Buotidae, a new family for the minute North American millipede *Buotus carolinus* (Chamberlin) 1940 (Diplopoda, Chordeumatida, Striarioidea)

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**Abstract**

*Buotus carolinus* (Chamberlin) 1940, a minute, rarely collected but relatively widespread millipede of the mid-Atlantic region of the United States, was originally described as a member of the order Polyzoniida, family Polyzoniidae. Shear (1981) correctly placed the species in the order Chordeumatida and argued for assignment to the suborder Craspedosomatidea, superfamily Brannerioidea, family Tingupidae. New studies of fresh specimens using the scanning electron microscope, however, revealed characters inconsistent with this placement and instead support inclusion of *Buotus* in the suborder Striariidea, superfamily Striarioidea. Because the species cannot be accommodated in any of the established families of this superfamily, a new family Buotidae is herein erected to receive it.

**Key words:** North Carolina, Virginia, taxonomy, morphology, Brannerioidea, Striariidae, Tingupidae, Rhiscosomididae, Apterouridae

**Introduction**

Chamberlin (1940) described the species *Buotus carolinus* based on a single female specimen (which Chamberlin thought immature) from the Duke Forest, Durham, North Carolina, that had been collected by Nell B. Causey. Chamberlin’s description was quite general and contained little diagnostic information. It is not clear why Chamberlin decided to place the genus and species in the family Polyzoniidae, since the specimen demonstrably does not possess (nor did Chamberlin refer to) any of the characters of that family, including free pleurites and strongly modified mouthparts. Only the clavate antennae and low paranota suggest any resemblance to a polyzoniid.

My reclassification of the North American chordeumatidan fauna (Shear 1972) presented a map of the distribution of the chordeumatidan family Tingupidae with a locality in western Virginia based on “…an immature 28-segmented female” which I assumed was a member of that family. But in 1976 I collected a few similar specimens in Montgomery Co., Virginia, and on the advice of Richard Hoffman, was impelled to examine the holotype of *Buotus carolinus*, deposited in the United States National Museum of Natural History (USNMNH). I found the earlier-collected female, the new specimens, which included males, and the holotype (a mature female, also with 28 segments) to be conspecific and typical chordeumatidans, but was unsure of a family assignment. In 1981, I decided that *Buotus carolinus* belonged in Tingupidae after all, and included it in a revision of that family, most members of which occur in the western United States. I followed up that study with more detailed work on the same specimens in 1998, in the context of describing another minute tingupid from Colorado, *Blancosoma scaturgo* Shear & Hubbard (Shear & Hubbard 1998).

Recently, yet more fresh material of *B. carolinus* was obtained from Patrick Co., Virginia, and collections of the species from the Virginia Museum of Natural History were also examined, through the cooperation of curator Dr. Richard Hoffman. This time I was able to study the species using a scanning electron microscope.
at East Carolina University, thanks to Dr. Jason Bond. The results of this study, together with a greater knowledge of the range of characters in the superfamilies Brannerioidea and Striarioidea, which belong to different suborders of Chordeumatida, show that *Buotus carolinus* is better accommodated in the latter superfamily. While evidently closest to species of the nominate family Striariidae, *Buotus* does not share several important synapomorphies of that family, and therefore must be placed in a family of its own.

**Taxonomy**

**Suborder Striariidea Cook 1895**

This suborder was originally proposed to include only the family Striariidae, but was expanded by me in 1972 and 2000 to contain also the families Caseyidae, Urochordeumatidae, Rhiscosomidae and Apterouridae. A superfamily Caseyoidea was established to accommodate Caseyidae and Urochordeumatidae, and the superfamily Striarioidea includes Striariidae, Rhiscosomidae and Apterouridae. The key character for the suborder is the swollen, button-like, single-articled telopodite of the male ninth leg (except in Apterouridae, where the ninth legs are strongly reduced). Male gonopods are characterized as separate and not fused to the sternite, with two or more angiocoxites and generally with unsclerotized, sac-like colpocoxites.

**Superfamily Striarioidea Cook 1895**

The superfamily Striarioidea includes heavily sclerotized millipeds, each of the included families with characteristic cuticular sculpture, the nature of which can often only be fully examined under the scanning electron microscope. The collum is usually enlarged and at least partly covers the head. The ninth leg telopodites of males are likewise heavily sclerotic and set with thorny tubercles. The anterior gonopod median colpocoxites are appressed in the midline, but the sternum does not extend between them.

**Key to families of Striarioidea**

1a. Collum hood-like, concealing much of the head when seen dorsally; metatergites ornamented with 10–12 macroscopic longitudinal ridges, most of which run the length of the metatergite and which may be elevated into large crests ................................................................................................................................................................. Striariidae.

1b. Collum not hood-like, at most concealing only the posterior margin of the head; metatergites without long ridges or crests, but with paranota............................................................................................................................................... 2.

2a. Collum narrower than head; paranota distinctly bilobed; ninth legs of males reduced to single article, concealed under anterior gonopods.................................................................................................................................................. Apterouridae.

2b. Collum wider than head; paranota not bilobed; ninth legs of males with coxae and single telopodite article, ninth leg coxae with coxites, partially concealing anterior gonopods ............................................................................................................. Rhiscosomidae.

3a. Paranota recurved to acute posteriolateral angle; segmental setae long, thin; epiproct entire, posterior margin evenly curved; spinnerets on posterior margin of epiproct; coxite of ninth legpair with ornament of dentate tubercles similar to telopodite ....................................................................................................................................... Rhiscosomidae.

3b. Paranota not recurved, square in outline (Fig. 4); segmental setae very small, apically branched (Fig. 7); epiproct with two distinct emarginations, giving 3-lobed appearance; spinnerets on ventral margin of epiproct; coxite of ninth legpair exceeding telopodites, without ornament ........................................................................................................... Buotidae, n. fam.

The family Striariidae currently includes three recognized genera, *Striaria* Bollman 1888, *Amplaria* Chamberlin 1941, and *Vaferia* Causey 1958. However, the validity of *Vaferia* is in doubt (Shear & Krejca 2007) and at least five new genera and many new species of striariids from the Pacific states of the United States await description. Apterouridae contains only the genus *Apterourus* Loomis 1966, with two species (Shear 1977, 2003a) from southern California. Rhiscosomidae is also monobasic (*Rhiscosomides* Silvestri
1909), with seven described species and at least an equal number undescribed, found in California, Oregon, Washington and British Columbia. Striarioids are most abundant and diverse in western North America west of the Continental Divide; only some species of *Striaria* and *Buotus carolinus* represent the superfamily in the eastern part of the continent.

**Comparisons with related families.** Argumentation for placing Buotidae in Striarioidea rather than in Brannerioidea is summarized in following table.

<table>
<thead>
<tr>
<th>Character</th>
<th>Brannerioidea</th>
<th>Striarioidea</th>
<th><em>Buotus carolinus</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Epiproct</td>
<td>Margin entire</td>
<td>3-lobed (Striariidae)</td>
<td>3-lobed</td>
</tr>
<tr>
<td>Spinnerets</td>
<td>At dorsal margin of epiproct</td>
<td>Under ventral margin of epiproct (Striariidae)</td>
<td>Under ventral margin of epiproct</td>
</tr>
<tr>
<td>Male 9th leg coxa</td>
<td>No coxite</td>
<td>Coxite present</td>
<td>Coxite present</td>
</tr>
<tr>
<td>Male 9th leg telopodite</td>
<td>2 or more reduced articles</td>
<td>Single bulbous article</td>
<td>Single bulbous article</td>
</tr>
<tr>
<td>Gonopods</td>
<td>Anterior angiocoxites fused as plate; sternal plate present; colpocoxite sclerotic, branched</td>
<td>Anterior angiocoxites separate; no sternal plate; colpocoxite weakly or partially sclerotic, often sac-like</td>
<td>Anterior angiocoxites separate, sternal plate absent, colpocoxite partly sac-like, poorly sclerotized</td>
</tr>
</tbody>
</table>

The main justification for the new family Buotidae lies in the combination of characters found in *Buotus carolinus*, which prevents the species from being confidently assigned to any of the existing families of Striarioidea. *Buotus carolinus* resembles the striariids in the three-lobed epiproct and in the ventral origin of the spinnerets, but differs in that the spinnerets do not fit into shallow depressions in the paraprocts. Undescribed new taxa among striariids are close to the size range of *Buotus*, but these species retain the characteristic hooded collum, metatergal ridges, carinae or crests of their family and so look very different from similar-sized *Buotus*. Metatergal ornament is entirely different. An additional resemblance to striariids that is suggested by careful examination of some of the scanning electron micrographs is the presence of a filmy layer of some kind of secretion over the cuticle of *B. carolinus*. Similar pictures of striariids show that the tergal surfaces are covered by a thick, waxy secretion that seems to originate from pores associated with morate tubercles like those of *Buotus*; the true surfaces of the tergites can only be seen if this waxy layer is scraped away. It cannot be removed by ultrasonic cleaning. Also as in the striariids, the ninth legs of males of *B. carolinus* have prominent coxites, albeit much longer and more prominent ones than seen in any known striariid. However, male striariids have an extensive suite of pregonopodal leg modifications affecting all legpairs from one to seven, many of which are evidently homologous to similar modifications in the distantly related Caseyiidae (and therefore perhaps plesiomorphic for the suborder), while *B. carolinus* has essentially unmodified legs anterior to the gonopods. Rhiscosomomids have broad, recurved paranota, long segmental setae and a very different pattern of metatergal ornament. But like buotids and striariids, they have coxites on the male ninth legs. Apterourids share a broad collum and paranota with rhiscosomomids and buotids, but their male ninth legs are reduced to single segments fused to the sternites and are entirely hidden under the gonopods.

While monobasic families may reduce the information content of the system by obscuring relationships, they also call attention to wide, distinctive morphological gaps between taxa. In this case, with our relatively small knowledge base on the striarioid millipeds, it is possible that the taxon Buotidae may change levels as we learn more, and that further subordinate taxa may be added to it (see Shear 2003a, 2003b, McAllister et al. 2009) for examples in other families).
Buotidae, new family

Type genus: Buotus Chamberlin 1940.

Diagnosis: Unique in Striarioidae in having the coxites of the ninth legs exceeding the telopodites (Fig. 9) and in the unusual metatergal sculpture (Fig. 6). Differing from Striariidae in lacking longitudinal carinae on the metazonites; striariids also have the head mostly or partly concealed by a hood-like collum. Rhiscosomididae have strongly recurved paranota and an entire margin of the epiproct, while in Buotidae the paranota are not recurved and (like Striariidae) the epiproct is three-lobed (Fig. 5). Apterouridae have bilobed paranota and much reduced male ninth legs that are completely concealed in ventral view by the anterior gonopods.

Description: Very small millipedes (less than 4 mm in length; Fig. 1). In single known species, males with 26 trunk segments, females with 28. Head broadest posteriorly (Fig. 2), with coarse ornament of sharp tubercles, ocelli absent but deep-lying pigment spot present on sides of head, possibly representing remnant of reduced ocellus. Antennae short, strongly clavate, fifth segment much the largest. Mandibles with serrate posterior margin on cardo. Collum broader than head, flaring laterally, with characteristic sculpture (Fig. 6). Prozonites of trunk segments bulging, with fine ridges; metazonites bearing short, squared paranota, metazonital sculpture similar to that of collum. Segmental setae small, reduced (Fig. 7). Epiproct (Fig. 5) three-lobed, spinnerets tucked under posterior margin of epiproct; paraaprocts with pair of long setae. Walking legs short, stout; only prefemora are longer than wide. Male pregonopodal legs unmodified. Gonopods (Figs. 8–10) with large, pyramidal sternum, anterior angiocoxites long, blade-like, covering narrower posterior coxites; colpocoxites consisting of poorly sclerotized basal lobe and more sclerotized rod-like part. Male ninth legs (Figs. 8–10) with reduced sternum, coxae bearing long, sinuous coxites flaring at tips; telopodites oval, heavily invested with low, sharp tubercles and setae. Legpairs 10 and 11 with coxal glands, coxae 11 with posterior processes.

Buotus carolinus Chamberlin 1940

Figs. 1–10, Map 1


The original description of Buotus carolinus lacked any diagnostic details, and indeed the species was placed far from its proper position in the Chordeumatidae—in the colobognath family Polyzoniidae, where it resided for more than 40 years until I restudied it (Shear 1981). I revisited the species in 1998 based on the same specimens and added more details regarding the gonopods (Shear & Hubbard 1998). However, the animals are so small (smaller mature males may be only 2 mm long or less) and the gonopods correspondingly minute, that an examination using a scanning electron microscope (SEM) revealed many new details.

Chamberlin (1940) described the species as having a single ocellus, which I found to be a rather poorly defined pigment spot, deep-lying in the head (Shear 1981). The SEM reveals that there is no external expression of this spot whatsoever and no cuticular lens—the characteristic sculpture of the head is continuous over the position of the pigment spot (Figs. 2, 3). The mandible has a posterior serrate margin on the cardo, which just can be seen in Fig. 3 between the first leg and the anterior margin of the collum. The first leg is not reduced in size. The seminal ducts of the male open through pores in the second coxae, as in all chordeumatidans yet studied. The sculpture or ornament of the collum and metaterga differs from the simple acute tubercles of the head (Figs. 2, 3 cf. 4, 6) and consists of a series of irregularly arranged, minute ridges on raised mounds. On the sides of the mounds and scattered among them are morate (mulberry-shaped, from morum, L., a mulberry) tubercles. At the posterior margin of the metazonite, the ridges and tubercles are abruptly replaced with a few rows of sharp-pointed, recurved teeth above the shallowly serrate limbus. The teeth of the limbus serrations are created by small ridges. On more posterior segments, the ridges become
more closely spaced and crowd out most of the interspersed morate tubercles. The segmental setae are very small, only about 20µm long, and hardly detectable using optical microscopy or even at low magnifications under the SEM (try to find them on Fig. 4). It may have been the apparent absence of these setae, characteristic of Chordeumatida, that caused Chamberlin not to consider that order as a place for Buotus. Nevertheless, they are present (Fig. 7); each seta arises from an elongate, tubular socket and presents a single, spiral twist. The tip of the seta is divided into five or six short processes, which give the whole a remarkable resemblance to a human arm and hand! The sculpture of the epiproct (Fig. 5) more closely resembles that of the head. The spinnerets arise, as in striariids (Shear 2008) from beneath the posterior margin of the epiproct; above each spinneret is an emargination in the epiproct which gives it a three-lobed appearance (also as in striariids).

FIGURES 1, 2. Buotus carolinus. 1. Mature female specimen, lateral view. 2. Head of male specimen, dorsofrontal view.
The gonopods (Figs. 8–10) are small even for the size of the animal and the tips of the flattened, blade-like angiocoxtes extend posteriorly between the ninth leg coxites, so that their tips rest in the coxal glands of the tenth legpair. Further details of the gonopods can be seen in Shear (1981) and Shear and Hubbard (1998). The ninth legs of males are typical of striarioids, with a well-sclerotized coxosternum (Fig. 8); from the coxal portion arise long, sinuate coxites with broad tips, that arch over the recumbent gonopods and probably serve to protect them (Figs. 8, 9). The telopodites are heavily sclerotized and set with acute tubercles and setae. Except for gland openings, the tenth coxae are not modified or enlarged, but the eleventh coxae have large, blunt posterior processes.


**Natural history and distribution of *B. carolinus***. Collections of *B. carolinus* have rarely been made by hand-searching, though R. L. Hoffman, W. A. Shear and R. M. Shelley found three specimens sorting leaf litter on Brush Mountain, Montgomery Co., Virginia, in March, 1976. All of the new records below are from Berlese samples of deciduous leaf litter, several from rhododendron, but also from litter under oak, cherry or beech. At least two localities are beside streams. Even using the Berlese technique, most samples consist of a single individual, rarely up to 3–5 specimens. *Buotus* specimens are easily overlooked; the species is a strong
contender for the title of the world’s smallest milliped, with males usually less than 3 mm, and some scarcely
2 mm long. Females rarely exceed 4 mm even if well-extended. In addition, my recent collections from
Quaker Field Branch, Campbell Co., Virginia, came from the deepest layers of duff, where litter and debris
had accumulated to a depth of nearly 20 cm. Most of the specimens have been taken at elevations at or
exceeding 3000 feet (1022 m), though the type locality is the North Carolina piedmont at an elevation of
about 350 ft. (106 m).

FIGURES 7–10. Buotus carolinus. 7. Lateral segmental seta from metatergite 12, dorsal view. 8–10 Gonopods (blue)

It is curious that all records aside from the type locality are from the Appalachians of Virginia and West
Virginia. Despite extensive collecting by R. M. Shelley and others in the North Carolina piedmont, the species
has not been found there since Causey’s collection of a single female in 1939. In his 1940 paper, most of the
specimens Chamberlin reports on are indeed from the Duke Forest, but a few came from other localities in the
North Carolina Appalachians. It is possible the Buotus specimens were only assumed to be from the Duke
Forest, but in fact came from one of the Appalachian localities. This hypothesis is weakened by the failure of
anyone to find the species in the North Carolina mountains, where extensive collecting has been done by
many people over the seven decades since 1939.

MAP 1. Distribution of Buotus carolinus. The type locality in Durham Co., North Carolina, is not shown but is about 110 miles (177 km) southeast of the nearest other localities, in Patrick Co., Virginia.

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Literature cited


