occurrence along US highway 70 (Causey 1957, Keeton 1959), which lies hundreds of miles to the north in North Carolina and runs west to Arizona, is obviously incorrect.

Diagnosis. Telopodite of anterior gonopod apically flattened and blunt, distal extremity directed ventromedial, coaxial with, and shallowly demarcated from, midlength. Caudal surface of posterior gonopod telopodite with extraneous, closely appressed, basal process.

Color in life. Uniformly slate gray (Deyrup 2012).

Holotype (adapted from Causey [1957] and Keeton [1959, 1960b]). Fragmented, about 92 mm long, maximum width 11.6 mm, maximum height 10.3 mm, W/L ratio 12.6%, depth/width ratio 88.8%; 49 rings.

Head smooth, glossy/glabrous, with only clypeal (6–6) and labral (9–9) setae. Epicranial suture strong, continuous through interantennal region with frontal suture and continuing to clypeus. Interantennal isthmus broad, 2.4 mm; antennae widely separated. Genae broadly rounded, without impressions, ends extending slightly beyond adjacent cranial margins; width across genal apices 3.6 mm. Antennae short and stout, extending backwards to midlength of collum; 2nd antennomere elongate, 3–6 clavate, 7 short and truncate, with four terminal sensory cones, no other sensory structures evident; relative lengths of antennomeres 2>3=4>1=5>6>7; 1–2 subglabrous, 3–4 with rows of hairs on dorsal surfaces, 5 with scattered hairs and long ones ventrad, 6 moderately pilose, 7 densely so. Around 63 ocelli arranged in sublinear, horizontal and vertical rows, forming irregularly rounded cluster directed ventrolaterad; vertical rows, medial to lateral, with 4, 7, 10, 10, 9, 9, 6, 5, and 3 ocelli.

Collum about 3x length of 2nd pleurotergite, narrowing ventrolaterad, slightly overhanging epicranium, anterior margin elevated into rim, demarcated by sharp groove. 2nd pleurotergite extending ventrolaterad below ends of collum, margin lightly scalloped; remaining pleuroterga subsimilar throughout body; prozona separated from mesozona by narrow lines, meso- and metazona separated by stronger ones. Ozopores strong, distinct, arising from mesozona just anterior to metazonal suture. Ventrolateral striae fewer on anterior segments but generally strong and distinct, becoming progressively more elevated and ridge-like/subcarinate ventrad, extending dorsad for around ¼ of pleurotergal circumferences.

Legs set close together with opposing coxae essentially touching; prefemora with small conical to rounded lobes, becoming progressively smaller and more rounded caudad. Postgonopodal legs subsimilar throughout body; coxae with slight lobes and a single ventral hair, becoming progressively smaller and more rounded caudad. Podomeres becoming progressively more hirsute distad with strong, stout, ventral setae; claws gently curved. Hypoproct glabrous, subtrapezoidal; distal margin linear, anterior corners prolonged laterad; paraprocts glabrous, slightly re-entrant and without rims, medial margins coriaceous to lightly rugulose.

Gonopod structure as follows (Fig. 14–17). Apices of anterior gonopod telopodites linear and blunt, directed ventromedial, weakly and shallowly demarcated from midlengths. Posterior gonopod leaning ventromedial *in situ*; prefemoral process (asterisk) an inconspicuous, nubbin-like structure; ventral branch of bifurcate projection (vb) from anterior acropodital surface (A) rounded and subupright, connecting through shallow indentation with stronger, broader dorsal branch (db), latter marginally sublinear with dorsal corner slightly prolonged; caudal acropodital surface (C) with apical lobe substantially broader than subapical, also with closely appressed, inconspicuous basal process extending medial beyond margin, corners slightly prolonged.

Female as characterized by Keeton (1959).

Variation. Without sexing them, Keeton (1960b) addressed variation among 25 adults from the ABS. Ring counts varied from 47–51, but 16 specimens possessed 48 rings and five had 49. Lengths varied from 60–92 mm and widths from 10.0–12.8 mm; labral setae varied from 13–24; and the number of ocelli per ocellarium ranged from 52–66. Though not specifically measured, the convexities on the gnathochilarial mentums seemed constant; however, the lobes on the ambulatory prefemora varied greatly and were often small and inconspicuous.

Ecology. According to Keeton (1959), topotypes collected in 1958 were found in a sandy locality with sparse palmetto vegetation. Being nocturnal, they actively crawled over the sand at nights but were inactive during days, resting under pieces of wood and old fence posts. The near topotypes he (Keeton 1960b) later received were found only in areas with woody plants, often fed on palmetto fruiting bodies, and were abundant under dead logs that were not deeply buried in sand, in contrast to *N. gordanus*, which was common in open areas. The latter made round tunnels and burrowed deeply into the sand, but *F. penneri* apparently did not do so. Deyrup (1994, 2012) observed that, in captivity, it fed on partly decomposed scrub oak leaves (*Quercus ?inopina*) and small twigs, refusing fresh leaves. Pitfall traps capture adults in the fall but rarely juveniles any time of year, suggesting that *F. penneri* may only be surface active during reproductive season.

Distribution (Fig. 13). Known only from the Lake Wales Ridge, Polk and Highlands cos. (Deyrup 1989, 1994, 2012; Hoffman 1999; Shelley 2001a), ranging from Lake Wales (city) to the vicinity of Venus, in southernmost Highlands Co. The species thus occupies a narrow, irregularly linear, “zigzagging” range that is roughly 91 km (57 mi) long and 16 km (10 mi) wide. Places where *F. penneri* has been taken include Camp Florida YMCA Camp on US hwy. 27 (now a housing development); Virginia Avenue in Highlands Park Estates; NE Lake Placid; and the ABS. In addition to the types, specimens were examined from the following two sites:

Florida: *Highlands Co.*, Hendry Ranch ENE Venus and US hwy. 27, M, 1 October 1987, M. Deyrup (NCSM); and Sebring, F, 10 June 1960, H. V. Weems, Jr. (FSCA).

Remarks. Keeton (1959) characterized the legs as “exceedingly short” and “hardly visible when the animal is walking.” As *Floridobolus*’ and *F. penneri*’s flattened, transversely ovoid profiles (Fig. 33) are wider than high, their bodies shield the legs in dorsal views (Fig. 3) and protect them from breakage in tight burrows; contrastingly, legs are partly visible from above in the rounded profiles of *Narceus* spp. Because juvenile ring counts correspond with those of adults, Keeton suggested that *F. penneri* rapidly attains the adult ring number then increases in size and sexual maturation in subsequent molts. Deyrup (2012) suggested that *F. penneri* matures slowly and recommended that it be considered a species of “conservation concern.”

***Floridobolus orini* Shelley, new species**

Figures 1–5, 18–21, 33

Type specimens. M holotype (NCSM) collected by S.D. Floyd and J.L. Jarzynka, 1 August 2012, ca. 13.8 km (8.6 mi) ESE Lynn and 19.2 km (12 mi) ESE Ocala, along USFS rd. 13 (SE 241st Ave., 1st road past USFS rd. 97), 6.0 km (3.7 mi) S FL hwy. 40 (29°07.380’N, 81°45.354’W), Ocala National Forest, Marion Co., Florida. 6M paratypes (3 each deposited in NCSM, FSCA) taken by S.D. Floyd, 29 July 2013, ca. 11.2 km (7.0 mi) NW of type locality, along USFS rd. 38 west of USFS 11 (labeled as USFS 76 and 88 [NE 231st Ave.], respectively, on Google and USFS maps), Ocala National Forest, Marion Co., Florida. A discrepancy exists between the road signs and the numbers cited on both the official USFS map and the Google maps website. The signs are in good condition; perhaps the roads have been renumbered and the maps have not been updated.

Diagnosis. Telopodite of anterior gonopod narrowly rounded apically, distal extremity directed ventrad, not coaxial with, and deeply demarcated from, midlength. Caudal surface of posterior gonopod acropodite without extraneous basal process.

Color in life (Fig. 1–5). Body mostly gray to dark grayish olive; anterior margin of collum and pleurotergal fringes near legs dark yellowish, latter becoming wider caudad. Epiproct, paraprocts, and hypoproct gray blending into dark yellowish margins. Head dark grayish brown blending into brown on frons with lighter clypeal fringe. Prozona gray to yellowish.

Holotype. Length 72.5 mm; maximum width 9.7 mm, height 5.9 mm, W/L ratio 13.4%, depth/width ratio 60.8%, 48 rings.

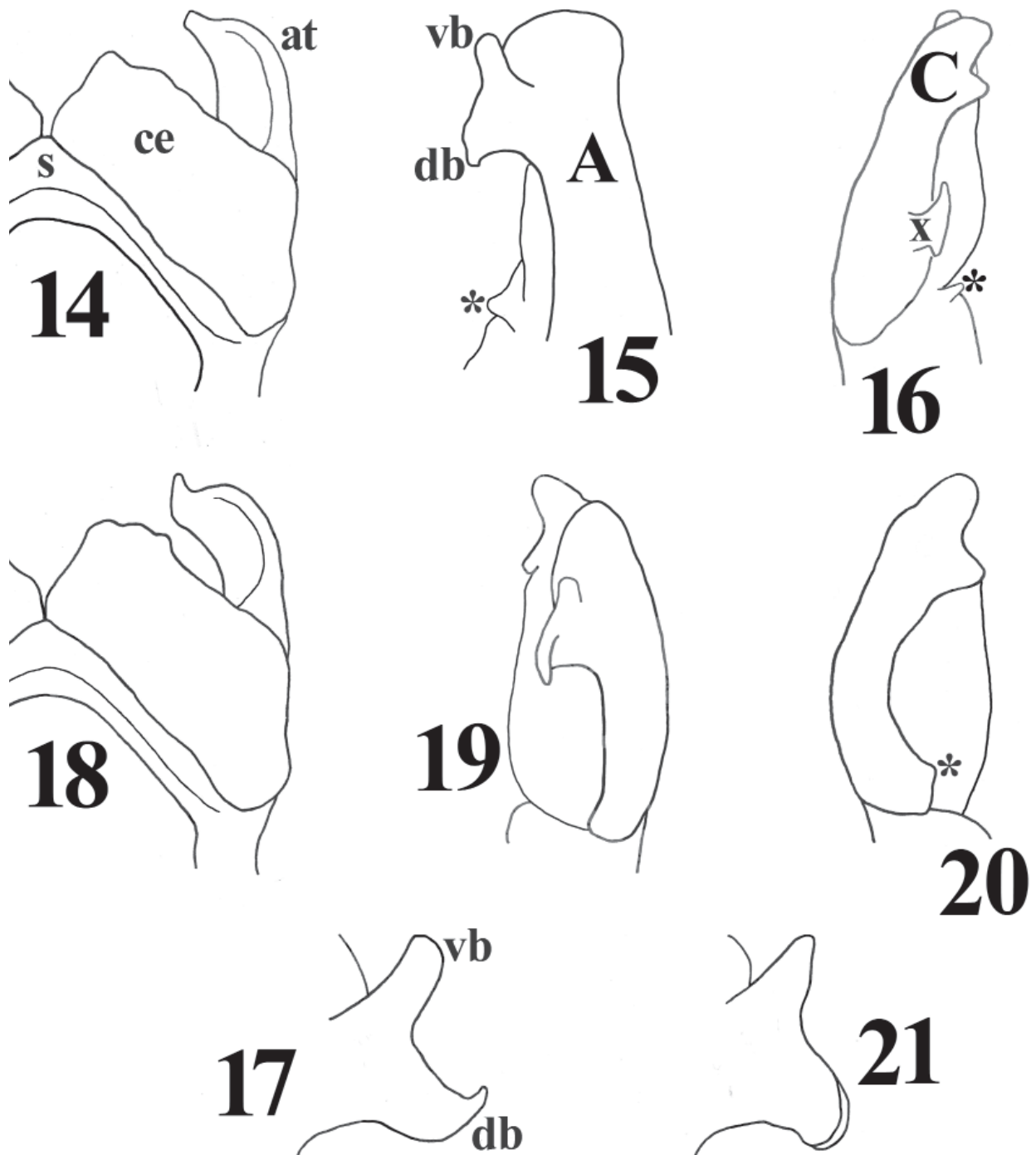
Somatic features agreeing closely with those of *F. penneri* with following exceptions:

Clypeal setae 4–4, labral 10–10, merging with clypeal series and continuing for short distances along genal margins.

Margins of 2nd pleurotergite rounded and lobe-like anteriorly with thickened rims (Fig. 2); meso- and metazona of remaining pleuroterga separated by faint grooves or sulci but not by clear, distinct lines; striae fainter, less elevated and ridge-like. Paraprocts smooth, margins not rugulose (Fig. 5).

1st and 2nd legs short and markedly crassate. Coxal lobes as in *F. penneri*.

Gonopod structure as follows (Fig. 18–21). Apices of anterior gonopod telopodites narrowly rounded, curved and directed ventrad, clearly demarcated from midlengths. Posterior gonopod leaning medially *in situ*; prefemoral process a short, stubby, basal enlargement of telopodital stem; ventral branch of



Figures 14–21. *Floridobolus* spp., gonopodal features. 14–17) *F. penneri* holotype. 14) Left anterior gonopod, anterior view. 15) Telopodite of left posterior gonopod, anterior view. 16) The same, caudal view. 17) Bifurcate projection of anterior surface of the same, anteriomedial view. 18–21) *F. orini* holotype. 18) left anterior gonopod, anterior view. 19) Telopodite of left posterior gonopod, anterior view. 20) The same, caudal view. 21) Bifurcate projection of anterior surface of the same, anteriomedial view. A and C, anterior and caudal surfaces, respectively, of posterior gonopod acropodite. at, anterior gonopod telopodite. ce, coxal endite. db, dorsal branch of bifurcate projection. s, sternum. vb, ventral branch of bifurcate projection. asterisk (*), prefemoral process. x, extraneous basal process.

bifurcate projection of anterior acropodital surface subtriangular, dorsal branch rounded and angling dorsad, with narrow marginal rim; caudal acropodital surface without basal process, subapical lobe narrowly rounded, extending beyond level of apical lobe.

Female unknown.

Paratypes. The paratypes agree closely with the holotype in somatic features and in the coxal lobes. Lengths range from 68.7–80.4 mm; maximal widths, caudal to midlengths, vary from 10.8–12.6 mm; W/L ratios range from 13.9–17.2%, and ring numbers, including the collum and epiproct, vary from 47–50, with an average of 47.8. The apices of the anterior gonopod telopodites can be slightly longer, shorter, broader, narrower, and more acuminate than the condition in the holotype. Branch proportions of the bifurcate projection of the anterior surface of the posterior gonopod acropodite vary, and the anterior branch is prolonged in two individuals.

Ecology (Fig. 22–26). The holotype was coiled under decaying sand pine (*Pinus clausa*) boards about 15 ft. from a dirt road in late afternoon in xeric “Big Scrub” habitat at an elevation of approximately 28 m (93 ft) (Fig. 22–23). The site, ca. 208 km (130 mi) to the north of *F. penneri*, appeared to have once been logged to restore habitat for the endangered Florida Scrub Jay (*Aphelocoma coerulescens*). Moisture remained from precipitation the previous day, which may have facilitated the discovery because the well drained, loose, sandy soil (Fig. 22) dries quickly and likely forces millipeds underground for extended periods of time. Predominant vegetation included three species of small, evergreen, shrubby oaks (Fig. 23) – myrtle oak (*Quercus myrtifolia*), Chapman’s scrub oak (*Quercus chapmanii*), and sand live oak (*Quercus geminata*) – interspersed with scrub palmettos (*Sabal etonia*) (Fig. 22–24), prickly pear cacti (*Opuntia humifusa ammophila*) (Fig. 22, 24–26), and scrub wild olives (*Cartrema floridana*). Younger sand pines were evenly scattered through the area with Florida rosemary (*Ceratiola ericoides*) in open spots. The roadside was bordered for most of its length with perennial dog fennel (*Eupatorium capillifolium*) to a width of around 3 m (10 ft). An expansive forest of mature sand pines (Fig. 26) with an understory of small endemic shrubs surrounded the more open spot where *F. orini* was discovered. The milliped is primarily nocturnal or crepuscular because daytime surface activity would render it vulnerable to desiccation. SDF has visited the type locality frequently over four years and found only *N. gordanus* until the serendipitous discovery of *F. orini*.

SDF surveyed spiroidolids on 9 July 2013 from 9:00 pm - 3:30 am along a three mile section of dirt road and recovered 38 individuals of *F. orini*, six designated paratypes. The area had received heavy precipitation two hours earlier, which likely induced millipeds to leave their burrows and wander; 33 individuals were walking on a dirt road, and five were less than 100 yards off it. The first individual was encountered at 10:45 pm, but the majority emerged a couple of hours later with peak activity being around 2:00 am when the ambient temperature dropped to 76°F. While mating and feeding were not observed, all individuals were actively moving on the sandy substrate; none were climbing in vegetation as often occurs with *C. spinigerus*. SDF searched for *F. orini* up to 16 km (10 mi) away but only *N. gordanus*, absent from the area where *F. orini* was found, was observed crossing roads. *Floridobolus orini* appears to prefer higher sandy elevations that lack the leafy detritus favored by *N. gordanus*, whose southern, Lake Wales Ridge population (Keeton 1960a) prefers sandy areas with little or no humus and leaf-mold, a different biotope from that of *F. penneri*. Individuals of *N. gordanus* burrow deeply into sand during day, forming round holes easily located by observers, and emerge at night to feed on rotting logs, the most ready source of food. *Floridobolus orini* may occupy a subsurface habitat and occur throughout sandy, “Big Scrub” habitat in the Ocala National Forest, which extends, east-west, from western Marion to western Volusia cos.; a graduate student is detailing its range.

Distribution (Fig. 13). Known only from the type and paratype localities, which are around 11.2 km (7 mi) apart in the Ocala National Forest, Marion Co., Florida.

Etymology. We are pleased to name this species for Orin McMonigle, who recognized the holotype as a form of *Floridobolus*, sent it to RMS, and agreed to its placement in the NCSM invertebrate primary type collection.



Figures 22–26. “Big Scrub” habitat at the type locality of *F. orini*. **22)** Sand Pine (*Pinus clausa*) boards that sheltered the holotype near the base of a scrub palmetto (*Sabal etonia*). **23)** Broad environmental view with young *Pinus clausa* beyond the boards. **24)** Lightly moist, porous sandy substrate, potential refuge for both *F. orini* and *N. gordanus*, beneath partly decayed *Pinus clausa* boards near base of *Sabal etonia*. **25)** Prickly pear cactus (*Opuntia humifusa*). **26)** Xeric *Pinus clausa* forest adjacent to more open scrub habitat where *F. orini* was discovered.

Remarks. Anatomical differences between the congeners are detailed in Table 4.

Tribe Tylobolini Keeton, 1960a, new status

Tylobolinae Keeton, 1960a:96–97. Buckett, 1964:23. Hoffman, 1980a:77; 1999:41. Kevan, 1983:2962. Shelley et al., 2000:23. Shelley, 2002a:98.

Type-genus. *Tylobolus* Cook, 1904.

Diagnosis. Rounded/cylindrical (Fig. 33), glabrous/glossy Spirobolidae, body tapering only at caudal end. Gnathochilarial mentum without convexity. 7th pleurotergites of males lengthened and/or expanded, noticeably distorting body to accommodate gonopods. Epiproct apically narrow, slightly produced but never completely obscuring paraprocts dorsally; latter with or without marginal rims, slightly re-entrant or not. Legs at most extending only slightly beyond lateral pleuroteral margins, partly visible in dorsal view. Males with pregonopodal lobes on 3rd, 4th, and 5th coxae. Anterior gonopod sternum widening mediad but without distinct lobes, only slightly separating coxal endites. Latter broad, margins curvilinear, medial corners usually noticeably extended or narrowed; telopodites apically uncinatate or not. Posterior gonopod coxal apodeme usually prolonged. Telopodite varying from subupright to leaning mediad or curving strongly dorsad and imparting uncinatate appearance to structure. Prefemoral process varying from a small lobe to slightly elongate. Anterior acropodital surface variably thickened and without processes, expanding into either two highly variable lobes or one lobe prolonged apically and strongly decurved. Caudal acropodital surface not extended.

Components. Two extant genera – *Tylobolus* Cook, 1904, and *Hiltonius* Chamberlin, 1918 – to which we add the Mongolian Cretaceous fossil genus, *Gobiulus* Dzik, 1975.

Distribution (Fig. 12). Extant forms occupy the four subfamilial regions in the western US, Mexico, and Guatemala, a latitudinal distance of approximately 4,272 km (2,670 mi) that extends from north of the Columbia River in Washington state, USA, to the western periphery of Guatemala. Apparent tylobolinine fossils have been discovered in southern Mongolia, Asia, where living representatives have never been encountered.

Origin. The differences between Tylobolini and Floridobolini, losses of the posterior gonopod sternal remnant and the extension of the caudal acropodital surface, are minor in comparison to those between Tylobolini and Spirobolinae and likely evolved rapidly. Tylobolini is thus the second clade to evolve/disperse, and we arbitrarily date its origin at ≤ 301 mya.

Remarks. Keeton (1960a) believed that Tylobolini (then Tylobolinae) probably arose from early spiroboline stock and considered *Hiltonius* the more “primitive” genus and the direct ancestor of *Tylobolus*. From the knowledge available then, these are remarkably prescient insights; we concur with both, although Tylobolini actually derived from floridoboline stock.

Gonopodally similar to Floridobolini, as evidenced by the acropodital lobe resemblances between *H. carpinus* and *Floridobolus* spp., Tylobolini have autapomorphically lost the extension of the caudal acropodital surface. In several respects, Tylobolini are intermediate, and bridge anatomical gaps, between Floridobolini and Spirobolinae. On the anterior gonopods, Floridobolini lack the medial sternal lobe and exhibit non-uncinatate telopodites whereas all spirobolines possess both the lobe and uncinatate telopodites; tylobolinines display both conditions in both structures. Tylobolinines display both long and short posterior gonopod apodemes, intermediate between the long ones of Floridobolini and the exclusively short ones of Spirobolinae. Tylobolinine prefemoral processes are intermediate in size between the nubbin-like ones in Floridobolini and the large structures in Spirobolinae. Additionally, the paraprocts in Floridobolini are slightly re-entrant whereas those in Spirobolinae possess distinct rims and lips; again, tylobolinines exhibit both conditions. Thus Tylobolini link these somatically and gonopodally dissimilar taxa, thereby substantiating confamilial status for Floridobolini/*Floridobolus*.

The latter are clearly related to Tylobolini, unequivocal spirobolids, so Floridobolini/*Floridobolus* must also belong to this taxon and not a separate, monotypic family.

Genus *Hiltonius* Chamberlin, 1918

Julus (*Julus*) (not Linnaeus) in part: Saussure, 1859:329; 1860:96.

Spirobolus (not Brandt) in part: Saussure and Humbert, 1872:74–75, 175.

Hiltonius Chamberlin, 1918b:166; 1943b:21; 1949:166. Loomis and Hoffman, 1951:51. Chamberlin and Hoffman, 1958:163. Hoffman and Keeton, 1960:15. Keeton, 1960a:97–99. Buckett, 1964:23. Loomis, 1966:25; 1968a:92; 1968b:392. Jeekel, 1971:199. Hoffman, 1980a:77; 1998b:64; 1999:41. Shelley, 2002a:98.

Type-species. *H. pulchrus* Chamberlin, 1918, by original designation.

Diagnosis. Generally stout, robust Tylobolini; paraprocts usually slightly re-entrant, with or without marginal rims. Posterior gonopod acropodite usually with two variably distinct distal lobes, only slightly prolonged if any, not curving strongly dorsad or decurved and not imparting uncinat appearance to overall appendage.

Components. Ten nominal species, both extant and fossilized; one species is divided into two subspecies: *H. mexicanus* (Saussure, 1859); *H. hebes* (Bollman, 1887); *H. reptans* (Porat, 1888); *H. australis* (Grinnell, 1908); *H. fossulifer* (Pocock, 1908); *H. pulchrus* Chamberlin, 1918; *H. mimus* Chamberlin, 1941; *H. erythropygus* Chamberlin, 1943; *H. carpinus carpinus* Chamberlin, 1943, and *H. c. vulcan* (Chamberlin, 1952); and *H. flavocinctus* Loomis, 1968 (Keeton 1960a; Hoffman 1999; Shelley 2002a, 2010).

Distribution (Fig. 12, black lines). Four segregated areas: southern California and adjacent Baja California Norte; southeastern Arizona; from southern Durango, Coahuila, and Nuevo León to Guerrero, Mexico; and the Guatamalan point locality. The distributions of *Hiltonius* and *H. pulchrus* extend from Ft. Tejon and the Santa Monica Mountains, Kern/Los Angeles cos., in northern metropolitan Los Angeles, to northern Baja California Norte and eastward to the vicinities of San Bernardino and Riverside.

Origin. Since *H. carpinus* occurs in southeastern Arizona, Guatemala, and the presumptive, central Mexican, familial source area, we believe it is the original, ancestral tyloboline and arose ≤ 301 mya.

Remarks. While *Hiltonius* was dispersing to California and Guatemala, divergences and evolution continued in the source area and Floridobolini were spreading northeastward.

Genus *Tylobolus* Cook, 1904

Spirobolus (not Brandt): Wood, 1867:129.

Tylobolus Cook, 1904:65. Brölemann, 1914:22, 32. Chamberlin, 1949:166–168. Chamberlin and Hoffman, 1958:168. Hoffman and Keeton, 1960:24. Keeton, 1960a:114–121. Buckett, 1964:23. Loomis, 1968a:93. Jeekel, 1971:208. Hoffman, 1980a:77; 1999:44–45. Kevan, 1983:2962. Shelley et al., 2000:23. Shelley, 2002a:98.

Californibolus Verhoeff, 1944:55. Chamberlin, 1949:165. Causey, 1955a:78. Chamberlin and Hoffman, 1958:161. Hoffman and Keeton, 1960:10. Jeekel, 1971:195.

Auxobolus Chamberlin, 1949:163. Chamberlin and Hoffman, 1958:160. Hoffman and Keeton, 1960:9. Jeekel, 1971:194.

Type-species. Of *Tylobolus*, *T. deses* Cook, 1904, by original designation; of *Californibolus*, *C. michelbacheri* Verhoeff, 1937, by monotypy; of *Auxobolus*, *A. ergus* Chamberlin, 1949, by original designation.

Diagnosis. Generally longer and more slender Tylobolini; paraprocts not or only slightly re-entrant, usually without marginal rims. Posterior gonopod acropodites with only one distal lobe, prolonged apically to varying degrees, usually curving strongly dorsad and imparting uncinat appearance to overall appendage.

Components. Eight nominal species, one divided into two subspecies: *T. uncigerus* (Wood, 1864); *T. deses deses* Cook, 1904, and *T. d. magnificus* Buckett and Gardner, 1966; *T. castaneus* Chamberlin, 1918; *T. claremontus* Chamberlin, 1918; *T. utahensis* Chamberlin, 1925; *T. viduus* Chamberlin, 1940; *T. monachus* (Chamberlin, 1949); *T. loomisi* Keeton, 1966 (Keeton 1960a, 1966; Shelley and Bauer 1997; Hoffman 1999; Shelley 2002a, 2010). In their treatment, Shelley and Bauer (1997) did not consider *T. fredricksoni* Causey, 1955, ostensibly from Lawrence, Douglas Co., Kansas, to be a valid species.

Distribution (Fig. 12, red line). The large, continuous tribal and familial areas along the Pacific Coast west of the crest of the Sierra Nevada and Cascade mountains, including the eastward extension to Utah and Arizona. The range completely overlies the small Pacific Coastal area of *Hiltonius*.

Origin. We concur with Keeton (1960a) that *Tylobolus* arose directly from *Hiltonius*, probably in the range overlap area in southern California, and arbitrarily date its origin at ≤ 297 mya.

Genus *Gobiulus* Dzik, 1975

Gobiulus Dzik, 1975:17.

Type- and only component species. *G. sabulosus* Dzik, 1975, by original designation.

Diagnosis. Body with 40 rings including collum and epiproct. Hypostome and gula large, covering part of mentum. Ocellaria widely separated, containing around 30 ocelli. 2nd pleurotergite extending below level of collum. Striae ventrolateral only. Paraprocts slightly re-entrant, without rims.

Distribution. Mongolia, Ömnögovı Prov., Gobi Desert.

Origin. The strata harboring these fossils derive from the late-Cretaceous Period, Mesozoic Era. They are thought to be from the Middle Campanian Stage, dating to 77 mya (Shear et al. 2009).

Remarks. Thirteen specimens of *G. sabulosus* were retrieved plus one with a less deeply incised and more rounded frontoclypeal region that Dzik (1975) thought might represent a second species but did not name. The head of the holotype (Dzik 1975, fig. 1b) clearly shows the frontal groove that is indistinct in the unnamed specimen, so we agree that Spirobolida is the correct order (Shear et al. 2009, Shear and Edgecombe 2010). Primarily from the shape of the mentum and sterna, Dzik allied *Gobiulus* with Rhinocricidae and Atopetholidae but then excluded the former because of the absence of protergal scobinae. However, scobinae, if present, would normally be overhung by the caudal edges of the preceding metaterga, probably fossilize poorly if at all, and some rhinocricids lack them, so this perceived absence in a juliformian fossil is not diagnostic. Dzik also thought that the indistinct tergal divisions eliminated *Gobiulus* from Atopetholidae, and he excluded Spirobolidae because of the shape of the mentum and the triangular mandibular stipes. He tentatively assigned *Gobiulus* to the exclusively North American/Mexican Atopetholidae, whose distribution he incorrectly reported as including Asia and North and South Africa (Chamberlin and Hoffman 1958; Hoffman and Orcutt 1960; Loomis 1968a; Hoffman 1980a, 1998b, 1999; Bueno-Villegas et al. 2004; Shear et al. 2009; Shear and Edgecombe 2010; Shelley and Golovatch 2011). From the published illustrations of *Gobiulus*, we note the slightly re-entrant paraprocts that lack rims (Dzik 1975, fig. 5a-c), which are consistent with both Atopetholidae and Tylobolini (Table 2, row 5; Keeton 1960a, pl. 3, fig. 21; Hoffman and Orcutt 1960); spiroboline paraprocts clearly possess rims and are not re-entrant. Additionally, the widely separated ocellaria, which lie dorsal to the antennal sockets and do not extend mediad, are also consistent with Tylobolini (Dzik 1975, fig. 1b,

6b; Keeton 1960a, pl. 1, fig. 6, pl. 2, fig. 11, 13); spiroboline ocellaria always extend mediad toward the epicranial suture and are closer together. With these anatomical similarities, we believe that *Gobiulus* is assignable to Spirobolidae/Floridobolinae/Tylobolini; Dzik's illustrations lack scale lines, but the individuals appear juvenile to us. We would never base a formal nomenclatural change of fossils solely on illustrations because rarely can associations of impression fossils with modern genera be certain, but we nevertheless think *Gobiulus* may be a synonym of *Tylobolus*, which the fossils resemble more closely than *Hiltonius*. Admittedly, our statements contain a degree of conjecture, but we do confirm Dzik's perception of affinity to North American rather than Asian spirobolidans, and the fossils are consistent with our concept of Spirobolidae. For the aforementioned reasons, we do not see Spirobolinae in Dzik's figures; *Gobiulus* seems to represent a rare tylobolinine that dispersed onto the Asian part of "Asiamerica" in the Cretaceous, became fossilized, and was transported to Mongolia. *Gobiulus* seems to support our spirobolid, "Asiamerica" hypothesis, which also applies to other North American taxa.

Subfamily Spirobolinae Bollman, 1893

Spirobolinae Bollman, 1893:156. Jeekel, 1971:210 (list). Kevan, 1983:2962.

Type-genus. *Spirobolus* Brandt, 1833.

Diagnosis. Body form rounded/cylindrical (Fig. 33). Anterior gonopod sternum with variably broad medial lobe substantially separating coxal endites; telopodites apically uncinat. Posterior gonopod telopodite with variably long, lobate prefemoral process overhung and enveloped to varying degrees by acropodite. Latter thin and laminate, variably cupulate with cavity/depression of varying depth; either short and marginally irregular with indentations, lobes, and spiniform projections, or long with smoothly curvilinear margins.



Figure 27. Distribution of Spirobolinae.

Components. Two tribes: Spirobolini Bollman, 1893, and **Aztecolini, new tribe.**

Distribution (Fig. 27). Four regions including the entire familial areas in Asia and eastern North America along with the point locality in Minnesota. Spirobolinae occur syntopically with Floridobolinae/Floridobolini in their Floridian locations and while absent from western North America and Guatemala, they partly overlap Floridobolinae/Tylobolini in central Mexico, occurring from northern Nuevo León to central Jalisco and northern Guanajuato (Fig. 28). The distance between Taiwan and Jalisco, the closest New World locality, is approximately 13,315 km (8,322 mi), one of the greatest subfamilial lacunas in the Diplopoda. Distances between areas in Mexico and the US are as cited in Table 3.

Origin. Substantial evolutionary changes had to take place for Floridobolinae/Tylobolini/*Hiltonius* to evolve into Spirobolinae/Aztecolini/*Aztecobolus*, so this divergence logically took longer than that which yielded Tylobolini. We arbitrarily allow 5 my for these changes and assign an age of ≤ 296 my to Spirobolinae, which likely evolved in Mexico before *Tylobolus* arose in California and perhaps before *Hiltonius* even reached this state.

Aztecolini Shelley, new tribe

Type-genus. *Aztecolus* Chamberlin, 1943.

Diagnostis. Posterior gonopod telopodite subupright or leaning slightly mediad. Prefemoral process with vaguely subtriangular basal part and longer, variably dactyliform distal part, positioned entirely outside of cupulate acropodite. Latter with shallow central cavity/depression, overhanging but not enveloping prefemoral process, either narrowing abruptly distad with terminal spiniform or bifurcate projection or anterior margin deeply incised distad with adjacent spiniform projection.

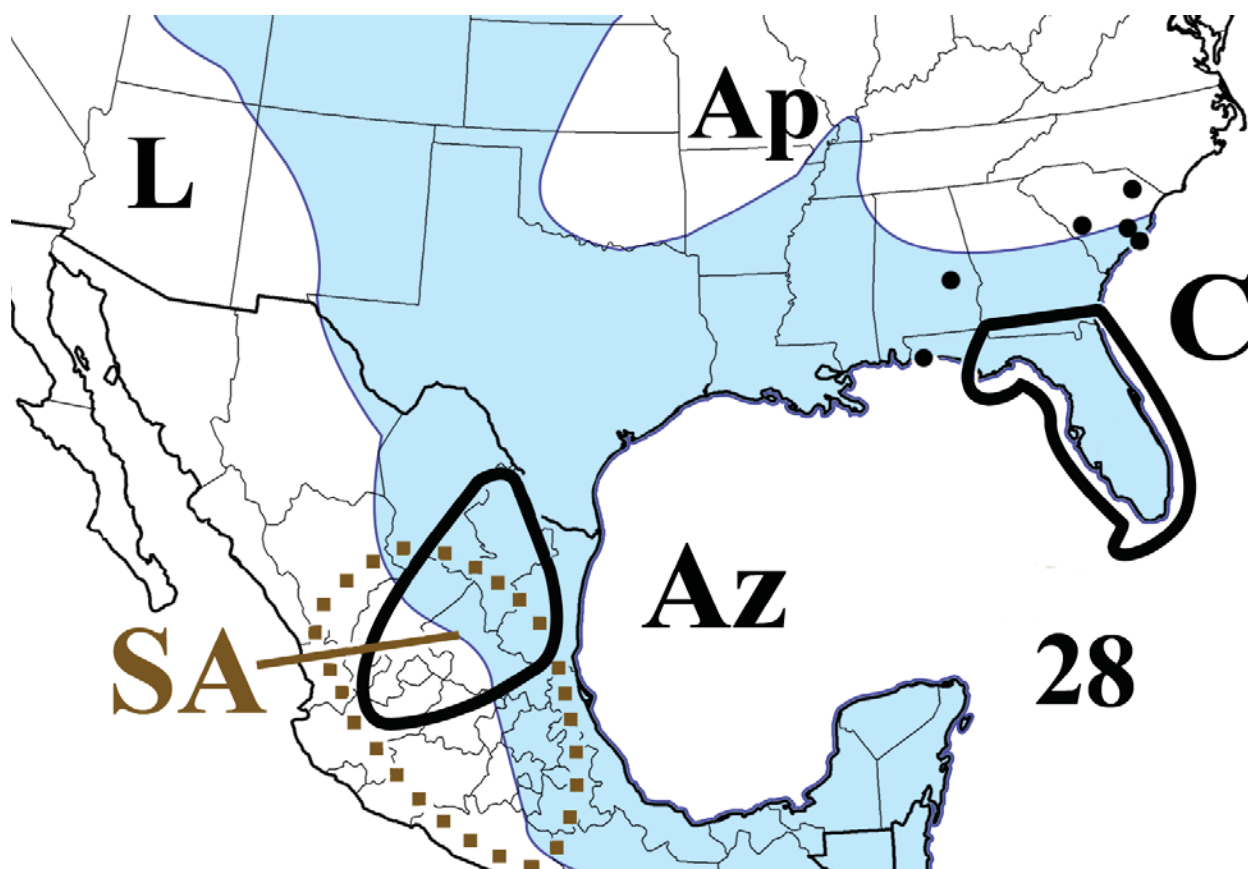


Figure 28. Distribution of Aztecolini plotted against Cretaceous land patterns; submerged, marine Florida terrane and approximate maximal dimensions of the Western Interior Seaway in light blue. Ap, Appalachia. AZ, *Aztecolus*. C, *Chicobolus*. L, Laramidia. SA, Presumptive Source Area in the “northern Mexican Highlands.” The area encircled with brown squares is that of Tylobolini/*Hiltonius*/*H. carpinus*; the area where *Aztecolus* and Tylobolini/*Hiltonius* overlap is plausibly the source area.

Components. Two genera: *Aztecolus* Chamberlin, 1943, and *Chicobolus* Chamberlin, 1947.

Distribution (Fig. 28). A divided taxon, Aztecolini inhabit two areas that span the Gulf of Mexico and are some 1,328 km (830 mi) apart. The eastern, in the southeastern US and occupied by *Chicobolus*, extends from Florence Co., South Carolina, to the south Florida Keys and westward to Pensacola, Escambia Co., Florida; the western, in northeastern/central Mexico and occupied by *Aztecolus*, extends from northern Nuevo León to central Jalisco and San Luis Potosí. We think the gap between the areas is larger than apparent because that in the US is probably shrinking, with *Chicobolus* being displaced by *Narceus*. *Chicobolus*' primary area (Fig. 28, black line) encircles the southern periphery of Georgia and the peninsula, Keys, and eastern Florida panhandle (westward to the Apalachicola River,

Fig. 13, AR). A smaller extant population, centering on the Francis Marion National Forest, inhabits Berkeley and Charleston cos., in coastal South Carolina. Other records, however, represent single samples; that from Alabama dates from 1898 and that from western Florida/Pensacola was taken by C.H. Bollman, who died in 1889. RMS and other collectors have investigated both areas in the past century without encountering *Chicobolus*, so these populations may already be extinct. If not, *Chicobolus* and *C. spinigerus* will soon be reduced to two populations, a small one in coastal South Carolina and a larger one from southern Georgia southward. The distance between the Mexican tribal area and that in peninsular Florida is about 1,475 km (922 mi).

Origin. As Aztecolini has remained in the presumptive northern Mexican source area, we conclude that it arose simultaneously with Spirobolinae, ≤ 296 mya, and before Spirobolini.

Remarks. Aztecolini can be considered incompletely developed Spirobolini, as their telopodites represent intermediate conditions that diverged during evolution of Spirobolini.

Genus *Aztecolus* Chamberlin, 1943

Aztecolus Chamberlin, 1943b:28. Hoffman and Keeton, 1960:9. Keeton, 1960a:33–35. Loomis, 1968a:92; 1968b:391. Jeekel, 1971:194. Hoffman, 1980a:76; 1999:37.

Type-species. *Spirobolus nigrior* Chamberlin, 1941, by original designation.

Diagnosis. Posterior gonopod telopodite subupright. Prefemoral process relatively long, extending beyond level of acropodital midlength. Anterior acropodital margin narrowing abruptly distad, terminating in spiniform or bifurcate projection.

Components. Three nominal species: *A. nigrior* (Chamberlin, 1941); *A. pabliko* Chamberlin, 1947; and *A. productus* Loomis, 1968 (Keeton 1960a, Hoffman 1999, Bueno-Villegas et al. 2004).

Distribution (Fig. 28, letter A). *Aztecolus* inhabits the Mexican tribal area where it is partly sympatric with Floridobolinae/Tylobolini/*Hiltonius/H. carpinus*. Aside from the minor overlap of Spirobolinae and Floridobolinae in Florida, this is the only region where the two subfamilies are sympatric. We believe they overlapped along the Pacific Coast of North America during the early Cretaceous, but only Floridobolinae/Tylobolini occur there today. Maximal dimensions of the area of *Aztecolus* are roughly 752 km (470 mi) north-south and 491 km (307 mi) east-west. The northernmost locality (Nuevo León, Cañon de las Anahuac) is only ~115 km (72 mi) south of the Rio Grande and Laredo, Webb Co., Texas, so Aztecolini/*Aztecolus* may inhabit this region of southernmost Texas, USA.

Origin. Occurring in the subfamilial and tribal source area, *Aztecolus* is the same age as these taxa, ≤ 296 my.

Genus *Chicobolus* Chamberlin, 1947

Chicobolus Chamberlin, 1947:46. Causey, 1955a:75–76. Chamberlin and Hoffman, 1958:162. Hoffman and Keeton, 1960:11. Keeton, 1960a:39–40. Jeekel, 1971:195. Hoffman, 1980a:76; 1999:37. Shelley, 2001a:244.

Incobolus Chamberlin, 1955:7. Hoffman and Keeton, 1960:15. Jeekel, 1971:199.

Type-species. Of *Chicobolus*, *C. pilsbryi* Chamberlin, 1947, by original designation; of *Incobolus*, *I. thaumastus* Chamberlin, 1955, by original designation.

Diagnosis. Posterior gonopod telopodite leaning mediad. Prefemoral process relatively short, at most extending only to level of acropodital midlength. Anterior acropodital margin deeply incised distal to midlength, with adjacent spiniform projection.

Component. Keeton's (1960a) concept, that *Chicobolus* is monotypic, has been accepted by all subsequent authors (Hoffman 1980, 1999; Shelley 2001a). We continue this pattern, although the strikingly different color pattern of populations in the Keys and southernmost peninsula suggests that they should be re-examined for structural differences justifying specific recognition (the name, *C. pilbryi* Chamberlin, 1947, is available), as should the South Carolina population.

Distribution (Fig. 28, letter C). *Chicobolus* and *C. spinigerus* are essentially restricted to the area in the four southeasternmost states that were completely inundated during the Cretaceous, and as noted in the tribal account, the taxa may already be gone from Alabama and western Florida. The northernmost locality is in Florence Co., South Carolina; the southernmost is on Big Pine Key, Monroe Co., Florida, where a thriving population apparently exists; and the westernmost is Pensacola, Escambia Co. Maximal dimensions are 1,110 km (694 mi), north-south, and 701 km (438 mi), east-west, but those for the continuous area with maximal abundance (Fig. 28, black line) are 760 km (475 mi), north-south, and 467 km (292 mi), east-west. We think the main population and that in coastal South Carolina, around 296 km (185 mi) to the north, will eventually be the only ones, with the latter subsequently disappearing leaving only the primary one, which will shrink to peninsular Florida and the Keys as *Narceus* ousts *Chicobolus* from Georgia and northern Florida. The area may continue shrinking, as *Narceus* spreads through the southernmost peninsula, and *Chicobolus* may eventually be restricted to the Keys, which are protected by marine barriers that the former cannot breach. However, rising sea levels coupled with the abundances of the introduced families Rhinocricidae and Trigoniulidae, which are overrunning the Keys and southernmost peninsula (Shelley and Edwards 2002, Shelley et al. 2005), may eliminate *Chicobolus* from these refugia.

Origin. We do not know exactly when in the Cretaceous the generically distinct US aztecolinine actually arose. It could have been anytime during aztecolinine dispersion, but separate generic status was finalized when the Western Interior Seaway severed the last strand of genetic continuity. We therefore arbitrarily select ≤ 104 mya, the mid-Cretaceous when we place all dispersions in Appalachia, as the origination date of *Chicobolus*.

Remarks. Again, Keeton (1960a) was remarkably prescient in regarding *Chicobolus* as deriving from an *Aztecolus*-like ancestor that lacked distal modifications of the posterior gonopod telopodite, which is essentially also our conclusion.

Tribe Spirobolini, new status

Type-genus. *Spirobolus* Brandt, 1833.

Diagnosis. Posterior gonopod telopodite curving broadly mediad. Prefemoral process with variably irregular or bulbous basal part and longer and variably dactyliform or short and irregularly broad distal part, recessed within or positioned outside of deeply cupulate acropodite. Latter with deep central cav-



Figure 29. Distribution of Spirobolini.

ity/depression, either lying beside prefemoral process or overhanging and enveloping latter, margins smooth and continuous, without irregularities, indentations, and projections.

Components. Two genera: *Spirobolus* Brandt, 1833, and *Narceus* Rafinesque, 1820.

Distribution (Fig. 29). Spirobolini occupy three separate areas. That in east Asia and the point locality in Minnesota are as characterized for the family and subfamily. That in eastern North America excludes southernmost peninsular Florida and the Keys, inhabited solely by Aztecolini/ *Chicobolus*. The shortest distance between the Asian (Taiwan) and eastern North American (southcentral Texas) areas is approximately 14,017 km (8,761 mi), one of the greatest tribal lacunas in the Diplopoda.

Origin. To originate in northern Mexico and occur in its present areas today, Spirobolini had to disperse northwestward/eastward through the “proto-southern US.” The Western Interior Seaway interrupted this process and bisected a previously subcontinuous fauna. The anatomical conditions in Aztecolini are enhanced in Spirobolini, which had to evolve soon after Aztecolini, and we arbitrarily date its origin at ≤ 294 mya.

Genus *Narceus* Rafinesque, 1820

Narceus Rafinesque, 1820:8. Hoffman and Crabill, 1953:80. Causey, 1955a:70–71. Hoffman, 1957:68; 1980a:77; 1999:38–39. Chamberlin and Hoffman, 1958:165. Hoffman and Keeton, 1960a:17. Keeton, 1960b:62–66. Jeekel, 1971:201. Shelley, 2000a:184; 2001a:244. Kevan, 1983:2962.

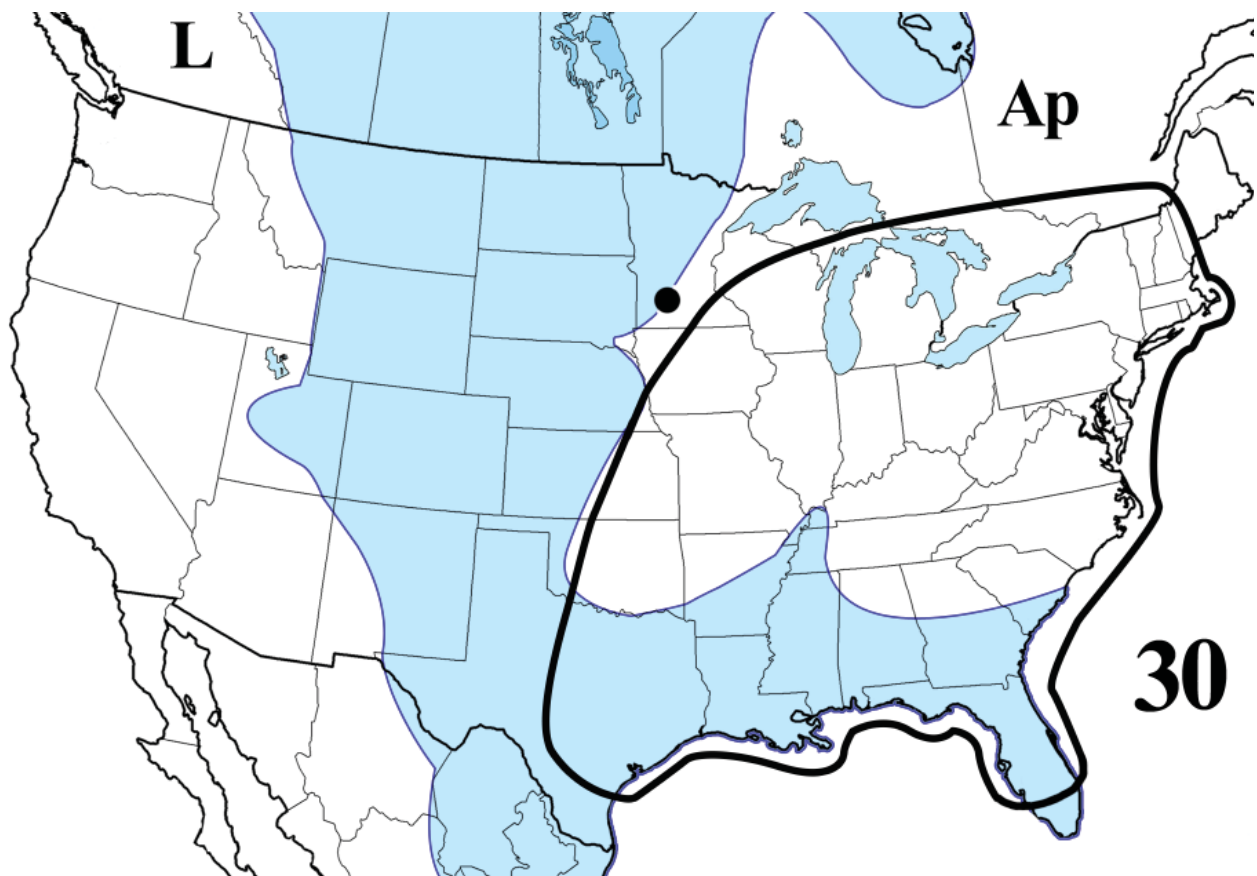


Figure 30. Distribution of Spirobolini/*Narceus* plotted against Cretaceous land patterns; submerged, marine Florida terrane and approximate maximal dimensions of the Western Interior Seaway in light blue. Ap, Appalachia. L, Laramidia.

Rhexenor Rafinesque, 1820:8. Hoffman and Crabill, 1953:81. Causey, 1955a:70. Hoffman and Keeton, 1960a:20. Jeekel, 1971:204.

Spirobolus (not Brandt): Newport, 1844:269. Wood, 1865:207. Bollman, 1887:28; 1893:118. Brölemann, 1914:2. Williams and Hefner, 1928:123. Chamberlin, 1947:44–46.

Arctobolus Cook, 1904:64. Hoffman and Keeton, 1960:8. Jeekel, 1971:192.

Type-species. Of *Narceus*, *N. tinctorius* Rafinesque, 1820, by monotypy; of *Rhexenor*, *R. annularis* Rafinesque, 1820, by monotypy; of *Arctobolus*, *A. onondaga* Cook, 1904, by original designation.

Diagnosis. Posterior gonopod prefemoral process long and subdactyliform, bulbous basally with distal part strongly prolonged, extending for at least 2/3 of length of acropodite, deeply recessed within and partly enclosed by latter.

Components. Four nominal species: *N. americanus* (Beauvois, 1817), *N. annularis* (Rafinesque, 1820), *N. gordanus* (Chamberlin, 1943), and *N. woodruffi* Causey, 1959 (Causey 1959; Keeton 1960a; Shelley 2002c, 2006; Shelley et al. 2006).

Distribution (Fig. 30). One of the four most widely distributed North American chilogath genera, along with *Oriulus* and *Aniulus* (Julida: Parajulidae) and *Underwoodia* (Chordeumatida: Caseyidae) (Shelley 1992, 2001b, 2002d), *Narceus* is the most commonly encountered diplopod genus in eastern North America. It is ubiquitous within its range and blankets the eastern familial/subfamilial/tribal areas except for southernmost peninsular Florida and the Keys, inhabited by Aztecolini/*Chicobolus*/*C. spinigerus*. Though erroneously including this southernmost area, Shelley et al. (2006) detailed its distribution.

Origin. From the Mexican source area, ancestral spirobolinine stock spread northward across the breadth of the “proto-southern US,” and the faunal continuity was broken by the Western Interior Seaway sometime during the Cretaceous. We can never know when the last thread of genetic continuity was severed, but we consider this the date when *Narceus* and *Spirobolus* simultaneously arose. We therefore arbitrarily select ≤ 290 mya as the date of origin of both taxa.

Remarks. Per present concepts, particularly that of Keeton (1960a), *Narceus* comprises **four species not three** (see components section above), including the often overlooked *N. woodruffi* Causey, 1959. It and *N. gordanus* are known only from peninsular Florida and are therefore considered endemics until authentic adult males are discovered elsewhere (Shelley and Bauer 1997, Shelley et al. 2006). The records of *N. gordanus* from Charleston Co., South Carolina, and Carter Co., Tennessee, are misidentifications of *N. americanus/annularis* and are based entirely on females. Consequently, Shelley and Bauer (1997, footnote 2) deleted *N. gordanus* from both states and implied endemism to peninsular Florida by noting that the only authentic records are from Alachua and St. Johns cos., southward; subsequently, Shelley et al. (2006) stated this outright. Hoffman (1999) overlooked Shelley and Bauer’s footnote and mistakenly reported, “the apparently disjunct record for Charleston, South Carolina, requires verification.” Known only from Alachua, Columbia, and Putnam cos., *N. woodruffi* has been overlooked in five works (Hoffman 1980 [by implication], 1999; Shelley and Bauer 1997; Shelley 2001a; Walker et al. 2009) and reported in five (Causey 1959; Keeton 1960a; Shelley 2002c, 2006; Shelley et al. 2006). Proposed by Causey (1959) for an adult male holotype and two female paratypes from Putnam Co., *N. woodruffi* missed inclusion in the first checklist (Chamberlin and Hoffman 1958) by one year as it also did the familial revision, then in press. Consequently, Keeton (1960a) could only acknowledge its existence, stating in footnote 4, p. 65, that he had not seen the types and would not evaluate the name. Although the holotype was lost, Shelley (2002c) redescribed *N. woodruffi* from the female paratypes and four samples with males (FSCA); four years later, he (Shelley 2006) reported the holotype after it was discovered in the general AMNH holdings. *Narceus woodruffi* is the smallest-bodied spirobolid and the second smallest North American spirobolidan behind southwestern arinolinine atopetholids. From the standpoint of body size, *N. woodruffi* more closely resembles a spirobolellid or large-bodied representative of Parajulidae (Julida), like a species of *Bollmaniulus* Verhoeff, 1926, along the Pacific

Coast. Somatically and gonopodally, *N. woodruffi* is a unique spirobolid that appears to constitute a distinct clade, so its omission from the molecularly-based generic analysis (Walker et al. 2009) seems one that could impact results/conclusions and hence necessitate redoing aspects of this work.

Genus *Spirobolus* Brandt, 1833

Spirobolus Brandt, 1833:203. Porath, 1872:14–17. Pocock, 1894a:484; 1894b:388; 1908:74–76. Attems, 1909:25 (list); 1910:90 (key). Brölemann, 1913:472–476; 1914:3, 20, 31–32. Hoffman and Crabill, 1953:80. Hoffman, 1957:67. Hoffman and Keeton, 1960:22. Jeekel, 1971:205. Wang and Zhang, 1993:845. Zhang et al., 1997:509. Golovatch and Hoffman, 2000:233.

Iulus (not Linnaeus): Gervais, 1847:137–138.

Prospirobolus Attems, 1910:90. Hoffman, 1957:67. Hoffman and Keeton, 1960:20. Jeekel, 1971:204.

Sinobolus Chamberlin and Wang, 1953:12. Hoffman, 1957:67. Hoffman and Keeton, 1960:21. Jeekel, 1971:205.

Type-species. Of *Spirobolus*, *S. bungii* Brandt, 1833, by subsequent designation of Pocock (1894); of *Prospirobolus*, *Spirobolus joannisi* Brölemann, 1896, by original designation; of *Sinobolus*, *Spirobolus joannisi* (sic) Brölemann, 1896, by original designation.

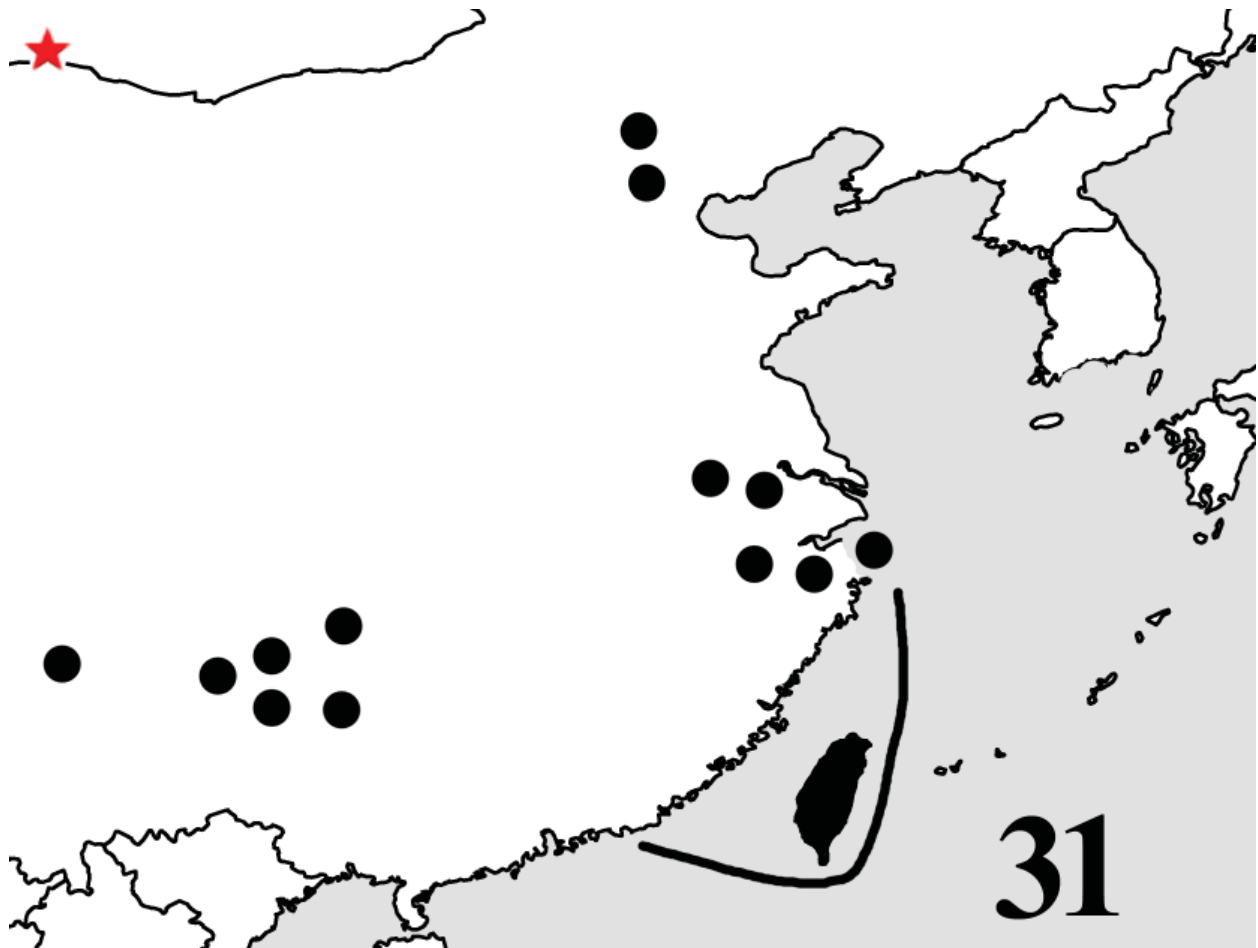


Figure 31. Distribution of Spirobolidea/idea/inae/ini in Asia. Black dots and complete shading of Taiwan, *Spirobolus* spp. Red star, approximate location of the Mongolian, Cretaceous fossils assigned to *Gobiulus* (Floridobolinae: Tylobolini).

Diagnosis. Posterior gonopod prefemoral process short and relatively broad, not dactyliform; lobes generally short, broad, and irregular, basal lobe generally broader than distal part; length no more than half that of acropodite, situated medial to and not overhung or enveloped by latter.

Components. Six nominal species: *S. bungii* Brandt, 1833; *S. walkeri* Pocock, 1895; and *S. umbobrochus*, *grahami*, *formosae*, all by Keeton, 1960; and *S. cincinnalis* D. Wang and Zhang, 1993 (Keeton 1960a, D. Wang and Mauriès 1996, Korsós 2004). D. Wang and Mauriès (1996) assigned *Trigoniulus niger*, *takahasii*, *segmentatus*, and *tertius*, all by Takakuwa (1940), *Spirostrophus lanyusis* Y. Wang, 1955, and *Spirobolellus takakuwai* Y. Wang, 1961, to Spirobolidae but left them in their original combinations. Korsós (2004) placed the last name in synonymy under *Paraspirobolus lucifugus* (Gervais, 1836) and returned *T. tertius* and *Spirostrophus lanyusis* to their original families. Likewise, we now return *T. niger*, *takahasii*, and *segmentatus* to Trigoniulidae, as the gonopodal illustrations in Takakuwa (1954) clearly refer them to the suborder Trigoniulidea.

Distribution (Fig. 31). The extant familial/subfamilial/tribal area in east Asia; we shade all of Taiwan because *Spirobolus*/Spirobolini/inae/idae/idea may occur subcontinuously in this small island. On the Asian continent, the taxa are known from eastern China, extending from Zhoushan Island, Zhejiang Prov., on the East China Sea, to central Sichuan Prov. north of the Laos/ Myanmar border, an east-west distance of around 1,926 km (1,204 mi) or around 59% of the country's breadth. North-south, they are known from the Great Wall of China in northern Beijing Prov. to northern Guizhou Prov., a latitudinal distance of around 1,389 km (868 mi), and *S. ?bungii* was encountered north of Beijing on the Wall itself by B.A. Snyder in 2011. To our knowledge, this is the northernmost Asian record of extant Spirobolini, but the locality of *Gobiulus sabulosus*, the Mongolian, Cretaceous fossil, is slightly more northern.

Origin. As discussed in the *Narceus* account above, we estimate the origin of *Spirobolus* at ≤ 290 mya.

Remarks. Keeton (1960a) opined that the closely similar gonopodal features of *Narceus* and *Spirobolus* indicate shared ancestry. We concur and must therefore formulate a hypothesis explaining how these sister taxa became so vastly separated, a stringent requirement with few options. Hoffman (1969) viewed *Narceus* and *Spirobolus* as “two ends of a long Trans-Beringian arc,” and Golovatch (1979) cited Spirobolidae as exemplifying a Trans-Beringian connection. We consider a Trans-Beringian hypothesis implausible. With all other extant Spirobolidae/inae/ini occupying, and originating in, North America (Fig. 11, 27, 29), *Spirobolus* also had to arise there, not Asia, and we question whether multitudinous generations of Spirobolini could have dispersed north-northwestward through today's central US, western Canada and Alaska, crossed the Bering Strait from east to west, dispersed westward and then southward through present-day eastern Russia, parts of Siberia, and Manchuria to eastern and southern China, then somehow managed to cross the Taiwan Strait to Taiwan while not spanning similar expanses and occurring today on Sakhalin Island, the Japanese mainland, the Ryu Kyu Islands, and the Philippines. This dispersion seems particularly unlikely in the short time period since the Cretaceous Seaway closed. The countless multitude of generations and epochs required for this trek militate against it, and the progeny also underwent considerably less anatomical divergence than did whole lineages evolving over equivalent or even shorter time spans. Even if generations of these mobile/vagile diplopods had marched along the Alaska highway, straight across the Bering Strait, and directly to their present areas, we question whether enough time has elapsed for this to have happened, and dispersals proceed in all directions, not in straight lines as if guided by maps or GPS units. Furthermore, an ostensible Trans-Beringian dispersion somehow happened without also leaving evidential populations in intervening or tangential areas, as occurred with *Hiltonius*' disjunct population in southeastern Arizona (Fig. 12; Shelley 2010) and the spread, over hundreds of millions of years, of ancestral European taxa to southeast Asia, leaving populations in the Central Asian Republics and around the Caspian Sea (Shelley and Golovatch 2011). In 2006–2007, RMS investigated the Alaskan panhandle, Kodiak Island, the vicinities of Anchorage, Palmer, Wasilla, Girdwood, Homer, Seldovia, Seward, Cordova, Valdez, and Glenallen, and connecting highways without finding a single spirobolidan in any life stage. He has also investigated northcentral and southern Alberta/British Columbia, Canadian regions that would logically be on such a dispersal route, with the same result and knows of no preserved samples from these areas. Likewise,

extant spirobolids have never been taken in any part of Siberia or Far Eastern Russia that would logically be on this route or in tangential places like the Korean Peninsula and Kamchatka and Sakhalin/Kurile Islands, Russia (Takakuwa and Takashima 1940; Paik 1958; Korsós 1980; Korsós and Ronkay 1988; Mikhaljova 1993, 2001, 2004, 2010, 2012; Mikhaljova and Pil 1993; Mikhaljova and Basarukin 1995; Mikhaljova and Golovatch 2000; Mikhaljova et al. 2000; Mikhaljova and Lim 2001; Mikhaljova and Nefediev 2002; Mikhaljova and Korsós 2003; Mikhaljova and Marusik 2004; Shelley and Golovatch 2011). Alaskan, Canadian, and Russian populations could have become extinct during the intervening eons of time, but we think their collective absences, coupled with the lack of even tribal-level divergence in the progeny during a length of time when such would be expected, render a Trans-Beringian hypothesis inoperative. We believe that *Gobiulus* and extant forms of Spirobolidea/idae/inae/ini/*Spirobolus* reached east Asia in a different manner, and we employ the “Asiamerica” concept as defined on (<http://palaeos.com/earth/paleogeography/asiamerica.htm>) to explain this vast allopatry; extensive searches by RMS, several colleagues, and the NCSM librarian have failed to produce a hard reference, so we cite this website. “Asiamerica” existed from the late-Cretaceous to the Eocene (Cenozoic), ca. 94–50 mya, and contained present-day Taiwan and parts of China, Mongolia, the western US, and Canada. It contained dinosaurs, archaic mammals, and, we think, spirobolid millipeds.

Florida’s Paleogeographic History

During most of the Paleozoic era, Florida was a marine terrace attached to the “proto-Africa” part of “Gondwana I” (Webb 1990); it rifted in the late Carboniferous, when Euramerica collided with “proto-South America” and Spirobolidea penetrated “proto-Mexico.” The terrane, still exclusively marine, drifted toward Euramerica and accreted near present-day Brunswick, Georgia, in the late Triassic (Mesozoic), ca. 220 mya, but the first permanent Floridian land emerged 195 my later, in the late-Oligocene (Cenozoic), ca. 25 mya. A substantial central-peninsular landmass existed that was connected on the north to “proto-Georgia” and supported mesic forests; it now constitutes the Central Highlands where *Floridobolus* occurs. Beginning in the Miocene (Cenozoic), around 23 mya, parts of this central landmass were periodically inundated, reconnected, reduced, and enlarged as sea levels rose and fell until the peninsula assumed its present configuration.

As we know them, *Floridobolus* and its species are thus ≤ 25 my old, the age of the land area to which they are restricted (Neill 1957, Webb 1990). However, *Chicobolus* inhabits environments throughout the peninsula and even on the Keys, and *Narceus* ranges southward to the latitude of Lake Okeechobee. Penetrations by ancestral stock, as “proto-peninsular Florida” grew and changed during the Cenozoic, were from the north, the only land avenue available. *Floridobolus* established a (sub)continuous population throughout the sand ridges that extend southward from present-day Baker and Columbia to Polk and Osceola cos. As sea levels fell in the Miocene and more land emerged, the dunes/peninsula expanded southward through Highlands Co., allowing *Floridobolus* to penetrate today’s Lake Wales Ridge. Sea level risings in subsequent Cenozoic periods sliced this continuous land into islands and partitioned the fauna into segregated populations. The southernmost, now *F. penneri*, became isolated on the Lake Wales Ridge; another, now *F. orini*, was isolated on the northern island containing the present Ocala National Forest; and additional populations were likely segregated on other islands.

On a clear day in January 2014, RMS flew northward over western Highlands and Polk cos. in a private plane at around 20,000'; the flight path continued northeastward over Orlando and the St. Johns Rivers. From this elevation there were no traces of ridge-like physiographic features; Florida appeared flat and studded with lakes. Thus, the Lake Wales and other ridges along this trajectory are not overwhelming from this height, but they are obvious on the ground and the former harbors this unique diplopod taxon. We believe that undiscovered populations and even species of *Floridobolus* exist in uninvestigated ridges and “Big Scrub” habitat in Florida and perhaps southernmost Georgia, and a graduate student is investigating them as part of his doctoral research.

An Evolutionary Hypothesis

As did Hoffman (1980a, 1982), we concur with Keeton (1960a) that the “northern Mexican Highlands,” the general part of Euramerica that actually contacted “proto-South America” in the Carboniferous, constitutes the center of origin and dispersal in Spirobolidae as it likely also does for Allopocockiidae, Atopetholidae, Hoffmanobolidae, Messicobolidae, Typhlobolellidae, and endemic leptodesmidean families. While this characterization is generalized and vague, the two spirobolid subfamilies occur sympatrically in a mountainous part of northern Mexico (Fig. 12, 28, 32) that is plausibly the source area for Spirobolidae though not necessarily other taxa. We also agree with Keeton (1960a) that Tylobolini arose from early stock and that *Hiltonius* is the more plesiomorphic genus; indeed, *Tylobolus* can be deemed a *Hiltonius* in which the distal lobe of the extended anterior surface of the posterior gonopod acropodite is prolonged and decurved. The tylobolinine genera are sympatric from Los Angeles Co., California, to Baja California Norte (Fig. 12), but *Hiltonius* occurs alone in southeastern Arizona, central Mexico, and Guatemala. *Hiltonius*’ fragmentation and larger overall distribution indicate greater age, in contrast to *Tylobolus*, which is continuous and the only representative in Oregon, Washington, Nevada, Utah, and northern Arizona. *Hiltonius* arose first, spread northwestward to the Pacific Coast, and gave rise, perhaps in the sympatric range area, to *Tylobolus*, which has dispersed northward and eastward, probably supplanting *Hiltonius* north of Los Angeles and doing so now where they overlap. The lobate posterior gonopod acropodite of *Floridobolus* resembles that of *H. carpinus* (Fig. 6–8), which inhabits the presumptive source area and is the most proximate tylobolinine, so one can reasonably conclude that Floridobolini also originated there. The second most proximate tylobolinine to *Floridobolus* is *T. utahensis* in northwestern Arizona, some 2,920 km (1,825 mi) to the northwest, which shares non-uncinate anterior gonopod telopodites. We regard these gonopodal similarities with *Hiltonius* and *Tylobolus* as incontrovertible evidence that *Floridobolus* is more closely related to geographically distant Tylobolini than to sympatric Spirobolinae.

Beyond the vastly allopatric spirobolinine genera, a hypothesis on the evolutionary history of Spirobolidae must also account for the restricted distribution of *Floridobolus*, the absence of taxa from most of the Central Plains, and the lack of sympatry except in the southeastern US, southern California/northern Baja, and central Mexico. As evidenced by broad east-west disjunctions between Floridobolini/Tylobolini and *Aztecobolus/Chicobolus*, all familial and generic taxa necessarily antedate the Cretaceous (Mesozoic), ~141–66 mya, when the Western Interior Seaway divided North America into separate eastern (Appalachia) and western (Laramidia) land masses (Stanley 1999, Skelton 2003, Shelley and Richart 2014). As Spirobolidae could **only** have penetrated North America via Central America **after** the Euramerica/“proto-South America” collision (Shelley and Golovatch 2011), all dichotomies except that forming *Tylobolus* had to take place in the 202 my between the Carboniferous and mid-Cretaceous, or between 306–104 mya. Furthermore, Spirobolidae/inae/ini/*Narceus/Spirobolus*, Floridobolinae/ini, *Hiltonius*, and *Aztecolini/Aztecobolus/Chicobolus* had to diverge and disperse into Appalachia and/or western/southern Laramidia during this same time span. Allowing time for evolution in the “Mexican Highlands,” we hypothesize four northwardly penetrations of the “proto-US” during this 202 my period, so while the Permian-Triassic extinction event was occurring 255–250 mya, with mass losses of land vertebrates and insects, spirobolid millipeds were proliferating and dispersing in these areas. Only relative dates can be inferred because the only time measures are geologically dated Cretaceous events and the fact that **ALL** taxa had to fully evolve and disperse into future Appalachia and Laramidia during the ~202 my **BEFORE** the Western Interior Seaway completely blocked passage and partitioned the lineages, and as stated, we place all taxa in these land areas by the mid-Cretaceous, ~104 mya. Dispersals occurred in most northerly directions, but the Waterway erased all progeny in its area, leaving only those that successfully reached Appalachia as founder populations for modern eastern taxa. A plethora of vacant spirobolidean niches were available in the “Mexican Highlands,” Appalachia, and Laramidia, and we suspect “species swarm” phenomena with rapid cladogeneses and familial divergences (Shelley and Golovatch 2011). Therefore, we arbitrarily date the origin of Spirobolidae/Floridobolinae/Floridobolini at ≤303 mya.

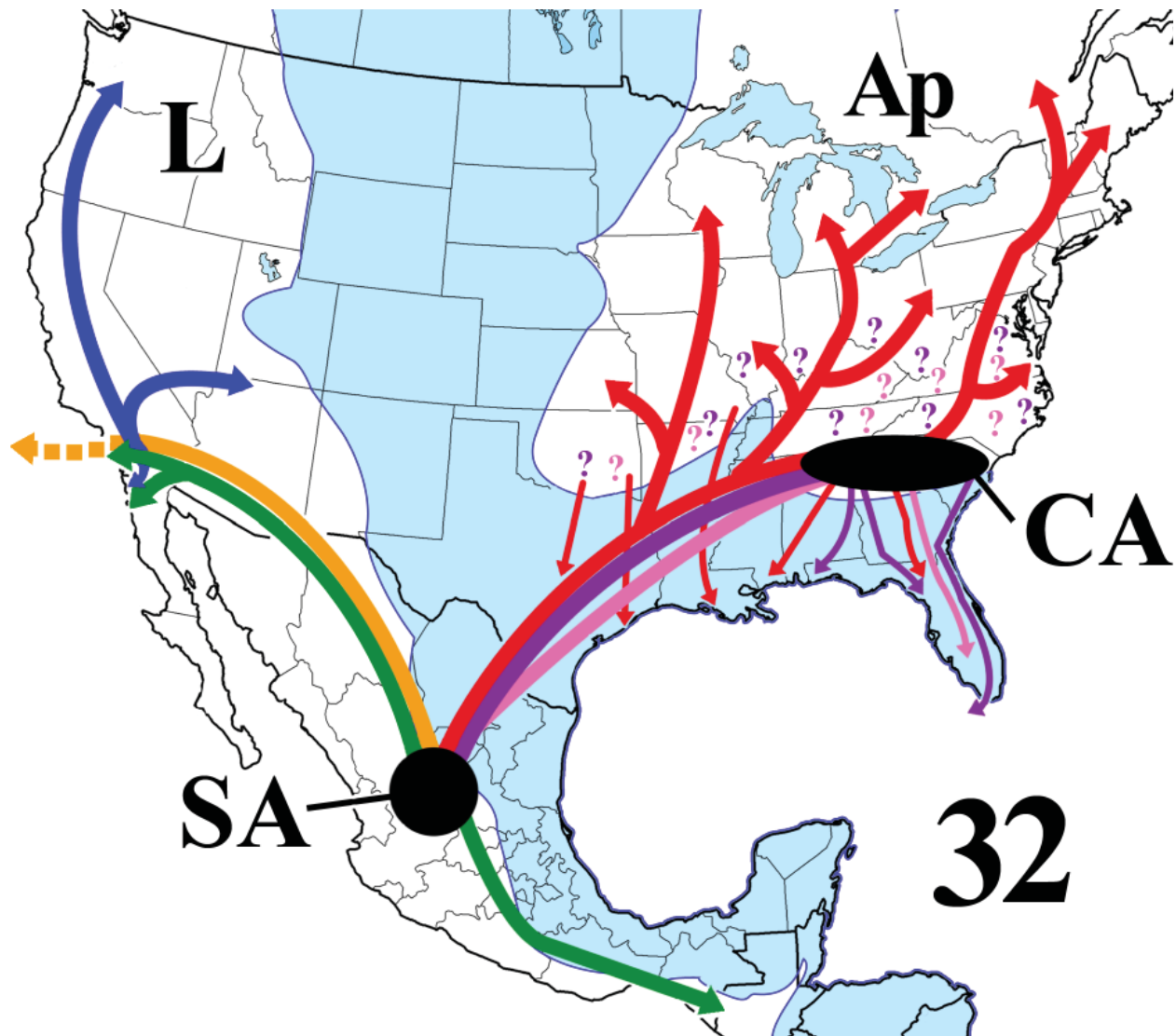


Figure 32. Inferred, pre-Cretaceous, spirobolid dispersal pathways plotted against Cretaceous land patterns; submerged, marine Florida terrane and approximate maximal dimensions of the Western Interior Seaway in light blue. Broad lines, primary dispersal routes (prior to Cretaceous Embayment); narrow lines, secondary dispersal routes (during and after retreat of the Seaway and emergence of peninsular Florida). Colors for dispersal lines and question marks (uncertain occurrences) as follows: Pink, Floridobolini/*Floridobolus*; Green, *Hiltonius*/Tylobolini; Dark Blue, *Tylobolus*/Tylobolini; Purple, Aztecolini/*Chicobolus*; Red, *Narceus*/Spirobolini; Gold, *Spirobolus*/Spirobolini. Ap, Appalachia. CA (blackened ovoid region in eastern lobe of Appalachia), Taxon Cluster Area in late-Cretaceous. L, Laramidia. SA (blackened rounded region in Mexico), Presumptive Source Area in the “northern Mexican Highlands.”

First and second invasions

The most plesiomorphic lineages that invaded the “proto-US” possessed thickened, lobate posterior gonopod acropodites. Floridobolini was first, <303 mya, followed relatively shortly by *Hiltonius*, after the posterior gonopod sternal remnant and extended caudal acropodital surfaces were lost. Floridobolini headed northeastward toward future Appalachia while *Hiltonius* spread southward to present-day Guatemala and northwestward to the Pacific Coast. We cannot speculate as to why Floridobolini apparently only spread northeastward, but perhaps *Hiltonius* headed southward/northwestward because Floridobolini had occupied all niches to the northeast and ones were available in these directions.

Populations that reached the future lands of Appalachia and Laramidia spread to the east and west coasts and dispersed unknown distances northward. *Tylobolus* subsequently diverged in California, perhaps in the present area of sympatry with *Hiltonius*, and the Western Interior Seaway eradicated forms between the lineages. We have no way of inferring the area that ancestral Floridobolini occupied nor the diversities of its former populations, which may have contained two or more genera and several species. However, today's *Floridobolus* mandates their occurrences in at least southeastern Appalachia to be able to penetrate South Carolina, Georgia, and Central Florida, and generate the modern fauna. We do not know and can only infer why floridobolinines disappeared from Appalachia and other areas that they once had to occupy, but being swamped and out-competed by *Chicobolus* and particularly *Narceus* seem obvious and at least partial explanations.

Third invasion

After Tylobolini diverged, spirobolid acropodites thinned, margins further expanded, and the pre-femoral process became a distinct projection. As evolution proceeded, Aztecolini split off, representing an incomplete developmental stage with a shallow acropodital cavity, incised margins with spiniform projections, and short prefemoral processes. As with *Hiltonius*, a population remained in the "Mexican Highlands" while Aztecolini spread to the Atlantic Coast and an unknown distance northward in Appalachia. Being apomorphic, Aztecolini probably ousted Floridobolini from some niches in its established range, and the Seaway partitioned the subcontinuous aztecolinine fauna leaving populations in Appalachia and Mexican Laramidia. As the waters receded, both spread into formerly inundated lands, and like Floridobolini, *Chicobolus* must have inhabited southeastern Appalachia to be positioned to penetrate South Carolina, Georgia, and later Florida. As Cenozoic sea levels fell, *Chicobolus* spread throughout the enlarged peninsula and was eradicated from some of this area as they rose again. However, small populations remained on insular refugia and survive today on the Keys.

Fourth invasion

As its posterior gonopod telopodite continues the developmental pattern of Aztecolini, which occupies the presumptive source area, Spirobolini logically also arose there although they no longer inhabit the region. The laminate acropodite expands into a smoothly margined, endomere-like hood with a deep cavity that overhangs and partly envelops the enlarged prefemoral process. This clade dispersed simultaneously northwestward and northeastward, traversed the boundaries of future Appalachia and Laramidia, spread to both the Atlantic and Pacific coasts, and was partitioned into eastern and western populations by the Seaway. By the time western forms reached the Pacific, *Tylobolus* had surely evolved, spread well northward, and fully occupied spirobolid niches west of the Sierra Nevada and Cascade mountains, leaving none for a confamilial competitor. Unable to oust tylobolinines from the niches in which they were entrenched, western spirobolinines found refuge in "Asiamerica," and *Spirobolus*, the only extant east-Asian spirobolid/ean, occurs today in Taiwan and China. When "Asiamerica" formed, it offered a plethora of vacant niches that "proto-*Spirobolus*" was able to penetrate and occupy; they were also available to tylobolinines, which were already entrenched and possibly could not compete with "proto-*Spirobolus*" without this advantage. While no extant tylobolinines have been taken in east Asia, the fossil genus, *Gobiulus*, seemingly a tylobolinine, was discovered in late-Cretaceous deposits in the Gobi Desert of southern Mongolia, where extant Spirobolida are unknown (Mikhailjova 2012), so Tylobolini apparently did venture onto the Asian part of "Asiamerica" but became fossilized. Implausible as this overall scenario may seem, it is one of the few that explain the present picture – *Spirobolus* completely in eastern China and Taiwan; *Narceus*, its sister, wholly in eastern North America; and extant Tylobolini wholly in the western US, Mexico, and Guatemala. Spirobolini could not have originated in either presently occupied area because (a) it is the apomorphic culmination of an evolutionary sequence that began in Mexico, two lineages occur there today, and it necessarily also had to arise there; (b) it would likely have been trapped by Cretaceous events and occupy only that one area today; and (c) evolution of *Narceus* or *Spirobolus* from the other is difficult to envision because of time and distance, if for no other reason.

At the height of the Seaway, *Narceus* was well established in Appalachia. As waters receded, it spread southward into vacant niches in Texas and along the Gulf Coast that it probably occupied prior to the Embayment. When the Wisconsin glaciation retreated 12,000 years ago, it expanded northward, perhaps for the second or more times, to southern Québec and western Maine (Shelley 1988, 2002b; Shelley et al. 2006). A highly successful taxon of vagile, mobile spirobolids, *Narceus* is ubiquitous within its range, having out-competed and evicted prior spirobolids from niches throughout essentially all of Appalachia. Its successfulness is evidenced by its vast range and obvious ability to respond, radiate, speciate, and adapt to a variety of climatic and environmental conditions, which neither *Chicobolus* nor *Floridobolus* can do. Floridobolini and *Chicobolus* spread southward along the Atlantic Coast as land became available from the Embayment's retreat, and all records of both taxa are either in or close to formerly submerged areas (Fig. 12, 28). We surmise that insufficient "post-Embayment" time has elapsed for *Narceus* to completely oust *Chicobolus* from areas outside of peninsular Florida and southern Georgia (Fig. 28), so the latter still occupies eastern South Carolina. *Floridobolus*, however, does not; perhaps the "double whammy" of both *Chicobolus* and *Narceus* eliminated any possibility of its survival elsewhere. That plesiomorphic *Floridobolus* persists in peninsular Florida in the presence of these younger and more successful spirobolines suggests that it holds a selective advantage in sandy "Big Scrub" environments but is unable to compete with them in other biotopes.

While *Narceus* penetrated Florida simultaneously with *Floridobolus* and *Chicobolus*, we believe it encountered difficulty in the unique peninsular environments. It readily pervaded coastal biotopes to the west (in the Florida panhandle, Alabama, Mississippi, Louisiana, and Texas), but those on the peninsula induced speciation, resulting in its largest- and smallest-bodied species, *N. gordanus* and *N. woodruffi*, respectively. A particularly robust form of the former occurs syntopically with, and may now be displacing, *F. orini*. Whereas environmental factors apparently fueled speciation in *Narceus*, this process in *Floridobolus* has resulted solely from partitioning and the subsequent development of different gene pools.

Except perhaps for relictual, insular populations of *Chicobolus*, we believe that *Narceus* will inevitably become the only indigenous spirobolid/ean in both peninsular Florida and eastern North America. *Chicobolus* had to once occupy a substantially larger area to the north, in Appalachia, but its range is now reduced to eastern South Carolina, eastern/southern Georgia, and peninsular Florida, with late 19th Century records from eastern Alabama and the western Florida panhandle (Appendix) reflecting populations that may no longer exist. *Narceus* has erased all traces of *Chicobolus*' prior range in Appalachia, and the latter survives only in or near formerly submerged lands in the southeastern corner of the US (Fig. 28). Though more adaptable and successful than *Floridobolus*, as evidenced by its greater range and apparent moderate resistance to *Narceus*, even *Chicobolus* cannot compete long-term with this far superior spiroboline. *Floridobolus* and *Chicobolus* are both declining, and man is fortunate to



Figure 33. Ring profiles in Spirobolidae. Left two rings, transversely ovoid profile shown by Floridobolinae/Floridobolini. Right two rings, rounded profile demonstrated by Floridobolinae/Tylobolini and Spirobolinae. Photo courtesy of O. McMonigle.

see the southeastern spirobolid fauna while their presences provide evidence of past events. If *Floridobolus* were extinct, we would draw different inferences about the past, and if *Chicobolus* were also gone, the narrative, with only *Narceus*, would be vastly different.

Our judgement is that *Narceus*, as constituted in the Oligocene, could not out-compete Floridobolini in sandy, xeric, “Big Scrub” biotopes, the only environment in which it could not do so; consequently, *Floridobolus* hangs on in them today. Even there its survival seems doomed because *Narceus* has speciated, and those habitats now also harbor *N. gordanus*, which may eradicate *Floridobolus* from them as well. As with the order Siphoniulida, now confined to southern Mexico and Guatemala with an 1888 Sumatran record that needs confirmation (Pocock 1894, Sierwald et al. 2003, Shelley and Golovatch 2011), we are seeing Floridobolini at its end, when it has declined nearly to extinction. It survives only in this last remaining stronghold where its days also seem numbered, and we think it can be appropriately termed a “living fossil.”

Overall perspective

The previous sections address lineage dispersions individually, but events happened concurrently; while one lineage was dispersing, one or more new clades likely evolved and began dispersing before the prior ones had reached their maxima. Evolution could only proceed one lineage at a time, but two or more likely reached different dispersal stages simultaneously. This seems particularly true for Floridobolini and *Hiltonius* (Tylobolini), whose similar posterior gonopod acropodites suggest rapid divergence, and for Aztecolini/Spirobolini, where the former represents an early developmental stage of the latter that seemingly would have split off without disrupting the overall process. An overview, focusing on Appalachia and eastern taxa, is essential, and we provide a summary depiction (Fig. 32). As we define it, the presumptive Mexican source area lay primarily in future Laramidia (Fig. 12, 28, 32), so westward dispersing taxa either arose in, or quickly penetrated, this area thus evading future inundation. At its maximum, the Western Interior Seaway extended some 352 km (220 mi) farther up the present course of the Mississippi River, thereby dividing the southern boundary of Appalachia into two lobes (Fig. 12, 28, 30, 32), the western extending about 928 km (580 mi) westward to near the Texas panhandle and the eastern extending some 848 km (530 mi) to the Atlantic Ocean around the present Pee Dee/Santee river deltas, South Carolina. The Western Lobe was closer to the presumptive source area, and tribal lineages had to disperse around 1,056 and 1,536 km (660 and 960 mi) to reach the boundaries of it and the eastern lobe, respectively. While we do not know expansion rates and assume spread in all directions, present distributions, the only evidence available, show that both Floridobolini and Aztecolini dispersed to the eastern lobe while Spirobolini spread to both. As all southeastern lineages presently occupy parts of the Atlantic Coastal region, they had to once cluster in the southernmost part of the eastern lobe (Fig. 32, CA), to be able to eventually expand into their present areas. Present data indicate that Spirobolini penetrated well northward into Appalachia, but we cannot infer how far Floridobolini and Aztecolini may have spread, as all populations have been eradicated, logically by *Narceus*. We can only infer that all three co-existed in the “cluster area” (Fig. 32) and surmise that they may have closely followed the receding waters southward just as *Narceus*, millions of years later, may have closely followed retreating glaciers northward. With Spirobolini/*Narceus*’ great advantage in adaptability, mobility, and vagility, why has not a Mexican population persisted, particularly in the presumed source area? Assuming none awaits discovery and despite the fact that *Narceus* has seemingly displaced *Chicobolus* from Appalachia, we can only surmise that *Hiltonius* and *Aztecolus* must be so entrenched in Mexican niches that not even these taxa could displace them. While *Narceus* was able to evict Floridobolini and *Chicobolus* from niches in Appalachia, its sister, *Spirobolus*, was unable to do so with *Hiltonius* and *Tylobolus* in western Laramidia. Since the next clade chronologically, Aztecolini, did not spread in that direction, perhaps the greater time span that tylobolinines had occupied western niches before another lineage’s penetration enabled them to become more firmly entrenched such that they could not be ousted.

While spreading southward into newly exposed land, did Floridobolini ever fully occupy a niche before being evicted by its accompanying, confamilial, and more successful competitors? Obviously it survived as it exists now in peninsular Florida, but perhaps it did so only by continually penetrating

newly exposed land that was not yet occupied by *Chicobolus* or *Narceus*. Perhaps floridobolinines slid into newly exposed niches, were quickly ousted by *Chicobolus* or *Narceus*, then penetrated others as the Seaway receded only to be quickly evicted again, and so on until this process ended when the waters fully receded. Floridobolini may have neared extinction, being confined between more successful competitors and uninhabitable ocean, when the Central Highlands emerged from the Florida Terrane to provide new opportunity for a moribund lineage. Floridobolini (now *Floridobolus*) and *Chicobolus* penetrated these new lands just as before but *Narceus* did not because, we believe, it could not handle the environmental conditions and xeric vegetation. Indeed, so much new territory emerged rather simultaneously that *Floridobolus* and *Chicobolus* expanded to the southern limit while *Narceus* remained some 400 km (250 mi) to the north speciating into a form that could thrive, or at least survive, in this environment. Speciation is a time-consuming process, and the smallest- and largest-bodied species evolved, *N. woodruffi* and *N. gordanus*, respectively (Shelley et al. 2006). The former is known only from four counties in the northern peninsula (Causey 1959; Shelley 2002c, 2006), and the latter has spread to around the latitude of Lake Okeechobee thus engulfing the known range of *Floridobolus*. By providing new territory to penetrate, the fortuitous emergence of Florida not only rescued Floridobolini from perhaps imminent extinction but the arid, sandy nature of this land and its xeric vegetation combined to halt the spread of *Narceus*, force it to speciate, and buy *Floridobolus* more time to adapt and spread. This additional time allowed *Floridobolus* to become entrenched in sandy ecological niches, and it survives today in at least the Lake Wales Ridge and Ocala National Forest. We suspect that undiscovered populations and species inhabit sandy ridges and “Big Scrub” environments throughout peninsular Florida, and a graduate student is pursuing this research topic.

As the first lineage to evolve and penetrate Appalachia, Floridobolini was also the first to encounter its vacant niches. Radiation and diversification in response to such opportunities are reasonable, and Floridobolini may have once comprised several species and even genera, all now extinct; today, it contains only one genus, occupies only one habitat, and occurs in only one state. The next eastward-dispersing lineage, Aztecolini, logically ousted Floridobolini from some of Appalachia’s niches, and *Narceus* subsequently eradicated both to become the only spirobolid in this vast sector of eastern North America. *Chicobolus* and *Floridobolus* now occur **only** in relatively new territory where *Narceus*’ total impact has not yet manifested itself. *Chicobolus* seems not to have adapted and changed to Floridian environments, because aside from the different color pattern of southern populations, males from Florida are anatomically close to ones from South Carolina. Individuals from the Keys and southernmost peninsula are subuniformly slate gray with little to none of the ventrolateral white that distinguishes ones from central Florida northwards and is the basis for the vernacular name, “Florida Ivory Milliped” (Walls 1995). With no populations outside the peninsula, we can only speculate on whether *Floridobolus* has adapted in response to the “Big Scrub” environments. Its forms are accomplished burrowers that venture forth only on cool, moist evenings and nights; their conspicuously different, transversely ovoid profiles (Fig. 33) seem a plausible adaptation that may be advantageous for burrowing in arid, sandy soil. By overhanging and sheltering the legs, obscure from above (Fig. 3), this body form also minimizes the risk of their breaking in tight burrows. Have floridobolinines always been ovoid? There is no way to know, but this body form plausibly may have evolved in association with these peninsular environments. Perhaps only after penetrating them did plesiomorphic *Floridobolus* derive a degree of selective advantage that has enabled it to survive longer than would otherwise have been possible.

This “rebirth” of *Floridobolus* mandates a highly speculative narrative as to why it, *Chicobolus*, and *Narceus* occupy peninsular Florida today while only the last two inhabit southern Georgia and coastal South Carolina and *Narceus* alone blankets the rest of the eastern tribal and (sub)familial ranges. Furthermore, Tylobolini alone occupies the west/southwestern US, and *Spirobolus* occupies eastern Asia along with one fossilized apparent tylobolinine. These facts are supported by data and specimens and are beyond debate. Notwithstanding the reasonable inferences and speculations that are unavoidable to fill gaps and formulate hypotheses, our biogeographic reconstructions fit the more broadly framed hypotheses on the early evolution and dispersal of the class (Shelley and Golovatch 2011). The unanticipated discovery of a second species of *Floridobolus* coupled with the sudden realization that a larger generic fauna exists than has been known for a half-century, compel an attempt at explaining this new reality, which can only be done in the broad context of the entire family. No longer is *Floridobolus* just that mysterious, monotypic, oddity in southcentral Florida; it now contains two

species with more seemingly awaiting discovery. With Florida unlikely to grow or expand and *Narceus* successfully evolving a syntopic competitor, the reprieve that the peninsula provided *Floridobolus* will probably be short lived geologically speaking. There is not now, nor is there ever likely to be, another sanctuary to rescue *Floridobolus* from extinction. Displacement by *N. gordanus* seems inevitable with *Chicobolus* inevitably being reduced to relictual “point populations” on the Keys, which are surrounded by marine barriers that *N. gordanus* cannot breach. Fortunately, peninsular Florida did emerge in time to allow this plesiomorphic “living fossil” to survive for millions of additional years, such that man can see it, study it, and gain different perspectives of the family, order, and class as a whole than would otherwise have been possible.

Could *Floridobolini*'s restricted occurrence be explained otherwise and perhaps more simply? Could it, for instance, have rafted across what is now the Gulf of Mexico and settled in Florida? No. As the first and most plesiomorphic lineage, *Floridobolini* evolved when Florida was a marine terrane and closer to Africa than Euramerica; *Floridobolini* could thus have rafted somewhere but not to Florida. Could *Floridobolini* have dispersed directly to Florida over lands exposed when sea levels fell? Again, the answer is “No.” As the initial lineage, *Floridobolini* arose long before sea level drops in the Pleistocene, when it had to already be embedded in Florida “Big Scrub” environments. It could have exploited sea bed exposures prior to 25 mya, but they would not have led it to Florida, which was then submerged. Furthermore, *Floridobolini* does not exist in a vacuum but in the context of the entire family, and a full understanding of this tribe requires elevated knowledge of the others. A hypothesis that just moves *Floridobolini* from Mexico to Florida is insufficient; it must also get the other tribes to their present locations because they all interact. We believe that a major reason why *Floridobolini* is restricted to Florida is that it has been supplanted elsewhere by *Aztecolini/Chicobolus* and then *Spirobolini/Narceus*, which also had to spread to their areas. No tangible evidence exists for these taxa directly extirpating *Floridobolini*, but there reasonably is such for *Narceus*' supplanting *Chicobolus*, and this can be reasonably extended to *Floridobolini*. A hypothesis must also transport *Tylobolini* to California **before** *Spirobolini* because otherwise (a) the latter would have occupied the vacant California niches and occur there today instead of, or in addition to, east Asia, and (b) *Tylobolini* might not occur at all in California or northern Baja. Consequently, while one may formulate other scenarios to move *Floridobolini* from Mexico to Florida, they must also transport *Tylobolini*, *Aztecolini*, and *Spirobolini* to their present locations, and few additional options viably meet all of these prerequisites. Ours does, and we therefore believe it is plausible and a close approximation to what actually happened.

The story with the western fauna is comparatively straightforward. *Hiltonius carpinus* evolved, spread southward to Guatemala and northwestward to the Pacific Coast, and left an isolated population in southeastern Arizona mountains. Four forms, presently nominal species, evolved in southern California as did *Tylobolus*, which spread northward to southern Washington (Chamberlin and Hoffman 1958; Keeton 1960a, 1966; Buckett 1964; Hoffman 1999; Shelley 2002a). *Spirobolini* arrived millions of years later but was unable to oust the firmly entrenched tylobolinines nor leave tangible evidence of its presence as *H. carpinus* did in Arizona. The only evidence of *Spirobolini*'s former presence in western North America is the taxon's current distribution; we infer that it had to be in California to be able to occupy east Asia today, and one apparent tylobolinine slipped into the Asian part of “Asiamerica” and became fossilized. We believe ours' is the only scenario that can yield today's reality, since we consider a Trans-Beringian pathway inoperative for previously stated reasons. We think that a Cretaceous “Asiamerican” landmass, encompassing parts of western North America, Taiwan, China, and Mongolia, is a more plausible explanation for such extreme allopatry than a pre- or post-Cretaceous trek that might not be complete even now. *Spirobolini* was in California when “Asiamerica” formed and simply penetrated vacant niches in the part that is eastern Asia today, which is also the exact region of eastern Asia region where *Spirobolini* occurs today. Aside from *Gobiulus*, they either out-competed *Tylobolini* for vacant Asiamerican niches and/or the latter remained entrenched in the Californian ones they already occupied.

Concordance between *Spirobolidea* and *Leptodesmidea* (Polydesmida)

We would be remiss not to digress to address this topic. The sudden availability of vacant niches in “proto-Mexico” after Euramerica collided with Gondwana I had no detectable impact on invading

Glomeridesmida, Siphonophorida, Spirostreptidea, and Stemmiulida, which remained stable at familial levels. The first two have not been investigated systematically, and only two such studies exist on Stemmiulida (Mauriès and Golovatch 2006, Mauriès et al. 2010), so detailed reviews may alter this impression. However, the new “proto-Mexican” niches triggered concordant bursts of evolution in Spirobolidea and Leptodesmidea (Polydesmida) that are manifested today by geographically restricted, endemic families. In addition to the six of Spirobolidea, four evolved in Leptodesmidea – Holistophallidae, Rhachodesmidae, Sphaeriodesmidae, and Tridontomidae – possibly also in the “northern Mexican Highlands.” These families have not dispersed as widely as the spirobolideans, for only Sphaeriodesmidae, represented by Desmoninae, have spread into the US – to Missouri, Kentucky, western Virginia, eastcentral Georgia, and northcentral Florida – and an additional sphaeriodesmid of unknown origin inhabits Guadeloupe, Lesser Antilles (Chamberlin and Hoffman 1958; Loomis 1968a; Mauriès 1980, Hoffman 1980a, 1999; Shelley 2000b; Shelley and Golovatch 2011; Shelley and Martinez-Torres 2013). The other endemic leptodesmidean families are restricted to Mexico and northern Central America, although like Stemmiulida (Shelley et al. 2012) and Aztecolini, Rhachodesmidae inhabit Nuevo León and Tamaulipas, the northeasternmost states, and like Allopocockiidae (Shelley and Hoffman 1995, Hoffman 1999), may traverse the Rio Grande into adjoining southern Texas. Represented by Chondrodesmini, the leptodesmidean family Chelodesmidae, dominant in South America but also occupying parts of Africa and Spain, inhabits the Yucatan peninsula (Loomis 1968a, Hoffman 1999, Bueno Villegas et al. 2004) but has not dispersed into the US; the tribal citation from Veracruz (state) (Hoffman 1999) seems erroneous as we cannot find a published record. In the polydesmidan suborder Polydesmidea, indigenous species of *Myrmecodesmus* (Pyrgodesmidae) have spread northward to northcentral Alabama and eastward along the Gulf Coast to the Apalachicola River (Shelley 2004), which also constitutes the western border of the primary area of *Chicobolus* (Fig. 13, AR, 28).

Conclusion

Once an inexplicable geographic oddity in southcentral peninsular Florida, *Floridobolus* can now be identified as the most plesiomorphic spirobolid, the lone component of its tribe, and the only surviving remnant of the family’s earliest dispersal into present-day North America. Restricted to central peninsular Florida, it is a relictual Paleozoic taxon most closely related to geographically distant Tylobolini in Mexico, Guatemala, and the southwestern US. Floridobolini, if not *Floridobolus* itself, had to inhabit present-day Georgia to be able to quickly penetrate the Central Florida Highlands when they arose from the sea. Additionally, Floridobolini had to occupy Cretaceous Appalachia, but they have been extirpated everywhere outside of peninsular Florida, apparently because they cannot compete with the younger and more successful spiroboline genera especially *Narceus*, whose dominant representative, the “*americanus/annularis* complex” (Shelley et al. 2006), blankets a vast sector of eastern North America. *Floridobolus* survives only in arid, “Big Scrub,” peninsular environments where its apomorphic transversely ovoid body form may confer a selective advantage for burrowing in loose, sandy soil. *Chicobolus* and *Narceus* also occupy these biotopes, but to do so, the latter had to speciate into a form that could survive in harsh, arid environments with scrub vegetation, and syntopic *N. gordanus* may now be actively displacing *Floridobolus* from its final refuge.

We are seeing Floridobolini/*Floridobolus* in the final stage of decline when, from a late-Carboniferous origin in the presumptive familial source area (Fig. 12, 28, 32), they are reduced to one genus and two species in a limited, distant refuge. To originate in Mexico, inhabit Florida today, and avoid inundation by the Western Interior Seaway in the Cretaceous, multitudinous generations of individuals had to disperse northeastward for multitudinous epochs into at least the southernmost part of the eastern lobe of Appalachia to become the founder population for today’s fauna. As sea levels receded at the end of the Cretaceous, the fauna had to spread southward into “proto-South Carolina/Georgia” to be positioned to penetrate the Central Florida Highlands when this sandy area arose in the Late Oligocene. When Floridobolini reached the haven of Appalachia, if not earlier, they had to continually maintain viable populations in the face of what may have been a reasonably continuous onslaught by younger confamilial competitors. Somehow, Floridobolini managed to survive until they gained a respite in the sanctuary of the Central Highlands, which posed an ecological impediment to *Narceus* and forced it

to speciate before proceeding farther. Our biogeographic reconstructions reveal that, for taxa of ostensibly poorly vagile soil arthropods, both Floridobolini and Spirobolidae as a whole have experienced amazing biogeographic odysseys; clearly their vagilities and perhaps those of other spirobolidans and even other diplopods have been under-estimated and under-stated. The magnitude of what had to take place can only be fully grasped by assessing the entire family, which comprises four overall clades and inhabits Mexico, northernmost Central America, the western US, and east Asia in addition to eastern North America. This distribution of Spirobolidae, unquestionably a monophyletic taxon, staggers one's preconceptions as to what millipedes are and what they can do given sufficient time. Explaining these cumulative realities compels speculation beyond a systematist's comfort level, but no alternative exists. Clearly *Floridobolus* did not arise anywhere near its present area, yet it exists there today, is well known from the Lake Wales Ridge, and is now documented from the Ocala National Forest. Beyond *Floridobolus*, Spirobolidae occupy three biogeographical regions, span the breadth of the world's third largest continent, and traverse its greatest ocean. Investigations are in order in peninsular Florida along with ones in the presumed source area to potentially discover new lineages that may be arising. A true grasp of Spirobolidae and the realization of what these soil arthropods have done shatters preconceptions and compels adoption of a much broader perspective of the diverse, intricate, and under-investigated Diplopoda.

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APPENDIX. Unpublished and unmapped records impacting spirobolid distributions. Missing data were not provided on vial labels; sexes and numbers of individuals are provided when known.

FLORIDOBOLINAE: TYLOBOLINI

Tylobolus utahensis Chamberlin, 1925

USA: **California, Inyo Co.**, China Lake Naval Weapons Station, Wild Horse Canyon, Coso Range (36°09' N, 117°43' W), F, 30 May 1997, D. Ubick, G. Pratt, W. Savary (CAS).

SPIROBOLINAE: AZTECOLINI

Aztecocolus nigrrior (Chamberlin, 1941)

MEXICO: Durango, 10 km (16 mi) W Santa Lucia de la Sierra (22°30' N, 104°20' W), MM, FF, 9 September 1984, W.J. Pulawski (CAS, NCSM) **New State Record. Nuevo León**, Sotano de Rancho Nuevo No. 3, M, 24 August 19073, R. Jameson (FSCA). Canyon San Juan Bautista, 8.8 km (5.5 mi) W Cienega, M, 14 July 1974, Liner, Johnson, and Chaney (NCSM) and 4.0 km (2.5 mi) E San Isidro, M, 22 July 1975, Liner, Johnson, Chaney (NCSM). 1.4 km (0.9 mi) S Esmeralda, 4M, F, 18 July 1975, Liner, Johnson, Chaney (NCSM).

Aztecocolus sp.

MEXICO: Jalisco, Ajijic, M, F, 20 June 1964. W.L. Nutting (UAZ) **New State Record for Genus.**

Chicobolus spinigerus (Wood, 1864)

USA: Alabama, Lee Co., Auburn, MM, FF, 1898, O.F. Baker (NMNH). **Florida**, Alachua Co., on waterlily on Orange Lake, F, 26 October 1976, M.R. and J.E. Cooper (NCSM). Broward Co., Ft. Lauderdale, F, 11 December 2000, P.D. Pratt (FSCA). Citrus Co., 3.2 km (2 mi) S Holder, F, 9 April 1936, J. Pen (NMNH). Duval Co., Jacksonville, F (FSCA). Escambia Co., Pensacola, 3F, C.H. Bollman (NMNH). Franklin Co., Apalachicola, 2 April 1915 (NMNH); Elfers, M, 14 April 1952, J.R. Vockeroth (CNC); and St. George I., Sugar Hill Area, 2F, 9 February – 23 March 1972, W.W. Baker (FSCA). Highlands Co., ABS, F, 30 March 1962, D.C. Ferguson (NMNH); and Welaka, 2F, 16 March – 11 April 1962, D.C. Ferguson (NMNH). Leon Co., Apalachicola Nat. For., along USFS rd. 360 nr. Harvey Cr., 10.4 km (6.5 mi) E Bloxham, M, 7 May 1989, J.C. Beane, S.L. Alford (NCSM). Liberty Co., Torreya St. Pk., M, 23 June 1956, T.J. Cohn (UMMZ). Miami-Dade Co., Miami, J.E. Benedict (NMNH), Monroe Co., Everglades Nat. Pk., Cape Sable (NMNH); on keys heading to Key West, 6 March – 18 April 1896, O. Bangs (MCZ); Upper Matecumbe Key, 3 January 1935 (NMNH); Key Largo, 3F, 2 July 1931, H.F. Loomis (NMNH) and M, 24 March 1978, H.V. Weems (FSCA); and Big Pine Key, 0.8 km (0.5 mi) N US Hwy. 1, F, 9 August 1967, R. Silbergleid (MCZ), and grassy pinelands, 6M, 8F, 2 juvs., 15-20 May 1990, S.B. Peck (NCSM). Polk Co., Lakeland, M, February 1963 (Florida Southern College). Seminole Co., Lake Mary (town), Liberty Park, M, F, 9 October 2002, K. Dabney (CAS). **Georgia**, Camden Co., St. Marys, 6 March – 18 April 1896, O. Bangs (MCZ). Seminole Co., 6.4 km (4 mi) SW Reynoldsville, M, 12 June 1956, T.J. Cohn (UMMZ). Thomas Co., Thomasville, F, June 1942, E. Ireland (NMNH). Ware Co., 11.2 km (7 mi) E Waycross, along US hwy. 23 just W of jct. GA hwy. 177, M, F, 13 September 1979, R.M. Shelley, P.T. Hertl (NCSM). **South Carolina**, Aiken Co., W of Tarplay, MM, FF, 23 September 1959 (FSCA). Berkeley Co., Francis Marion Nat. For., 7.3 km (4.7 mi) NNW Huger, 2M, 1 May 1988, J.C. Beane, S.L. Alford, and 5.6 km (3.5 mi) SW Honey Hill, M, 28 June 1998, J.C. Beane, P.D. McMillan (NCSM). Charleston Co., James Island, MM, FF, juvs. 16 September 1926, 3 August 1929, and 24 May 1969 (NMNH) and 2 September 1939, J.T. Pressley (NMNH). Florence Co., near Florence, M, F, 7 August 1925 (NMNH).

SPIROBOLINAE: SPIROBOLINI

Narceus americanus (Beauvois, 1817)

USA: Florida, Wakulla Co., Wakulla Springs, M, 13 July 1934 (KMNH). **Kansas**, Douglas Co., Lawrence, M, 2 November 1914 (KMNH). **Texas**, Milam Co., Rockdale, F, 24 March 1961, R.W. Fredrickson (KMNH).

Narceus gordanus (Chamberlin, 1943)

USA: Florida, Highlands Co., Lake Placid, ABS, in clump of reindeer moss in slash pine, turkey oak, and sand pine scrub, M, 12 August 1960 (ABS); 6.4 km (4 mi) E ABS; and 12.8 km (8 mi) S ABS. Lake Co., Ocala Nat. For., USFS rd. 538 at jct. FL hwy. 19, under board in sand, F, 6 October 2004, D.G. Cooper (NCSM). Marion Co., Ocala Nat. For., along USFS 90, 4.3 km (2.7 mi) E jct. USFS 65, F, 7 October 1904, D.G. Cooper (NCSM), and along USFS 97, 2.2 km (1.4 mi) N FL hwy. 40, M, 7 October 2004, D.G. Cooper (NCSM). Polk Co., Lakeland, F, 23 July 1963 (Florida Southern College). St. Lucie Co., Ft. Pierce, M, 18 February 1983, Hibbard (FSCA).