

**THE STATUS OF *HEIKERTINGERELLA*, *MONOTALLA*, *PSEUDODIBOLIA*,
AND *SPHAERODERMA* (COLEOPTERA: CHRYSOMELIDAE: ALTICINAE)
IN THE NEW WORLD**

VILMA SAVINI AND DAVID G. FURTH

(VS) Museo del Instituto de Zoología Agrícola Francisco Fernández Yépez (MIZA), Facultad de Agronomía, Universidad Central de Venezuela, Apdo. 4579, Maracay 2101-A, Aragua, Venezuela (vsgioia@telcel.net.ve); (DGF) Department of Entomology, National Museum Natural of History, Smithsonian Institution, Washington, D.C., 20560-0165, U.S.A. (e-mail: furth.david@nmnh.si.edu)

Abstract.—Based primarily on characters of the metatibia and head, justification of the validity and status of the genera *Heikertingerella*, *Monotalla*, *Pseudodibolia*, and *Sphaeroderma* in the New World is given. Two species of *Sphaeroderma* reported in the New World are transferred to other genera. *Neosphaeroderma* is described as a **new genus**. **New combinations** are *Pseudodibolia opima* (LeConte) and *Neosphaeroderma coerulea* (Jacoby). The genus *Monotalla* Bechyné previously placed as a synonym of *Pseudodibolia*, is considered valid. *Monotalla* has only 10 segmented antenna a rare character in the Alticinae.

Resumen.—Se provee una justificación de la validez de los géneros de Nuevo Mundo *Heikertingerella*, *Montalla*, *Pseudodibolia* y *Sphaeroderma* basada en caracteres de la metatibia y cabeza. Dos especies de *Sphaeroderma* registradas para el Nuevo Mundo son transferidas a otros géneros. Se describe *Neosphaeroderma* como un **género nuevo**. Se establecen dos **combinaciones nuevas** *Pseudodibolia opima* (LeConte) y *Neosphaeroderma coerulea* (Jacoby). Se revalida el género *Monotalla* considerado anteriormente un sinónimo de *Pseudodibolia*. *Monotalla* posee un carácter muy raro en la Alticinae, sólo 10 segmentos en la antena.

Key Words: Neotropical, flea beetles, new combination, new genus, *Neosphaeroderma*, key

For some years, those interested in New World Chrysomelidae, specifically of the subfamily Alticinae, have questioned the correct status of the genera *Heikertingerella* Csiki, *Monotalla* Bechyné, *Pseudodibolia* Jacoby and *Sphaeroderma* Stephens, in particular the species placed in some of these genera.

The first question arose when Furth (1989) studied on the jumping apparatus (metafemoral spring) in 91 Neotropical Al-

ticinae genera in which he arranged them into morphological groups already established from studies of the Palearctic and Nearctic genera (Furth 1985). Furth (1989) mentioned for the first time that there were morphological similarities among *Pseudodibolia*, *Heikertingerella* and “*Sphaeroderma*,” and indicated that “*Sphaeroderma opima*” LeConte is not congeneric with the Palearctic species of *Sphaeroderma*. He (Furth 1989) presented some figures dem-

onstrating the similarity of the metatibia of *S. opima* and *Pseudodibolia*. Later Furth in Flowers et al. (1994), discussing the host plants of Florida Alticinae, mentioned that "*Sphaeroderma opima*" was not a true representative of the genus *Sphaeroderma* from the Old World. Furth (in Flowers et al. 1994) said that a narrow relationship may exist between that species and those of *Heikertingerella* and *Pseudodibolia*; however, at that point he considered *S. opima* to be nearer to *Heikertingerella* than to *Pseudodibolia*.

During recent studies of a variety of Neotropical Alticinae by the authors, we discovered that several genera with similar external morphological features caused some confusion in attempting to identify specimens. These characters are primarily a round to globose, very convex body shape (coccinelliform) and the pronotum with a bisinuate, lobed, projecting, posterior margin. There is no other particular apparent relationship of these genera and the primary purpose of this study is to clarify the nomenclatural status of these genera. Because of this confusion, we conducted studies that would help clarify the correct status of each taxon, concentrating primarily on the study of the external morphology of some representatives of the genera in question. For practical reasons (e.g., ease of identification purposes for general users), we have chosen here to only concentrate on external morphological characters. We have also found some more detailed internal characters, but these will be presented in a more comprehensive morphological study in the future (Savini in preparation).

MATERIALS AND METHODS

Specimen were examined from the following museums: (USNM): National Museum of Natural History, Smithsonian Institution, Washington, DC; (MIZA): Museo del Instituto de Zoología Agrícola Francisco Fernández Yépez, Facultad de Agronomía, U.C.V., Maracay, Venezuela; (MCZC): Museum of Comparative Zoolo-

gy, Harvard University, Cambridge, MA (F. C. Bowditch collection); (INBIO): Instituto Nacional de Biodiversidad, Costa Rica; (NHMB): Naturhistorisches Museum, Basel (Frey Collection), Switzerland; BMNH: The Natural History Museum, London, United Kingdom; (FAMU): Florida A. M. University, Tallahassee, FL; Hungarian Natural History Museum, Budapest, Hungary (HNHB).

We made many dissections of specimens of *Heikertingerella*, *Pseudodibolia*, and *Sphaeroderma*. The body parts were disarticulated to allow examination of the maximum number of possible external characters and to prepare them for the Scanning Electron Microscope photos; however, in the current study we use only external characters. For the genus *Monotalla*, dissections were not made, because the only specimens to be studied were the holotype and paratype of *Monotalla guadeloupensis* Bechyne; therefore, only external characters were examined, studied and illustrated by line drawings.

The terminology for external morphological characters generally follows Snodgrass (1935). However, in this study we have used some different terminology as follows. The frontoclypeus is the area between the clypeo-labral suture to and including the inter-antennal space. This area is defined as the frontoclypeus because when we made a detailed examination of the internal morphology of the head capsule, we were able to observe that the anterior tentorial arms are just underneath the inferior border of the antennal cavities. According to classical morphological theory, the tentorial pits define the division between the clypeal and frontal regions and the suture between these pits is called the epistomal suture. However, when the epistomal suture is absent, such as with the genera studied here, it is more appropriate to name this area the frontoclypeus. The term frontal sulcus is applied in this study to include the orbital sulcus plus the supracallinal sulcus (sensu Konstantinov and Vandenberg 1996).

Once dissected, the parts were submerged in 10% KOH for about 10 hours to eliminate the maximum amount of material that could obstruct visibility of the characters to be studied. Next, the parts were submerged in distilled water and then in ammonia for approximately one hour, in order to eliminate the fat tissue. Once this procedure was complete, the parts were dried and each dissected specimen was mounted onto a metal stub for metallic coating and photography using AMRAY 1810 Scanning Electron Microscope.

Also, we present a key for the identification of the genera and a diagnosis for each genus accompanied by some illustrations of the characters studied.

RESULTS

KEY TO THE GENERA *HEIKERTINGERELLA*,
MONOTALLA, *NEOSPHAERODERMA*,
PSEUDODIBOLIA, and *SPHAERODERMA*

All genera except *Sphaeroderma* (= *Neosphaeroderma*) can be identified using the key of Scherer (1962, 1983); however, *Pseudodibolia* and *Monotalla* are contained in the same couplet of that key to Neotropical genera because of the synonymy established by Scherer (1962).

- 1. Dorsal outer edge of metatibia serrate (Figs. 6–9, 17) 2
- Dorsal outer edge of metatibia not serrate (Figs. 10–12, 14–16) 3
- 2. Head without frontal sulcus (Fig. 5). Metatibia with a very long apical spur, almost half length of first metatarsomere (Figs. 16–17). Metasternum very short, approximately equal length of prosternum and mesosternum processes together *Monotalla*
- Head with frontal sulcus strongly impressed (Fig. 1). Metatibia with a very short apical spur (Fig. 7). Metasternum longer than prosternum and mesosternum processes together *Pseudodibolia*
- 3. Metatibia with preapical tooth on dorsal outer edge (Figs. 10–11) *Heikertingerella*
- Metatibia smooth, without tooth on dorsal outer edge (Figs. 12–15) 4
- 4. Head with horizontal frontal sulcus (Fig. 3). Anterior coxal cavities open *Sphaeroderma*
- Head with frontal sulcus obliquely angled and convergent towards antennal socket (Fig. 4).

Anterior coxal cavities closed
..... *Neosphaeroderma*, n. gen.

Heikertingerella Csiki 1940:350
(Figs. 2, 10–11)

Type species: *Homophyla adusta* Harold 1877:138 (Peru).

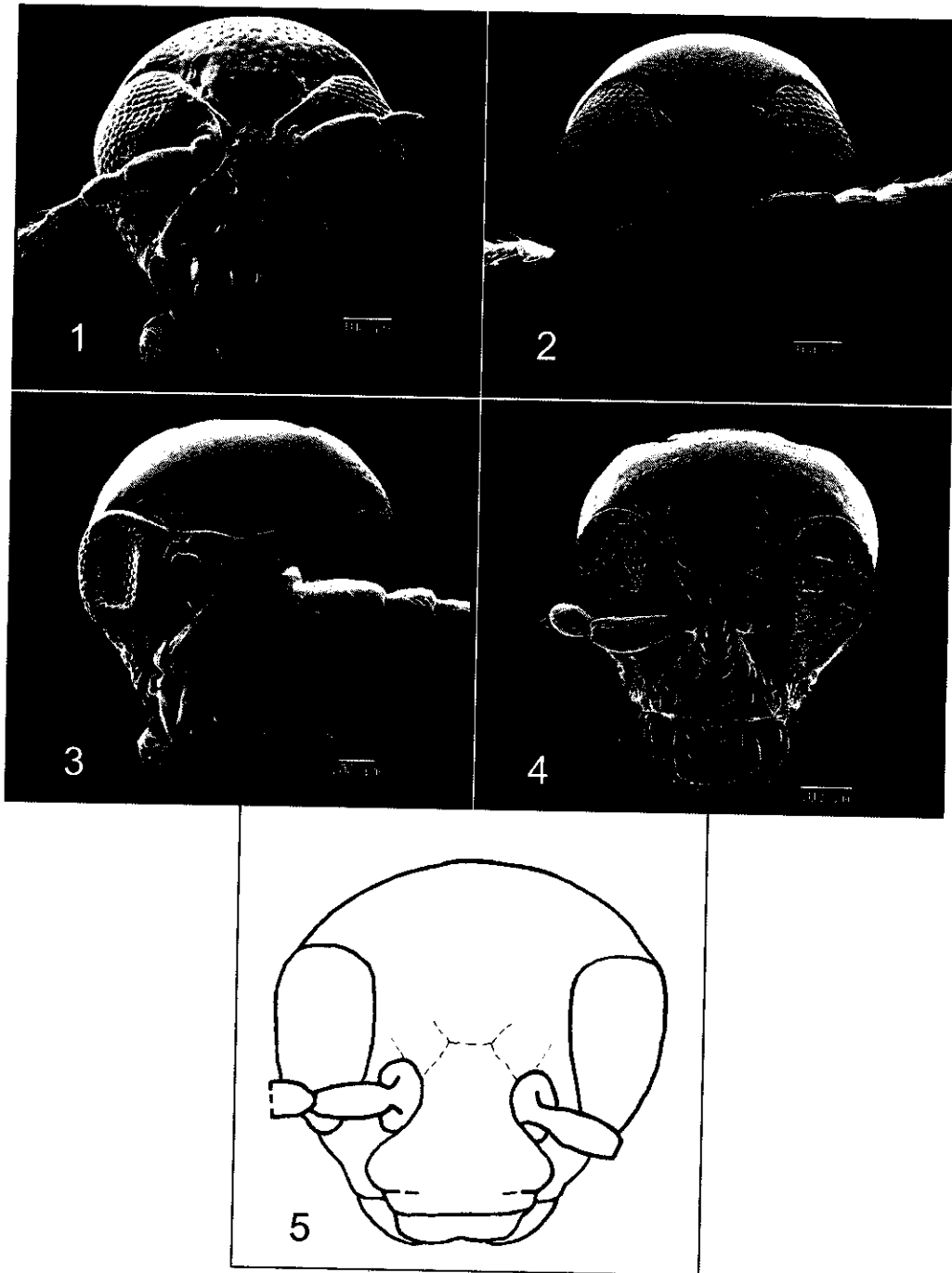
Heikertingerella Csiki 1940:350 (established as a replacement name due to homonymy).

Homophyla Harold 1877:138. Type species *H. adusta* Harold.

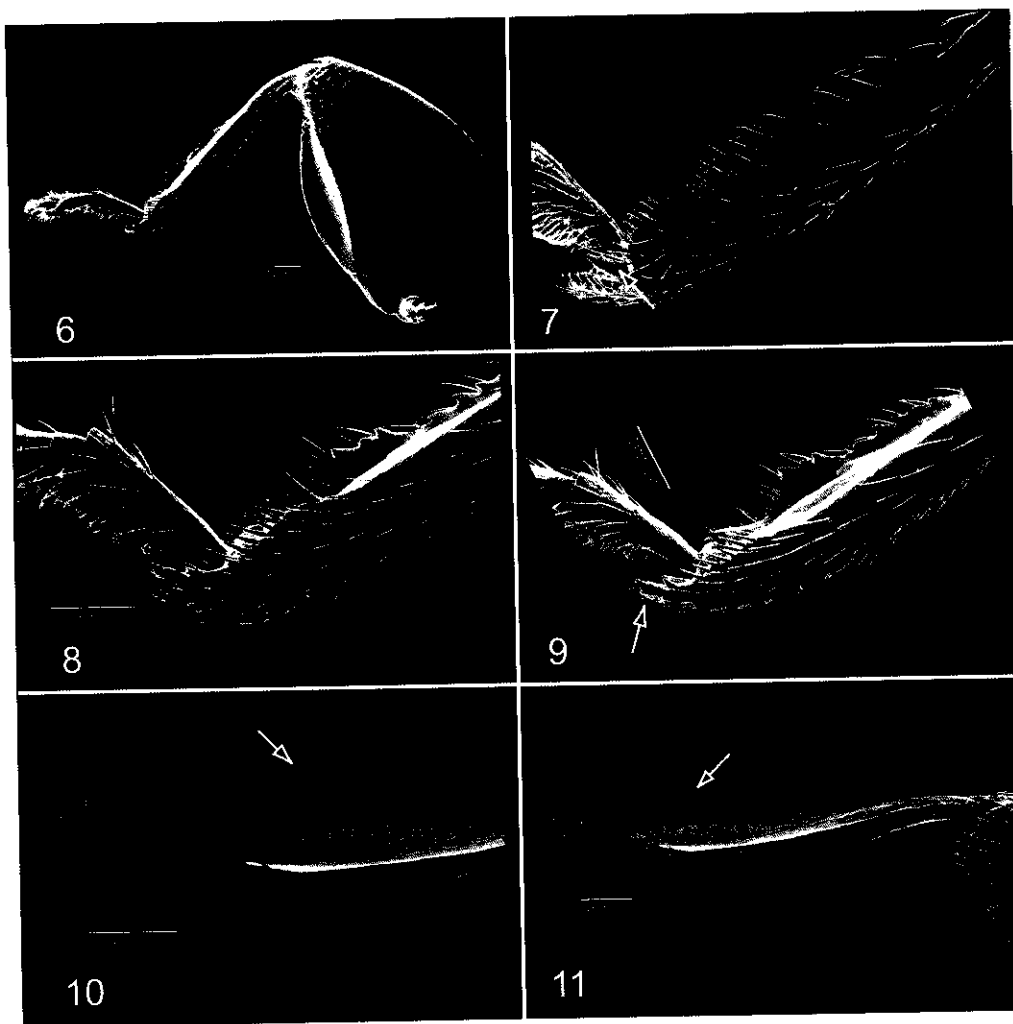
Euplectroscelis Jacoby 1885:392 (not Crotch 1873:57, 75), see also Remarks below.

Description.—Body oval short, broad, very convex, color not metallic. *Head*: Frontoclypeus with longitudinal carina always present; clypeal transverse carina present or evident only laterally. Frontal sulcus always present oblique and convergent towards antennal socket. Supraantennal calli absent or very narrow (Fig. 2). *Thorax*: Pronotum convex and without prebasal transverse impression; anterolateral angle beveled. Anterior coxal cavities open. Metasternum as long as or longer than length of prosternal and mesosternal processes together. *Legs*: Metafemur thickened but narrower than width of abdomen. Metatibia dorsally flattened in middle with raised edges from approximately apical half and with one preapical tooth; outer edge smooth; inner edge apically somewhat widely prolonged posteriorly (Figs. 10–11). First metatarsomere generally subcylindrical. Apical spur distinct but short. *Elytra*: Punctuation fine and confused, sometimes with tendency to form striae; epipleura slightly broadened, but somewhat wider towards anterior ¼, laterally visible and gradually tapered toward apex.

Remarks.—The genus *Heikertingerella*, currently includes 125 species and 3 subspecies (Savini 1999) most of these are recorded from South America and 19 from Central America (Furth and Savini 1996).



Figs. 1-5. Heads. 1, *Pseudodibolia opima*. 2, *Heikertingerella* sp. 3, *Sphaeroderma testaceum*. 4, *Neosphaeroderma coerulea*. 5, *Monotalla guadeloupensis*.



Figs. 6-11. Metatibiae. 6-9, *Pseudodibolia opima* (fig. 7, arrow = apical spur. fig. 9, arrow = apical spur). 10-11, *Heikertingerella* sp. (arrows = preapical tooth on outer edge).

Since 1940, no taxonomic work has been published indicating confusion with other related genera. *Heikertingerella* is actually very diverse; however, we predict, based on recent examination of material from various Neotropical countries (Savini and Furth, unpublished), that its recorded diversity will increase greatly and that possibly its distributional range will be greatly expanded in the New World. We examined many specimens of several species from Costa Rica (INBIO, FAMU). Baly (1877:319-322), mistakenly described 6 species of *Homophyla* as *Euplectroscelis* Crotch.

Monotalla Bechyné 1956:588, revised
status
(Figs. 5, 16-17)

Type species: *Monotalla guadeloupensis* Bechyné 1956:588 (Guadeloupe) by monotypy.

Pseudodibolia Jacoby 1891 (Scherer 1962: 583 placed *Monotalla* in synonymy).

Description.—Micropteris insects. Body oval, very short and wide, strongly convex, color not metallic. Head: 10-segmented antenna, segments 1-2 elongate somewhat swollen, 3-5 tiny and thin, 6-10 larger,

swollen, rounded and almost spherical. Without frontal carina. Frontoclypeus triangular, inflated; longitudinal and traverse carinae barely evident. Supraantennal calli faint (Fig. 5). *Thorax*: Pronotum convex and without prebasal transverse impression; anterior angles almost rounded, not beveled. Anterior coxal cavities open. Metasternum very short, approximately length of prosternal and mesosternal processes together. *Legs*: Metafemur greatly thickened, only slightly narrower than width of abdomen. Metatibia flattened laterally, consequently toward ventral area of tibia a carinae is present from near base until apex; dorsally metatibia flattened with raised edges from near base to the apex; inner edge serrate from approximately apical half (Fig. 17); outer edge smooth, but with distinct preapical excavation (Fig. 16). Apical spur very long, half length of first tarsal segment, clearly wider at base. (Figs. 16–17). First metatarsomere subcylindrical. *Elytra*: Punctures arranged in striae of 9 impressed longitudinal rows, but confused apically; epipleura totally visible in lateral view and ending abruptly at apex.

Remarks.—A very special discovery in the current study is that *Monotalla* has only 10-segmented antennae. This is only the third genus known in the Alticinae (with over 500 genera worldwide) with less than 11 segments in the antennae. The others are *Psylliodes* Latreille with 10 segments and *Nonarthra* Baly with 9 segments. Until now only two species were known in the genus *Monotalla*: *M. guadeloupensis* Bechyné (Guadeloupe) and *M. nigrita* (Jacoby) (Grenada). The male holotype (NHMB) and the female paratype (HNHM) specimens of *M. guadeloupensis* were examined. We have examined all known syntypes of *M. nigrita* (MCZC [2], BMNH [7]) and have determined that it is not con-generic with *M. guadeloupensis*. *Monotalla nigrita* was originally described in the genus *Glyptina* LeConte; however, we do not believe it belongs in that genus either. The placement of *M. nigrita* will need to be resolved at some

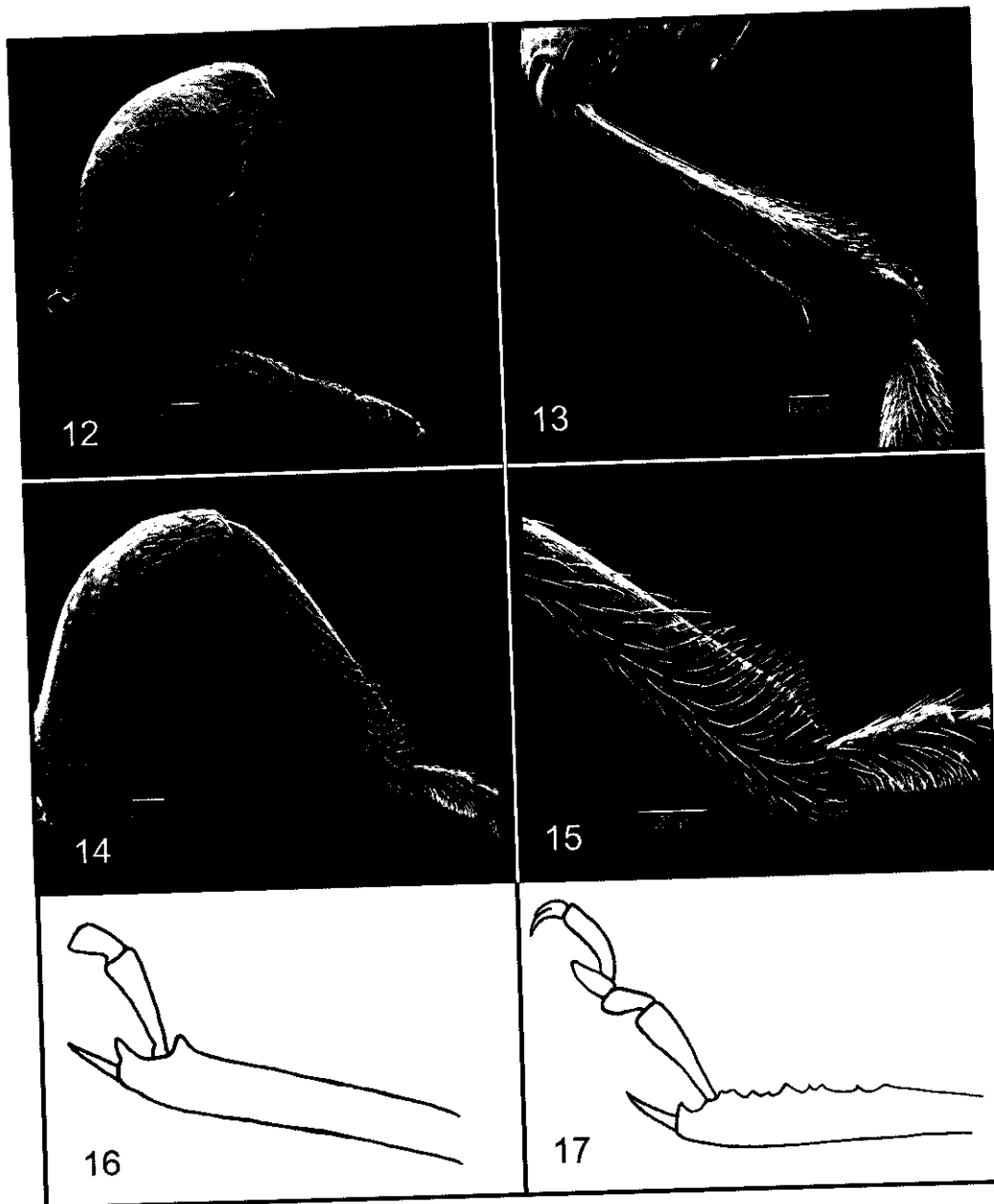
time in the future. During the review of the status of *Monotalla* and specimens from many collections, we have been able to discover some new genera distributed in South and Central America with similar external morphology to *Monotalla* (Savini and Furth in preparation).

Pseudodibolia Jacoby 1891:291
(Figs. 1, 6–9)

Type species: *Pseudodibolia picea* Jacoby 1891:291 (Mexico) by monotypy.

Description.—Body oval, short, wide, convex, not metallic. *Head*: Frontoclypeus triangular; longitudinal and transverse carina faint. Frontal sulcus present, oblique and convergent towards antennal socket (Fig. 1). Supraantennal calli faint or absent. *Thorax*: Pronotum convex, without prebasal transverse impression; anterior angles beveled. Anterior coxal cavities open. Metasternum longer than prosternal and mesosternal processes together. *Legs*: Metafemur thickened but narrower than width of abdomen. Metatibia slightly flattened dorsally in apical half; outer and inner edges distinct only in approximately apical half (Figs. 6–7); inner edge serrate in apical half and excavated near apex; apex of inner edge of tibia prolonged posteriorly (Figs. 8–9). First metatarsomere generally subcylindrical. *Elytra*: Striate punctuation distributed in 9 longitudinal rows but not very regular. Epipleura as in *Heikertingerella*.

Remarks.—In contrast to *Heikertingerella*, the genus *Pseudodibolia*, originally described from Mexico, has been confused with the genus *Monotalla* Bechyné (1956). Scherer (1962, 1983) synonymized it with *Pseudodibolia*. However, based on the current study, these genera are different, as demonstrated by differences in certain morphological characters. *Monotalla* was originally described from the Guadeloupe Isle in the West Indies. We suppose that this synonymy was based only on the original description of *Pseudodibolia* (Jacoby 1891) and that Scherer (1962) made an erroneous



Figs. 12–17. Metatibiae. 12, 13, *Sphaeroderma testaceum*. 14, 15, *Neosphaeroderma coerulea* (outer view). 16, 17, *Monotalla guadeloupsis* (inner edge and outer edge, respectively).

interpretation of the characters described by Jacoby. This synonymy established by Scherer, resulted in *Pseudodibolia* appearing to have a wider distribution, because it included West Indian *Monotalla*. We have examined the syntypes of *P. picea* (BMNH [2], MCZC [4], USNM [2]) all from Tea-

pea, Tabasco, Mexico. Also, *Sphaeroderma opima* LeConte has been placed in *Sphaeroderma* by many authors for a long time (see Introduction), but Furth (1989) and Flowers et al. (1994) began to question this. Based on external morphological characters, the current study has shown that *S. op-*

ima belongs in the genus *Pseudodibolia* (Figs. 1, 6–9) (**new combination**). This species is recorded from the northeastern (Ohio, Maryland), midatlantic (North Carolina), southeastern (Florida) and south central (Texas) states of the USA (Wilcox 1975, Flowers et al. 1994). We have examined *P. opima* specimens from Florida (USNM).

Sphaeroderma Stephens 1831:328
(Figs. 3, 12–13)

Type species: *Altica testacea* Fabricius 1775:114 (Europe) by subsequent designation of Maulik 1926:316.

Description.—Body spherical in shape, wide, very convex. *Head*: Frontoclypeus subtriangular; frontal sulcus horizontal from upper margin of compound eyes toward center of front (Fig. 3). Supraantennal calli present. *Thorax*: Pronotum convex, without prebasal transverse impression; anterior angles projected anteriorly, thickened, very blunt and not beveled. Anterior coxal cavities open. Metasternum longer than prosternal and mesosternal process together. *Legs*: Metafemur not greatly thickened, evidently narrower than width of abdomen. Metatibia dorsally rounded, without excavation on outer edge of tibia and without preapical tooth (Fig. 13). First metatarsomere triangularly enlarged and very thick. *Elytra*: Very fine and confused punctuation, with tendency to form striae. Epipleura totally visible laterally, very wide in anterior half then gradually tapering apically almost reaching apex of elytron.

Remarks.—The current distribution of *Sphaeroderma* is composed of over 150 species in the Old World, mostly in the Oriental and Afrotropical regions (Konstantinov and Vandenberg 1996, Heikertinger and Csiki 1940, Furth 1989, Flowers et al. 1994); however, LeConte (1878) and Jacoby (1891) reported two species in the New World: *Sphaeroderma opima* LeConte (USA) and *Sphaeroderma coerulea* Jacoby (Panama), respectively (see also Furth and

Savini 1996). The taxonomy and the status of these two species has not been previously reviewed; however, we now realize that both species should be placed in two different genera: *S. opima* should be placed in the genus *Pseudodibolia* and *S. coerulea* needs to be placed in a new genus (see Remarks sections for *Pseudodibolia* and *Neosphaeroderma*, respectively). We have examined specimens of *S. testaceum* F. from Europe (USNM) and *S. seminigrum* Jacoby from China (USNM).

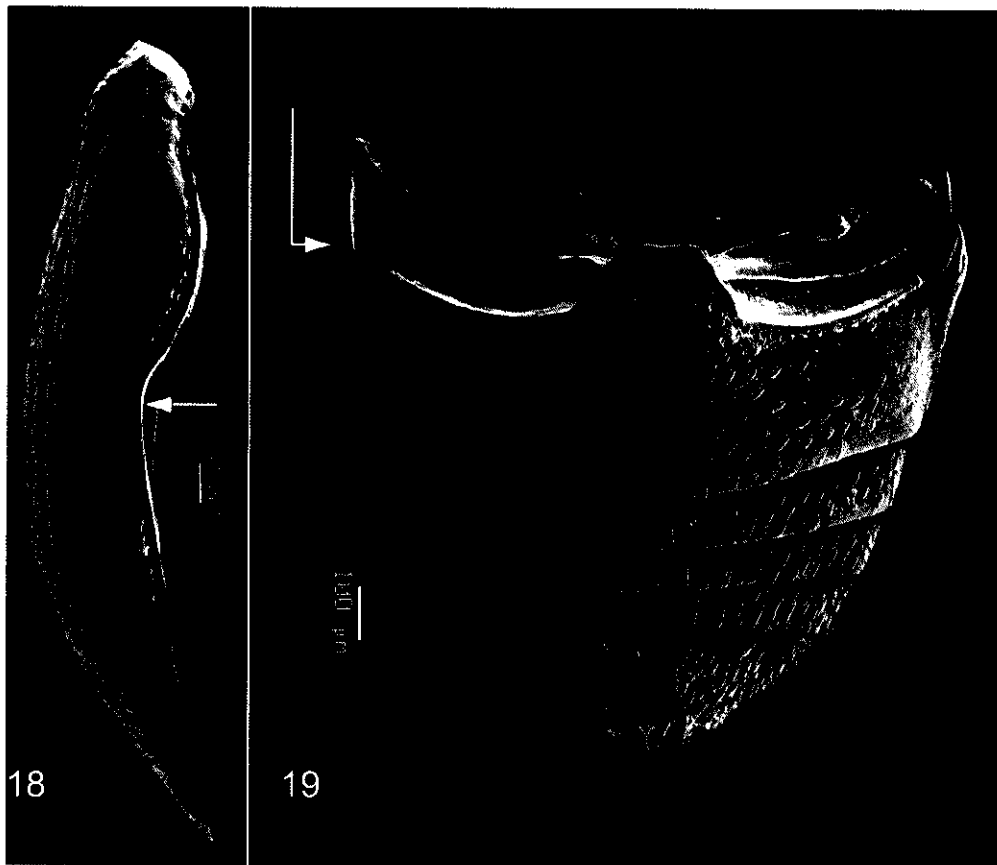
Neosphaeroderma Savini and Furth,
new genus

(Figs. 4, 14–15, 18–19)

Type species: *Sphaeroderma coerulea* Jacoby 1891:310 (Panama).

Neosphaeroderma coerulea (Jacoby), **new combination**.

Description.—Body oval, short, very convex, not metallic. *Head*: Frontoclypeus subtriangular and with abundant setae; coarse punctuation on dorsal half; longitudinal carina present, but not very inflated; transverse carina absent. Frontal sulcus present oblique and convergent towards antennal socket (Fig. 4). Supraantennal calli present. Antenna with 10 segments. *Thorax*: Pronotum convex, with only a slight impression near base, but laterally more evident; 1.6 times wider than long; anterior angles rounded and thickened, not projecting. Posterior angles not evident. Posterior border bisinuate and with well-developed central lobe. Anterior coxal cavity closed. Prosternal process wide, almost as long as wide, with coarse punctures on both sides and with many setae. Metasternum as wide or wider than length of prosternal and mesosternal processes together. *Legs*: Metafemur like *Sphaeroderma*. Metatibia dorsally rounded, without preapical tooth on outer edge (Figs. 14–15). First metatarsomere slightly subtriangular. *Elytra*: Punctuation striate in 9 longitudinal rows; epipleura not very wide, with an evident concavity where



Figs. 18–19. 18, Elytron and epipleuron: *Neosphaeroderma coerulea* (right lateral view). 19, Abdomen: *Neosphaeroderma coerulea*. (ventral view, arrow = lateral projection of first abdominal segment).

lateral projection from first abdominal segment fits (Figs. 18–19).

Remarks.—The last elytral character mentioned (epipleura concave, Fig. 18) was used by Bechyné to group the Crepidoderini and Chaetocnemini (Bechyné and Bechyné 1975). We have examined the syntypes of this species (MCZC [# 19385], BMNH [1]) both from Bugaba, Panama, as well as other specimens from Costa Rica (INBIO La Amistad, Sect. Altamira, Buenos Aires, Prov. Punta, 1,200 m, 21 Feb.–10 Mar. 1994, R. Delgado [7], Sector Cerro Cocori, Fca. De E. Rojas, 150 m, Prov. Limón, May 1993, E. Rojas [2]). Further details of external morphology can be found in the original description of *S. coerulea* Jacoby (1891:310, plate 42: fig. 22).

ACKNOWLEDGMENTS

We thank Alexander Konstantinov (USDA) for providing specimens from the USNM and for very useful comments about the manuscript. We are also grateful to R. Wills Flowers (FAMU) for lending us specimens and for helpful comments on the manuscript and to Otto Merkl (HNHB) for the loan of the paratype of *Monotalla guadeloupensis*. We also thank Susan Braden (USNM) for advice and assistance with the Scanning Electronic Microscope. Lucrecia Rodríguez, (USDA) has been very helpful for support and advice for the electronic improvement of the images and the composition of the figures for publication. We thank Concejo de Desarrollo Científico y Human-

ístico (CDCH) through the Universidad Central de Venezuela, Maracay, for support for the studies for one year of the first author at USNM.

LITERATURE CITED

- Baly, J. S. 1877. Descriptions of new genera and of uncharacterized species of Halticinae. Transactions of the Entomological Society of London, Part IV: 283-323.
- Bechyné, J. 1956. Über die Altíciden-Sammlung Heikertinger (Col. Phytophaga). Entomologische Arbeiten Museum G. Frey 7(2): 577-598.
- Bechyné, J. and B. S. Bechyné. 1975. Notas sobre la serie filetica de *Monomacra* y sus formas convergentes (Col. Phytophaga, Altícidae). Revista de la Facultad de Agronomía (Maracay) 8(4): 25-140.
- Crotch, G. R. 1873. Materials for the study of the Phytophaga of the United States. Proceedings of the Academy of Natural Sciences, Philadelphia 25: 19-83.
- Fabricius, J. C. 1775. Systema Entomologiae. Flensburgi et Lipsiae, Korte. 832 pp.
- Furth, D. G. 1985. Relationships of Palearctic and Nearctic genera of Altícinae. Entomography 3: 375-392.
- . 1989. Metafemoral spring studies some Neotropical genera of Altícinae. Entomography 6: 497-510.
- Furth, D. G. and V. Savini. 1996. Checklist of the Altícinae of Central America, including Mexico (Coleoptera: Chrysomelidae). Insecta Mundi 10(1-4): 45-67.
- Flowers, R. W., D. G. Furth, and M. C. Thomas. 1994. Notice on the distribution and biology of some Florida leaf beetles (Coleoptera: Chrysomelidae). The Coleopterists Bulletin 48(1): 70-89.
- Harold, E. 1877. Beiträge zur Kenntniss der Peruanischen Käferfauna (Haltícinae) auf Dr. Abendroth's Sammlungen basirt. Deutsche Entomologisches Zeitschrift 25: 129-152.
- Heikertinger, E. and Csiki, E. 1940. Chrysomelidae, Haltícinae. Coleopterorum Catalogus. Volume XXV, Pars 169. pp. 337-635. Uitgeverij Dr. W. Junk, Gravenhage.
- Jacoby, M. 1885. Biologia Centrali-Americana, Insecta, Coleoptera, Supplement to Phytophaga 6(1): 263-625.
- . 1891. Biologia Centrali-Americana, Insecta, Coleoptera, Supplement to Phytophaga 6(1): 1-374.
- Konstantinov, A. S. and N. J. Vandenberg. 1996. Handbook of Palearctic Flea Beetles (Coleoptera: Chrysomelidae: Altícinae). Contributions on Entomology, International, Associated Publishers. Gainesville, Florida, 439 pp.
- LeConte, M. D. 1878. Additional descriptions of new species. In Schwarz, E. A. The Coleoptera of Florida. Proceedings of the American Philosophical Society 17: 373-434.
- Maulik, S. 1926. The Fauna of British India, including Ceylon and Burma. Coleoptera, Chrysomelidae (Chrysomelinae and Haltícinae). Taylor and Francis, London. 442 pp.
- Savini, V. 1999. The género *Heikertingerella* Csiki (Coleoptera: Chrysomelidae: Altícinae) en Venezuela. Boletín de Entomología Venezolana 14(2): 95-190.
- Scherer, G. 1962. Bestimmungsschlüssel der neotropischen Altícinen-Genera (Coleoptera: Chrysomelidae: Altícinae). Entomologischen Arbeiten Museum G. Frey 13(2): 497-607.
- . 1983. Diagnostic key for the Neotropical Altícinae genera. Entomologischen Arbeiten Museum G. Frey 31/32: 1-89.
- Snodgrass, R. E. 1935. Principles of Insect Morphology. McGraw-Hill, New York. 667 pp.
- Stephens, J. F. 1831. Illustrations of British Entomology. Mandibulata IV. Coleoptera. 414 pp. Baldwin and Cradock.
- Wilcox, J. A. 1975. Checklist of the beetles of Canada, United States, Mexico, Central America and the West Indies. The Leaf Beetles (Red Version). North American Beetle Fauna Project 1(7): 1-166.