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The Giant Pill-Millipedes of Madagascar

Revision of the Genus *Sphaeromimus*, with a Review of the Morphological Terminology (Diplopoda, Sphaerotheriida, Sphaerotheriidae)

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The Malagasy sphaerotheriid genus *Sphaeromimus* DeSaussure and Zehntner, 1902 is revised. Known heretofore from a single male specimen, the genus now contains three species, *Sphaeromimus musicus* (DeSaussure and Zehntner, 1897), *Sphaeromimus splendidus* sp. nov. and *Sphaeromimus inexpectatus* sp. nov. The female of *S. musicus* is described here for the first time. The mouthparts of giant pill millipedes were observed for the first time using scanning electron microscopy and species- and genus-level characters are illustrated. Intraspecific variation of the female stridulatory organ, the 'washboard' is described. For the first time in Malagasy Sphaerotheriida, some ecological comments are given. Characters found in the male telopods and the female stridulatory organ (the washboard) indicate that characters employed previously for the definition of subfamilies and tribes cannot be maintained and the monophyly of such groups remains questionable.

KEYWORDS: *Sphaeromimus*, Sphaerotheriida, giant pill-millipedes, Madagascar, Diplopoda.

Based on its species-richness and high level of endemism (Myers et al. 2000), Madagascar was recently listed among the eight eminent biodiversity hotspots of the world. Madagascar, as the fourth largest island of the world, harbors a diversity of different ecosystems, resembling in this regard a small continent. Due to its over 150 million years of isolation from the closest continental landmass Africa (Rabinowitz et al. 1983; Wells 2003), its flora and fauna are unique and very distinct from that of other regions of the world. Furthermore, the fauna and flora of Madagascar are extremely poorly known, as is the case for many species-rich regions outside northwestern Europe and North America. Ongoing faunistic research on the island of Madagascar continues to discover numerous new species, even among vertebrates (Jenkins 1993; Glaw and Vences 1994; Sparks and Stiassny 2003). Since the destruction of natural habitats is advancing on the island at an alarming rate, alpha-taxonomic research with regards to invertebrates is extremely urgent, as many species may vanish before ever being described. Three Malagasy ecosystems, the east coast littoral forest, highland vegetation and the western dry deciduous forests have shrunk by over 90% of their former distributions and belong now to the most threatened ecosystems of the world (Ganzhorn et al. 2001; de Gouvenain and Silander 2003; Vincelette et al. 2003).

The millipede genus *Sphaeromimus* revised below illustrates the understudied invertebrate diversity as well as the threatened status of its species. The diverse arthropod class Diplopoda is

one of the severely understudied animal groups. Over 9,000 species have been described so far (an exact species catalog does not yet exist) and estimates of millipede species richness are given as approximately 80,000 species worldwide (Hoffman 1980). As far as it is known, millipede species are often microendemic with very small distribution ranges; in some cases related species may occur just 20 km apart (Enghoff 1983; Hamer and Slotow 2002; Mesibov 1998). Despite the fact that most millipedes are macroinvertebrates (adult size from a few millimeters to 28 cm body length in *Archispirostreptus gigas* (Peters 1855)) and are of considerable ecological importance for litter breakdown within the decomposition cycle (Wolters and Ekschmitt 1997; Curry 1994; Crawford 1992; Schaefer 1990), biological research on the class suffers from lack of alpha-taxonomic attention, mainly due to the paucity of taxonomic experts for the group.

The Malagasy giant pill-millipede genus *Sphaeromimus* was heretofore known from a single male specimen of *Sphaeromimus musicus*. Among recently collected material by the senior author and from survey work by Goodman (Field Museum) and Griswold (California Academy of Sciences), female specimens of *S. musicus* and material of two new species of the genus were discovered. The four-jointed anterior telopods are the distinguishing feature of the genus. In *Zoosphaerium* Pocock, 1895, the other genus of giant pill-millipedes occurring in Madagascar, the anterior telopods have only three joints. Furthermore, features of the female vulva in *Sphaeromimus* do not agree with characters used by Jeekel (1974) in the most recent classification of the millipede order Sphaerotheriida and further phylogenetic analyses of the order will be required to clarify its internal classification.

The two newly discovered species of *Sphaeromimus* described below are each known only from small, isolated remnants of the southern littoral forest on Madagascar. This very limited distribution, the still ongoing anthropogenic influence in these remaining littoral forest patches and further possible disturbance of the habitat by mining projects may make these two new species likely to be among the most endangered millipede species of the world.

Material and methods

The senior author (T.W.) collected specimens of the two new species described here during fieldwork in Madagascar in March and April 2003. Specimens of *S. musicus* were borrowed from the California Academy of Sciences (CAS) and the Field Museum (FMNH).

Specimens were euthanized using ethyl acetate, straightened and preserved in 70% ethanol. All measurements are in mm.

Dissections, illustrations.— Dissections were made with a scalpel, in very small specimens with a dissecting pin. The following structures were dissected (a) the anterior and posterior pair of telopods, which were separated from each other using a needle; (b) the left leg of the 9th pair in males and females; (c) the 2nd leg pair in females; (d) the 1st leg pair with 1st sternite in females and males, (e) the subanal plate with 'washboard' in females; and (f) a section of the endotergum from a tergite in the center of the body, removed using scissors. Dissected specimen parts were cleared in clove oil. Drawings were done using a camera lucida mounted on a dissecting or compound microscope depending on size of specimen. Small specimens were held in position using clean sand at the bottom of dissecting dishes.

For scanning electron microscope examinations the following parts were dissected: (a) The right/left antennae were cut off with a scalpel near the insertion in the head. (b) The gnathochilarium was removed by cutting along its base with a scalpel and separating the tentorium with scissors. After removal of the gnathochilarium, (c) the mandibles were cut easily at the first joint with scissors and scalpel. (d) The epipharynx was separated from the head with a needle and then pulled

out with forceps. (e) The remaining head capsule was separated from the body using forceps. (f) The 2nd leg coxa of males was removed from the body.

SEM PREPARATIONS.— Specimens were dehydrated through a series of alcohol to 100% ethanol, mounted on stubs using sticky tabs and air-dried overnight. The 2nd leg coxa of the male with the gonopore was critical point-dried. Stubs were sputter-coated with gold and observed with an AMRAY 1810 SEM (Field Museum).

TERMS

As is true for many millipede groups, systematic treatments of the order Sphaerotheriida are scant and were done by a few authors, e.g., Verhoeff (1927, 1928, German) and Attems (1897, German), Silvestri (1917, Latin), Jeekel (1974, English) and recently by VandenSpiegel et al. (2003, English). Authors used terms in the various languages and the equivalency of such terms in the different treatments is sometimes difficult to determine. Since millipede morphology is less well known than that of other arthropod groups, which in the past have been explored more extensively with high quality light microscopy and scanning electron microscopy, the nomenclature of several morphological terms is currently neither standardized nor stabilized in the Diplopoda. For that reason we list terms used in this paper, along with terms used by other authors for apparently the same structure. Our use of such terms does not necessarily imply homology.

Anal shield.— Formed by the fused tergites of the last 3(?) diplosegments (= pygidium of authors, e.g., VandenSpiegel et al. 2003). In males of some sphaerotheriid species the anal shield is invaginated in the middle (Fig. 1IH). Such invagintion may play a role in mating behavior.

Antennae.— The first visible joint of the antennae, inserting in the antenna socket, is termed 1st antennomere.

Anterior paratergite depressions.— Denotes the anterior rim of the lateral extensions of the tergites (Paratergite, see below), a well circumscribed slightly concave area which glides under the posterior margin of the proximal tergite during volvation (Figs 1, 28–29, 50). Recent treatments on Sphaerotheriida did not explicitly discuss this morphologically distinct area.

Bursa.— Jeekel (1974) applied this term for the structures of the female vulva below the operculum. The 'bursa' consists of two sclerites, the exterior and inner plate (EP and IP) (Figs 5, 33, 55).

Endotergum.— The underside of the posterior margin of the tergites carries crenulations, spines and bristles, often in a species-specific arrangement (see VandenSpiegel et al. 2003; 'Unterblatt' *sensu* Verhoeff 1928: plate 10, fig. 123).

Gnathochilarium.— Since homologies with sclerites of helminthomorph gnathochilaria are unresolved (see Hoffman 1976:125), the sclerite terminology used here for sphaerotheriid gnathochilaria is descriptive. Usage of the term lamellae linguales below does not constitute a statement of homology.

Harp.— A set of ridges located on a discrete plate on the first joint of the anterior telopods of males (Figs 8, 37, 58).

Inner horns of posterior telopods.— Lobe-like projections attached mesally to the syncoxite, termed coxal horn by VandenSpiegel (2002), and 'Hörner des Syncoxit' by Verhoeff (1928:676). Indicated here by IH = inner horn. Also, see below under 'Telopods' (Figs 11, 35, 57).

Lamellae linguales.— Two longitudinal sclerites between the left and right paramentum of the gnathochilarium. In *Sphaeromimus*, the two sclerites are partly fused. At the distal tip of the lamellae linguales are pads carrying sensorial cones (Fig. 48). These pads were termed 'Zäpfchenkappen' by Verhoeff (1928:872). The homology of these two sclerites with the lamellae

linguales of the Helminthomorpha is questionable (see Hoffman 1976).

Male gonopore.— Opening of the vas deferentia on the posterior wall and the inside margin of the coxa of the 2nd leg pair (Fig. 27). Verhoeff (1928:695) stated that in Sphaerotheriida the male genital opening consists of a small, inconspicuous pore; other authors (e.g., VandenSpiegel et al. 2003) described somewhat more complex structures and denoted them with the terms penes and pseudopenes. DeSaussure and Zehntner (1897/1902) illustrated the male gonopore in several species and genera of the Sphaerotheriida showing different structural elements.

Molar plate process.— Elongated process attached to the upper side of the molar plate towards the roof of the head (Figs 18, 40), as it occurs in the millipede clade Pentazoniida (comprising the orders Glomerida, Glomeridesmida and Sphaerotheriida). This structure is very prominent in sphaerotheriids and can be found on illustrations of other pentazonid mandibles (e.g., in glomerids by Köhler and Alberti 1990, fig. 2-3; in sphaerotheriids by Silvestri 1917, fig. 2). No term has been coined for this structure.

Paratergite (Verhoeff 1928:385, German).— Lateral extensions of the tergites. The anterior paratergite depressions (see above) are located on the dorsal side of the anterior margin of the lateral extensions of the tergites (Figs 1, 28–29, 50). Verhoeff (1928:385) also used the term 'Seitenlappen.' These lateral tergite extensions were sometimes called paranota. Paranota is commonly used for the metazonite extensions in Polydesmida. Since the latter denotes a different anatomical part than the 'Paratergite' *sensu* Verhoeff in the Pentazonia, we prefer to call the structure lateral tergite extensions or paratergite.

Sensorial cones.— Myriapods feature a variety of sensorial structures, one of which are cones with a small pore on their tip. All such structures called sensorial cones in this paper have this particular anatomy. The distribution of such cones may reveal species- or genus-specific characters.

Subanal plate.— Hypoproct or ventral scale of authors, equipped with a stridulatory organ (washboard) in females of *Sphaeromimus*.

Telopods.— In the Pentazonia, males have two pairs of modified legs, the anterior and posterior telopods, at the end of their bodies. These telopods are involved in mating behavior and sperm transfer. It is commonly assumed that these are homologous to walking legs and thus the most proximal joint is called the coxite. In Sphaerotheriida, the coxites of each telopod pair are fused, forming a 'syncoxite.' The homology of the more distal joints with podomeres is uncertain. Here, the joints distal to the syncoxite are indicated by numbers 1–3 (posterior telopods) or 1–4 (anterior telopods) respectively. Some authors (Mauriès 2001) distinguish between the anterior and posterior telopod by using the terms 'paratelopod' (anterior telopod) and telopod (posterior telopod).

Thoracic shield ('Brustschild' *sensu* Verhoeff 1928:473).— Formed by the enlarged tergite of the 2nd body segment, the one following the collum. It features wide lateral lobes with a distal concave groove ('Gruben des Brustschildes' *sensu* Verhoeff 1928:473) and a conspicuously raised brim, involved in volvation (Verhoeff 1928:473).

Vulva.— The vulva consists of the bursa and the operculum. Many authors used the term 'cyphopods' for the female organs in millipedes.

Washboard.— A stridulatory apparatus termed washboard by Jeekel (1999) is located on the subanal plate (=Hypoproct or ventral scale) at the caudal end of the body of females (Figs 7, 34, 55).

Abbreviations

CAS	California Academy of Sciences, San Francisco, USA
FMNH	Field Museum of Natural History, Chicago, USA
MNHN	Muséum National d'Histoire Naturelle, Paris, France

12T	12th tergite
AI	Anal shield invagination
AS	Anal shield
EP	Exterior plate of vulva
IH	Inner horns on syncoxite of posterior telopods.
IP	Inner plate of vulva
O	Operculum of vulva
PL	Pleurite
S	Sternite
TO	Tömösváry organ

RESULTS

Genus *Sphaeromimus* DeSaussure and Zehntner, 1902

Sphaeromimus DeSaussure and Zehntner, 1902.
Sphaeromimus, Attems 1942.— Jeekel 1971, 1974, 1999 — Enghoff 2003.

TYPE SPECIES.— *Sphaeropoeus musicus* DeSaussure and Zehntner, 1897. Other species included: *Sphaeromimus splendidus* sp. nov., *Sphaeromimus inexpectatus* sp. nov.

The Malagasy sphaerotheriid genus *Sphaeromimus* was first described by DeSaussure and Zehntner (1902) in their important work on the Diplopoda of Madagascar. Originally, the genus contained a single species, *Sphaeromimus musicus* (DeSaussure and Zehntner, 1897, sub *Sphaeropoeus*), known only from a single male. Consequently, only male sexual characters were given with descriptive details focusing on the telopods. The unusual features of the species prompted Jeekel (1999) to suggest that the then known *Sphaeromimus* specimen may have been "mislabelled or [represents] an introduced Indian sphaerotheriid". With the collection of male and female specimens of *S. musicus* at three different localities and the discovery of two new *Sphaeromimus* species, described below, it is now demonstrated that *Sphaeromimus* forms an established part of the endemic Malagasy fauna. Since the genus is no longer monotypic, genus-specific characters can be given.

The genus *Sphaeromimus* can be distinguished from the only other Malagasy sphaerotheriid genus *Zoosphaerium* Pocock, 1895, on the basis of numerous characters. The genus description given below includes the characters DeSaussure and Zehntner (1902) mentioned in the original description of the genus.

DIAGNOSIS.— Members of the genus *Sphaeromimus* can be distinguished from *Zoosphaerium* by the following combination of characters: antennae short, with six joints, antennomeres without small spines and first antennomere without indentation. Apical antennomere rounded with numerous (up to 77) sensorial cones (apical antennomere cylindrical with four or more sensorial cones in *Zoosphaerium*), number of cones species-specific. Tarsi in *Sphaeromimus* broad (2.5–3 times longer than broad, *Zoosphaerium* up to 4.5 times longer than broad), tarsal tip densely covered with ventral spines. Anterior telopods with four joints (*Zoosphaerium* with three joints). Males with numerous strong stridulatory ridges on a plate termed 'harp' located on the first joint of the anterior telopods. Females with prominent, long stridulatory ridges on the subanal plate called 'washboard.' Washboard divided into two parts by a suture of variable length depending on species. Cyphopod sclerites in the bursa of *Sphaeromimus* of unique shape. In *Sphaeromimus,* operculum of vulvae much longer than the 2nd leg coxa, without a central depression (operculum subreniform in *Zoosphaerium*). This high number of characters allows easy differentiation between the two Malagasy sphaerotheriid genera.

DESCRIPTION.— Known members of the genus range from 15 to 35 in body length, thoracic shield width ranges from 6.8 to 17.6.

Head: only antennae with genus-specific characters, remaining features of head agree well with those found in most other sphaerotheriids. Eyes with numerous greenish ocelli, two of which are larger and one ocellus laterally displaced and separated (Figs. 24–25). Clypeus with single tooth (called labrum tooth by other authors), surrounded by hairs set in small pits. Tömösváry organ developed as a small round pit as in all known members of the order (Fig. 25). Center of posterior edge of head with or without patch of very small bristles (Figs 14, 39).

Antennae: antennae short, six visible antennomeres more or less short and rounded. First antennomere without spines, 6th antennomere prominent, big, flat and longer than the others, carrying many (40–77) sensorial cones (Figs 20, 43, 61).

Mouth parts: external tooth of mandible with a distinct 'step' (Figs 18, 40), with 6 or 7 pectinate lamellae, apical teeth of pectinate lamellae broad and short (Figs 19, 41), number of teeth declining from apical to proximal pectinate lamellae. Gnathochilarium more or less hairy, with a few sensorial cones lateral of the palpi (Figs. 15–16, 47, 49). Centrally located pads (='Zäpfchenkappen' *sensu* Verhoeff) on the anterior edge of the lamellae linguales with sensorial cones (Fig. 48). Tip of palpi with numerous sensorial cones distributed regularly around the tip. Epipharynx very similar in shape as known from other sphaerotheriid taxa (see Verhoeff 1928:841, fig. 419) (Fig. 45).

Thoracic shield: ridges on lateral lobes of thoracic shield absent. Anterior rim of lateral lobes broad, used in volvation.

Tergites: surface varies somewhat but mostly hairless and almost polished, except for the anterior paratergite depressions (see Material and Methods) which are more or less densely covered with hairs. Tergites always without a median keel. Tergites 3–12 each with a black carina ventrally on the anterior section of the tergites. Carinae apparently function as a locking device (Verhoeff 1928:479), fitting over the rim of the lateral extension of the thoracic shield (Figs. 1, 28–29, 50). Endotergum variable, species-specific crenulations, marginal ridge and bristle patterns, marginal bristles branched (Figs. 17, 23, 44, 62).

Sternite: first sternite with a sclerotized ledge along the anterior sternite lobe (Figs 4, 31, 53). Sternite lobe long, curved towards the legs, reaching the apical edge of coxa. Coxae and sternites without spines, but sternites three and beyond with a spine-like process which reaches about to the stigma opening of the anterior sternite.

Anal shield: shape of anal shield not variable within genus. Males of *S. musicus* with a small invagination as described in other sphaerotheriids (VandenSpiegel et al. 2003; Jeekel 1986). Anal shield sometimes with a few small isolated hairs and a patch of hairs in the corners towards the 12th tergite. Ventral side of anal shield with single black locking carina (='Verschlussleiste' Verhoeff 1928:479) on each side, locking carina with a slight central constriction (Figs. 3, 30, 52).

Legs: remarkably short and broad, especially the tarsus, being only 2.5–3 times longer than broad. Tarsi of first two leg pairs with three to five ventral tarsal spines and a straight apical claw. Tarsi of leg pair 3–21 with 10–15 ventral spines on the apical part and a curved apical claw with one apical spine. Coxal lobes present, with small black triangular spines, variable in the genus. Femur with toothed ridge (Figs. 2, 26, 33, 51). Prefemur of last pair of legs basally with a small sclerotized knob on posterior side.

Female sexual characters: subanal plate with washboard, consisting of well-developed stridulation ridges. Stridulation ridges always very long, ending just in front of the anterior margin of the washboard. Washboard with distinct median longitudinal groove, posterior rim of washboard with a central invagination. Shape of vulva unique. Operculum rounded and very long, always longer

than the coxa and can reach about half of the length of the prefemur. Exterior and inner plates (EP, IP) below the operculum (termed bursa by Attems 1928; Jeekel 1974). Cyphopod sclerites consisting of two triangular apical sclerites and a much larger smoothly rounded third sclerite, all visible as dark structures near the suture of the vulva between inner and exterior plate (Figs. 5, 32).

Male sexual characters: male gonopore conspicuous, located slightly above the middle and near the inside margin of the coxa of second pair of legs. Gonopores apparently complex, partially closed by a round sclerotized plate carrying a few long hairs and featuring at least two membranous folds (Figs. 6, 27). *Anterior telopods:* with four joints in addition to the syncoxite. Harp on plate of first joint with three or more prominent stridulation ridges (Figs 8, 37, 58). Posterior side of second joint always with a large immovable lobe-like flat projection. Lobe-like projection with some crenulation on the border juxtaposed the third and fourth joints. Fourth joint much thinner and longer than the proximal joints, about as long as the second and third joint combined. Apically with a single long sclerotized spine (spine A) on posterior surface, basally with two non-sclerotized spines (spines B). Spination sometimes variable within individuals, especially on the fourth joint. Distally with fringe of thick, long hairs (Figs. 9, 10, 38, 59). *Posterior telopods*: Syncoxite mesally with lobe-like projections, termed inner horns (IH). Tips of inner horns (IH) with apical thorn and patch of hairs; terminal portion of inner horn bent posteriorly more than 90°. Subanal lobe densely covered with hairs (Figs. 11, 56). The 2nd joint forms an immovable finger, the third joint forms a movable finger. Three characteristic non-sclerotized spines on the inside of immovable finger, spaced at ⅓ intervals. Small triangular non-sclerotized lobe next to most proximal spine. Stout tip of immovable finger hook-shaped. Posterior face of movable finger with several sclerotized ridges.

Variation.— Members of *Sphaeromimus* are small in comparison to *Zoosphaerium*, the latter can reach a length of 100 mm (e.g., *Z. hippocastanum*), but moderate in size when compared to others in the order Sphaerotheriida. The number of stridulation ridges on the female washboard is correlated with the length of the individual, with three ridges on each side in the smallest females of *Sphaeromimus splendidus* sp. nov. and up to five ridges in the largest females. The number of ridges on each side of the washboard may vary in the same specimen.

Natural history, behavior.— Life observations of the two newly described species revealed that the first pair of legs is not used when walking on flat ground. The first pair of legs is held up, above the ground and next to the head. Upon encountering an obstacle such as a leaf or twig (personal observations, senior author), the first pair of legs touches the obstacle. The first leg differs morphologically from the remaining legs by having fewer ventral spines and lacking the typical apical spine. The 3rd–21st leg pair show identical characters with little variation, even in the same leg pair, regarding to the number of ventral spines and length of the claw.

Living animals of *S. splendidus* sp. nov. and *S. inexpectatus* sp. nov. seem to avoid climbing on steeply inclined twigs. When lightly touched while on branches the animals quickly roll up and drop down. Haacker and Fuchs (1972) reported a different behavior from apparently arboreal species observed in South Africa: when touched while sitting on a branch, the animals coil up the head and anterior body, but hold on firmly to the branch using the posterior legs. Only after repeated and aggravated disturbance the animals roll up and drop from the branch. One of the authors (T.W.) observed identical behavior as described by Haacker and Fuchs (1972) in one *Zoosphaerium* species found in Sainte Luce and Mandena, where they co-occur with the *Sphaeromimus*-species. This *Zoosphaerium* species was sometimes also found up to 250 cm high on trees and shrubs, feeding on the trunk. The behavioral differences may indicate different ecological niches for these sympatric sphaerotheriid species.

Discussion.— Currently, too few specimens are known to evaluate sexual dimorphism with

regards to the number of sensorial cones on the antennae as is known to occur in other sphaerotheriid genera (Verhoeff 1928: 791). Regenerated antennae were observed in some specimens. In these, the number of sensorial cones was reduced.

The black locking carinae on the inside of the anal shield show a central invagination in some specimens, which may indicate a fusion of originally two separate carinae. Verhoeff hypothesized that the anal shield of sphaerotheriids results from a fusion of at least two segments, the 13th segment and the telson (Verhoeff 1928:448, Bitelotergit). The characteristics of the carinae described here represent further support for this notion.

Species-specific characters found on the endotergum have also been reported from the South African genus *Sphaerotherium* (VandenSpiegel et al. 2003).

The distribution of the here observed toothed ridge on the femora of all walking legs within the order is currently unknown, it may have been overlooked by other authors (Silvestri 1917: figs. 5-10 and 17, Jeekel 1986, fig. 4). This ridge is present in all Malagasy sphaerotheriids examined to date by the senior author. Because of the rarity of female specimens, the vulvae were not dissected. Thus, the exact form of the cyphopod sclerites cannot be illustrated here.

The movable finger of the chela of the posterior telopods carries sclerotized ridges on its posterior surface. DeSaussure and Zehntner (1902) suggested these to represent another stridulation organ (Figs. 11–12, 35–36, 56–57). Haacker (1969:455) and VandenSpiegel et al. (2003) describe a similar feature in the South African *Sphaerotherium* and suggest that it may provide a better grip on the female legs during mating and we agree with this suggestion. The lobe-like projection on the 2nd joint of the anterior telopods with its small crenulations may serve a similar purpose. The function of the inner horns of the syncoxite of the posterior telopods is uncertain. It can be suggested that the big spine on the inner horn of the syncoxite is used to open the female vulvae or to transfer the sperm, while the posterior and anterior telopods hold the female. Unfortunately, matings have been reported for only one sphaerotheriid species (Haacker 1968, 1969, 1974) who mentioned transfer of a spermatophore with the male legs. His observations appeared to indicate that females take the spermatophore into their mouths shortly after transfer of the spemathophor. However, dissections of the entire male and female head and SEM studies of the mouth parts revealed no special structure in the male mouth parts for sperm transfer and no visible sperm bag in the female's head.

Conservation.— The two new species were found in two of the four remaining small patches of the southern littoral rainforest, in Mandena (1,103 ha, 160 ha slated as conservation area) and Sainte Luce (1,947 ha; Ramanamanjato et al. 2002, Vincelette et al. 2003). More field collecting in other areas may reveal other species of this interesting genus. Considering the fast destruction of the last isolated remaining forest patches (e.g., Green and Sussman 1990) and the endemism of the here described new *Sphaeromimus* species in Madagascar, new studies in other areas of the island are urgently needed.

Sphaeromimus musicus (DeSaussure and Zehntner, 1897)

Figs 1 – 27

Sphaeropoeus musicus DeSaussure and Zehntner, 1897 (publication of figure).
Sphaeromimus musicus, Saussure and Zehntner 1902 (publication of description).— Jeekel 1999 (lists species name) — Enghoff 2003 (lists species name).

Material examined.— Type material: Male holotype; Madagascar, Province: unknown, coll. A. Grandidier, MNHN, CH038, vidi, without telopods, specimen figured in atlas published 1897, plate 4, figure 1 a-e. Non-type material: 16 males, 3 females. Madagascar, Province: Toliara, coll. RNI Andohahela, par-

cel II, camp 6, ~120m NN, 24°49.0′S 46°36.6′E, 7-15.XII.1995, leg. S.Goodman, 2 males, 1 female; FMNH 5378. 2 males; FMNH 5372. 1 male; FMNH 5409. 1 male, pitfall trap 16-18; FMNH 5407. Province: Toliara, 1 male coll. Foret Analavelona, mid altitude forest with western and eastern elements, ~1050m NN, 9-15.III.1998, 22°40.7′S 44°11.5′E, leg. S. Goodman, 1 male; FMNH 5439. 2 males; FMNH 5427. Province: Toliara, coll. RP Berenty, Foret Bealoka, Mandrare River, gallery forest; ~35m NN, 24°57′25″S 46°16′17″E; 3-8.II.2002, leg. B.L. Fisher et al., 5 males; 2 females, BLF 5315; CAS. 2 males, BLF 5314; CAS.

Diagnosis.— *Sphaeromimus musicus* can be most easily distinguished from any other Malagasy sphaerotheriid by its unique coloration and pattern (Fig. 13), which identifies the species unambiguously. The body is orange, with an irregular black pattern near the posterior margin of each tergite. Each of the paratergites wears a median distinct thick black stripe. *S. musicus* is markedly more hairy than the other species of the genus, with hairs covering the head, legs, gnathochilarium, sternites and anal shield (Figs. 1–2, 4, 14–15). The anterior paratergite depressions carry an elongated patch of hairs on each. The body is less highly arched than in *S. splendidus* sp. nov. The coxal lobes of the walking legs are only weakly developed, but somewhat bigger than in *S. inexpectatus* sp. nov. (Fig. 2). Remarkable is also the high number of over 75 sensual cones (Fig. 21) on the last antennomere, which is much higher than those of *S. splendidus* sp. nov. (Fig. 43). The female washboard (Fig. 7) and the male harp (Fig. 8) are the biggest known in all Malagasy sphaerotheriids, with the highest number of stridulation ridges in the genus *Sphaeromimus*. The shape of the female operculum is unique and shorter in *S. musicus* than in the other species of the genus. Its mesal margin is more strongly developed than in its congeners (Fig. 5). The lower part of the inner plate (IP) of the female vulvae is not sclerotized and carries some triangular black spines. Molar plate process of the mandible with a single step (Fig. 17). In *S. musicus*, the endotergum features a distinct band of flattened nodules between the marginal bristles and the internal area covered with short spines and hairs (Fig. 17).

Description.— Body length: 17.2–34.5; width of thoracic shield: 13.3–17.6; height of thoracic shield 7.5–10.1.

Habitus: In general, the tergites of this species seem to be higher than in most other Sphaerotheriida, with the exception of *Sphaeromimus splendidus* sp. nov.

Coloration: body orange, with irregular black pattern near the posterior margin of each tergite. Each paratergite with a distinct thick black stripe, thoracic shield with even thicker black stripe, collum mostly black. Anal shield almost completely black (Fig. 13); head, antennae and legs orange-red. In alcohol, pattern and coloration, especially orange and red, are lost over time, either through exposure to light and/or alcohol; black stripe may fade completely, the black pattern becomes very irregular. The illustrated specimen in the original description shows this loss of coloration clearly. For this study, we examined a number of specimens in different stages of coloration and pattern loss, from specimens featuring almost lifelike color and pattern to the stage illustrated by DeSaussure and Zehntner (1897).

Head: with numerous hairs and setiferous pits mostly around the clypeus and lateral of the eyes. Some long, isolated hairs around the eyes and more distributed over the rest of the head. Posterior margin of the head towards the collum with dense field of very small hairs (Fig. 14).

Antennae: shape as given in genus description. Length of antennomeres: 1>2>3=4=5<6; 6th antennomere being broadest and longest (Fig. 20), flat, reaching broadest point near the middle and does not taper towards the sensual plate, with up to over 75 sensual cones (Fig. 21).

Mouth parts: *mandible* with six pectinate lamellae; number of teeth of pectinate lamellae declining from apical to proximal (Fig. 19). Molar plate process with a sharp single step near the apical border (Fig. 18). *Gnathochilarium* ventrally with many hairs on the lamellae linguales. Field of four sensorial cones, three grouped together, the fourth displaced towards posterior margin,

located laterally of the palpi (Fig. 16). *Epipharynx* as in the genus description.

Collum: anterior margin with two rows of isolated long hairs, posterior margin only with few isolated hairs, rows of hairs of the endotergum visible.

Thoracic shield: with an area of numerous thick hairs on the concave lateral extension ('Brustschildgruben' *sensu* Verhoeff) towards the marginal rim. Anterior rim of the lateral extensions broad (Fig. 1).

Tergites: posterior margins of tergites three to seven with a visible fringe of short hairs, which originates from the endotergum. The anterior paratergite depressions of the tergites four to ten are densely covered with hairs, anterior paratergite depressions of the anterior tergites with several ridges each. Anterior paratergite depressions of tergites 11 and 12 also with pads of dense hair, but ridges not visible in intact specimens. Tips of posterior margins of paratergites project posteriorly. The endotergum features a distinct band of flattened nodules between the marginal ridge and the internal area covered with short spines and hairs (Fig. 17). *1st Sternite:* lobe long, reaching beyond the length of the coxa, covered with many long hairs and curved towards the leg pair (Fig. 4). The upper margin is smoothly rounded and completely covered with individual long hairs, lower margin hairless (Fig. 4).

Anal shield: rounded, neither bell-shaped nor tapered, in males there is a weak invagination not seen in females and less distinct than in the South African genus *Sphaerotherium* (Fig. 1:AI). The anal shield carries on both sides a black locking carina, sloping towards the posterior end of the anal shield (Fig. 3). The locking carinae in this species are well-developed, but narrow and of medium length compared to other species.

Legs: tarsi of leg pair one and two with only four ventral spines and only weakly curved claws. Claws of the tarsi of following legs are curved wearing 12–14 ventral spines. Ninth pair of legs with a small lateral lobe and many small black triangular spines (Fig. 2). Coxae of all legs at the inside margin densely covered with many long hairs, also on the following leg joints at the inside margin some very long, isolated hairs.

Female sexual characters: second pair of legs with coxal lobe. Operculum (Fig. 5:O) of vulvae very broad and long, reaching ⅓ of the prefemur length. Mesal section of operculum drawn out apically and longer than lateral section. Center of operculum without indentation (=not subreniform), lower margin straight. Exterior plate (Fig. 5:EP) of vulvae long and broad, its anterior margin reaches around the base of the operculum. Inner plate (Fig. 5:IP) not as long as exterior plate, anterior margin of former ends below base of operculum. Posterior margin of inner plate not sclerotized, sloping lower than exterior plate, with short, triangular black spines (Fig. 5).

Subanal plate rounded, center of anterior margin with a broad shallow invagination. The washboard with six strong, symmetrical stridulation ribs which end just in front of the anterior margin. Subanal plate divided by central suture not reaching anterior and posterior margins of subanal plate (Fig. 7).

Male sexual characters: second pair of legs with a pronounced coxal lobe (Fig. 6). Anal shield with a weak invagination (Fig. 1:AS). *Anterior telopods*: first joint with a large stridulation harp and 5 stridulation ridges (Fig. 8), posterior side of second joint with a lobe-like projection, which reaches the 4th joint (Fig. 9). On its inside face two long, thin non-sclerotized spines (Figs. 10:G–H). The outside face of the lobe carries a patch of very small (sensorial) hairs (Fig. 9:H). The third joint is short and slightly invaginated towards the lobe of the second joint. Near the invagination insert two short (E) and one longer thin non-scletorized spine (F) (Figs. 9:E–F). The 4th joint carries basally a low knob (C) and a lateral non-sclerotized thin spine (D) (Figs. 9:C–D). The apical portion of the 2nd joint lobe is juxtaposed the low basal knob of the 4th joint (Figs. 9–10). *Posterior telopods*: telopod syncoxite densely covered with hairs. Outer surface of 2nd joint basal-

ly with hairs, apically hairless. Stout tip of immovable finger hook-shaped. Chela without species-specific characters, movable finger with genus-specific dentition and row of crenulated teeth. The opposite finger (2nd joint) features crenulations juxtaposed to the crenulated teeth of the movable finger. Base of movable finger laterally with some long hairs, more densely towards the outer margin, apical section with a few sensorial hairs (Fig. 22).

Distribution and ecology.— According to current collection records, *S. musicus* appears to be restricted to the southwestern region of Madagascar. To date, *S. musicus* is known from three localities, indicating a wider distribution range than some other sphaerotheriid species on Madagascar, e.g., *S. inexpectatus* sp. nov. and *S. splendidus* sp. nov. *Sphaeromimus musicus* was collected in gallery forests as well as in over 1,000 m elevation. It is remarkable that no specimens of this species were found in the spiny dry forest so widespread in its range, but the species appears to be restricted to semi-humid habitats such as gallery forests. The species was not found among other sphaerotheriid material, e.g., of the genus *Zoosphaerium*, collected in the eastern Hylaea areas or the western dry-deciduous forest. Collections took place during the wet season, December, February and the first half of March. Members of the genus *Zoosphaerium* were found at all three sites (Fig. 65) from which *S. musicus* were collected. No eggs were found in a dissected female collected during the wet season (Dec. 7–15, 1995 in RNI Andohahela, parcel II). It is unknown whether this species is active in the dry season.

Conservation.— The currently fragmented distribution of *S. musicus* is most likely the result of the continuing destruction of the natural vegetation. Habitat protection is vital for the survival of highly endemic species such as the type species of the genus *Sphaeromimus.*

Discussion.— Males and females in Sphaerotheriida molt after maturity (pers. obser.). Ontogenetic changes of characters described above have not been investigated to date, e.g., it is possible that the number of stridulation ridges increases with the age and size of the animal. This seems to be the case in females, the number of stridulation ridges on the male harp remain constant (Table 1). The small size of the vulva in this species is remarkable when compared to the relatively larger female vulvae in the much smaller females of *S. splendidus* sp. nov. and *S. inexpectatus* sp. nov.

Table 1. Variation in *S . musicus*. * indicates specimens used for drawings and SEM; m: male; f: female; TS w: width of thoracic shield; SR: number of stridulation ridges of harp in males and washboard in females on left/right body side.

Sex	*TS w*	*SR*	*Location*
m*	17,0	5/5	RNI Andohahela, parcel 2
m*	16,0	5/5	RNI Andohahela, parcel 2
f*	14,5	6/6	RNI Andohahela, parcel 2
m	17,4	5/5	RNI Andohahela, parcel 2
m	15,8	5/5	RNI Andohahela, parcel 2
m	17,0	5/5	RNI Andohahela, parcel 2
m	16,5	5/5	RNI Andohahela, parcel 2
m	15,9	5/5	Foret Analavelona
m	15,4	5/5	Foret Analavelona
m	15,6	5/5	Foret Analavelona
m	17,4	5/5	RP Berenty
m	16,7	5/5	RP Berenty
m	16,7	5/5	RP Berenty
m	16,7	5/5	RP Berenty
m	13,3	5/5	RP Berenty
f	16,2	8/8	RP Berenty
f	15,5	7/8	RP Berenty
m	17,6	5/5	RP Berenty
m	16,5	5/5	RP Berenty

Sphaeromimus splendidus sp. nov.

Figs 28–49

Material examined.— Type material: 1 female holotype; paratypes: 1 male; 3 females, 1 male immature, coll. Madagascar, Province: Toliara: Sainte Luce, littoral forest, 24°47′S 47°10′E; 08.IV.2003, leg. Wesener; FMNH 6702, 6703. 1 female (mature), identical collecting data; CAS. Other material examined: 2 males (immature), 2 females (immature), coll. Madagascar, Province: Toliara: Sainte Luce, littoral forest;

24°47′S 47°10′E, 06.04.2003, leg. Wesener, 2 juvenile, (width of thoracic shield: 3.4 mm, 2.9 mm; body length 7.6 mm, 7.0 mm), same collection data; vouchers, deposited at the Université Antananarivo.

Diagnosis — *S. splendidus* is distinguishable from other *Sphaeromimus* species by its completely black coloration and tergites with a satin sheen. This species is almost hairless, with only a few individual hairs on the anterior paratergite depressions and on the thoracic shield (Figs. 28–29). The body is more highly arched than in other *Sphaeromimus*-species. The coxal lobe is very long and well-developed which is one of the main characters by which this species can be distinguished from *S. musicus* and *S. inexpectatus* sp. nov. (Fig. 33). Remarkable is also the small number of only 20–45 antennal cones and the 6th antennomere (Fig. 43) is very slender. The male anterior telopods differ from the telopods in *S. musicus* by possessing a small pointed process on the anterior side of the first joint, reaching the 3rd joint. The operculum of the vulva reaches over the middle of the prefemur; its anterior margin is well rounded. The black locking carinae of the anal shield are shorter than in the other two species. The molar plate process of the mandible possesses one small and one big step (Fig. 40). The endotergum features only one row of marginal bristles and unique, rounded crenulations between the marginal ridge and the internal area, which is covered with short spines and hairs (Fig. 44).

Description.— Body length up to 23.6; width of thoracic shield: 8.2–11.8 (mature); height of thoracic shield up to 6.5.

Habitus: In general, the tergites of this species seem to be higher than in other Sphaerotheriida and higher than in all other species of this genus (Figs. 28–29).

Coloration: The body is shiny black. Smaller specimens are crème-white with only a black posterior margin at each tergite. As the animals grow the black margins on the tergites expand until the tergites are completely black. Head and collum brown, antennae olive-blackish, but antennomeres five and six remarkably lighter in color. Legs also olive-blackish, but apically lighter in color.

Head: with numerous hairs and setiferous pits mostly around the clypeus and lateral of the eyes. Few long, isolated hairs around the eyes and distributed over the rest of the head. Posterior margin of head towards the collum hairless (Fig. 39). Field of little crenulated teeth near the antennal socket with one small spine (Fig. 46).

Antennae: shape as given in genus description. Length of antennomeres: 1>2>3=4=5<6. Sixth antennomere being longest (Fig. 42), flat, reaching broadest point near the middle, but is not broader than other antennomeres. Tapering only slightly towards sensorial disc. Only 20 to 45 sensorial cones (Fig. 43).

Mouth parts: mandibular molar plate process with two steps near apical end (Fig. 40); with seven rows of pectinate lamellae, teeth short and broad; apical pectinate lamella with 18 teeth, number of teeth declining proximally (Fig. 41). *Gnathochilarium* ventrally with few hairs (Fig. 47), group of 4 sensorial cones located in a pit laterally of the palpi (Fig. 49). *Epipharynx* genus-like (Fig. 45).

Collum: anterior margin with some isolated long hairs, posterior margin only with few isolated hairs.

Thoracic shield: with only very few small hairs on the concave lateral extension of the thoracic shield towards the margin. Brim of anterior margin of lateral extension only slightly broader than remaining brim.

Tergites: hairless, shiny, only the anterior paratergite depressions and their anterior margins with very few short hairs. Anterior paratergite depressions of the anterior tergites with several ridges each. Anterior paratergite depressions of tergite 12 also with few hairs, but ridges not visible in intact specimens. Tips of posterior margins of paratergites project posteriorly, stronger in ter-

gites 9–11 (Figs. 28–29).

1st Sternite: lobe as long as coxa and curved to the leg pair. Upper margin smoothly rounded, isolated long hairs near the border. Rest of sternite hairless (Fig. 31: S = sternite).

Anal shield: rounded, neither bell-shaped nor tapered (Figs. 22–23). Anal shield with distinct, broad, but short black locking carinae on each side, sloping towards the posterior end (Fig. 30). Remarkable is a very small invagination at the middle of the carinae.

Legs: 9th leg pair with a pronounced coxal lobe and many small black triangular spines (Fig. 33). Tarsi of first two leg pairs with only three to four ventral spines and only weakly curved claws. Tarsi of following leg pairs curved, with 10–14 ventral spines and the apical spine. Coxae mesally with many dense long hairs; other podomeres with few, very long, isolated hairs.

Female sexual characters: second pair of legs with well-developed coxal lobe. Operculum (*O*) of vulvae: very broad and long, reaching over ½ of prefemur length; reaches its maximum length in center. Anterior margin without indentation (=not subreniform), lower margin with invagination in center. Exterior plate (EP) of vulvae long and broad, its anterior margin ends below base of operculum. Inner plate (IP) not as long as exterior plate, anterior margin of former extends below base of operculum (Fig. 32: O = operculum, IP = inner plate, EP = exterior plate).

Subanal plate rounded, center of anterior margin with a very broad shallow invagination. Washboard with three to five strong, symmetrical stridulation ribs, ending just in front of anterior margin. Washboard divided by central suture reaching anterior and posterior margins of subanal plate (Fig. 34)

*Male sexual characters: s*econd pair of legs with coxal lobe. *Anterior telopods*: first joint with a small harp and three stridulation ridges (Fig. 37) and on its posterior side with a very small projection, reaching the third joint. Posterior side of 2nd joint with a lobe-like projection, reaching 4th joint (Fig. 38: A = big spine; B = two small spines). Third joint short, 4th as described in genus description (Figs. 37–38). *Posterior telopods*: telopod syncoxite nearly hairless. Chela without species-specific characters, movable finger with genus-specific dentition and row of crenulated teeth. Opposite finger (2nd joint) features crenulations juxtaposed the crenulated teeth of the movable finger. Base of movable finger laterally with some hairs. Stout tip of immovable finger hook-shaped (Figs. 35–36). Immature males with bud-shaped anlagen (primordia) in the place of telopods as in mature male.

Distribution and ecology.— Some females collected in the beginning of April were carrying up to eight eggs, suggesting that the breeding season was in progress. Assuming a single annual breeding season and collecting adult egg-carrying females and juveniles with 19 leg pairs at the same time suggest that the adults are at least 2 years of age.

So far this species of *Sphaeromimus* was collected only from a fragment of littoral rainforest on sand in Sainte Luce. This particular patch of littoral rainforest is virtually undisturbed and may represent the best preserved of all four still existing southern littoral forest patches (Dumetz 1999; Vincelette et al. 2003; deGouvenain and Silander 2003). Juveniles and adults could be found in thick (30–80 mm) leaf litter, containing mostly big leaves of trees. The leaf litter was wet and did contain also a large numbers of Spirostreptida, Isopoda, winged Blattodea, Diplura and Collembola. In this assemblage, the giant pill-millipedes were the biggest arthropods found. This species was found together with two species of the genus *Zoosphaerium* (description in progress) one of which occurs also in the littoral rainforest in Mandena and in the eastern lowland rainforest. The second *Zoosphaerium* species appears to be restricted to Sainte Luce. The forest patch of Mandena was intensively searched for 18 days without success for *S. splendidus* sp. nov. In addition, *S. splendidus* sp. nov. was not found in any other collection samples. These observations suggest that *S. splendidus* sp. nov. is endemic to the littoral forest patch of Sainte Luce. Also, with

regards to the isopod fauna and vegetation (Dumetz 1999), the littoral forests of Mandena and Sainte Luce, albeit separated by a distance of only 20 km, display distinct faunal and floral differences. Currently, both patches of littoral forests are separated by pseudosteppe with apparently little humus and soil arthropods (pers. observation). Maps showing forest distribution dating back to 1950 indicate that continuous forest vegetation disappeared before 1950. Lehtinen et al. stated 2003: "*At present, the landscape at Mandena and Sainte Luce is a series of littoral rainforest fragments in a matrix of extremely degraded anthropogenic sand-scrub. This barren sand-scrub is the result of previous forest clearing, burning, and attempts at cattle grazing and is presumably a hostile environment for forest-dwelling organism* (p. 1359)." Our studies are comparable with this suggestion: no pill millipedes or other soil arthropods were found in the sand-scrub, no humus layer is visible in the pseudosteppe. Actually, there are no geographic barriers between the Mandena's and Sainte Luce's littoral rainforest, such as rivers and hills, which in other cases often form borders of a millipede species ranges. The only difference between the two localities is the annual precipitation, with higher rainfall in Sainte Luce (Donque 1972).

Conservation.— The forest at Sainte Luce is subject to human impact and wood removal as one of us (T.W.) observed. Protecting this unique and still relatively pristine littoral forest should receive highest priority.

Discussion.— Coloration not suitable for field identification, since shiny black *Zoosphaerium* species occur sympatrically. The only male known also shows the juvenile coloration, but has fully developed telopods and thus is most likely sexually active.

Table 2. Variation in *S. splendidus* sp. nov. * indicates specimens used for drawings and SEM; m = male; f = female; TS w: width of thoracic shield; SR: number of stridulation ridges of harp in males and washboard in females on left/right body side. * small, bud-shaped anlagen (primordia) of telopods present.

Sex	status	TS w	SR
m	mature	8,0 (4th segment!)	3/3
f (type)	mature	11,8	5/5
f	mature	11,2	5/5
f	mature	9,0	4/5
f	mature	8,4	4/5
f	mature	8,2	4/5
m	immature	5,1	*
m	immature	4,7	*
m	immature	3,1	*
f	immature	6,2	4/4
f	immature	5,1	3/3
?	juvenil	3,4	–
?	juvenil	2,9	–

Sphaeromimus inexpectatus sp. nov.

Figs. 50–63.

Type material.— 1 male holotype (width of thoracic shield: 7.3mm), 1 female paratype, in parts (width of thoracic shield: 6.8mm); Madagascar, Province: Toliara, Mandena; littoral forest; in leaf litter with small fruits. 24°57′15″S 046°39′22″E ; IV.2003; leg. Wesener; FMNH 6701.

Diagnosis.— Coloration unique in the genus, males of *S. inexpectatus* pink to red (Fig. 63). Species almost hairless, except for some isolated hairs on the anterior paratergite depressions and thoracic shield (Fig. 50). Sixth antennomere broader than in the other two *Sphaeromimus* species, with well over 70 antennal cones (Figs. 60–61).

Coxal lobes only weakly developed. Lobe-like projection at the 2nd joint of the anterior telopods protruding laterally and reaching the distal end of the 3rd joint (Fig. 58: F = one thin spine), a unique feature for this species. *Sphaeromimus inexpectatus* sp. nov. differs from *S. musicus* by the possession of a small process inserting on the anterior side of the first joint of the anterior telopods, extending to the 3rd joint. Very remarkable is the curved, hook-like end of the immovable finger of the posterior telopods (Figs. 56–57). The operculum of the vulva is large and extends

over the middle of the prefemur. Its anterior margin is well rounded. The black locking carina of the anal shield is longer than in the other two species (Fig. 52: AS = anal shield; PL = pleurite). External tooth of the mandible with one big and a second small step. The endotergum features only one row of marginal bristles, which are separated by a wavy marginal ridge from the intermediate area covered with short spines and hairs (Fig. 62).

Description.— Body length: circa 15; width of thoracic shield: 6.8 (f)–7.3; height of thoracic shield up to 4.5.

Habitus: In general, the tergites of this species seem to be lower than in all other species of this genus.

Coloration: body of mature male pink, posterior margin of each tergite with thin black line; immature female crème-white to reddish, posterior margin of each tergite with a broad, brown line. Head and collum in male type pink, anterior paratergite depressions gray to reddish; antennae and legs remarkably silver-gray to yellow.

Head: with numerous hairs and setiferous pits mostly around the clypeus and lateral of the eyes. There are some long, isolated hairs around the eyes and more distributed over the rest of the head. The posterior margin of the head towards the collum is hairless.

Antennae: shape as given in genus description; length of antennomeres: 1>2>3=4=5<<6, last antennomere as long as antennomeres 4+5 combined; last Antennomere flat and very broad (Figs. 60–61).

Mouth parts: mandibular molar plate process with one big and a second smaller step near the apical tip; with seven pectinate lamellae, 20 teeth in apical pectinate lamella, number declining proximally.

Collum: anterior margin with some isolated long hairs, posterior margin only with few isolated hairs.

Thoracic shield: with only very few short hairs on the concave lateral extension of the thoracic shield towards the marginal rim. Rim around anterior margin only slightly broader than around the rest of the thoracic shield.

Tergites: hairless with very few short hairs in the anterior paratergite depressions and with some more longer hairs on the anterior margin. Tips of posterior margins of paratergites do not project posteriorly (Fig. 50).

1st Sternite: lobe as long as coxae, with some isolated long hairs, curved towards leg pair, upper margin irregularly rounded with two invaginations (Fig. 53: S = sternite), a few isolated long hairs near the margin. Rest of the sternite hairless.

Anal shield: rounded, neither bell-shaped nor tapered. Anal shield with black locking carinae on each side, sloping towards the posterior end of the anal shield (Fig. 52: AS = Anal shield; PL = pleurite). The locking carinae in this species are well-developed and broad, remarkably longer than those of the other *Sphaeromimus* species. Locking carinae with distinct but very small invagination at the center.

Legs: the first leg pair with only three, the 2nd with four to five ventral spines and only weakly curved claws. Claws of the following leg pairs are curved. Coxal lobe at 9th leg pair very weakly developed, with many small black triangular spines (Fig. 51). Tarsi of remaining legs with 12-15 ventral spines and one apical spine (damaged in specimen). Coxae at mesal margin with many dense long hairs, also on following podomeres some very long, isolated hairs.

Female sexual characters: 2nd pair of legs without coxal lobe but with one black spine. Operculum (*O*) of vulvae very broad and long, reaching ½ of the prefemur length, maximum length in the center. Center of operculum rim without indentation (=not subreniform), lower margin with weak invagination in the center. Exterior plate (EP) of vulvae long and broad, its anterior margin

ends below the base of the operculum. Inner plate (IP) is not as long as exterior plate, anterior margin of former ends below base. (Fig. 54: O = operculum, EP = exterior plate, IP = inner plate)

Subanal plate rounded, center of anterior margin with a broad invagination. The washboard with three strong, symmetrical stridulation ribs, ending just in front of the anterior margin. 1st and 3rd ribs smaller than 2nd . Subanal plate divided by short median suture only in the center (Fig. 55).

Male sexual characters: 2nd pair of legs without a coxal lobe. *Anterior telopods*: 1st joint with small harp and three stridulation ridges (Fig. 58: F = one thin spine), posterior side of 1st joint with a small projection which reaches the 3rd joint. Lobe-like projection laterally on posterior side of 2nd joint reaching 4th joint (Figs. 58–59). 3rd joint short and slightly invaginated towards the lobe of the second joint, with one longer thin non-scletorized spine (F) juxtaposed the second joint lobe (Figs. 58–59: A = big spine, B = two small spines, D = small lateral spine, F = longer spine). *Posterior telopods*: Movable finger of chela with genus-specific dentition and row of crenulated teeth. The opposite finger (2nd joint) features crenulations juxtaposed to the crenulated teeth of the movable finger and also one non-slerotized spine on its anterior side (Fig. 56). Movable finger almost hairless. 2nd joint with some hairs on the immovable finger. Stout tip of immovable finger curved and hook-shaped (Figs. 56–57). Telopod coxa densely covered with hairs.

Distribution and ecology — So far this species of *Sphaeromimus* was collected only from a fragment of littoral rainforest on sand in Mandena. This particular patch of littoral rainforest is little disturbed, with 50–75% forest cover (QIT Madagascar forest map). The holotype was found in thin (5–30mm) dry leaf litter, containing mostly leaves and some tree fruits. A few winged Blattodea were found as well. A new species of genus *Zoosphaerium* (unpublished/in preparation), which occurs also in the littoral rainforest in Sainte Luce and in the eastern lowland rainforest, was common in this area (>300 mature and mostly immature where detected).

Body rings of spirostreptid and small sphaerotheriid tergites were found in a layer of arthropod remains around ant holes of a big red ant species. It is unknown how the ants are able to hunt these well-armored animals. Rolled up sphaerotheriids were placed near ants, but the ants showed no interest. A large *Zoosphaerium* specimen (34 mm long, 16 mm broad (2nd segment)) was put in a cage with one Carnivora: *Galidia elegans* inside, which was caught and kept at the Pepinière in Mandena. *Galidia* was able to detect the rolled up specimen, broke the tergites with a few bites of the lateral teeth and ate internal parts, ignoring the intestine tergite pieces. It is likely that *Galidia elegans* may represent a predator of pill millipedes, including *Sphaeromimus inexpectatus*. Predation of pill millipedes by mongoose was reported by Eisner and David (1969).

The female collected in the middle of April was carrying two eggs, suggesting that the breeding season was in progress. The forest patch of Mandena was intensively searched for 18 days during rain and at night without locating more specimens. This fact prompts us to suggest that *S. inexpectatus* is either a very rare species or was not active during the collection time. *S. inexpectatus* was not found in any other collection samples or in nearby littoral forest patches of Petriky and Sainte Luce. Additionaly it was not present in the collections of CAS, FMNH or in the huge collections of the MNHN. People living in the area are familiar with pill millipedes, calling them "Mia," but were not aware of this red-colored species. These observations may indicate that *S. inexpectatus* is endemic or now restricted to the littoral forest patch of Mandena. According to the isopod fauna and vegetation (Dumetz 1999), the littoral forests of Mandena are different from those of Petriky and Sainte Luce, albeit a distance of only 20–30 km separates these.

Conservation.— Currently, the observed patch of littoral forests is separated by pseudosteppe or *Eucalyptus* plantations with apparently little humus and soil arthropods (per. observation). In the past 50 years almost 73% of the original forest was destroyed (Vincelette et al. 2003). Currently, the small study area is efficiently protected by QIT Madagascar. It is however, uncer-

TABLE 3. Species separation in *Sphaeromimus*. No. = Number; gn = gnathochilarium; a.t. = anterior telopods; p.t. = posterior telopods; SR = stridulation ridges.

Character:	*Sphaeromimus musicus*	*Sphaeromimus splendidus* sp. nov.	*Sphaeromimus inexpectatus* sp. nov.
Tergite coloration:	orange with black pattern	black	pink
Body length:	up to 34.5 mm	up to 23.6 mm	at least 15 mm
No. of SR in female	7-Aug	5-May	3
No. of SR in male	5	3	3
antennal cones	up to 75	up to 45	up to 75
Sensorial cones lateral of gn-palpi	4, 1 displaced	4, all together	?
Surface of tergites	few hairs	bald	bald
Patch of hairs on the head towards the collum	present	absent	absent
Molar plate process of mandible	with 1 large step	with 2 steps	with 2 steps (2nd small)
No. of pectinate lamellae	6	7-Jul	7
No. of ocelli	>80	50–60	?
Coxal lobe of legs	weakly developed	strongly developed	nearly absent
Endotergum: marginal ridge	straight	straight	curved
Endotergum: flattened nodules	oval	rounded	rounded
Endotergum: No. of rows of marginal bristles	3-Mar	1–2	1
a.T. process of 2nd joint visible	only posterior of joint 3&4	only posterior of joint 3&4	posterior and lateral of joint 3&4
p.t.: 2nd joint	apical end stout	apical end stout	apical end hook-like

tain, whether the protected area is large enough to sustain viable populations of this species. The senior author noted the lack of old large trees in the area and wood removal by humans is ongoing.

DISCUSSION

The three species of *Sphaeromimus* are easily distinguished from each other, see Table 3. Jeekel (1974, Fig. 64 B) presented the most recent classification of the order Sphaerotheriida, while Hoffman (1976) and Mauriès (2001) modified Jeekel's classification of the sphaerotheriid family Sphaeropoeidae (Fig. 64 A). Jeekel employed characters found in the shape of the female vulva and the stridulation organs (harp in males, washboard in females) to separate tribes and subfamilies. The genus *Sphaeromimus* belongs to the family Sphaerotheriidae, sharing the main synapomorphy of its genera: basis of the vulval operculum embraced by the bursa (consisting of the exterior and inner plate, Fig. 64, character 1). Jeekel considers the presence of a female stridulation organ, the washboard (Fig. 64, character 2) as the synapomorphy for the subfamily Arthrosphaerinae, to which the genus *Sphaeromimus* is currently assigned. The other synapomorphy of the subfamily cited by Jeekel, the median protrusion of the bursa, is not present in *Sphaeromimus* (Fig. 64, character 3). In Jeekel's classification, *Zoosphaerium* and *Sphaeromimus*, the two Malagasy sphaerotheriid genera, are placed in the tribe Zoosphaeriini, based on the possession of the harp in the males (occurs in both genera, character 4). Jeekel also listed the shape of the subreniform

female operculum (character 5), as it occurs in *Zoosphaerium*, as an apomorphy of the tribe. However, now that females of *Sphaeromimus* are known, this latter apomorphy cannot be supported. Females of *Sphaeromimus* have a round operculum with a smooth edge.

Furthermore, *Sphaeromimus* shares characters with members of the Indian genus *Arthrosphaera*, currently placed by Jeekel (1974) in the tribe Arthrosphaerini of the Arthrosphaerinae. Such shared characters are: 6th antennomere flat and broad (cylindrical in *Zoosphaerium*, Fig. 64, character 8), and the four-jointed anterior telopods (Attems 1936, Fig. 64, character 9). Thus, males of *Sphaeromimus* share on the one hand a characters with the genus *Arthrosphaera* (characters 8 and 9) and on the other hand a character, the harp (character 4), with the genus *Zoosphaerium* (DeSaussure and Zehntner 1902; Pocock 1895). In *Sphaeromimus*, the washboard features a rather deep median groove (character 10) of variable length. The presence of the groove may indicate the fusion of two separate plates. In contrast, all *Zoosphaerium* species examined to date possess a completely fused subanal plate without a suture or groove. A groove is also present in at least one species of the Indian genus *Arthrosphaera*. Unfortunately, the form of the subanal plates are known for only few members of both genera. These morphological details indicate clearly that the current classification scheme (Fig. 64) lacks sufficient character support and that more characters are needed to define monophyletic clades within the Sphaerotheriida unequivocally.

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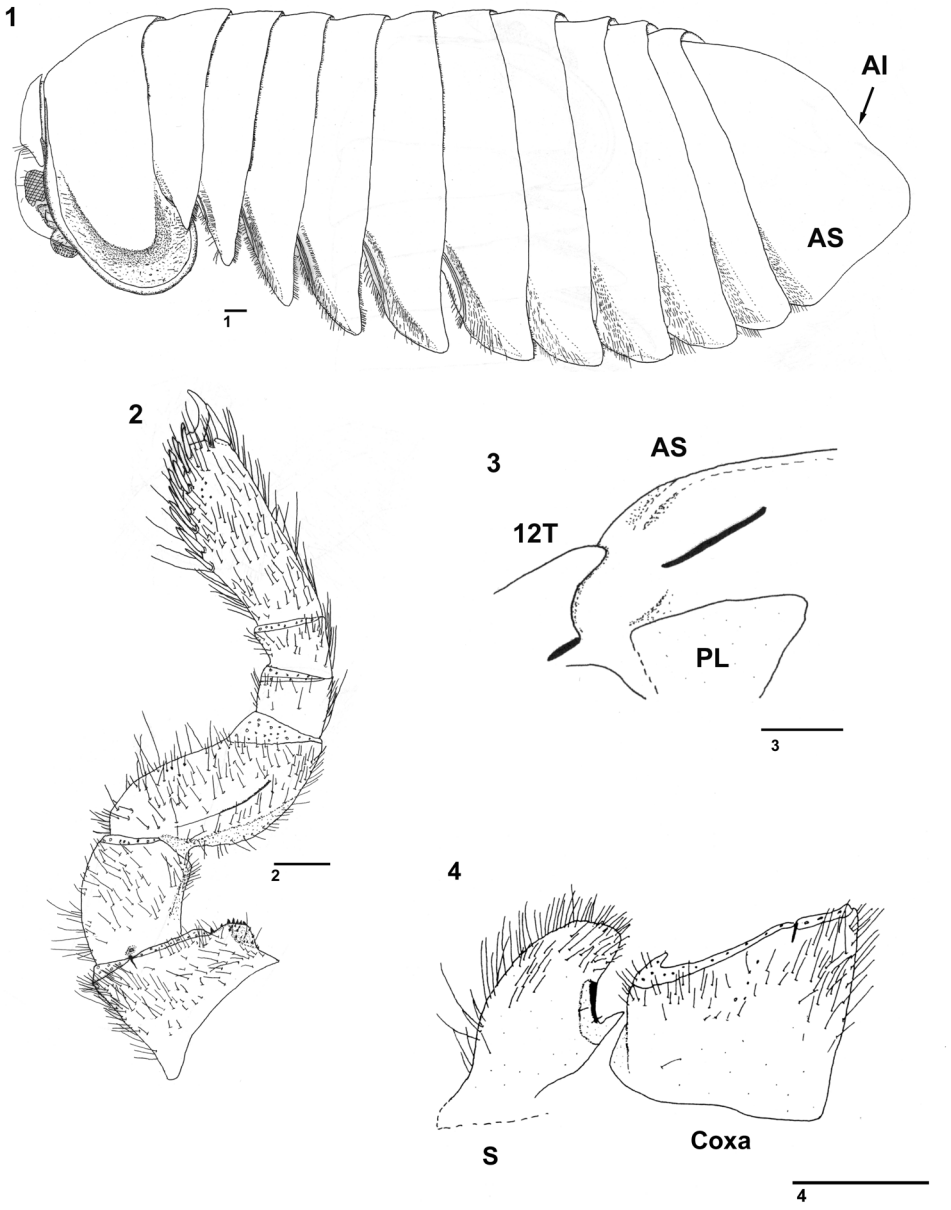
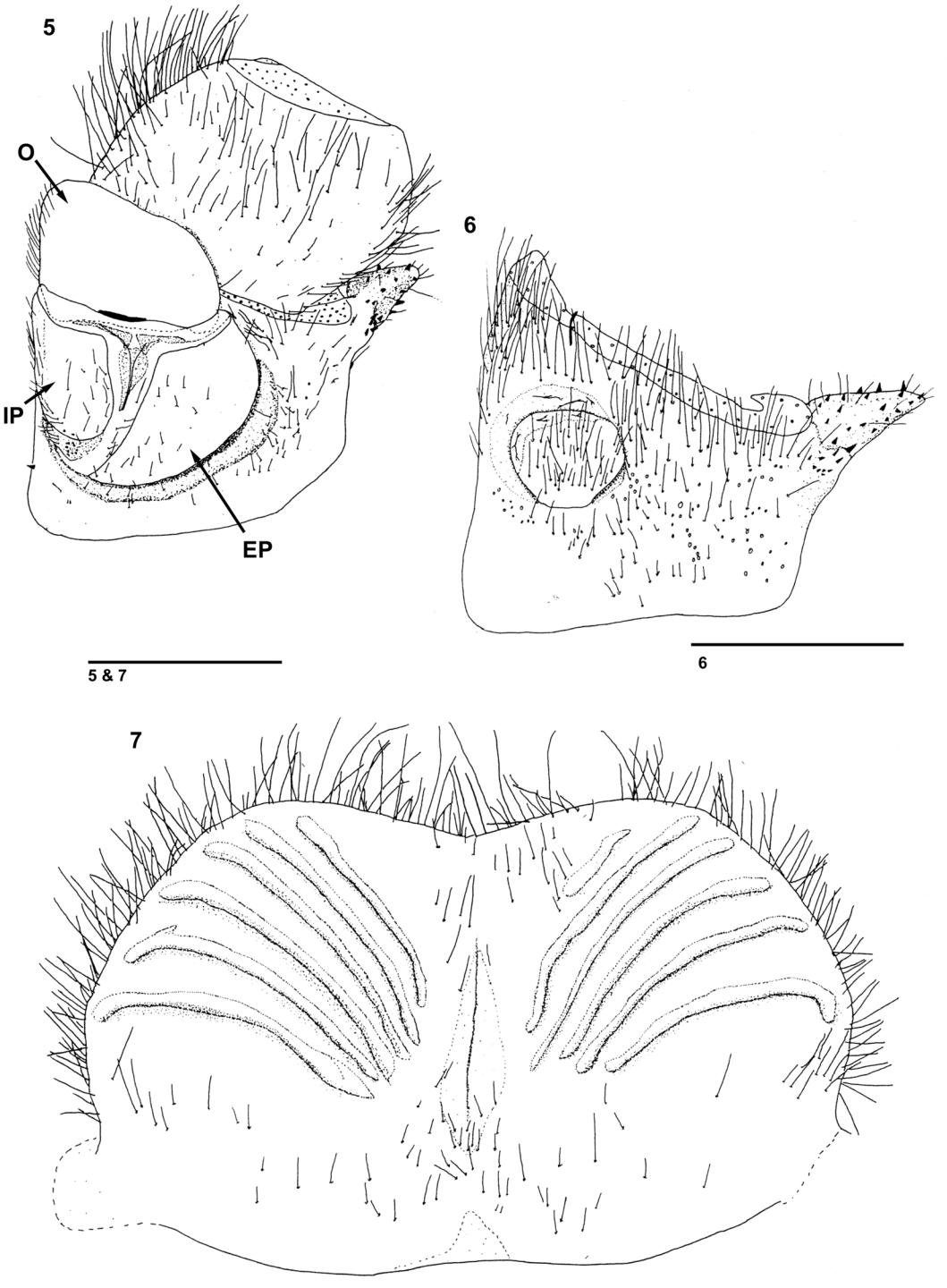
ILLUSTRATIONS



FIGURES 1–4. *Sphaeromimus musicus*, male. 1: habitus; 2: left 9th leg, posterior view; 3: anal shield, dorsal view of black locking carinae; 4: 1st right sternite with coxa of 1st pair of legs. AI = invagination of anal shield; 12T = 12th tergite; PL = pleurite; AS = anal shield; S = sternite. Scale bars: 1 mm.



FIGURES 5–7. *Sphaeromimus musicus*, female and male. 5: 2nd left leg: coxa (female) with vulva; 6: 2nd left leg: coxa (male), posterior view; 7: washboard. O = operculum; IP = inner plate; EP = exterior plate. Scale bars: 1 mm.

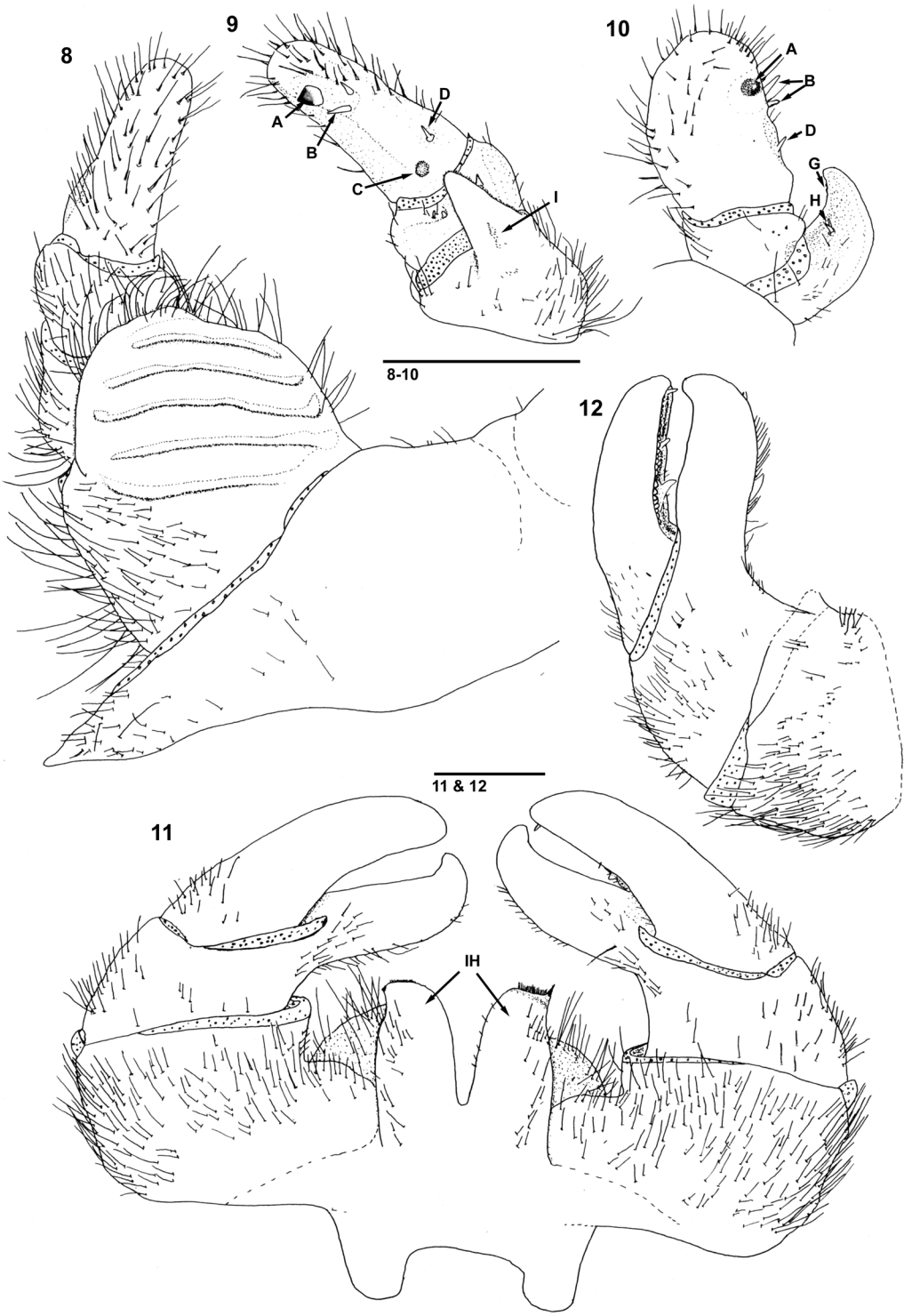

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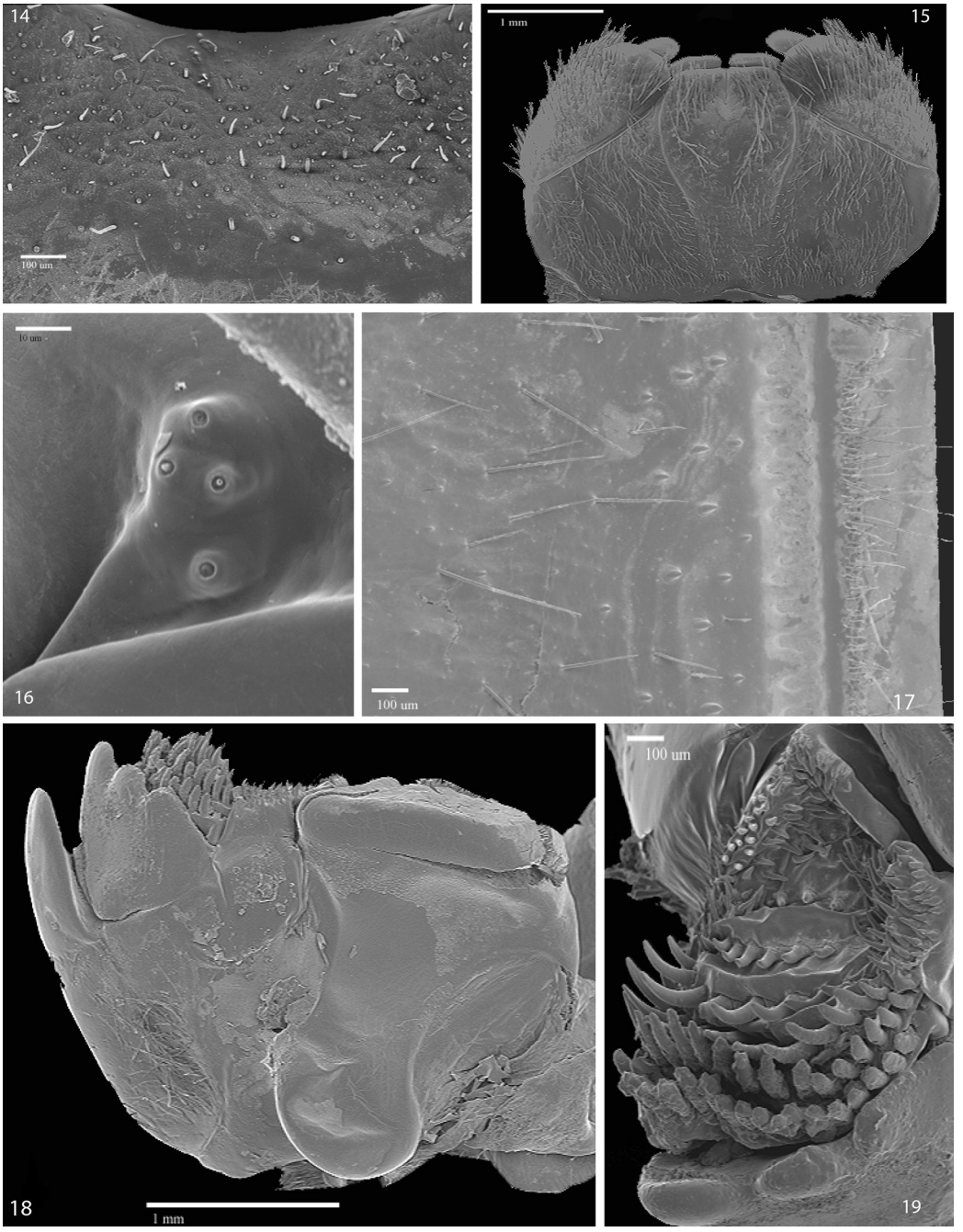
FIGURE 13 (above). *Sphaeromimus musicus*. Photo of freshly preserved male.

FIGURES 8–12 (left). *Sphaeromimus musicus*, male. 8: left anterior telopod, anterior view; 9: left anterior telopod, posterior view; 10: anterior telopod, lateral view; 11: posterior telopods, anterior view; 12: posterior right telopod, posterior view. A = 4th joint big spine; B = 4th joint 2 small spines; C = 4th joint knob; D = 4th joint 1 small lateral spine; I = 2nd joint sensorial hairs; G = 2nd joint lobe crenulation; H = 2nd joint lobe 2 spines; IH = inner horns. Scale bars: 1 mm.



FIGURES 14–19. *Sphaeromimus musicus*, male SEM. 14: patch of hairs on head to collum; 15: gnathochilarium, ventral view; 16: field of sensorial cones lateral of palpi of gnathochilarium; 17: endotergum 18: right mandible, general view; 19: right mandible, pectinate lamellae.

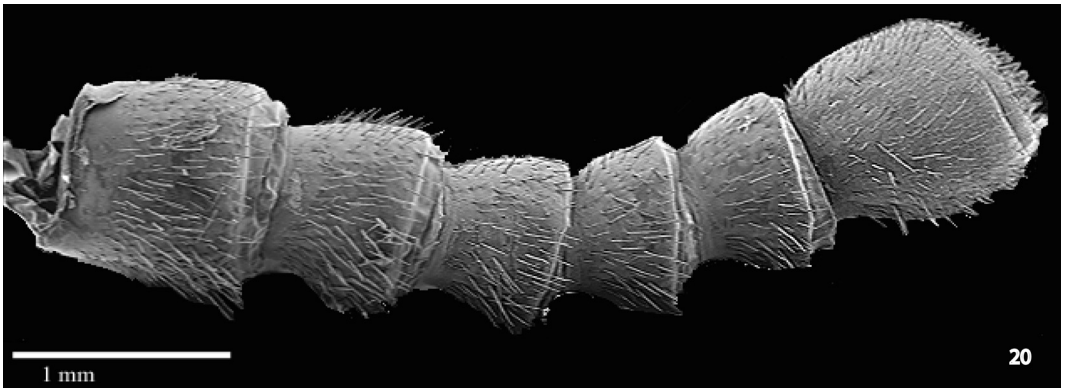
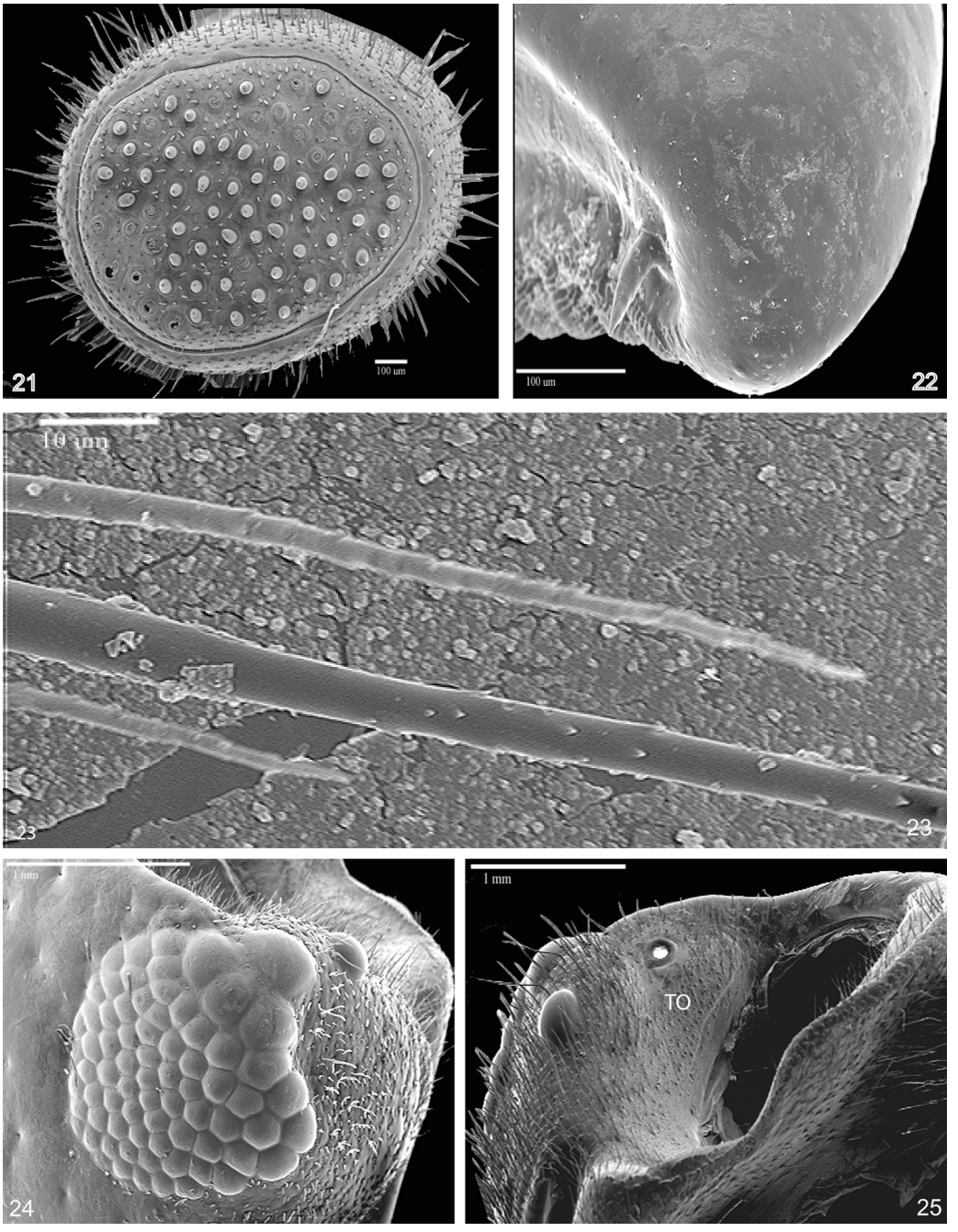
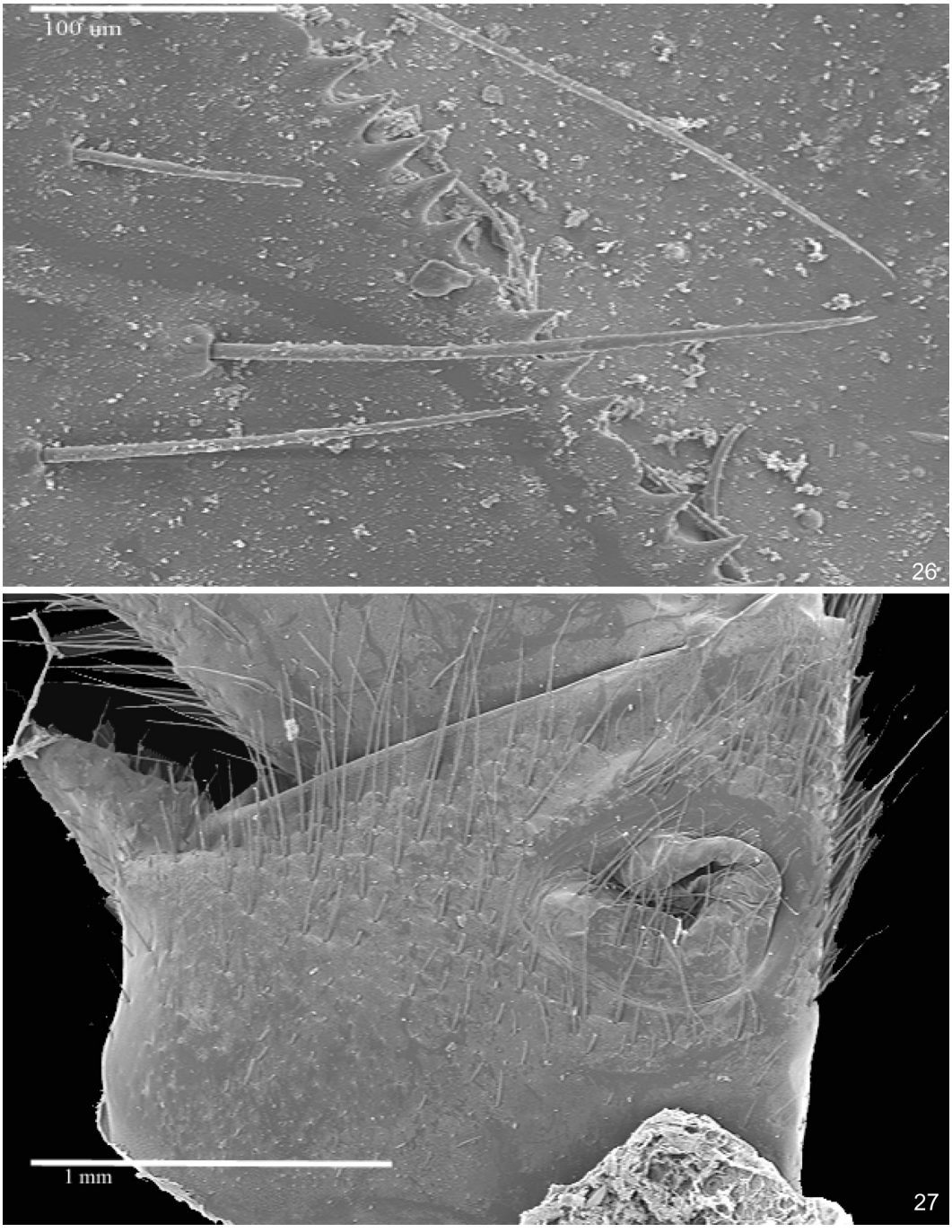


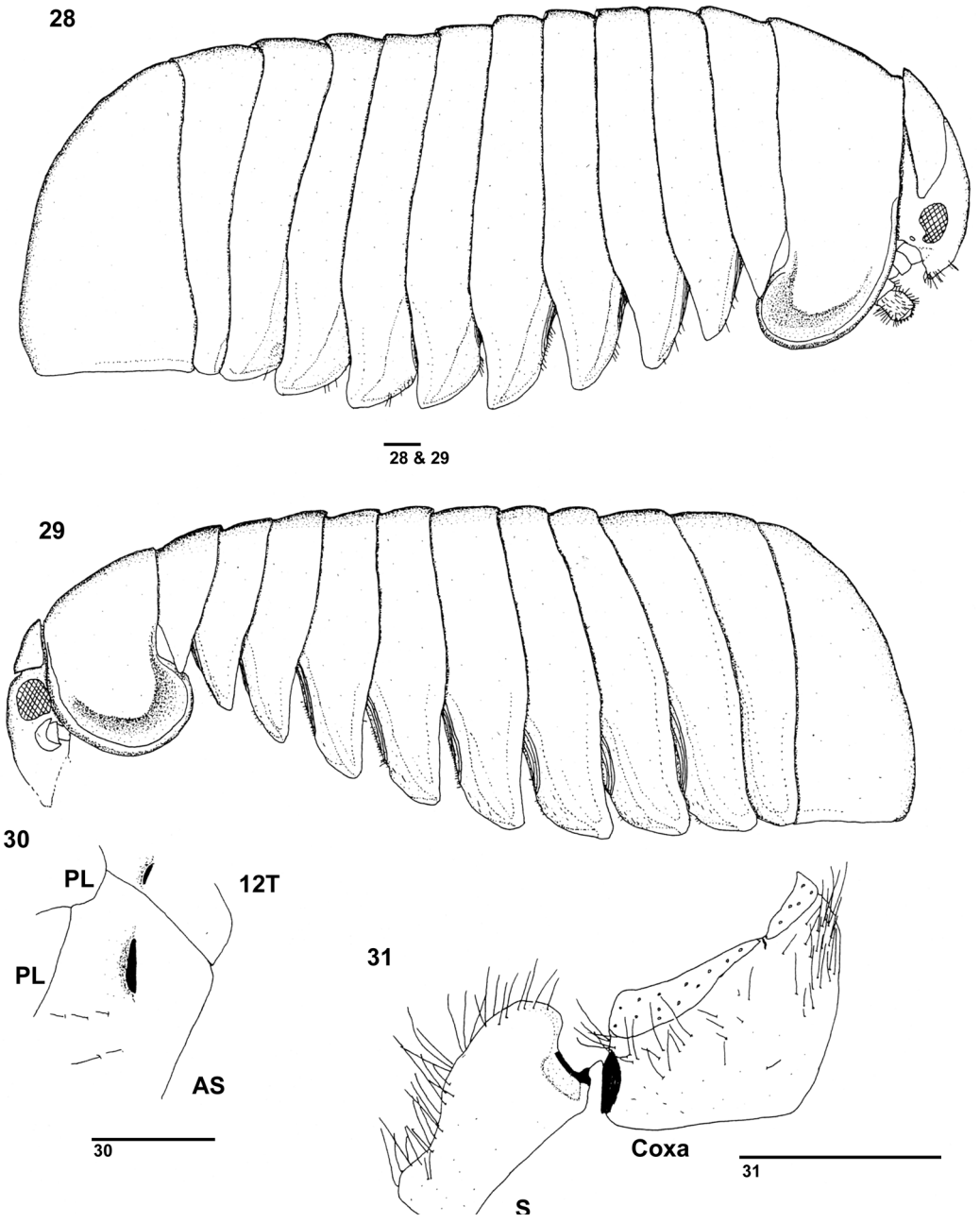
FIGURE 20. *Sphaeromimus musicus*, male SEM, antennae, lateral view.



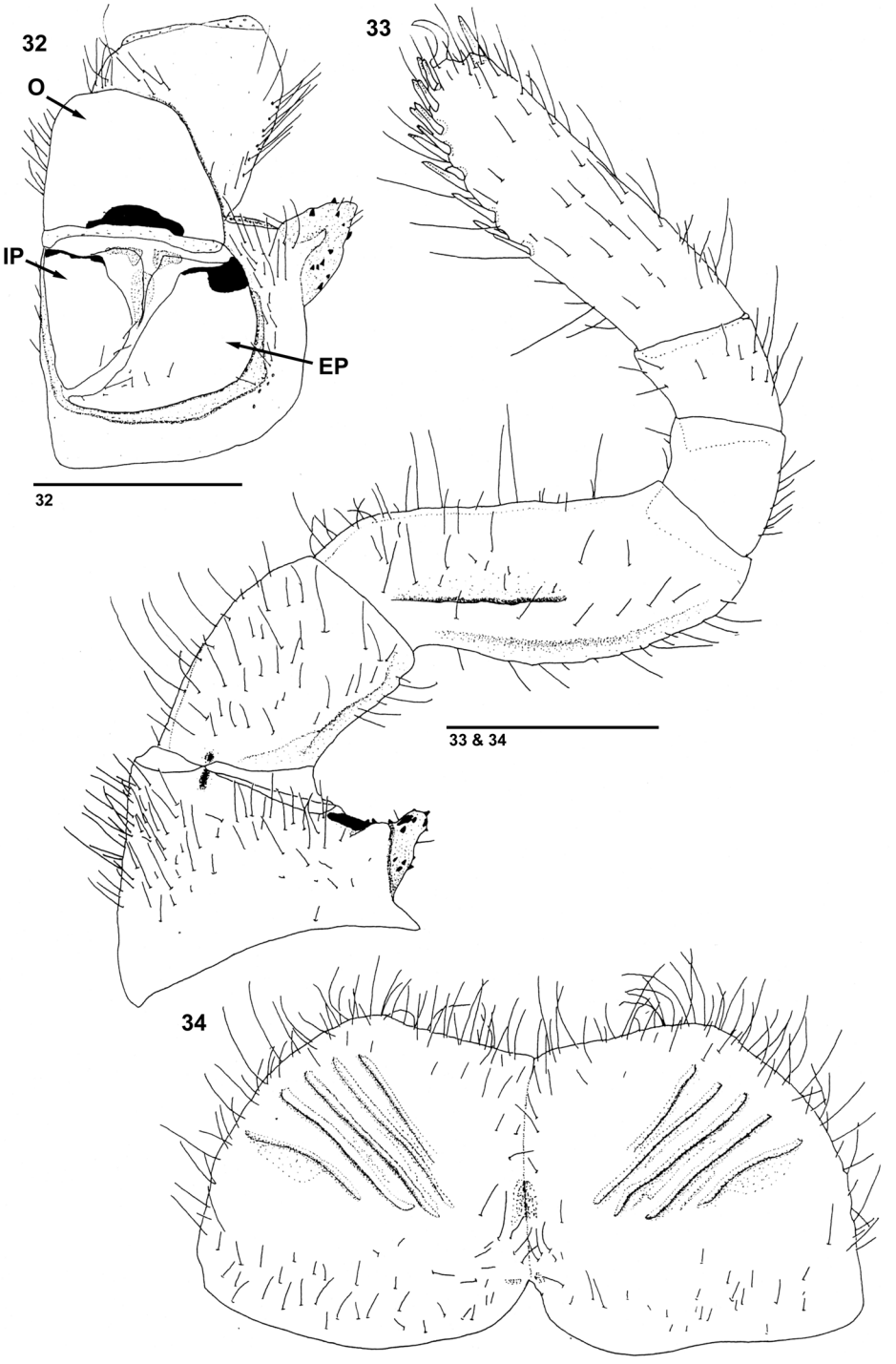
FIGURES 21–25. *Sphaeromimus musicus*, male SEM. 21: 6th joint of antennae; 22: apical part of movable finger of posterior right telopod; 23: bristle of endotergum; 24: right ocelli; 25. antennal groove with Tömösváry organ (TO) and aberrant ocellus.



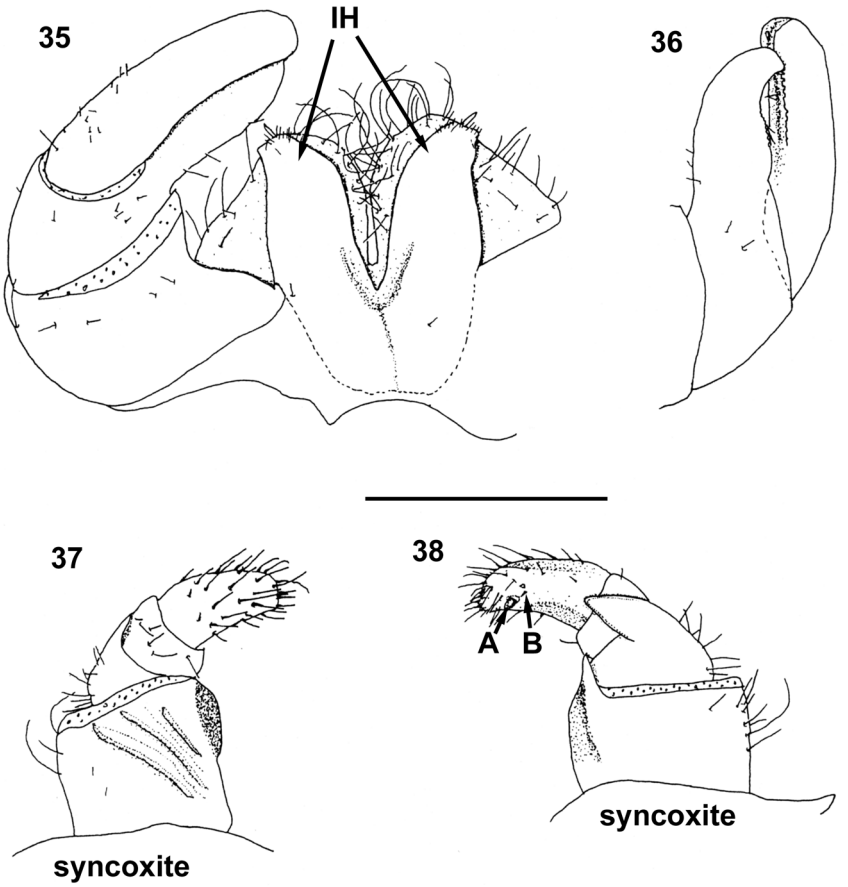
FIGURES 26–27. *Sphaeromimus musicus*, male SEM. 26: posterior side of 9th femur with toothed ridge; 27: 2nd coxa, posterior view, coxal lobe and male gonopode.



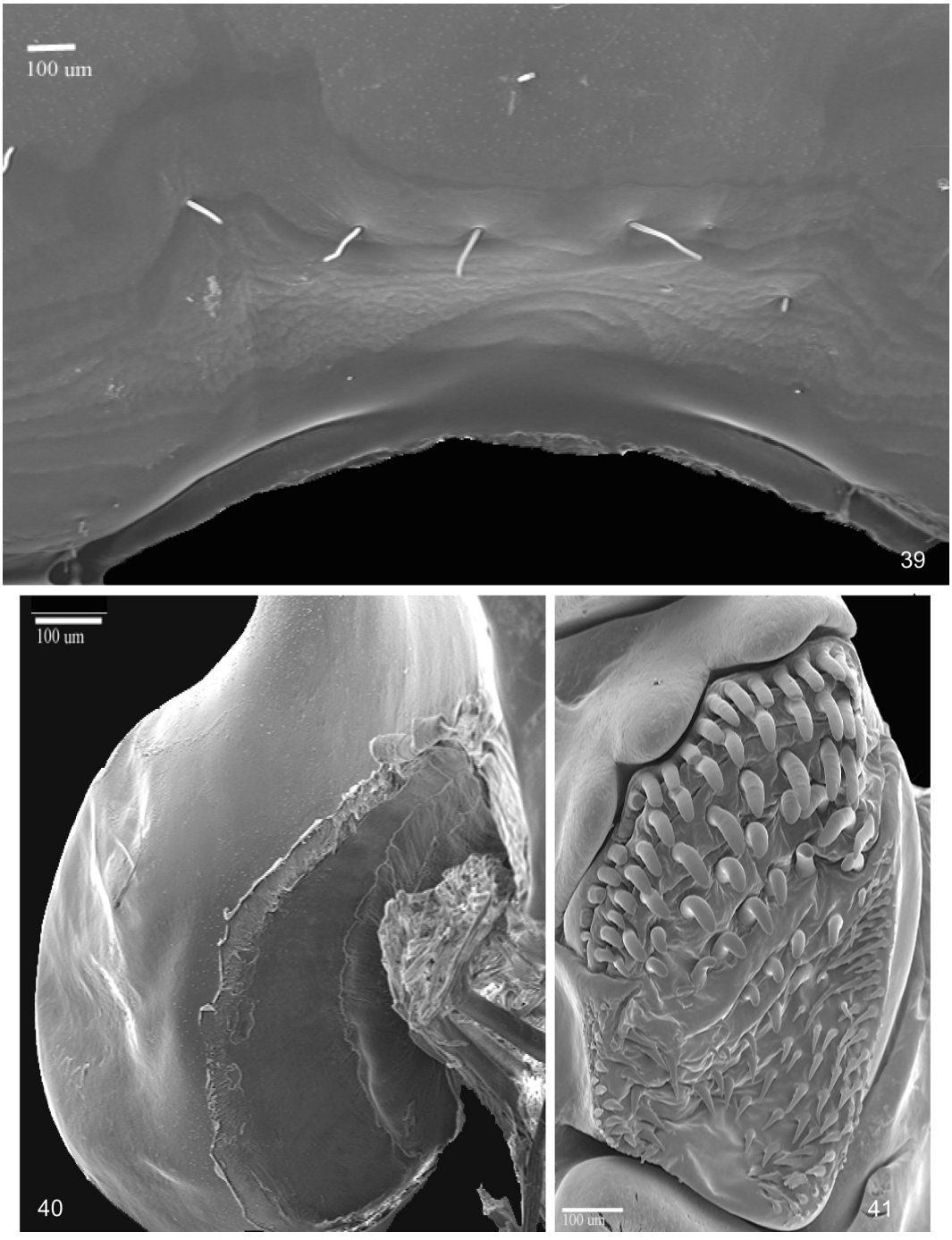
FIGURES 28–31. *Sphaeromimus splendidus*, female holotype. 28: habitus, right side; 29: habitus, left side; 30: anal shield, dorsal view of black locking carinae; 31: 1st right sternite; 12T = 12th tergite; AS = anal shield; PL = pleurite; S = sternite. Scale bars: 1 mm.



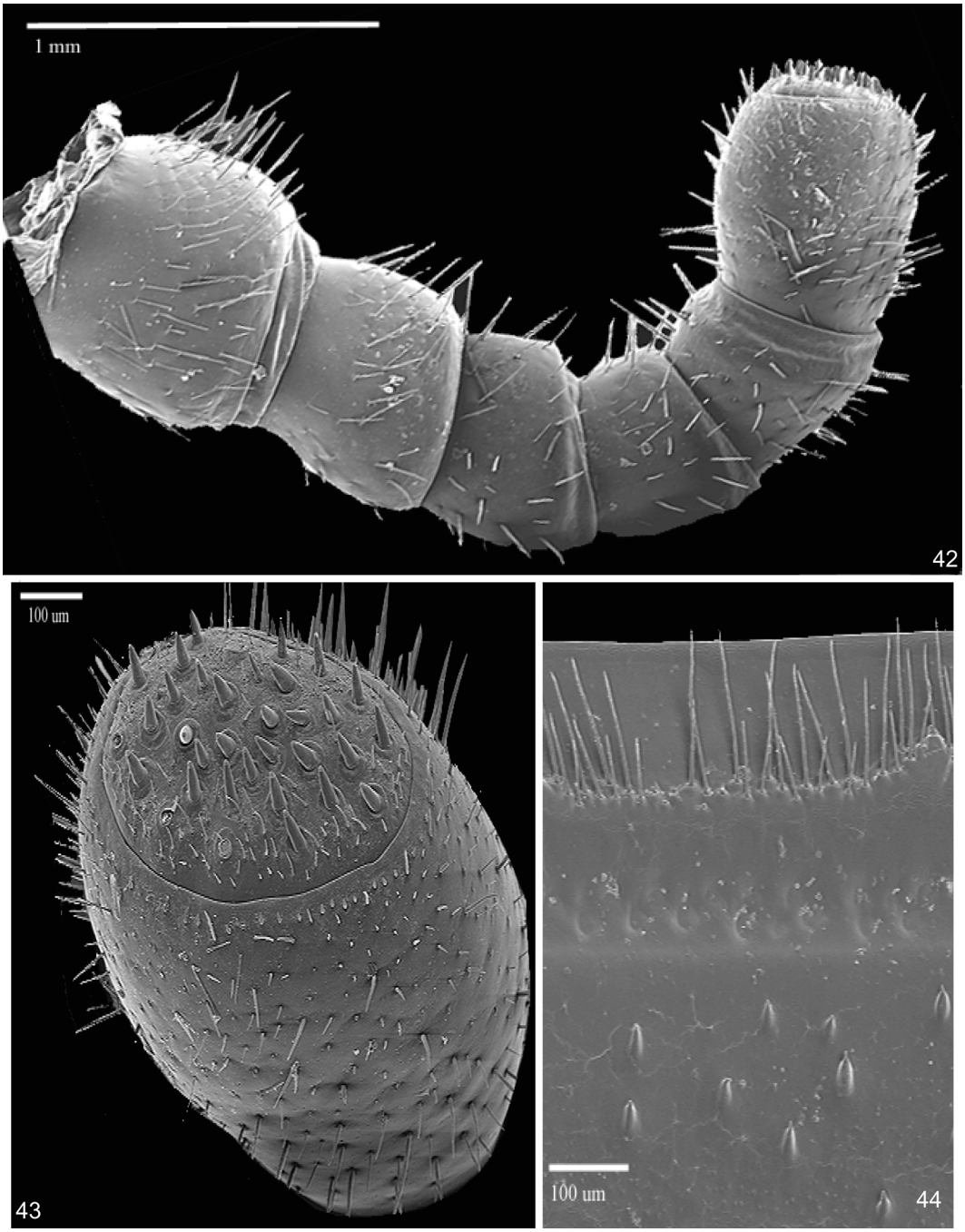
FIGURES 32–34. *Sphaeromimus splendidus*, female holotype. 32: left vulva; 33: left 9th leg, posterior view; 34: washboard; O = operculum; IP = inner plate; EP = exterior plate. Scale bar: 1 mm.



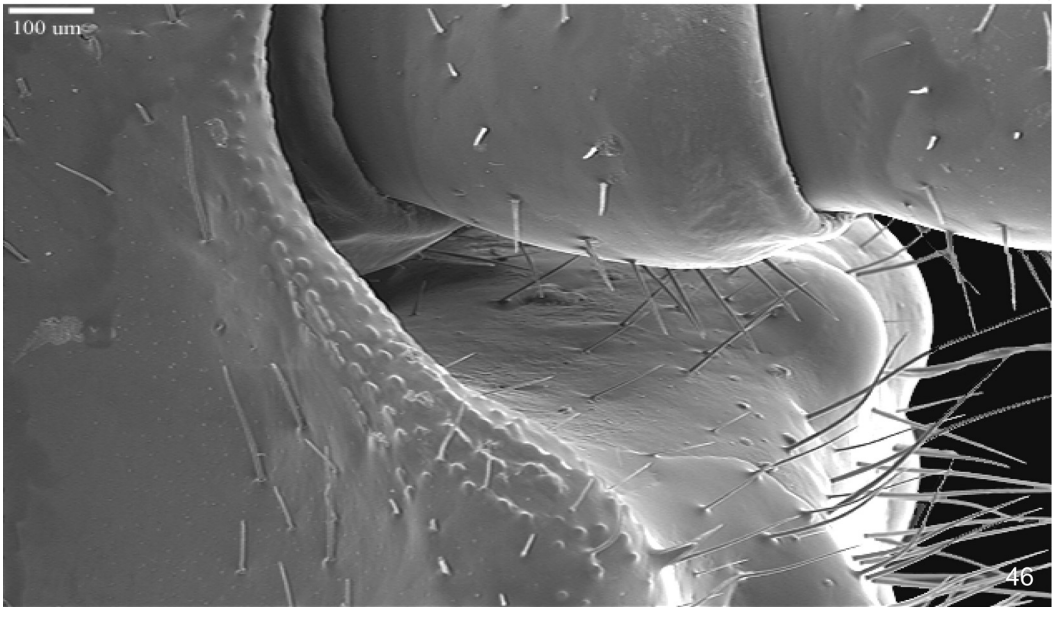
FIGURES 35–38. *Sphaeromimus splendidus*, male paratype. 35: left posterior telopod, anterior view; 36: left posterior telopod, posterior view; 37: left anterior telopod, anterior view; 38: left anterior telopod, posterior view; A = big spine; B = two small spines; IH = inner horns. Scale bar: 1 mm.



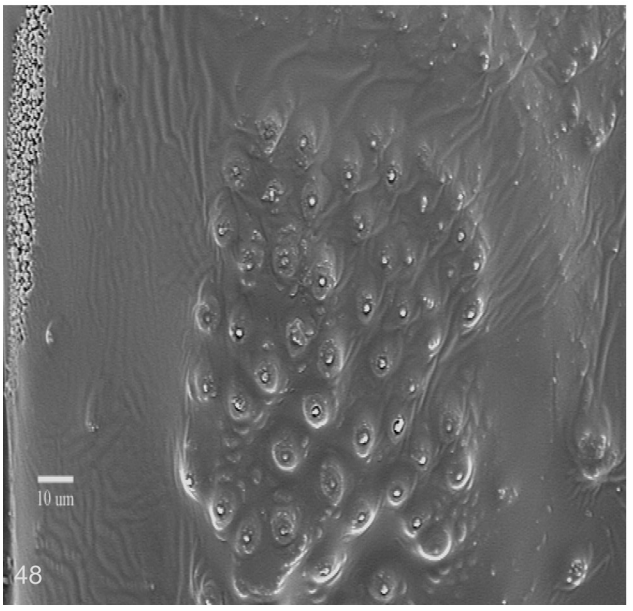
FIGURES 39–41. *Sphaeromimus splendidus*, female SEM. 39: patch of hairs on head to collum; 40: right mandible, molar plate process; 41: right mandible, pectinate lamellae.

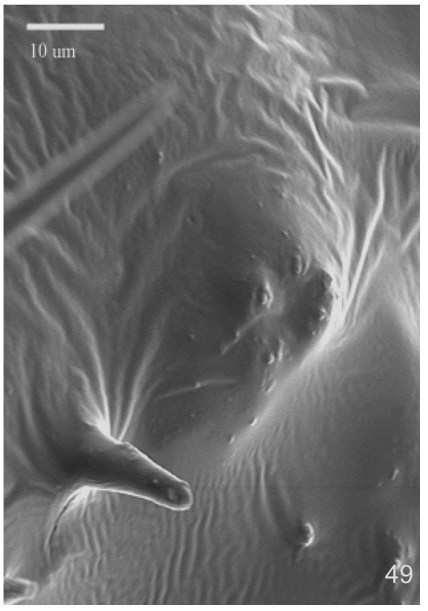


FIGURES 42–44. *Sphaeromimus splendidus*, female SEM. 42: antennae lateral; 43: 6th antennomere; 44: endotergum.

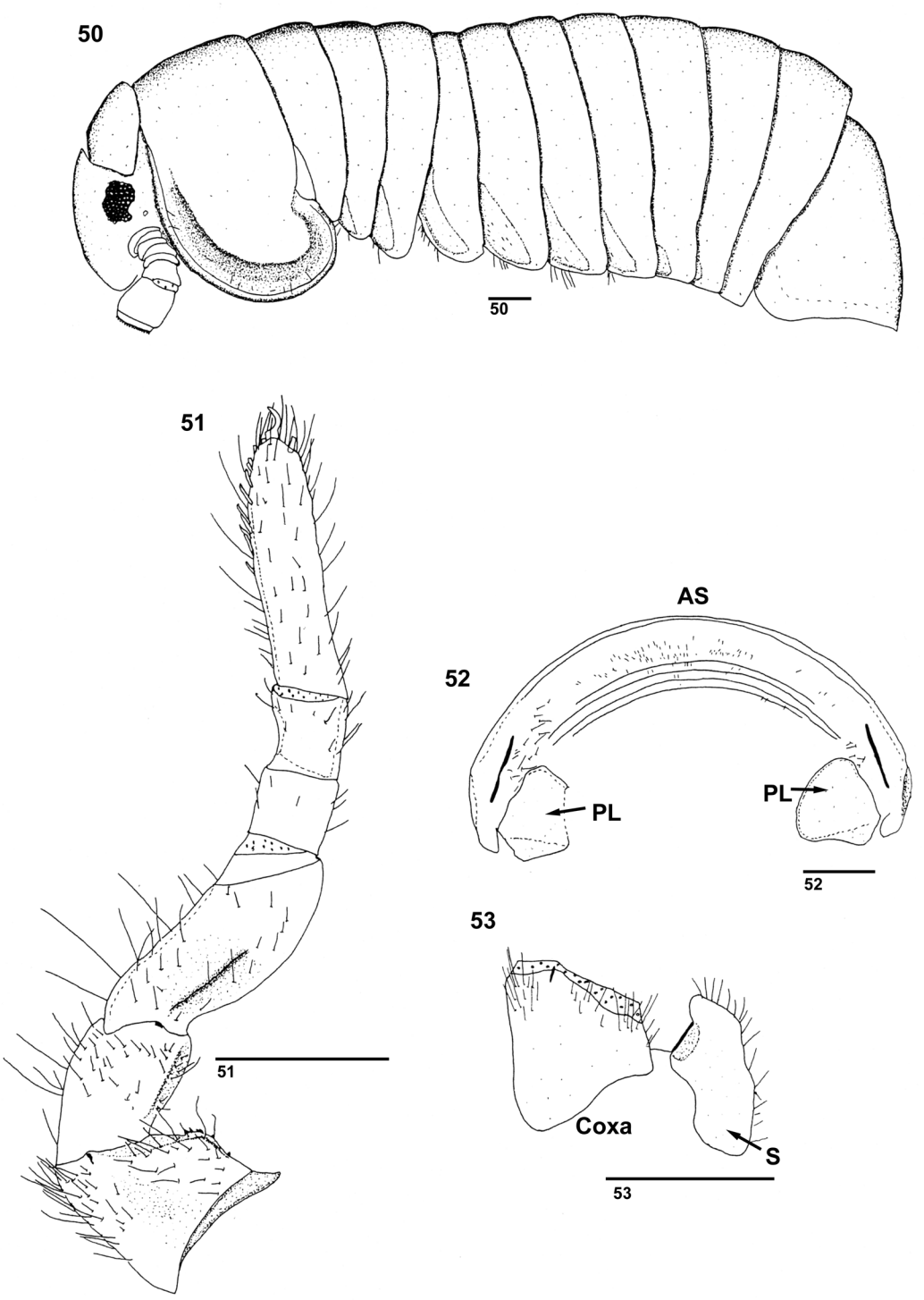


FIGURES 45–46. *Sphaeromimus splendidus*, female SEM. 45: epipharynx, anterior side; 46: edges of antennal groove with crenulated teeth and one spine.

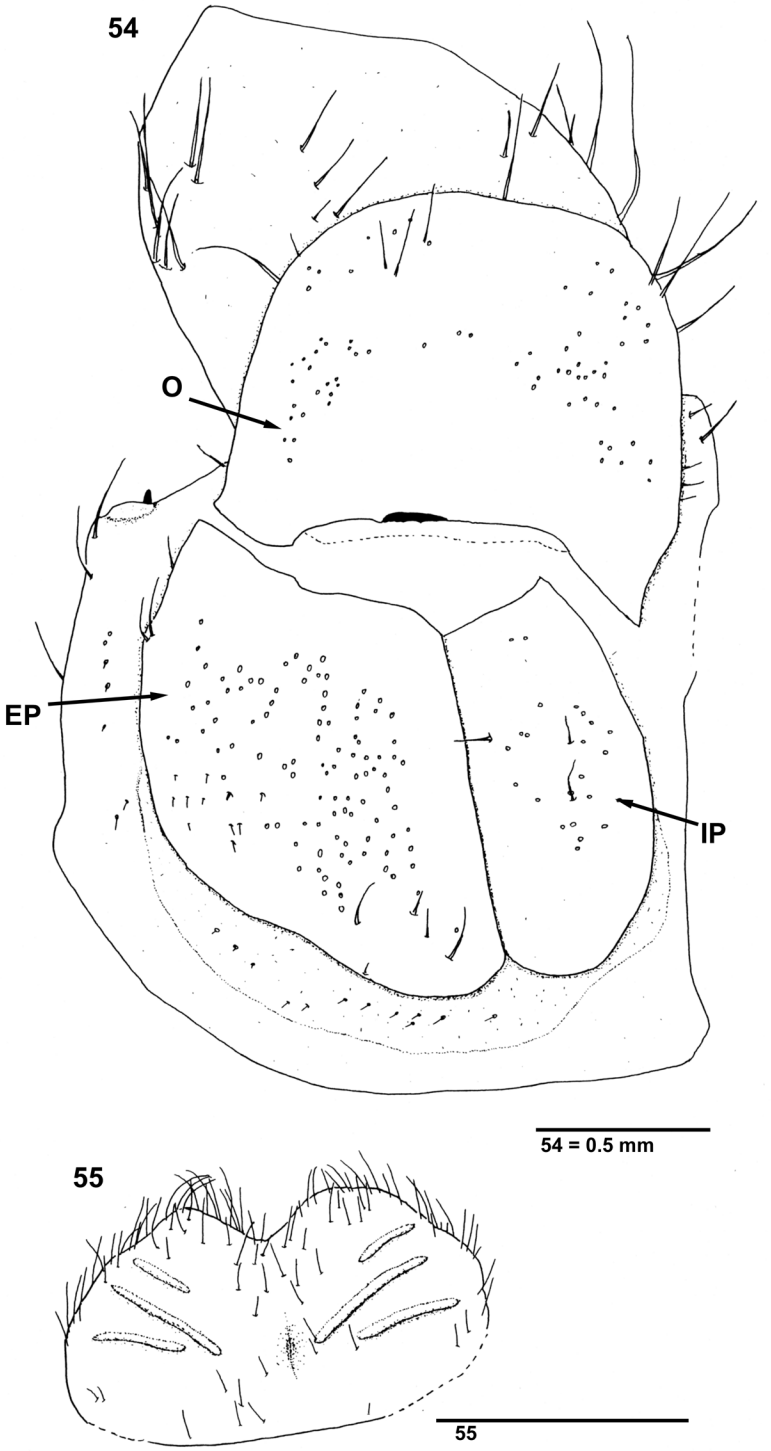




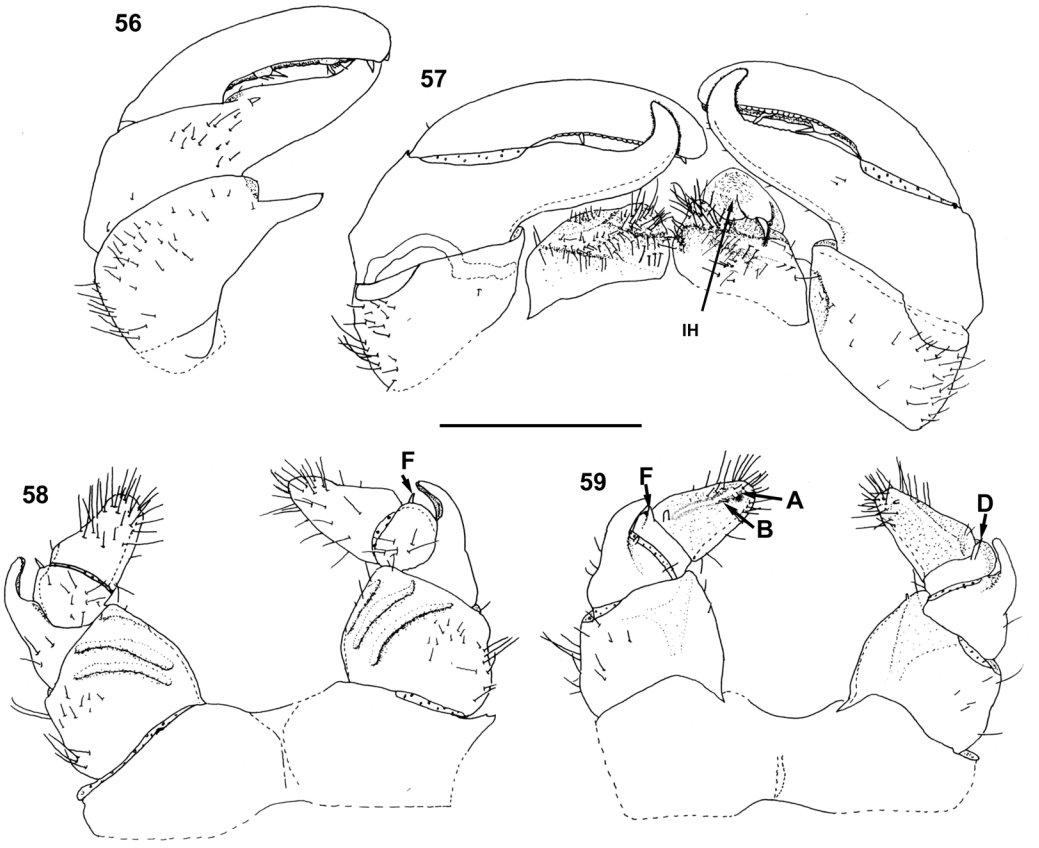
FIGURES 47–49. *Sphaeromimus splendidus*, female SEM gnathochilarium. 47: gnathochilarium, ventral view; 48: sensual cones on medial pads; 49: pit laterally of palpi with sensual cones.



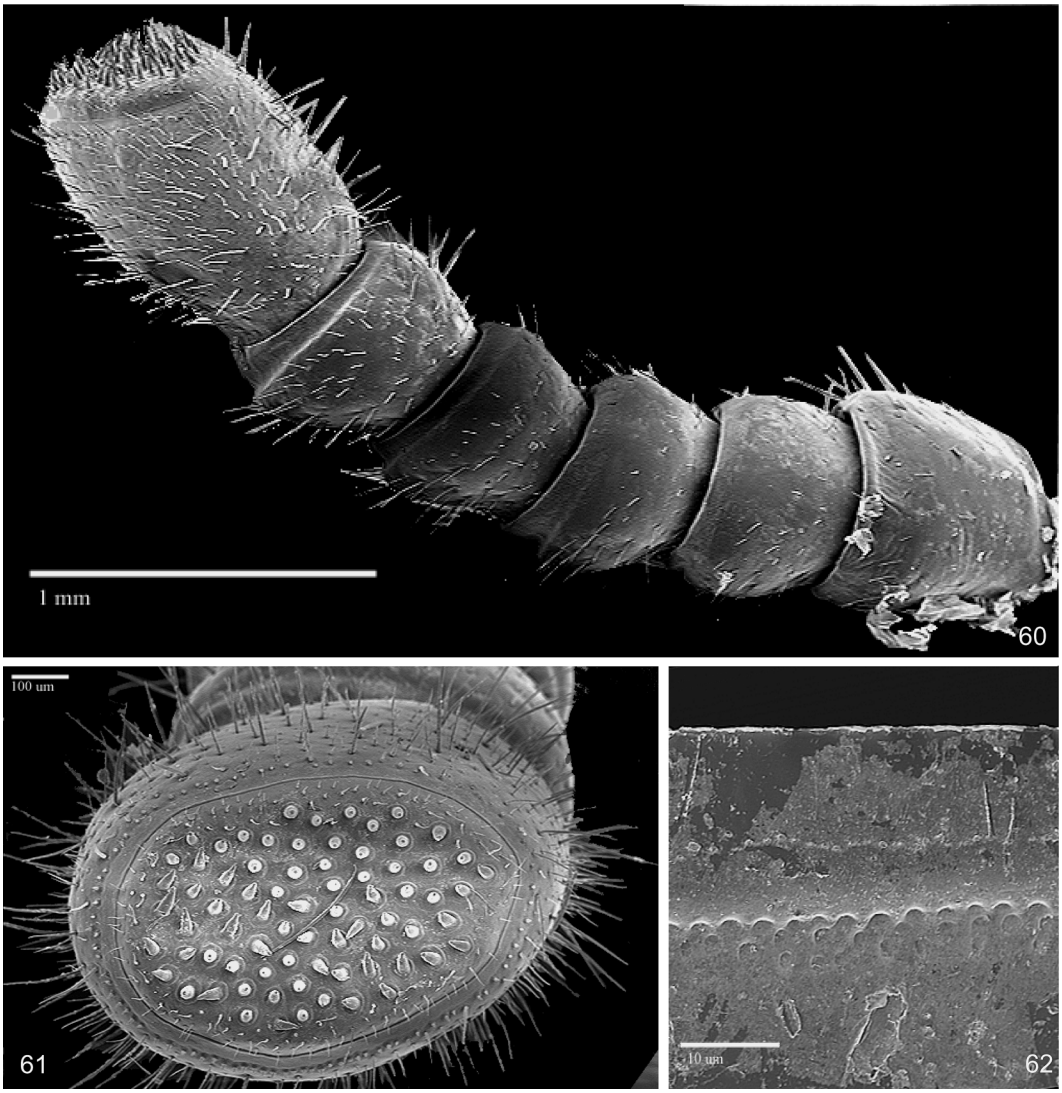
FIGURES 50–53. *Sphaeromimus inexpectatus*, male holotype. 50: habitus; 51: left 9th leg, posterior view; 52: anal shield, dorsal view of black locking carinae; 53: left 1st sternite; AS = anal shield, PL = pleurite; S = sternite. Scale bars: 1 mm.



FIGURES 54–55. *Sphaeromimus inexpectatus*, female paratype; 54: vulva (macerated); 55: washboard right; O = operculum; IP = inner plate; EP = exterior plate. Scale bars: 0.5 and 1 mm.

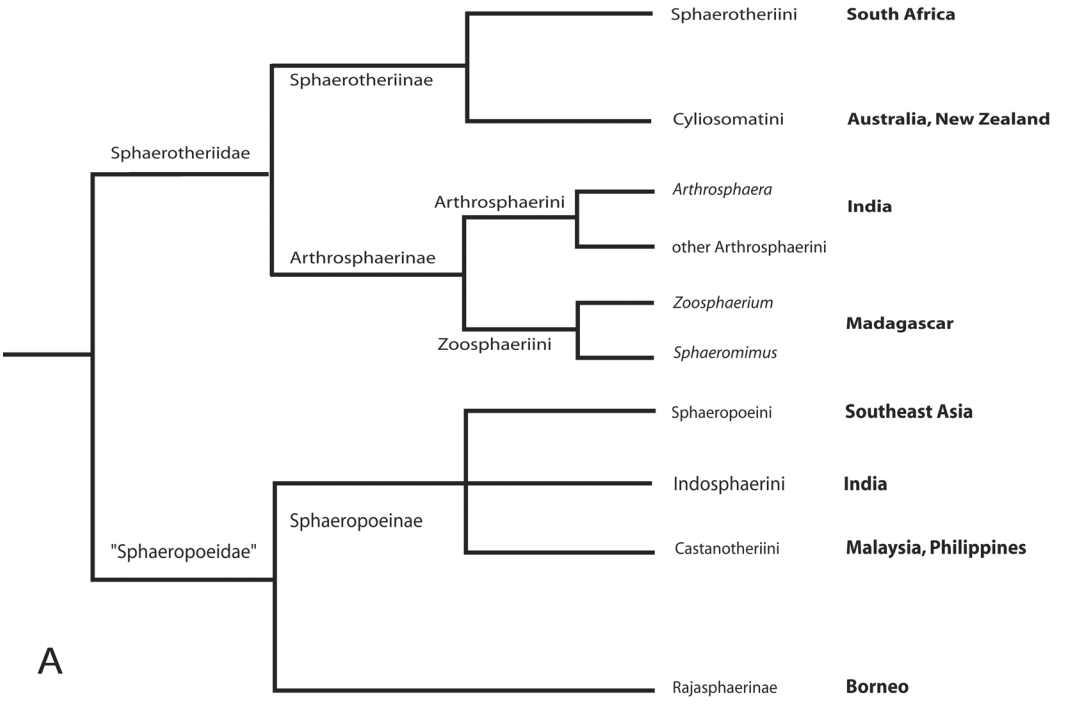


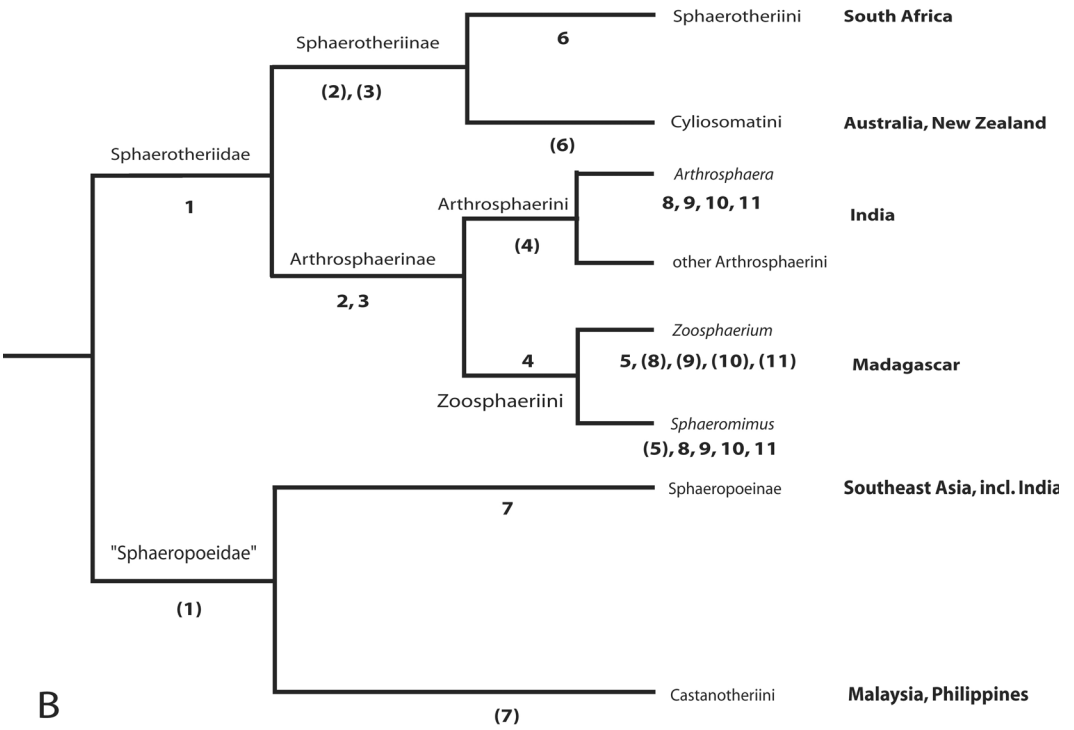
FIGURES 56–59: *Sphaeromimus inexpectatus*, male holotype; 56, left posterior telopod, posterior view; 57, posterior telopods, anterior view; 58, anterior telopods, anterior view; 59, anterior telopods, posterior view; A = big spine; B = two small spines; D = small lateral spine; F = longer spine; IH = inner horns of posterior telopod. Scale bar: 1 mm.



FIGURES 60–62. *Sphaeromimus inexpectatus*, male holotype SEM. 60: antennae lateral; 61: 6th antennomere; 62: endotergum.

FIGURE 63. *Sphaeromimus inexpectatus*, male holotype, photo.


Sphaerotheriini
South Africa
Sphaerotheriinae
Cyliosomatini
Australia, New Zealand
Sphaerotheriidae
Arthrosphaerini
Arthrosphaera
India
other Arthrosphaerini
Arthrosphaerinae
Zoosphaerium
Madagascar
Zoosphaeriini
Sphaeromimus
Sphaeropoeini
Southeast Asia
Indosphaerini
India
Sphaeropoeinae
Castanotheriini
Malaysia, Philippines
"Sphaeropoeidae"
Rajasphaerinae
Borneo
A


Sphaerotheriini
South Africa
6
Sphaerotheriinae
(2), (3)
Cyliosomatini
Australia, New Zealand
(6)
Sphaerotheriidae
Arthrosphaera
1
Arthrosphaerini
8, 9, 10, 11
India
(4)
other Arthrosphaerini
Arthrosphaerinae
2, 3
Zoosphaerium
4
5, (8), (9), (10), (11)
Madagascar
Zoosphaeriini
Sphaeromimus
(5), 8, 9, 10, 11
Sphaeropoeinae
Southeast Asia, incl. India
7
"Sphaeropoeidae"
(1)
Castanotheriini
Malaysia, Philippines
(7)
B

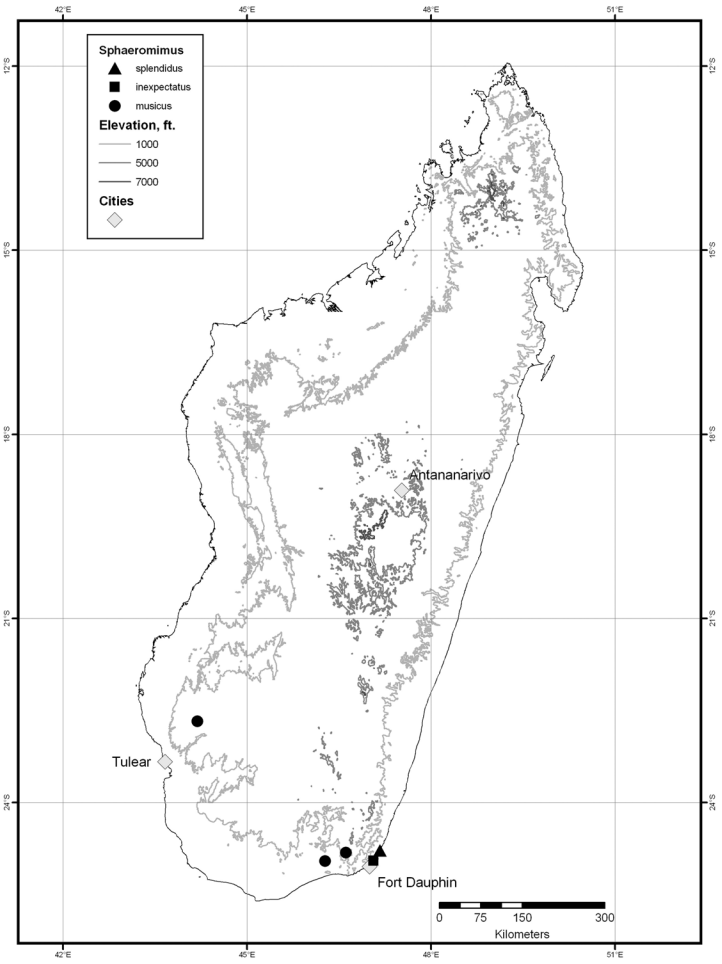


FIGURE 65. Distribution map of *Sphaeromimus.*

FIGURE 64 (left). Classification of the order Sphaerotheriida translated into a cladogram, with geographical distributions of clades. A. After Hoffman 1976, 1980, with modifications by Mauriès 2001 incorporated. B. After Jeekel 1974. Shelley (2003) recommended use of the family name Zephronidae instead of "Sphaeropoeidae." Numbers 1-7 on branches of Fig. 64 B indicate group-defining characters used by Jeekel (1974), numbers in parentheses indicate absence of character; 1=vulval operculum embraced by bursa, 2=female washboard present, 3= medium protrusion of bursa, 4= male harp present at anterior telopod, 5= vulval operculum subreniform, 6= stridulation organ on posterior male telopods, 7= movable digit of posterior telopod consists of two distinct podomeres, (7)= movable digit of posterior telopod consists of single podomere. Numbers 8-10 indicate characters and their distributions discussed in this study: 8= 6th antennomere flat and broad, (8)=6th antennomere cylindrical, 9= four-jointed anterior telopod in males, 10= female washboard divided (known from only a single *Arthrosphaera* species), (10)= female washboard undivided (with other variable features in *Zoosphaerium*), 11= operculum well rounded, (11)= operculum with central depression.