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# *Carinobolus* gen. nov. and *Costabolus* gen. nov., two new, remarkably crested, monospecific genera of spirobolidan millipedes from West Africa, with the proposal of a new tribe, Amblybolini tribus nova (Diplopoda, Spirobolida, Pachybolidae)

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## Abstract

Two new genera, *Carinobolus* **gen. nov.** and *Costabolus* **gen. nov.**, both belonging to the very large, widespread, pantropical family Pachybolidae, are described based on *Carinobolus complex* **sp. nov.** and *Costabolus baculus* **sp. nov.**, respectively. Chiefly based on the posterior gonopod being distinctly articulated at midlength, both new genera seem to be especially similar to *Amblybolus* Keeton, 1964a (three species in western Africa) and *Atlanticobolus* Hoffman, 1979 (one species from an island off the Brazilian coast), all of them meriting a separate tribal category, Amblybolini **tribus nova**. A key is proposed to distinguish all four presently accepted genera of the new tribe. The new genera and species are clearly distinguished in showing unusually strongly crested/ribbed metazonae, a character that is only very seldom observed in Pachybolidae generally, and apparently unique among Afrotropical members. Being rather similar in many respects, both new genera and species differ from each other sufficiently well in gonopodal and leg structure, even though both come from forests in southeastern Nigeria close to the border to Cameroon.

**Key words:** Afrotropics, key, new species, Nigeria, taxonomy

## Introduction

The highly diverse, widespread and basically tropical millipede order Spirobolida is one of the largest in the whole class Diplopoda, presently known to comprise 900+ species, 120+ genera, and 8–11 families in three suborders (Pitz & Sierwald 2010; Enghoff *et al*. 2015). Despite such an outstanding diversity, Spirobolida with distinctly ornamented bodies are surprisingly few. Thus, the Papuan genus *Acanthiulus* Gervais, 1844, both accepted species of which, i.e., *A. blainvillei* (Leguillou, 1841), the type-species, polymorphous and widespread, endemic to New Guinea and the adjacent Aru Archipelago, and *A. subcostulatus* Golovatch, 2021, from Papua New Guinea, show more or less evident longitudinal crests, carinae or costulae, often also strong spines, on most metazonae (Golovatch *et al*. 2021; Golovatch 2021). Superficially, *Eucentrobolus* Pocock, 1903, with the sole currently recognized, and type species *E. maindroni* (Bouvier, 1903), from southern India, so strikingly resembles *Acanthiulus* that it was originally described in the latter genus (Bouvier 1903; Golovatch & Wesener 2016). The smallest and shortest Pachybolidae, also from southern India, *Komphobolus* Carl, 1941, monospecific, with *K. mimicus* Carl, 1941, albeit acarinate, shows two peculiar, stout, dorsal projections flanking the epiproct (Carl 1941). Finally, Porat (1894) described three strongly carinated juliformian species from Cameroon, one of which he erroneously assigned to *Acanthiulus*; however, presently all these three species are treated within the order Spirostreptida (Golovatch *et al*. 2021). As a result, no Spirobolida ribbed similarly to *Acanthiulus* have unequivocally been recorded yet from Africa.

The more so important seems to be the discovery of as many as two monospecific genera of strongly carinate Pachybolidae in Nigeria. Both are quite similar to each other in sharing numerous traits, including the ribbed metazonae and the peculiar gonopodal conformation, especially the two-segmented posterior gonopod. Overall, they seem to be particularly similar to the acarinate genera *Amblybolus* Keeton, 1964a (three species in western Africa) and

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*Atlanticobolus* Hoffman, 1978 (one species from an island off the Brazilian coast), all rather small (30–40 mm long) and short (only 36–38 body rings), with a well-developed antennal groove etc. (cf. Hoffman 1978; Enghoff *et al*. 2015), chiefly because the posterior gonopod is distinctly articulated at midlength. A new tribe, Amblybolini **tribus nova**, is thereby proposed to accomodate these four genera.

The present paper continues our efforts in revealing the remarkably rich and diverse millipede fauna of tropical Africa.

## Material and methods

This study is based on material borrowed from the NHMD and VMNH collections. All samples are stored in 70% ethanol. Photographs were taken with a Leica DFC 500 digital camera mounted on a Leica MZ16A stereo microscope. Images were processed with a Leica Application Suite programme. Following a "destructive analysis agreement" signed between the VNHM and the RMCA, specimens for scanning electron microscopy (SEM) were air-dried, mounted on aluminium stubs, coated with gold and studied using a JEOL JSM-6480LV scanning electron microscope. Line drawings were prepared using a camera lucida. A distribution map was produced by plotting the coordinates of the type locality (Calabar) on a free blank map (Wikipedia Commons).

## Museum collection acronyms and abbreviations:

**NHMD**: Natural History Museum of Denmark (Zoological Museum), University of Copenhagen, Denmark
**RMCA**: Royal Museum for Central Africa, Tervuren, Belgium
**SEM**: Scanning Electron Microscopy
**VMNH**: Virginia Museum of Natural History, Martinsville, VA, U.S.A.

Abbreviations of particular structures are explained directly in the figure captions and in the text.

## Results

### Class Diplopoda de Blainville in Gervais, 1844

### Order Spirobolida Cook, 1895

### Family Pachybolidae Cook, 1897 *sensu* Hoffman, 1980

### *Carinobolus* gen. nov.

Type species: *Carinobulus complex* **sp. nov.**, by present designation.

**Name.** To reflect the bimodally crested metazonae characteristic of the genus, and '-bolus', a common suffix for genus-group names in the Spirobolida; masculine in gender.

**Diagnosis.** This new genus and species is remarkable not only in the bimodally crested metazonae (slightly, but clearly concave in the middle), which in itself is unique in the family, but also in the anterior gonopods being particularly elaborate and complex, multiramous and rather palm-shaped. In addition to the bimodal crests, *Carinobolus* **gen. nov.** differs from the similar *Costabolus* **gen. nov.** by the absence of prominent prefemoral protuberances from male legs 2 and of prominent coxal protuberances from male legs 3, and by the overall shape of the anterior gonopods which are palm-like rather than subtriangular. See also Key below.

**Distribution.** Only known from the type locality in southeastern Nigeria (Fig. 8).

***Carinobolus complex* sp. nov.**
Figs 1–3

**Material examined.** Holotype male (NHMD), southeastern NIGERIA, 56 km from Calabar, 13.VI.1963, collector unknown.

Paratypes: 1 male, 1 female (NHMD), 1 male (SEM, RMCA), same data as holotype.

**Name**. Complex, a noun in apposition referring to the particularly complex anterior gonopods.

**Diagnosis**. Basically as in the genus. Body short, up to 26 mm long, with 38 body rings plus telson. Metazonae bimodally crested, epiproct slightly projecting caudally. Tarsal pads present, coxal projections absent. Legs and antennae short. Anterior gonopods particularly complex, multiramous, rather palm-shaped, with a paramedian pair of antero-apical processes and a two-segmented telopodite.

**Description.** *Measurements*: male holotype with 39 body rings (38 + telson), ca 26 mm long, 3 mm wide. Male paratypes same as holotype; female paratype slightly longer than male (ca 28 mm long), broken into several pieces.


**FIGURE 1**. *Carinobolus complex* **sp. nov.**, male holotype (NHMD). **A**. Habitus, lateral view. **B & C**. Anterior part of body, lateral and ventral views, respectively. **D**. Posterior part of body, ventral view. **Scale bars:** 4 mm (**A**), 1 mm (**B–D**).

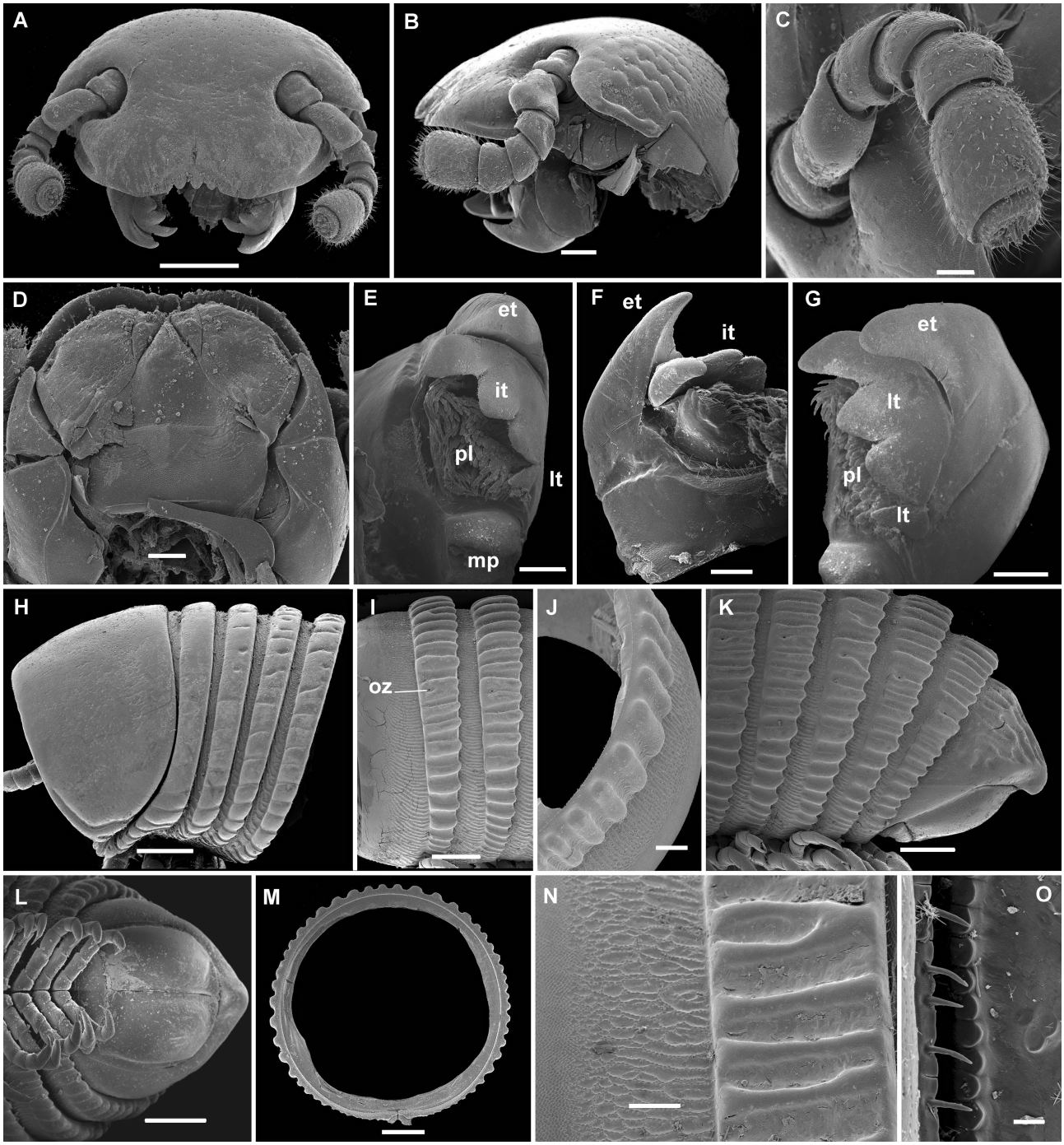


**FIGURE 2**. *Carinobolus complex* **sp. nov.**, male paratype (RMCA). **A & B**. Head, frontal and lateral views, respectively. **C**. Tip of antenna, sublateral view. **D**. Gnathochilarium, ventral view. **E**, **F & G**. Right mandible, submesal, mesal and subfrontal views, respectively. **H**. Anterior part of body, lateral view. **I**. Midbody rings with ozopores (oz), lateral view. **J**. A midbody metazona showing bimodal crests. **K & L.** Posterior part of body, lateral and ventral views, respectively. **M**. Cross-section of midbody ring, frontal view. **N**. Details of a midbody ring, lateral view. **O**. Limbus of a midbody ring, lateral view. **Abbreviations**: **et**, external tooth; **it**, internal teeth; **lt**, lateral tooth; **mp**, molar plate; **oz**, ozopore; **pl**, pectinate lamella. **Scale bars:** 500 µm (**A**, **I**, **K**, **L**, **M**), 200 µm (**B**, **D**, **H**, **J**), 100 µm (**C**, **E**, **F**, **G**, **N**), 10 µm (**O**).

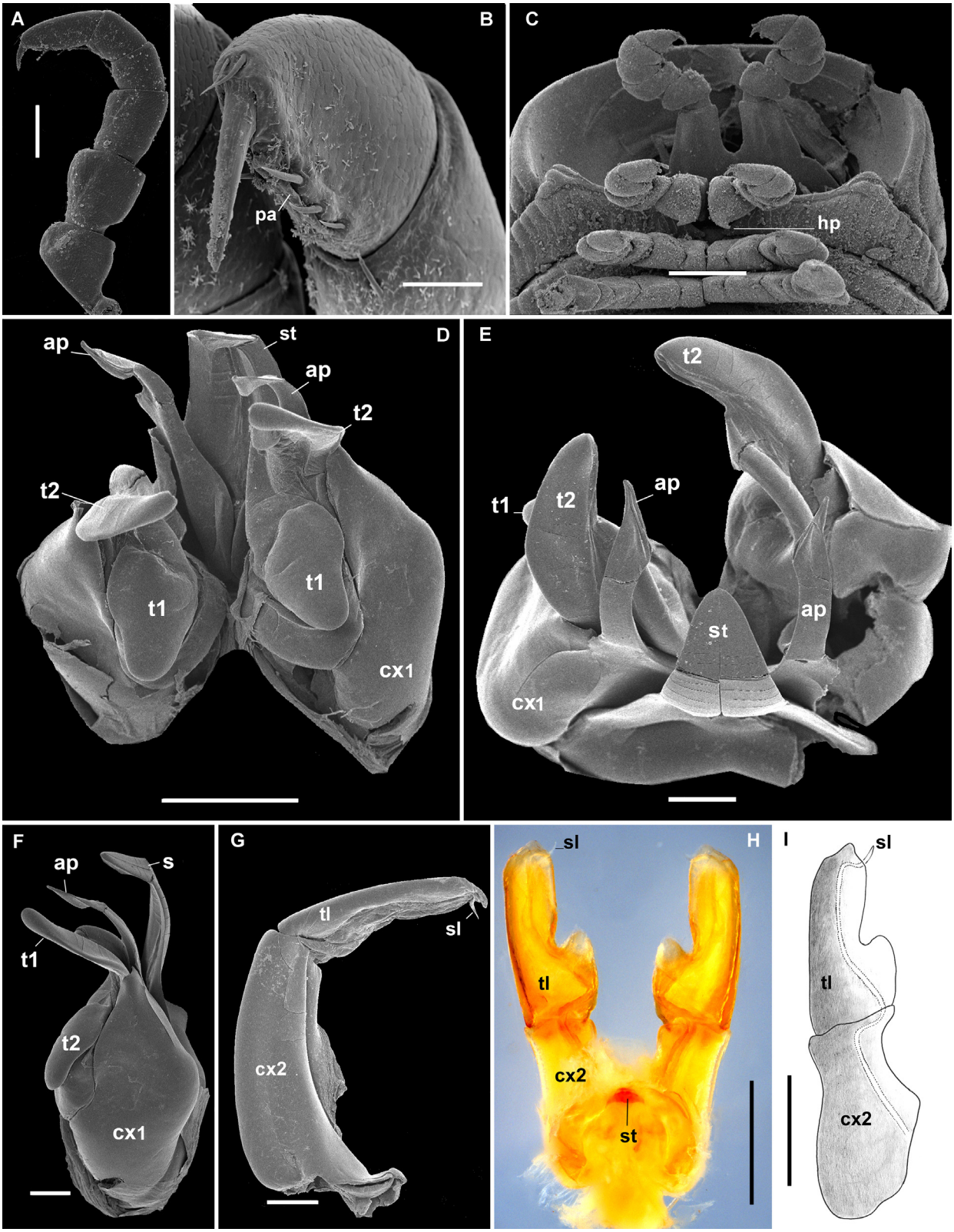


**FIGURE 3**. *Carinobolus complex* **sp. nov.**, male paratype (RMCA). **A**. Midbody leg, lateral view. **B**. Apical parts of a post-gonopodal leg with a tarsal pad, subventral view. **C**. First three legs, ventrocaudal view. **D & E**. Anterior gonopods, posterior and anterior views, respectively. **F**. Left anterior gonopod, lateral view. **G.** Right posterior gonopod, lateral view. **H**. Posterior gonopods**,** caudal view**. I**. Drawing of right posterior gonopod, caudal view. **Abbreviations**: **ap**, antero-apical process; **cx1**, coxite of anterior gonopod; **cx2**, coxite of posterior gonopod; **hp**, basal projection of prefemur 2; **pa**, tarsal pad; **sl**, solenomere; **st**, sternite; **t1** and **t2**, telopoditomeres 1 and 2; **tl**, telopodite. **Scale bars:** 200 µm (**A**, **E**, **F**, **G**), 50 µm (**B**), 500 µm (**C**, **D**), 0.5 mm (**H**, **I**).

*Coloration* faded in alcohol, but two darker stripes still visible on each side of body. Head, antennae, legs and telson slightly brownish, ommatidia and medial part of frons dark brown (Fig. 1).

*Head* capsule with a median suture, this being especially distinct on labrum; ca 20 ommatidia located in an irregular oval cluster (Fig. 2B). Labrum as usual, with three irregular teeth and a single row of 10–12 stout marginal setae. Clypeus with two setiferous foveolae on each side (Fig. 2A). Incisura lateralis closed (Fig. 2B). Antennal cavity/groove present, antennae shorter than body diameter. Relative lengths of antennomeres: 3=4=5<1<6<2 (Fig. 2A, B). Terminal antennomere with four large sensory cones clustered together inside a membranous area. Antennomeres 5 and 6 each with an apicolateral field of specialized sensilla (Fig. 2C).

*Gnathochilarium* as usual, of spirobolidan conformation. Stipites separated in basal portion, each bearing three apical setae, but not setose on ventral surface. Lamellae linguales separated by anterior portion of mentum (Fig. 2D), each with two usual setae located behind one another, mentum devoid of a large swollen area apically between both lamellae linguales, but subdivided basally by a well-marked suture (Fig. 2D).

*Mandible:* external tooth (**et**) large and prominent, inner tooth (**it**) with three smaller inner teeth, a thin lateral tooth (**lt**), five rows of pectinate lamellae (**pl**), molar plate (**mp**) with a few (2–3) transverse furrows (Fig. 2E–G).

*Collum*, with a prominent groove along anterior margin, lateroventral margin broadly rounded, not extending ventrad as far as ventrolateral corner of body ring 2 (Fig. 2H).

*Body rings:* Metazonae heavily crested/ribbed, crests being bimodal, slightly, but clearly concave in the middle (Figs 1A, B, 2H–K, M, N); mesozonae with longitudinal impressions, these being especially clearly visible ventrally; pre-anal ring with dorsal tip of epiproct clearly overhanging the paraprocts (Fig. 2K); hypoproct rounded; anal valves well-rounded and devoid of spines or setae. Posterior margin of paraprocts in lateral view without distinct lips (Figs 1D, 2L). Ozopores (**oz**) small and inconspicuous, starting with ring 6 (Fig. 2I), suture between putative pleurotergite and sternite visible. Pleurotergal tips of body ring 2 gaping ventrally, not connected to sternite; pleurotergal tips of body ring 3 fused to sternite and forming a complete ring. Pleurotergal tips of male body ring 7 fused ventrally. Limbus membranous, overtopped by a row of short, parallel and regularly spaced spinicles (Fig. 2O).

*Legs:* Male leg-pairs 1 and 2 modified, coxae of legs 1 fused medially at base only, each prefemur of legs 2 with a small, unciform, basal projection (Fig. 3C, **hp**). Midbody legs ca 0.5 x body diameter, with coxa as long as the other podomeres. Tarsus ventrally with three pairs of spines and apically with a pair of setiform spines (Fig. 3B). Male tarsi 3 up to midbody legs with a tarsal pad not protruding past base of claw (Fig. 3B, **pa**). Tarsal claw of male leg pair 1 normal in size, subequal to tarsal claws of postgonopodal legs (Fig. 3A, B).

*Anterior gonopods* (Fig. 3D–F) especially complex, clearly branched; sternite (**st**) elongated into a triangular process with a blunt tip; a paramedian pair of slender, membranous, acuminate, antero-apical processes (**ap**); coxite (**cx1**) subtending much of anterior gonopods; telopodites 2-segmented, each consisting of a smaller, roundish, basal telopoditomere (**t1**) and a much larger, higher, complex, lobe-shaped, distal telopoditomere (**t2**).

*Posterior gonopods* (Fig. 3G–I) connected by a small, triangular, sclerotized sternite (**st**), clearly and rather regularly curved, slender, 2-segmented, both segments (a thicker and slightly longer coxite (**cx2**) and a more slender and shorter telopodite (**tl**) distinctly separated near midway subtransversely by a deep seminal groove; a rudimentary solenomere (**sl**) subapically. Sperm channel running at mesal margin of coxite through telopodite's subapical part (Fig. 3I).

*Vulvae* in the single female missing (apparently, removed and lost by Richard L. Hoffman at VNHM).

### *Costabolus* gen. nov.

Type species: *Costabolus baculus* **sp. nov.**, by present designation.

**Name**. Reflecting the longitudinal costae/ribs on the metazonae, and '-bolus', a common suffix for genus-group names in the Spirobolida; masculine in gender.

**Diagnosis**. Distinguished from all pachybolid genera but *Carinobolus* **gen. nov.** by strongly crested metazonae, from *Carinobolu*s **gen. nov.** by the crests being simple, even, not bimodal, by the presence of prominent prefemoral protuberances on male legs 2 and of prominent coxal protuberances on male legs 3, and the anterior gonopods being subtriangular in overall shape, *vs*. rather palm-shaped in *Carinobolu*s **gen. nov.** See also Key below.

**Distribution.** Only known from the type locality in southeastern Nigeria (Fig. 8).

***Costabolus baculus* sp. nov.**
Figs 4–7

**Material examined.** Holotype male (with exposed gonopods, body broken into two pieces) (VNHM 198), Nigeria, 27 km NE of Calabar, 20 m inside native forest, 12.VIII.1984, collector unknown.

Paratypes: 2 males (VNHM 198), same data as holotype; 1 female (VMNH 154), Nigeria, 27 km NE Calabar (Ekang road), under logs on fairly dry soil in new canopy forest farmed to young maize, 28.IV.1984, collector unknown; 1 male, 1 female (VMHN 199), Nigeria, 27 km N of Calabar, between trees, native forest, 20 m off logging road, 12.VIII.1984, collector unknown.

**Name**. *Baculus* in Latin means "crutch", referring to the long coxal processes on male legs 2 and 3; a noun in apposition.

**Diagnosis**. Basically as in the genus. Body short, up to 27 mm long, with 38 body rings plus telson, metazonae with simple longitudinal crests/ribs, epiproct slightly projecting caudally. Male with tarsal pads and prominent coxal projections on leg-pairs 2 and 3.


**FIGURE 4**. *Costabolus baculus* **sp. nov.**, male holotype (VNHM 198). **A & B**. Habitus, lateral and ventral views, respectively. **Scale bars:** 5 mm.

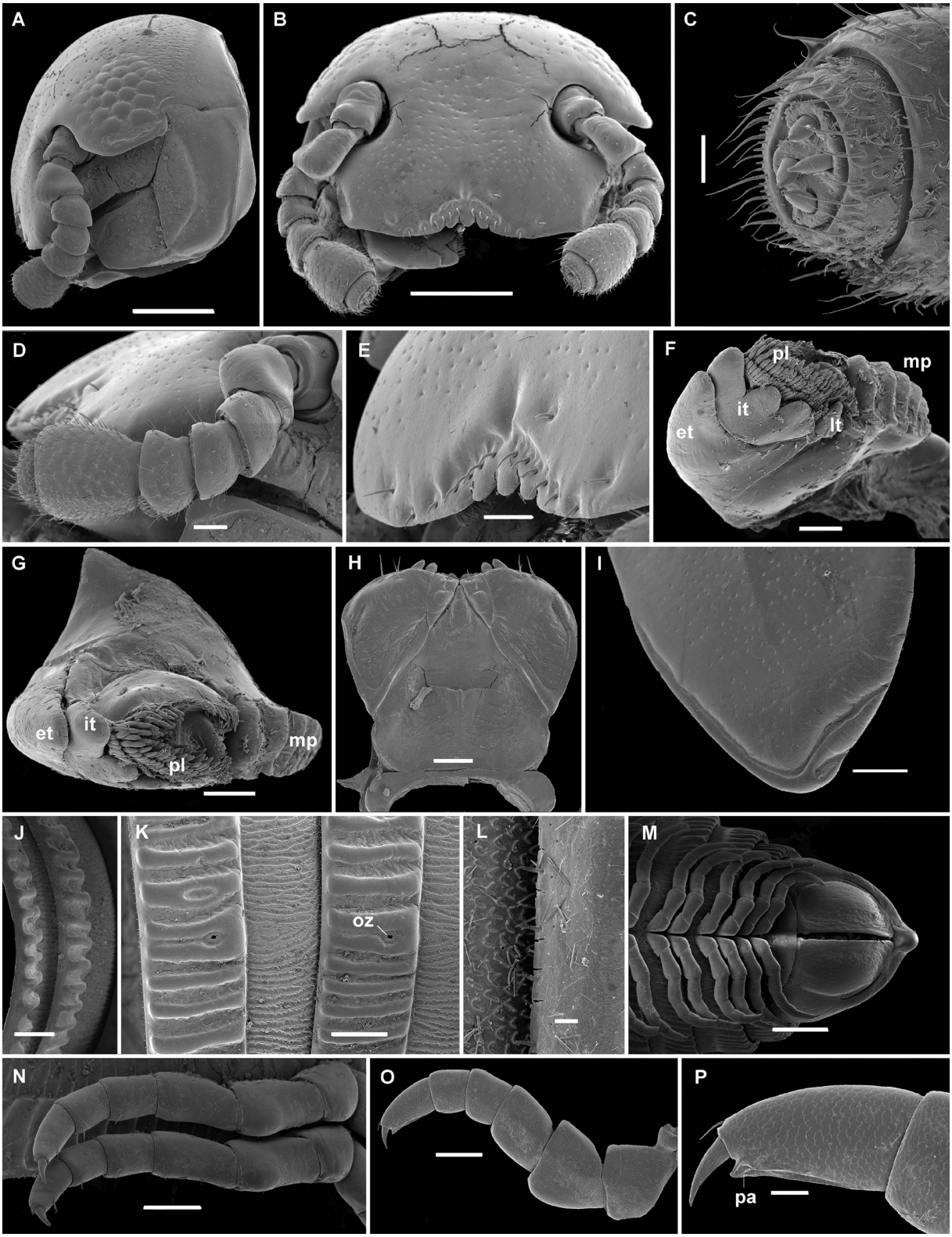


**FIGURE 5**. *Costabolus baculus* **sp. nov.**, male paratype (VNHM 198). **A & B**. Head, lateral and frontal views, respectively. **C**. Tip of antenna. **D**. Left antenna, lateral view. **E**. Clypeus, frontolateral view. **F & G**. Mandible, ventral and mesal views, respectively. **H**. Gnathochilarium, ventral view. **I**. Right lateral margin of collum, lateral view. **J**. A midbody metazona. **K**. Ozopore. **L**. Limbus of a midbody ring. **M**. Posterior part of body, ventral view. **N & O**. Midbody legs, ventral and lateral views, respectively. **P**. Tarsus of a midbody leg, lateral view. **Abbreviations: et**, external tooth; **it**, internal teeth; **lt**, lateral tooth; **mp**, molar plate **oz**, ozopore; **pa**, tarsal pad; **pl**, pectinate lamella. **Scale bars:** 500 µm (**A**, **B**), 100 µm (**D**, **E**, **F**, **G**), 50 µm (**C**, **P**), 200 µm (**L**, **H**, **J**, **K**, **N**, **O**), 10 µm (**L**).

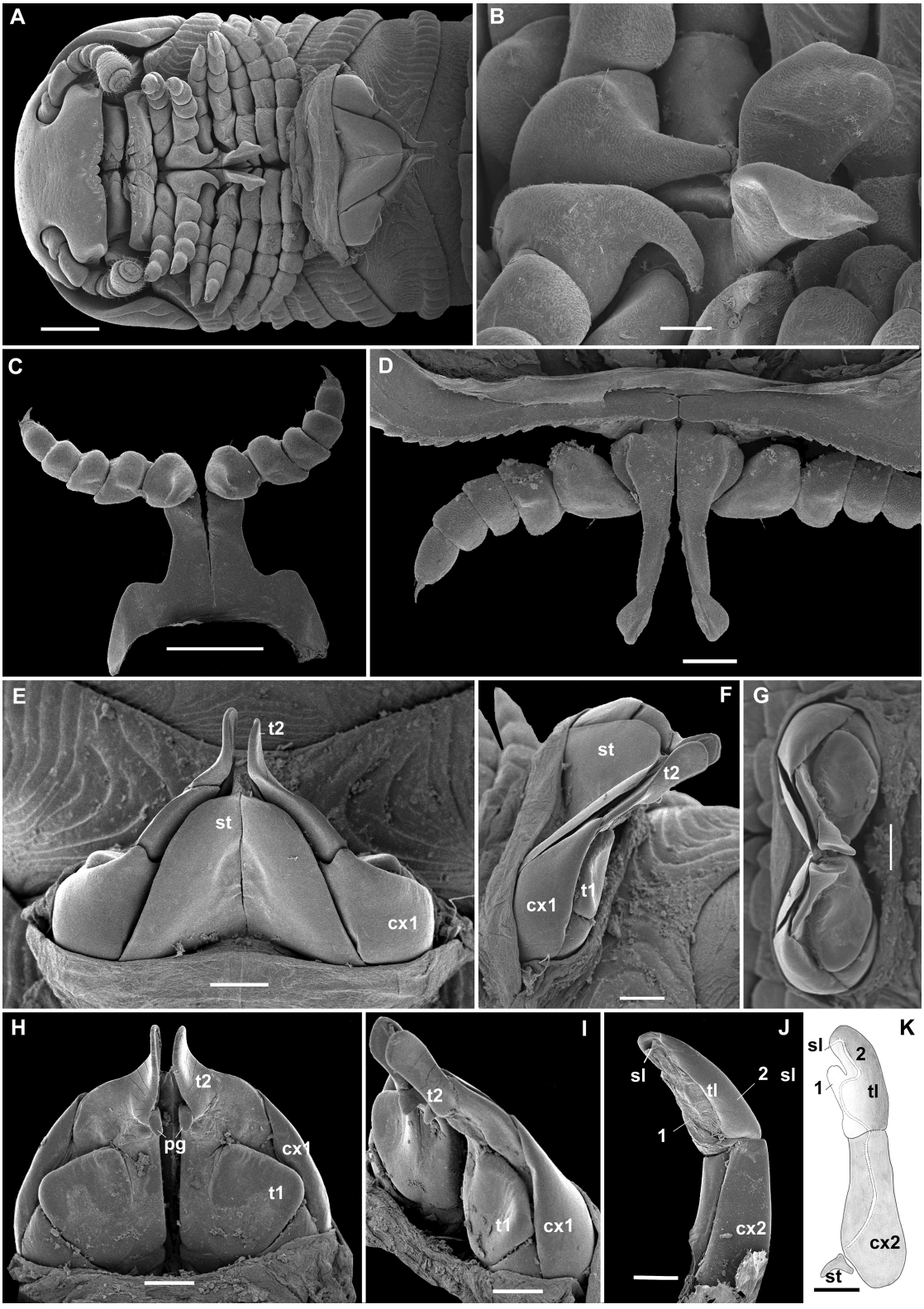


**FIGURE 6**. *Costabolus baculus* **sp. nov.**, male paratype (VNHM 198). **A**. Anterior part of body, ventral view. **B**. Coxal projections on leg-pairs 2 and 3. **C**. Leg-pair 2, posterior view. **D**. Leg-pair 3, posterior view. **E-I**. Everted gonopod block, anterior, ventrolateral, ventral, posterior and posterolateral views, respectively. **J**. Right posterior gonopod, lateral view. **K.** Drawing of left posterior gonopod, caudal view. **Abbreviations**: **1**, median membranous area of telopodite; **2**, lateral sclerotized area of telopodite; **cx1**, coxite of anterior gonopod; **cx2**, coxite of posterior gonopod; **pg**, posterior gonopod; **hp**, basal projection of prefemur 2; **st**, sternite; **sl**, solenomere; **t1** and **t2**, telopoditomeres 1 and 2 of anterior gonopod; **tl**, telopodite of posterior gonopod. **Scale bars:** 500 μm (**A**, **C**), 100 μm (**B**), 200 μm (**D**, **E**–**K**).

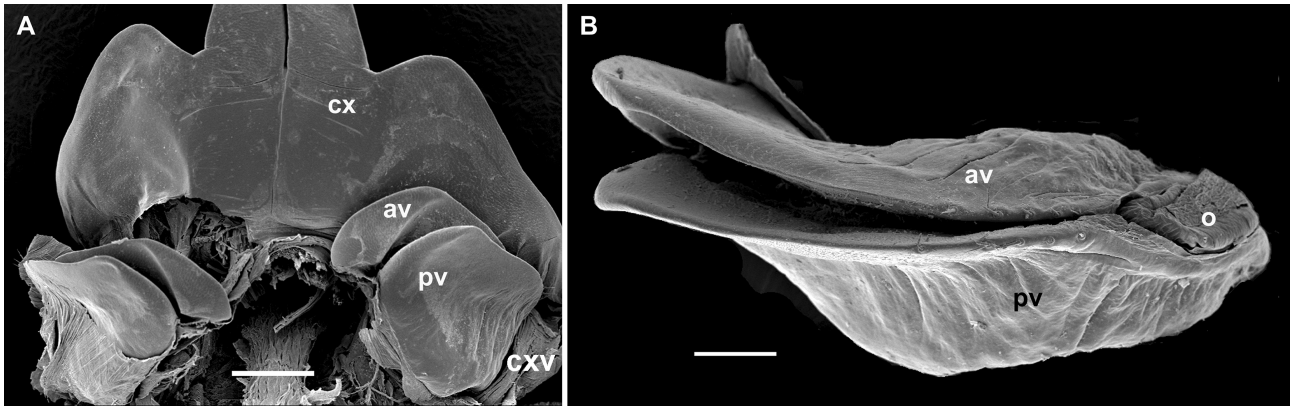


**FIGURE 7**. *Costabolus baculus* **sp. nov.**, female paratype (VMNH 154). **A**. Ventral view of both vulvae, **B**. Left vulva, lateral view. **Abbreviations: av**, anterior valve; **cx**, coxite of leg 1; **cxv**, coxite of vulva; **o**, operculum; **pv**, posterior valve. **Scale bars:** 500 µm (**A**), 200 µm (**B**).

**Description.** *Measurements*: male holotype with 39 body rings (38 + telson), ca 27 mm long, 3 mm wide. Paratypes, both male and female, same as holotype.

*Coloration* faded in alcohol, but a darker pattern still visible dorsally and laterally, yellowish ventrally. Head, ommatidia and anterior part of collum dark brown, antennae, legs and telson yellowish (Fig. 4).

*Head* capsule with an axial suture, this being especially distinct on labrum; ca 22 ommatidia located in an irregular oval cluster (Fig. 5A).

*Labrum* as usual, with three irregular teeth and a single row of 12 stout marginal setae. Clypeus with two setiferous foveolae on each side (Fig. 5E). Incisura lateralis closed (Fig. 5A, D). Antennal cavity/groove present, length of antennae ca 1.3 mm; antennae shorter than body diameter. Relative lengths of antennomeres: 3=4=5<1<6<2 (Fig. 5D). Terminal antennomere with four large sensory cones clustered together inside a membranous area (Fig. 5C). Antennomeres 5 and 6 each with an apicolateral field of specialized sensilla (Fig. 5D).

*Gnathochilarium* as usual, of spirobolidan conformation. Stipites separated in basal portion, each bearing three apical setae, but no setae on ventral surface. Lamellae linguales separated by anterior portion of mentum, each with two usual setae located behind one another; mentum without a large swollen area apically between both lamellae linguales, subdivided basally by a well-marked suture (Fig. 5H).

*Mandible:* external tooth (**et**) prominent, inner tooth (**it**) with three smaller inner teeth, a thin lateral tooth (**lt**), six rows of pectinate lamellae (**pl**), molar plate (**mp**) with five transverse furrows (Fig. 5F, G).

*Collum* with a prominent groove along anterior margin, lateroventral margin broadly rounded, not extending ventrad as far as ventrolateral corner of body ring 2 (Fig. 5I).

*Body rings:* Metazonae heavily crested (Fig. 5J–L); mesozonae with longitudinal impressions, these being especially distinct ventrally (Fig. 5K), caudal fringe/limbus membranous, with very small and regularly spaced spinicles (Fig. 5L). Pre-anal ring with a small dorsal tip of epiproct overhanging the paraprocts (Figs 4A, 5M); hypoproct rounded; paraprocts (anal valves) well-rounded and devoid of spines or setae (Fig. 5M). Posterior margin of paraprocts in lateral view without distinct lips (Fig. 5M). Ozopores (**oz**) starting with body ring 6.

*Legs:* Midbody legs ca 1.4 mm long, with prefemur longer than coxa and as long as the other podomeres; with small tarsal pads (**pa**) (Fig. 5O, P). Male tarsi 3 up to midbody legs with a small tarsal pad not protruding past base of claw, and with a pair of setiform apical spines (Fig. 6D). Male leg-pairs 1, 2 and 3 modified, coxae 1 fused medially at base only, each prefemur 2 with a well-developed, unciform, basal projection (**hp**) (Fig. 6B, C), each coxa 3 with a long and spoon-shaped coxal process (**cp**), this being almost as long as the leg itself (Fig. 6B, D).

*Anterior gonopods* stout and relatively simple (Fig. 6E–I); sternite (**st**) produced into a wide, broadly rounded lobe, bearing clear traces of axial fusion (Fig. 6E); coxite (**cx1**) subtending much of anterior gonopods; telopodites basically 2-segmented, each consisting of a smaller, roundish, apically flattened, basal telopoditomere (**t1**) with a very small, accessory, subtriangular segment at base (Fig. 6H, I), and a much larger, lobe-shaped, distal telopoditomere (**t2**).

*Posterior gonopods* (Fig. 6J, K, **pg** in H) *in situ* almost completely concealed inside anterior gonopods, clearly divided into a slender coxite (**cx2**) and a shorter telopodite (**tl**), both being slender (Fig. 6J) and connected by a

tiny triangular sternite. Telopodite consisting of two components: (1) a median membranous area, and (2) a lateral sclerotized area. Sperm channel running at mesal margin of coxite through telopodite's membranous area, ending up subapically on a rudimentary solenomere (**sl**) (Fig. 6J, K).

*Paratypes. Males* as holotype. *Female* similar in size and appearance to males, but devoid of prefemoral or coxal projections on leg-pairs 2 and 3, respectively. Vulva simple, consisting of two simple, sclerotized plates, bivalve-like and subequal in size (Fig. 7). Both coxite (**cxv**) and operculum (**o**) of vulva very small and inconspicuous. Both valves only basally with one row of setae directed towards the opening. Anterior valve (**av**) slightly larger than posterior one (**pv**) (Fig. 7).

## Tribal position

The above results show that the fauna of Afrotropical Spirobolida is still quite poorly known. This seems to hold especially true of the *Amblybolus*-like Pachybolidae whose systematics and evolutionary relationships still remain largely unresolved (Enghoff *et al.* 2015).

Just a single tribe, Pachybolini, has been delimited so far in the entire family Pachybolidae, one that encompasses only very few genera in western and eastern tropical Africa, as well as one genus from Madagascar (Wesener *et al.* 2008; Enghoff 2011). None of the remaining numerous pachybolid genera have been assigned to a tribe yet.

Taking the definition of Pachybolini as a model (Wesener *et al.* 2008), we are able to formulate the following diagnosis of Amblybolini **tribus nova** as its counterpart, in order to harbour the genera *Amblybolus* (= *Tonkouibolus* Demange & Mauriès 1975a, synonymized by Hoffman 1979, 1980) (Keeton 1964a, 1964b; Demange & Mauriès 1975a, 1975b), *Atlanticobolus* (Hoffman 1979; Enghoff *et al.* 2015), *Carinobolus* **gen. nov.**, and *Costabolus* **gen. nov.**

## Amblybolini new tribe

**Type genus: *Amblybolus* Keeton, 1964a**

= *Tonkouibolus* Demange & Mauriès 1975a, synonymized by Hoffman (1979).

**Type species:** *Amblybolus mitis* Keeton, 1964b, from Mount Coffee and Bushrod Island near Monrovia, Liberia (Keeton 1964b), by monotypy.

## Other species included:

*Amblybolus flagellatus* (Demange & Mauriès 1975a), from the summit of Mont Tonkouï, Ivory Coast (Demange & Mauriès 1975a), the type species of *Tonkouibolus*, by monotypy.

*Amblybolus levieuxi* (Demange & Mauriès 1975b), from Téké Forest near Abidjan, Ivory Coast (Demange & Mauriès 1975b).

All three species have been keyed by Hoffman (1979).

## Other genera included:

### *Atlanticobolus* Hoffman, 1979

**Type species:** *Spirobolus noronhensis* Pocock, 1890, from Ilha Fernando de Noronha, Brazil (Pocock 1890), by subsequent designation (Hoffman 1979).

No other species known.

***Carinobolus* gen. nov.**

**Type species:** *Carinobolus complex* **sp. nov.**, from Nigeria, by present designation.
No other species known.

***Costabolus* gen. nov.**

**Type species:** *Costabolus baculus* **sp. nov.**, from Nigeria, by present designation.
No other species known.

**Diagnosis**. A tribe of the family Pachybolidae characterized by the following putative apomorphies or synapomorphies:

- incisura lateralis closed (Figs 2B, 5D), a synapomorphy shared with Pachybolini (Wesener *et al.* 2008);

- setae on lamellae linguales apical (Figs 2D, 5H), a synapomorphy shared with Pachybolini (Wesener *et al.* 2008);

- vulva subreniform and bivalve (Fig. 7A, B), a synapomorphy shared with Pachybolini (Wesener *et al.* 2008), but devoid of a central ridge, this being an apparent plesiomorphy.

- both posterior gonopods mostly connected by a tiny sternite, each distinctly biarticulate near midlength (Figs 3G–I, 6J–K), telopodite clearly twisted based on a subtransverse course of the seminal groove dividing the coxite and telopodite.

**Key to the accepted four genera of Amblybolini tribus nova:**

1(2) Metazonae smooth, only slightly vaulted at most. . . . . 3
2(1) Metazonae strongly carinate (Figs 1 and 4) . . . . . 5
3(4) Antennal groove/cavity below eyes shallow. Posterior gonopods suberect, devoid of a central sternal rudiment. . . . *Amblybolus*
4(3) Antennal groove/cavity below eyes very deep and clear-cut. Posterior gonopods strongly curved and showing a small, but distinct, central, sternal rudiment . . . . . *Atlanticobolus*
5(6) Metatergal crests simple, even, not concave in the middle. Prominent prefemoral or coxal protuberances present on male legs 2 and 3, respectively. Anterior gonopods subtriangular in overall shape (Figs 4–7) . . . . . *Costabolus* **gen. nov.**
6(5) Metatergal crests bimodal, slightly, but clearly concave in the middle. Male legs 2 and 3 devoid of prefemoral or coxal protuberances. Anterior gonopods more complex and palm-shaped in overall shape (Figs 1–3) . . . . . *Carinobolu*s **gen. nov.**

## Conclusion

As a result, the only remarkable and clear-cut apomorphy that defines the Amblybolini **tribus nova** as opposed to the remaining Pachybolidae, including the tribe Pachybolini, is the structure of the posterior gonopod, in particular its being biarticulate near midlength, and the telopodite twisted against the coxite as the course of the seminal groove distinctly shows. It seems also noteworthy that all species of Amblybolini **tribus nova** appear to be among the smallest and shortest Spirobolida known to date.

Biogeographically, the delimitation of the new tribe also makes sense, since most of the generic diversity of Pachybolidae is confined to tropical Africa (Enghoff *et al.* 2015). The distribution of Amblybolini **tribus nova** is rather coherent, too, three genera being encountered in western Africa (two nearly sympatric, Fig. 8). Only *Atlanticobolus* superficially represents an outlier found on a small island off the Atlantic coast of Brazil. However, it seems very likely to have been introduced from Africa or South America, either through commerce or because the island lies astride the South Equatorial Current, or both (Hoffman 1979).


**FIGURE 8**. Distributions of *Carinobolus complex* **sp. nov.** and *Costabolus baculus* **sp. nov.**

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