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TAXONOMY AND SYSTEMATICS

A Synopsis of the New World Genera of Phileurini (Coleoptera: Scarabaeidae: Dynastinae), with English and Spanish Keys to the Genera

Sinopsis de los Géneros de Phileurini (Coleoptera: Scarabaeidae: Dynastinae) del Nuevo Mundo, con Claves en inglés y español para los Géneros

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ABSTRACT

The 22 genera of New World Phileurini are briefly reviewed and characterized, and English and Spanish keys to all the genera are provided for the first time, thus facilitating generic identifications. *Chiliphileurus* Endrödi (a junior synonym of the Asian genus *Eophileurus* Arrow), *Moraguesia* Dechambre (transferred to *Oxyligyrus* Arrow in the tribe Pentodontini), and *Platyphileurus* Ohaus (transferred to the tribe Oryctini) are no longer part of the New World phileurine fauna. The monobasic *Phileucourtus* Dechambre is considered a junior synonym of *Hemiphileurus* Kolbe.

Keywords. Taxonomy, classification, phileurine scarab beetles, identification key.

RESUMEN

Se revisan brevemente y se caracterizan los 22 géneros de Phileurini del Nuevo Mundo y se presentan por la primera vez claves en inglés y español para todos los géneros, facilitando la identificación de ellos. *Chiliphileurus* Endrödi (un sinónimo junior del género asiático *Eophileurus* Arrow), *Moraguesia* Dechambre (transferido a *Oxyligyrus* Arrow en la tribu Pentodontini) y *Platyphileurus* Ohaus (transferido a la tribu Oryctini) ya no son parte de la fauna de Phileurini en el Nuevo Mundo. El género monobásico *Phileucourtus* Dechambre se propone como sinónimo junior bajo el género *Hemiphileurus* Kolbe.

Palabras clave: Taxonomía, clasificación, escarabajos phileurinos, clave para identificación

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INTRODUCTION

Species in the tribe Phileurini are found in nearly all regions of the world, although most species occur in the tropics. The world fauna is comprised of 35 genera (Endrödi 1985) with 300 currently recognized species. In the New World, there are now 22 genera and 189 valid species. Endrödi (1977, 1978, 1985) provided the most recent, comprehensive review of the entire tribe, but new genera and 114 new species (37 % of all species currently known) have been described in the past 38 years.

Adult phileurines are recognized by their generally flattened body; large mentum that covers the bases of the labial palpi; a clypeal apex either acuminate or rounded; frons with one or two tubercles or horns; pronotum often with a longitudinal, median furrow and subapical tubercle; elytra usually flattened and either smooth or striate; protibia with three or four teeth; and apex of metatibia truncate or armed with one to three teeth (Endrödi 1977, 1978). In some species, the concavity of the vertex on the head differs between the sexes, with the male having a deeply hollowed pit, while the female does not.

Adult phileurines are nocturnal, and many species are known by only a few specimens. Their rarity may result from genuinely small and/or dispersed populations, inadequate methods for attracting or collecting them, and our lack of knowledge of where to look for them. Adults of a few species have been attracted to lights, but in our experience phileurines are not as readily attracted to lights as are many other dynastines. This may be because adults live in and on rotting tree trunks and stumps where they do not usually "see" the occasional light trap. Some species are inquilines with ants or termites (Vanin *et al.* 1983, Ratcliffe and Skelley 2011), while others live in decaying wood in a fashion similar to that of passalids, although without subsociality.

The larval stages, life history, and larval development are poorly known. There is evidence that adults of some species may be predaceous on other insects (McCleve 2007, Ratcliffe *et al.* 2020). A few larvae have been collected from rotting wood or termite or ant nests. There is a genuine need for laboratory rearing, so that larvae and their subsequent descriptions can be associated with adults. This opportunity will fall largely to resident entomologists in the countries in which these species occur, since visiting researchers on short collecting trips cannot hope to efficiently accomplish this task.

The purpose of our paper is to provide an updated key to identify the genera of the New World Phileurini in the scarab subfamily Dynastinae and a short synopsis of each genus. All the images are by the authors except where indicated. We dedicate this work to the memory of our colleague, Germán Amat García.

RESULTS AND DISCUSSION

Key to the Genera of Adult Phileurini of the New World

1. Outer side of mandibles tridentate....2

1´. Outer side of mandibles simply curved...7

2. Protibia quadridentate...3

2´. Protibia tridentate...4

3. Frons with a single horn or tubercle (Fig. 4c)...***Oryctophileurus* Kolbe, 1910**

3´. Frons with 2 tubercles or large, recurving horns (Fig. 1c)...***Amblyodus* Westwood, 1878**

4. Metatibial apex with small teeth...5

4´. Metatibial apex truncate, lacking teeth....6

5. Metatibial apex with 3 small teeth. Pronotum with narrow, shallow, longitudinal furrow (Fig. 3a) and lacking depression either side of furrow...***Goniophileurus* Kolbe, 1910**

5´. Metatibial apex with 4 small teeth. Pronotum with broad, deep longitudinal furrow (Fig. 4a) with elongate depression each side of furrow...***Metaphileurus* Kolbe, 1910**

6. Clypeal apex obtusely acuminate. Frons with 2 tubercles. Pronotum with simple, longitudinal furrow (Fig. 4b)...***Microphileurus* Kolbe, 1910**

6´. Clypeal apex narrowly, weakly bidentate. Frons with 2 erect, flattened horns (Fig. 5d). Pronotum anteriorly declivous, quadrituberculate...***Trioplus* Burmeister, 1847**

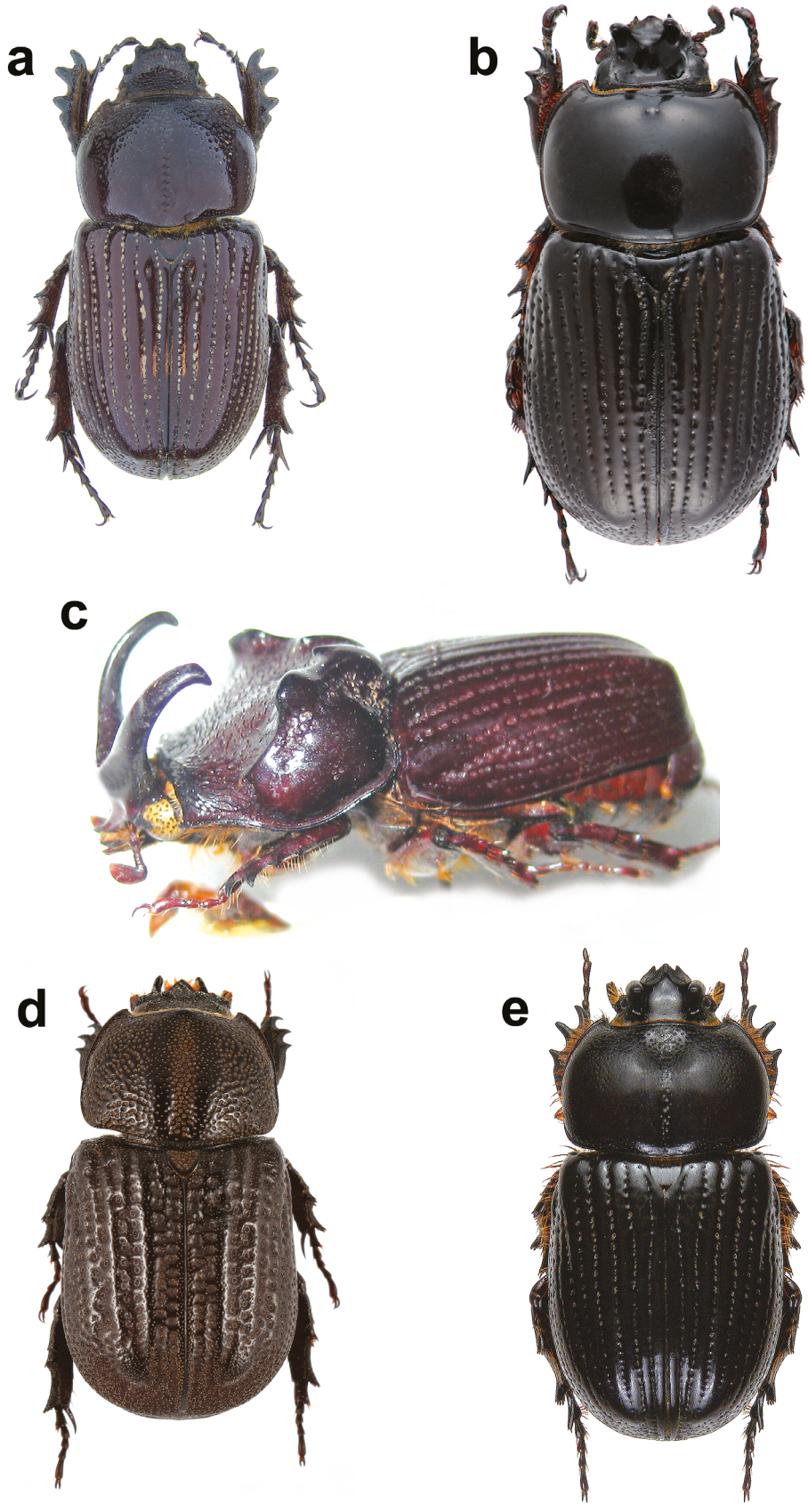

Fig. 1. a: *Actinobolus radians* Westwood. b: *Allophileurinus cavifrons* Dupuis and Dechambre holotype male at the Muséum National d'Histoire Naturelle (MNHN). Image © MNHN Antoine Mantilleri. c: *Amblyodus castroi* Grossi and Grossi. d: *Amblyoproctus chalumeaui* Endrödi. e: *Archophileurus chaconus* (Kolbe).

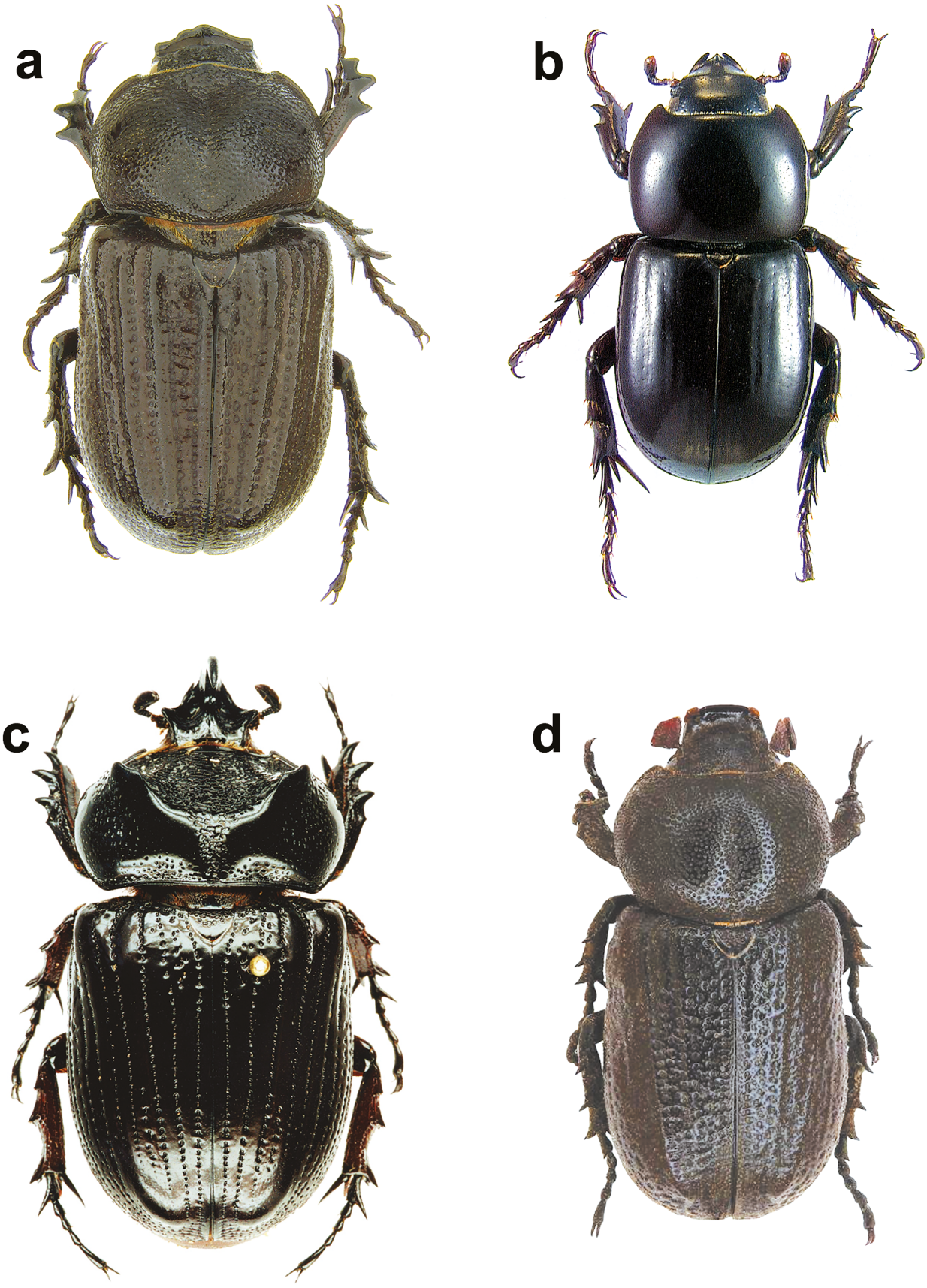

Fig. 2. a: *Argentophileurus litoralensis* Penco and Zubarán. b: *Caymania nitidissima* Ratcliffe and Cave. c: *Ceratophileurus lemoulti* Ohaus. Image courtesy of Alain and Marcel Galant. d: *Cnemidophileurus personatus* Kolbe. Image courtesy of Inventaire National du Patrimoine Naturel

7. Metatibia with truncate apex, lacking teeth...8

7´. Metatibia with at least upper apical angle produced as a sharp tooth, usually with 1–3 additional teeth as well...10

8. Male protarsomere 4 usually with a small ventral lobe that projects beneath tarsomere 5; protarsomere 5 short, slightly to distinctly enlarged. Prosternal process large, bulbous... ***Planophileurus*** **Chapin, 1932**

8´. Male protarsomeres 4–5 subcylindrical, 4 without ventral lobe, 5 not enlarged. Prosternal process small, laminate, and either subtriangular, subquadrate, or columnar...9

9. Frons with a single tubercle or horn (Fig. 3b)...***Haplophileurus*** **Kolbe, 1910**

9´. Frons with 2 tubercles or short horns (Fig. 1e)...***Archophileurus*** **Kolbe, 1910**

10. Clypeal apex with a long, recurving horn (Fig. 2c)... ***Ceratophileurus*** **Ohaus, 1911**

10´. Clypeal apex lacking a long, recurved horn...11

11. Clypeal apex rounded...12

11´. Clypeal apex not rounded, instead acute or broadly emarginate...13

12. Clypeal apex with 3–5 lobes (Fig. 1a)...***Actinobolus*** **Westwood, 1841**

12´. Clypeal apex broadly rounded, lacking lobes (Fig. 2d)...***Cnemidophileurus*** **Kolbe, 1910**

13. Clypeal apex broadly, weakly emarginate. Antennomere 1 at apex bulbous, subequal in length and width to club...***Argentophileurus*** **Penco and Zubarán, 2013**

13´. Clypeal apex acute. Antennomere 1 cylindrical, not enlarged at apex...14

14. Pronotum simply convex, lacking tubercles or a longitudinal furrow (a row of punctures at most)...15

14´. Pronotum at least with a longitudinal furrow or fovea...17

15. Pronotum punctate. Elytra dull (Fig. 4d). Apical angle of metatibia angulate. Length greater than 20 mm...***Palaeophileurus*** **Kolbe, 1910**

15´. Pronotum smooth, shiny. Elytra shiny. Apical angle of metatibia spiniform...16

16. Elytra with weak rows of minute to small punctures, striae absent (Fig. 2b). Length less than 12 mm...***Caymania*** **Ratcliffe and Cave, 2010**

16.´ Elytra coarsely punctate-striate (Fig. 1b). Length greater than 18 mm...***Allophileurinus*** **Dupuis and Dechambre, 2001**

17. Apex of metatibia with 3–4 small teeth...18

17´. Apex of metatibia with 1–3 large teeth or at least upper angle strongly produced...19

18. Mandibles slender, external edge slightly curved (Fig. 1c). Posterior pronotal angles rounded. Metatibial apex with 3 small teeth...***Amblyoproctus*** **Kolbe, 1910**

18´. Mandibles broad, external edge strongly angulate. Posterior pronotal angles obtusely angulate. Metatibial apex with 4 small teeth...***Mictophileurus*** **Ohaus, 1911**

19. Apex of metatibia with 3 large teeth...***Homophileurus*** **Kolbe, 1910**

19´. Apex of metatibia with 1–2 large teeth...20

20. Tubercles or horns of frons located near center of head, away from lateral margins. Pronotum lacking fovea or anterior declivity (Fig. 3c); longitudinal furrow variable, all but 1 species lacking subapical tubercle...***Hemiphileurus*** **Kolbe, 1910**

20´. Tubercles or horns of frons located near lateral margins of head. Pronotum with anterior, foveate cavity or broad declivity; longitudinal furrow strong, usually with distinct tubercle at anterior end...21

21. Prosternal process with large conical knob on posterior surface. Length 20 mm or less...***Paraphileurus*** **Endrödi, 1978**

21´. Prosternal process variable, but never with posterior surface produced backward as an angulate projec-

tion. Length greater than 20 mm except for *P. valgus*... ***Phileurus* Latreille, 1807**

Clave para los Adultos de los Géneros de Phileurini del Nuevo Mundo

1. Margen externo de las mandíbulas tridentado...2

1´. Margen externo de las mandíbulas simplemente curvado...7

2. Protibia cuadridentada...3

2´. Protibia tridentada...4

3. Frente con un cuerno o tubérculo (Fig. 4c)...***Orycto-phileurus* Kolbe, 1910**

3´. Frente con 2 tubérculos o cuernos grandes y curvados (Fig. 1c)...***Amblyodus* Westwood, 1878**

4. Ápice de la metatibia con diente pequeños...5

4´. Ápice de la metatibia truncado, sin dientes...6

5. Ápice de la metatibia con 3 dientes pequeños. Pronoto con surco longitudinal estrecho (Fig. 3a) y no profundo, sin depresión en cada lado del surco...***Goniophileurus* Kolbe, 1910**

5´. Ápice de la metatibia con 4 dientes pequeños. Pronoto con surco longitudinal ancho y profundo (Fig. 4a), una depresión alargada en cada lado del surco...***Meta-phileurus* Kolbe, 1910**

6. Ápice del clípeo obtusamente acuminado. Frente con 2 tubérculos. Pronoto con surco longitudinal simple (Fig. 4b)...***Microphileurus* Kolbe, 1910**

6´. Ápice del clípeo estrechamente y ligeramente bidentado. Frente con 2 cuernos aplanados y erectos (Fig. 5d). Pronoto con declive anterior, cuadrituberculado...***Trio-plus* Burmeister, 1847**

7. Metatibia con el ápice truncado, sin diente...8

7´. Metatibia con al menos el ángulo apical superior producido como un diente agudo, usualmente con 1–3 dientes adicionales...10

8. Protarsómero 4 del macho usualmente con un lóbulo pequeño ventral que se proyecta debajo del tarsómero 5; protarsómero 5 corto, ligera a evidentemente engrosado. Proceso prosternal grande, bulboso...***Planophileurus* Chapin, 1932**

8´. Protarsómeros 4–5 del macho casi cilíndricos, no engrosados. Proceso prosternal pequeño, laminado y casi triangular, casi cuadrado o columnar...9

9. Frente con un tubérculo o cuerno (Fig. 3b)...***Haplo-phileurus* Kolbe, 1910**

9´. Frente con 2 tubérculos o cuernos cortos (Fig. 1e)...***Ar-chophileurus* Kolbe, 1910**

10. Ápice del clípeo con un cuerno largo y curvado (Fig. 2c)...***Ceratophileurus* Ohaus, 1911**

10´. Ápice del clípeo sin cuerno largo y curvado...11

11. Ápice del clípeo redondeado...12

11´. Ápice del clípeo no redondeado, sino agudo o anchamente emarginado...13

12. Ápice del clípeo con 3–5 lóbulos (Fig. 1a)...***Actinobo-lus* Westwood, 1841**

12´. Ápice del clípeo anchamente redondeado, sin lóbulos (Fig. 2d)...***Cnemidophileurus* Kolbe, 1910**

13. Ápice del clípeo anchamente y débilmente emarginado. Antenómero 1 bulboso en el ápice, casi igual al tamaño de la maza...***Argentophileurus* Penco y Zubarán, 2013**

13´. Ápice del clípeo agudo. Antenómero 1 cilíndrico, no engrosado en el ápice.....14

14. Pronoto simplemente convexo, sin tubérculos o un surco longitudinal (a lo más una fila de puntos)...15

14´. Pronoto con un surco longitudinal o fóvea...17

15. Pronoto punteado. Élitros opacos (Fig. 4d). Ángulo apical de la metatibia angulado. Longitud mayor de 20 mm...***Palaeophileurus* Kolbe, 1910**

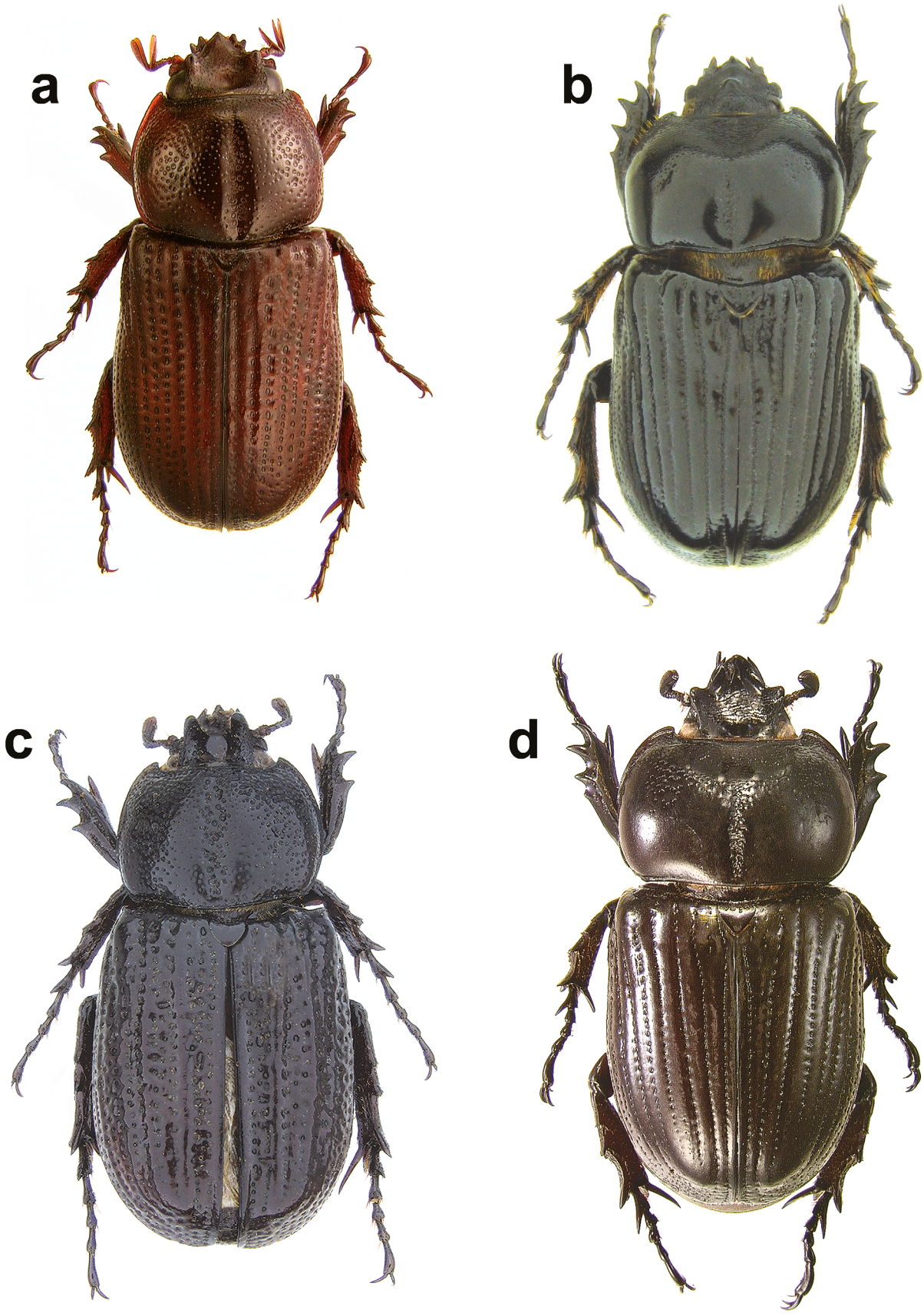

Fig. 3. a: *Goniophileurus femoratus* (Burmeister). b: *Haplophileurus caudipenis* Dupuis. c: *Hemiphileurus costatus* Endrödi. d: *Homophileurus quadritubercu-latus* (Palisot de Beauvois).

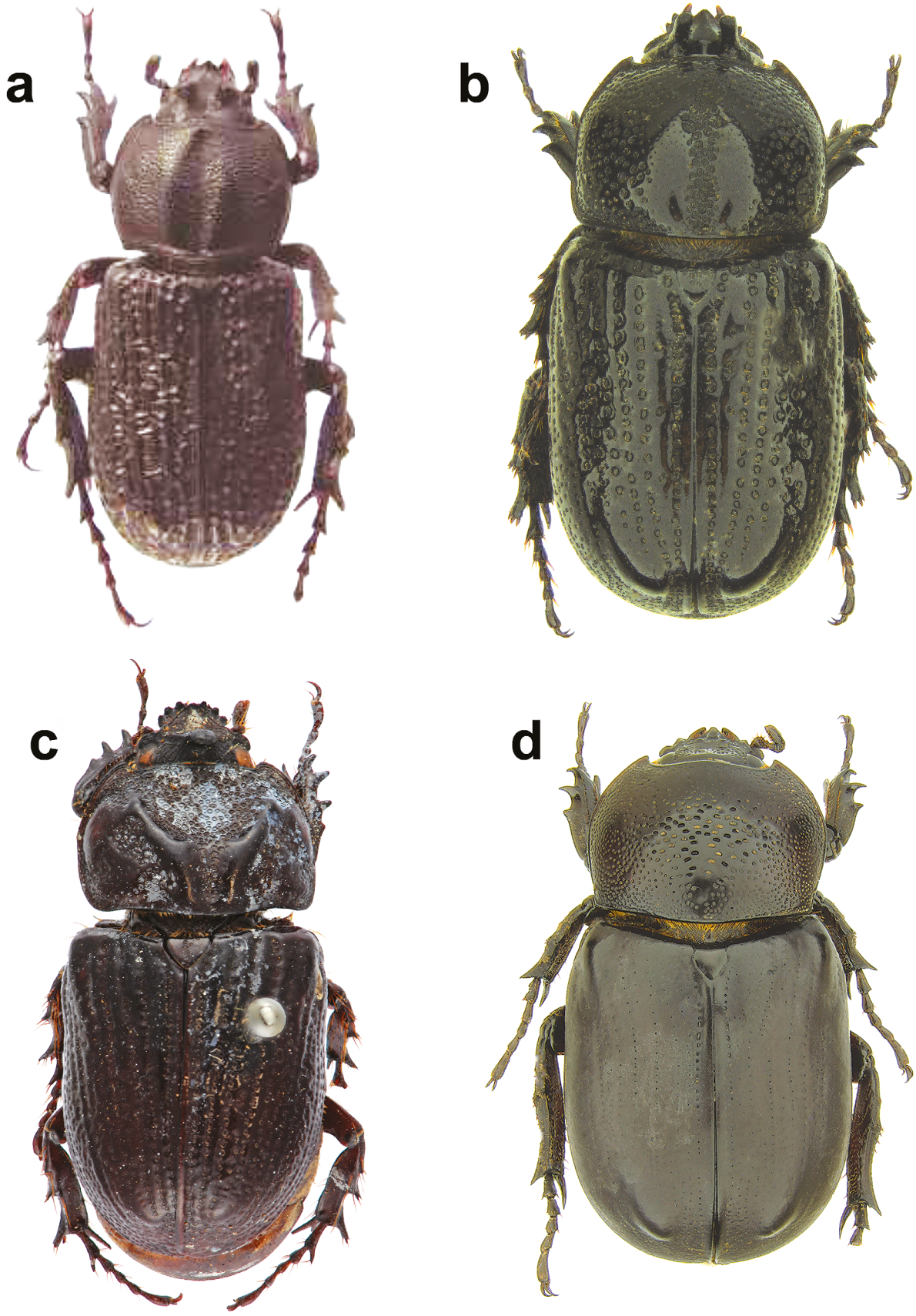

Fig. 4. a: *Metaphileurus lacunosus* (Burmeister). Image courtesy of Joachim Willers. b: *Microphileurus subulo* Prell. c: *Oryctophileurus nasicornis* (Burmeister). Image © MNHN/Antoine Mantilleri. d: *Palaeophileurus erebus* Ratcliffe.

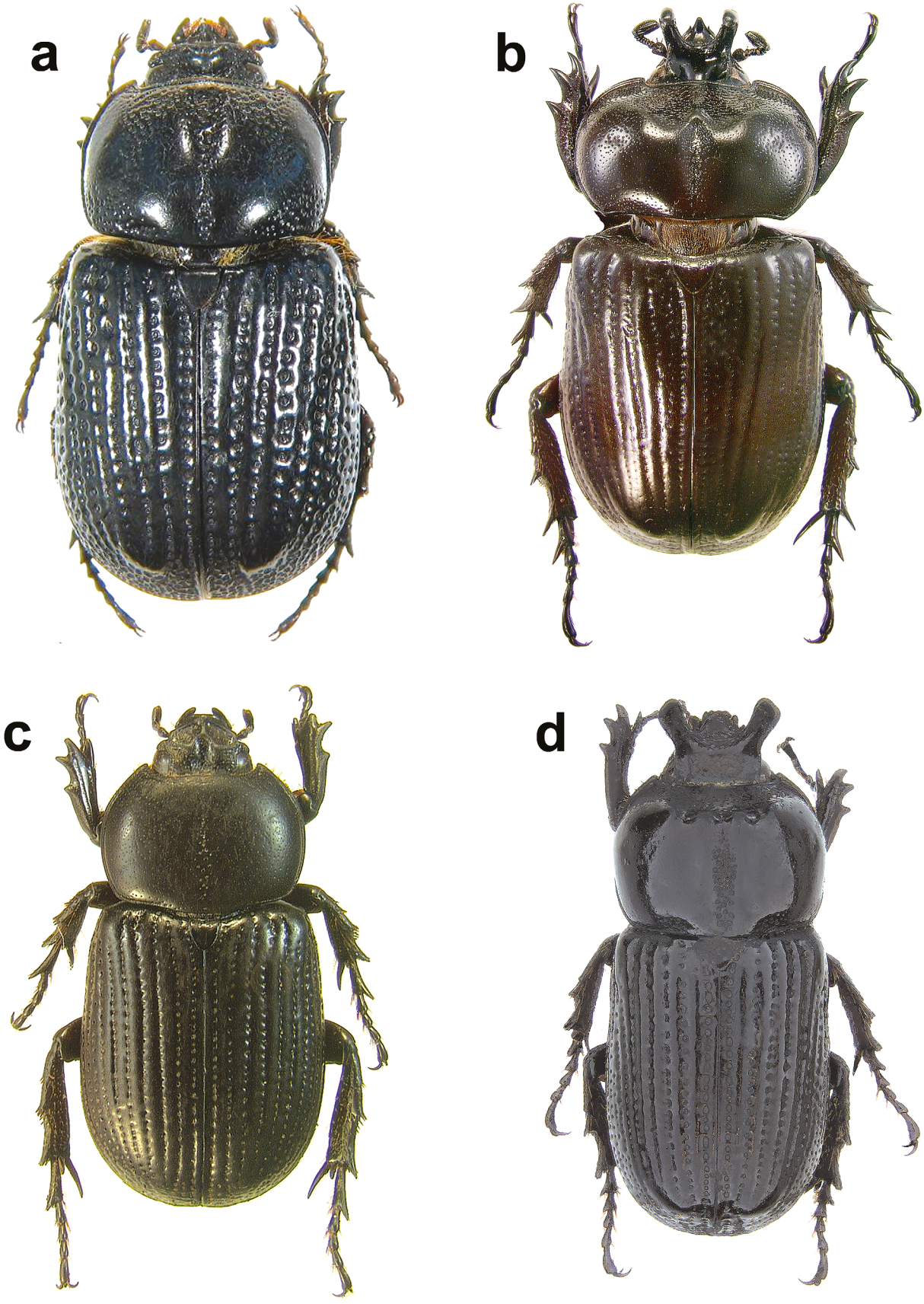

Fig. 5. a: *Paraphileurus ventricosus* Endrödi. Image courtesy of Inventaire National du Patrimoine Naturel. b: *Phileurus truncatus* (Palisot de Beauvois). c: *Planophileurus ypsilon* Ratcliffe and Cave. d: *Trioplus cylindricus* (Mannerheim).

15´. Pronoto liso, brillante. Élitros brillantes. Ángulo apical de la metatibia espiniforme...16

16. Élitros con filas débiles de puntos diminutos a pequeños, estrías ausentes (Fig. 2b). Longitud menor de 12 mm...***Caymania*** **Ratcliffe y Cave, 2010**

16´. Élitros toscamente punteado-estriados (Fig. 1b). Longitud mayor de 18 mm...***Allophileurinus*** **Dupuis y Dechambre, 2001**

17. Ápice de la metatibia con 3–4 dientes pequeños...18

17´. Ápice de la metatibia con 1–3 dientes grandes o al menos el ángulo superior fuertemente producido...19

18. Mandíbulas delgadas, margen externo ligeramente curvado (Fig. 1c). Ángulos posteriores del pronoto redondeados. Ápice de la metatibia con 3 dientes pequeños... ***Amblyoproctus*** **Kolbe, 1910**

18´. Mandíbulas anchas, margen externo fuertemente angulado. Ángulos posteriores del pronoto obtusos. Ápice de la metatibia con 4 dientes pequeños...***Mictophileurus*** **Ohaus, 1911**

19. Ápice de la metatibia con 3 dientes grandes...***Homophileurus*** **Kolbe, 1910**

19´. Ápice de la metatibia con 1–2 dientes grandes...20

20. Tubérculos o cuernos en la frente ubicados cerca del medio de la cabeza, distanciados de los márgenes laterales. Pronoto sin fóvea o declive anterior (Fig. 3c); surco longitudinal variable, todas excepto 1 especie sin tubérculo cerca del margen anterior...***Hemiphileurus*** **Kolbe, 1910**

20´. Tubérculos o cuernos en la frente ubicados cerca de los márgenes laterales de la cabeza. Pronoto con cavidad anterior hundido o declive ancho; surco longitudinal fuerte, usualmente con un tubérculo distinto en su ápice anterior...21

21. Proceso prosternal con protuberancia grande y cónica en su superficie posterior. Longitud 20 mm o menos... ***Paraphileurus*** **Endrödi, 1978**

21´. Proceso prosternal variable, pero nunca con superficie posterior producida hacia atrás como una proyección angulada. Longitud mayor de 20 mm excepto *P. valgus*... ***Phileurus*** **Latreille, 1807**

Actinobolus **Westwood, 1841**

Actinobolus Westwood 1841: 38.

The genus *Actinobolus* (Fig. 1a) contains nine species (Endrödi 1978, 1985, Dupuis and Dechambre 1998, Dupuis 2019b), all of which occur in South America, with one species extending into Central America. The species are characterized by a rounded or multilobed clypeal apex; concave head lacking a tubercle; protibia with four teeth (occasionally appearing tridentate due to fusion of basal teeth); and the metatibial apex with three short teeth. *Actinobolus* species are all saproxylophagous and develop inside termitaria (Lüderwaldt 1910, 1911, Vanin *et al.* 1983, Dupuis and Dechambre 1998, Dechambre and Lumaret 1986).

Allophileurinus **Dupuis and Dechambre, 2001**

Allophileurinus Dupuis and Dechambre 2001: 201.

Dupuis and Dechambre (2001) established *Allophileurinus* (Fig. 1b) to include two new species: *A. cavifrons* Dupuis and Dechambre, 2001 and *A. mediopunctatus* Dupuis and Dechambre, 2001, both from Ecuador (Ratcliffe *et al.* 2020). *Allophileurinus* species are characterized by a broadly subtriangular clypeal apex; smooth and shiny pronotum that lacks a median, longitudinal furrow; shiny, punctate-striate elytra; metatibia with two transverse carinae; and apical angle of the metatibia with a stout, triangular tooth. The form of the parameres for each species is unique. Members of *Allophileurinus* approach those of *Paraphileurus* in the form of the body, clypeus, frons, and prosternal process. Their life history is unknown.

Amblyodus **Westwood, 1878**

Amblyodus Westwood 1878: 32.

The genus *Amblyodus* (Fig. 1c) contains two species, with *A. taurus* Westwood, 1878 occurring in Costa Rica, Panama, and Nicaragua (Bates 1888, Ratcliffe 2003a) and *A. castroi* Grossi and Grossi, 2011 found in Peru and Brazil (Grossi and Grossi 2011). Endrödi (1977) indicated he saw a specimen from Colima, Mexico, but we remain unconvinced of the veracity of this record. Miguel Morón (personal communication to BCR, May 1997) said he knew of no Mexican records.

Amblyodus species are easily recognized by their distinctive head horns and flattened pronotum. It is one of only two genera of phileurines in Central America whose species possess dentate mandibles and quadridentate protibiae, whereas species of *Goniophileurus* (the other genus whose much smaller species have dentate mandibles) have tridentate protibiae.

Other than being attracted to lights (although perhaps not strongly so), nothing is known of the biology of the species in this rarely collected genus. Endrödi (1977, 1985) reviewed the genus.

Amblyoproctus Kolbe, 1910

Amblyoproctus Kolbe 1910: 335.

Amblyoproctus (Fig. 1d) contains twelve species (Endrödi 1985, Lamant-V 1995, Ratcliffe 1988, 2003a, Dechambre 2008a, Ponchel 2009), all from South America with one species reaching Central America. In our opinion, several of Dechambre's (2008a) species may be variations of previously known species, and additional study is warranted. The species of *Amblyoproctus* are all small (none exceeding 17 mm); possess two or three small spinules on the apical angle of the metatibia; have narrow mandibles lacking teeth; have a median, longitudinal furrow on the pronotum; and the apex of the prosternal process projects angularly backwards. Nothing is known of the natural history of *Amblyoproctus* species other than they live under the bark of rotting logs, and adults are occasionally attracted to lights. Endrödi (1977, 1985) provided the most recent review of the genus, although new species have been described since.

Archophileurus Kolbe, 1910

Archophileurus Kolbe 1910: 334.

Amblyphileurus Kolbe 1910: 334 (synonym).

Periphileurus Kolbe 1910: 334 (synonym).

Anisophileurus Prell 1912: 182 (described as a subgenus of *Amblyphileurus*; synonym).

Archophileurus (Fig. 1e) currently contains 33 species (Endrödi 1977, 1985, Morón 1990, Lamant-V 1995, Dechambre 2006, Ratcliffe and Cave 2015, Di Iorio *et al.* 2017, Dupuis 2018). The species are widely distributed, mostly in southern South America, although three species occur in Mesoamerica, and *A. cribrosus* (LeConte, 1854) is found in the southwestern USA. Dupuis (2019a) synonymized *Oxyligyrus larssoni* Endrödi, 1969 with *Archophileurus fodiens* (Kolbe, 1910). The species of *Archophileurus* are characterized by the presence of two tubercles or short horns on the head; apex of the metatibia truncate and with numerous small spinules; and a distinctive fringe of reddish-brown setae arising from beneath the lateral pronotal margins. Many species are rarely collected, often as singletons, and a female not associated with a male at the time of collection is virtually impossible to identify. Specimens in older collections are frequently misidentified, especially if the essential parameres have not been examined to determine their form, and so the distributional data based on undissected museum specimens is questionable.

The immature stages and life history are unknown for all species. Endrödi (1977, 1985) provided the most recent synopses of *Archophileurus*, but seven species have been described since his latest synopsis. Di Iorio *et al.* (2017) reviewed in detail the species from Argentina.

Argentophileurus Penco and Zubarán, 2013

Argentophileurus Penco and Zubarán 2013: 23.

Penco and Zubarán (2013) established the genus *Argentophileurus* (Fig. 2a) to accommodate a single new species, *A. litoralensis* Penco and Zubarán, 2003, characterized by simply curved mandibles; a metatibial apex with three blunt teeth; unique form of the parameres; and the first antennomere bulbous at its apex and subequal in size to the entire club that is almost twice as long as antennomeres 2–7. This species occurs in Argentina. Nothing is known of the life history of *A. litoralensis* except that adults come to lights (Mario Ibarra Polesel, personal communication 2022).

Caymania Ratcliffe and Cave, 2010

Caymania Ratcliffe and Cave 2010: 11.

The monobasic genus *Caymania* (Fig. 2b) is known only from Little Cayman Island in the West Indies. Its species, *C. nitidissima* Ratcliffe and Cave, 2010, is characterized by small size (9.5–11.5 mm); strongly shiny and minutely punctate dorsal surface; dark reddish brown to almost black

color; body slightly flattened dorso-ventrally; head lacking tubercles; small eyes (interocular width equals 9.0 transverse eye diameters); pronotum lacking a median furrow; elytra lacking striae; tridentate protibiae; and symmetrical parameres. The specimens of the type series were found beneath a rock. Nothing is known of the species' life history.

Ceratophileurus Ohaus, 1911

Ceratophileurus Ohaus 1911a: 171.

The rare *Ceratophileurus lemoulti* Ohaus, 1911 (Fig. 2c) is found in French Guiana and Suriname (Gillett *et al.* 2010). It is distinctive because of the long, recurved horn arising from the frons in both sexes. Well-developed specimens have a short, laterally compressed, truncate tubercle on each side of the pronotum. The few adult specimens known were all taken at lights, and the life history and immature stages remain unknown (Gillett *et al.* 2020).

Cnemidophileurus Kolbe, 1910

Cnemidophileurus Kolbe 1910: 335.

Cnemidophileurus personatus Kolbe, 1910 (Fig. 2d) occurs in Amazonian Brazil and is the only species in the genus. It is morphologically unique in having a broadly rounded clypeal apex; a broad mentum; frons with two tubercles; pronotum with small, dense punctures and simply convex with a broad, shallow, longitudinal furrow; tridentate protibiae; metatibial apex with two large teeth; and form of the parameres. Dupuis and Perrin (2020) reported that this species is found in termite nests in French Guiana, but otherwise little is known of its life history.

Goniophileurus Kolbe, 1910

Goniophileurus Kolbe 1910: 333.

The genus *Goniophileurus* (Fig. 3a) is distinguished by tridentate mandibles; tridentate protibia; pronotum with a narrow, longitudinal furrow; and metatibiae at the apex with three small teeth (one small tooth between two larger teeth).

Goniophileurus was reviewed by Endrödi (1977, 1985) who recognized a single species, *G. femoratus* (Burmeister, 1847). Dupuis and Mantilleri (2013) transferred *G. explanatus* (Burmeister, 1847) from *Metaphileurus* Kolbe and synonymized it with *G. femoratus*. *Goniophileurus* is known from South America east of the Andes (Colombia, Ecuador, Venezuela, French Guiana, Bolivia, and Brazil), and it also extends into Central America (Panama, Costa Rica, Honduras, El Salvador, and Mexico) (Endrödi 1977, Ratcliffe 2003a, Ratcliffe and Cave 2006, Ratcliffe *et al.* 2013). Nothing is known of the natural history of the species in this genus other than some specimens were collected at lights. These are small, rarely collected scarabs. The immature stages are unknown.

Haplophileurus Kolbe, 1910

Haplophileurus Kolbe 1910: 335.

Haplophileurus (Fig. 3b) currently contains three species, all from Andean South America. *Haplophileurus* species are very similar to *Archophileurus* species but have only one tubercle on the head. The immature stages and life history are unknown for all species, and the female is known for only *H. caudipenis* Dupuis, 2011. Dupuis (2011) provided the most recent synopsis of *Haplophileurus* species.

Hemiphileurus Kolbe, 1910

Hemiphileurus Kolbe 1910: 340.

Epiphileurus Kolbe 1910: 336 (synonym).

Neosyrichthoschema Ferreira 1965: 3 (synonym).

Phileucourtus Dechambre 2008b: 156 (**New Synonym).**

Hemiphileurus (Fig. 3c) is a large genus with 60 species. Endrödi (1977, 1978, 1985) was the last to comprehensively review the genus, although many new species have been described since (Howden 1978, Chalumeau 1981, 1988, Ratcliffe 1988, 2001, 2003a–b, 2014, Ratcliffe and Ivie 1998, Dechambre 2000, Dupuis and Dechambre 2000, Dupuis 1996, 2004a, Ratcliffe and Cave 2006, 2015, Neita-M and Ratcliffe 2010, Ratcliffe et al. 2023). There are now twelve species in the West Indies, 30 species in South America (some shared with Central America), 21 species in Mesoamerica, and one species in the USA. The genus *Hemiphileurus* continues to grow in number of species as new localities are explored and unidentified specimens already residing in research collections are studied. Compare, for example, Endrödi's (1985) listing of 24 known species with, just 38 years later, the 60 species now recognized. Many species are rarely collected, often as single-

tons, and a female not associated with a male at the time of collection is almost impossible to identify. Specimens in older collections are frequently misidentified, especially if the essential parameres have not been examined to determine their form, and so the distributional data based on undissected museum specimens is suspect.

The genus is characterized by having acute, simply curved mandibles; clypeus triangularly acuminate and reflexed; frons with two tubercles (usually) or horns (occasionally) arising far from the lateral margin of the head (less distinct when horns are large with a larger basal footprint); pronotum with a longitudinal furrow but lacking an anterior fovea or strong declivity; apex of metatibia with a single, large tooth or spine on the upper angle and usually with several minute serrations and short spinules below the large tooth; and apex of the first metatarsomere extended into a long, acute spine. Most of the species are moderate in size at 16–24 mm in length. Because most species are so similar externally, great reliance must be placed on the form of the parameres for accurate identifications. Accordingly, most females can only be reliably identified when collected with males.

Our knowledge of the natural history and habits of these beetles remains scant as a result of the secretive habits of most of the adults and larvae. Adults are attracted to lights at night, and this is where virtually all specimens in collections were taken. Until our search pattern for collecting goes beyond light traps (such as employing extensive excavation of rotting logs), specimens of most *Hemiphileurus* species will remain uncommon in collections.

The larval stage for only three species, *H. illatus* (LeConte, 1854) (USA and Mexico), *H. dispar* Kolbe, 1910 (Hispaniola), and *H. elbitae* Neita-Moreno and Ratcliffe, 2010 (Colombia), are described (Ritcher 1966, Ocampo and Morón 2004, Neita-M and Ratcliffe 2010, respectively). Larvae for the remaining species remain unknown or undescribed. Larvae presumably live in decaying wood where they feed on the wood or associated fungi. Obtaining larval life history information will probably require on-site research and lengthy periods of laboratory rearing.

Dechambre (2008b) briefly described *Phileucourtus bicornutus* as a new genus and species from Peru. Our examination of conspecific material from Peru indicates that the characters defining *Phileucourtus* are, in all respects, the same as those for *Hemiphileurus* except for the swollen protarsomeres of *P. bicornutus*. We do not believe that the enlarged protarsi are sufficient evidence for establishing a new genus and so reduce *Phileucourtus* to synonymy with *Hemiphileurus*. The presence or absence of an enlarged protarsus also occurs between species in other dynastine genera: *Euetheola humilis* (Burmeister, 1847) (enlarged) and *Euetheola bidentata* (Burmeister, 1847) (simple); *Ligyrus peruvianus* (Endrödi, 1970) (enlarged) and *Ligyrus burmeisteri* Steinheil, 1872 (simple). The body character states and especially the form of the parameres of *P. bicornutus* are identical with those of *H. howdeni* Endrödi, 1978, also from Peru, except for the swollen protarsi of *P. bicornutus*.

***Homophileurus* Kolbe, 1910**

Homophileurus Kolbe 1910: 336.

Homophileurus (Fig. 3d) is a relatively small genus consisting of ten species. Five species are found exclusively in South America, one is indigenous to Cuba and another to Central America, and three occur from Mexico to Brazil, with one of these also present in the West Indies (Endrödi 1978, 1985, Ratcliffe and Cave 2006, Dupuis 2012b, Ratcliffe *et al.* 2013).

Species in the genus are distinguished by the tubercles of the frons placed near the lateral margins of the head; quadridentate protibiae; and apex of the metatibia with three large teeth. Some of the larger species in the genus *Phileurus* are similar in overall appearance, including some with quadridentate protibiae, but none have three large teeth on the apex of the metatibia. The genus was comprehensively reviewed by Endrödi (1978, 1985).

Only the larva and pupa of *H. luederwaldti* (Ohaus, 1910) and the larva of *H. integer* (Burmeister, 1847), both South American species, are described (Costa *et al.* 1988, Ratcliffe and Skelley 2011, respectively). Little is known of the biology of any of the species. The larvae of some species probably live in rotting wood, while others are known to live in the nests of termites (Vanin *et al.* 1983, Costa *et al.* 1988, Neita and Ratcliffe 2011, Ratcliffe and Skelley 2011). Adults are attracted to lights at night.

***Metaphileurus* Kolbe, 1910**

Metaphileurus Kolbe 1910: 334.

Metaphileurus (Fig. 4a) is comprised of two species that occur in South America. Dupuis (2014) removed a former third species, *M. explanatus* (Burmeister, 1847), to *Goniophileurus*. Species are characterized by bi- or tridentate mandibles; tridentate protibiae; and metatibial apex with four small teeth. The life histories of the species remain unknown.

***Microphileurus* Kolbe, 1910**

Microphileurus Kolbe 1910: 333.

The small genus *Microphileurus* (Fig. 4b) contains two small species from South America, one known from Brazil and Argentina and the other rare species known from Peru. Species in the genus are characterized by tridentate mandibles, obtusely acuminate clypeal apex, and frons with two small tubercles.

***Mictophileurus* Ohaus, 1911**

Mictophileurus Ohaus 1911a: 169.

Mictophileurus is another monobasic phileurine genus, with only the southern Brazilian *M. punctulatus* Ohaus, 1911 as its included species. It shares many morphological characteristics with other genera of phileurines but can be distinguished by a combination of an acuminate clypeus; broad mandibles angled laterally; long, broad, and deep longitudinal pronotal furrow with a shallow fovea on each side; elytral intervals strongly convex; tridentate protibiae; metatibial apex with four small teeth; and form of the parameres. The natural history and immature stages of the species are unknown.

***Oryctophileurus* Kolbe, 1910**

Oryctophileurus Kolbe 1910: 334.

Oryctophileurus (Fig. 4c) contains four uncommon species found in Colombia, Peru, and Bolivia, which are characterized by tridentate mandibles; the presence of a horn or large tubercle on the frons; and quadridentate protibiae (Gasca-Á and Amat-G 2010, Perger and Grossi 2013). The immature stages and life history remain unknown for all species.

***Palaeophileurus* Kolbe, 1910**

Palaeophileurus Kolbe 1910: 335.

Kolbe (1910) described *Palaeophileurus* (Fig. 4d) for a single species, *Phileurus sclateri (*Bates, 1887), from Guyana. The genus now has ten species distributed only in South America (Ratcliffe 1988, 2002, Dechambre 1997, Dupuis 2012a, Neita and Ratcliffe 2012, 2017). Dechambre's (1997) *P. panamensis*, supposedly from Panama, is an erroneous country record because the type specimen is actually from Leticia, Amazonas, Colombia.

Dechambre (1996b) proposed three new species but did not include a description of the species. All of these names are *nomina nuda* because they were not accompanied by a description or diagnosis in words as required by Article 13a (i) of the International Code of Zoological Nomenclature that was in effect at that time or by the most recent code (Article 13.1.1) (International Commission on Zoological Nomenclature 1985, 1999). Dechambre (1997) corrected this oversight by proposing the names again but accompanied by a brief description of each. The date for those three species, therefore, is 1997 and not 1996.

Species of *Palaeophileurus* are characterized by two adjacent tubercles on the head with the surface slightly concave between the tubercles; pronotum lacking a median furrow, fovea, or tubercle; nearly smooth, opaque black elytra; metatibial apex with a single apical tooth; simple basal metatarsomere; and long, stout prosternal process with a trilobed apex.

Specimens of *Palaeophileurus* are usually uncommon, although occasionally locally abundant. Their rarity may result from genuinely small and/or dispersed populations or inadequate methods for attracting or collecting them. A few specimens have been attracted to lights, but, in our experience, phileurines are not as readily attracted to lights as are many other dynastines.

***Paraphileurus* Endrödi, 1978**

Paraphileurus Endrödi 1978: 98.

Paraphileurus (Fig. 5a) is a small genus comprised of only three species, all of which are known from northern South America, with one species reaching Panama (Ratcliffe 2003a). *Paraphileurus* is similar to *Hemiphileurus* but is distinguished by the presence of a broadly foveate pronotal cavity with an apical tubercle. In *Hemiphileurus*, the longitudinal furrow of the pronotum varies from indistinct to broad and from shallow to narrow and deep but never wid-

ened anteriorly into a broad depression nor with an apical tubercle. In addition, *Paraphileurus* has a prosternal process that is produced posteriorly into a large, conical knob.

The life history and immature stages of the species are unknown. Endrödi (1978, 1985) provided the most recent synopsis of the genus.

Phileurus Latreille, 1807

Phileurus Latreille 1807: 103.

The genus *Phileurus* (Fig. 5b) has 27 species (Endrödi 1978, 1981, 1985, Ratcliffe 1988a, Dechambre 1996a, 1998, Dupuis 2004b, Krajcik 2005, Ratcliffe and Cave 2015) distributed from the southeastern and south-central USA to southern South America and with three species in the West Indies. *Phileurus* was reviewed by Kolbe (1910) and comprehensively treated by Endrödi (1978, 1985), although new species have been described since.

Phileurus species are characterized by a sharply acuminate clypeus; slender, externally arcuate mandibles; pronotum with a longitudinal furrow, subapical tubercle, and fovea or declivous area; and the apical margin of the metatibia with the dorsal angle produced into a single large, acute tooth or two teeth. Most of the species are moderately large beetles, with only some specimens of *P. valgus* (Olivier, 1789) measuring less than 20 mm in length.

The larval stage is described for only two species in the genus, *P. didymus* (Linnaeus, 1758) and *P. valgus* (under the name *P. castaneus* [Haldeman, 1843]) (Ritcher 1966). The natural history of *Phileurus* species is largely unknown. Adults and larvae have been collected from rotting logs and stumps (Ritcher 1966; BCR and RDC personal observations), where the larvae probably feed on decaying wood and/or associated fungi. Adults are frequently encountered at lights. Adults have been observed beneath streetlights in Mexico, where they were tearing open and feeding on the abdomens of *Heterogomphus chevrolatii* Burmeister, 1847 (Scarabaeidae: Dynastinae) (Ratcliffe and Morón 1997). McCleve (2007) observed an adult female on the branch of a tree where it was feeding on a lepidopteran larva. Albert Thurman (personal communication to BCR, June 2015) posted a video (www.youtube.com/watch?v=AY-dcJWvS-Po) of a *Phileurus* adult, probably *P. truncatus* (Palisot de Beauvois, 1806), feeding on a large dung beetle (*Dichotomius* species) in Panama. Adults of *P. carinatus* Prell, 1914 were observed consuming an adult female *Golofa eacus* Burmeister, 1847 after both were confined together in a terrarium in Ecuador (Ratcliffe *et al.* 2020). These observations demonstrate that some phileurine adults are predaceous. Little else is known of their natural history.

Planophileurus Chapin, 1932

Planophileurus Chapin 1932a: 307.

The genus *Planophileurus* (Fig. 5c) contains three species known from Cuba, the Bahamas, and the Dominican Republic (Ratcliffe and Cave 2015). *Planophileurus* species are noticeably dorsoventrally flattened relative to most other phileurines, and males are distinguished from all West Indian phileurines by their enlarged protarsal claws. The frons has two nearly obsolete tubercles, the pronotum lacks a longitudinal furrow (a row of punctures at most), the basal bead is obsolete in front of the scutellum, the prosternal process is large and bulbous, male tarsomere four usually has a small ventral lobe that projects forward beneath tarsomere five, male tarsomere five is short and slightly to distinctly enlarged, and the medial claw is usually enlarged.

The females are best identified by association with the males when collected but also by their broadly oval pronotum that is reminiscent of the shape seen in species of *Palaeophileurus* from South America (best seen with comparative material). The natural history and immature stages for these rare beetles are completely unknown. Their dorsoventrally flattened body form suggests they live under bark.

Trioplus Burmeister, 1847

Trioplus Burmeister 1847: 147.

Trioplus (Fig. 5d) contains only one species, *Trioplus cylindricus* (Mannerheim, 1829), found in Brazil, Paraguay, and Argentina. The larval and pupal stages were described and illustrated by Costa *et al.* (1988).

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Chiliphileurus Endrödi, 1977

Chiliphileurus Endrödi 1977: 19.

Ratcliffe *et al.* (2021) determined that the single species in this genus, *Chiliphileurus tuberculatus* Endrödi, 1977, is a junior synonym of the Asian *Eophileurus cingalensis* Arrow, 1908. The male holotype of *C. tuberculatus* is labeled "Valdivia, Chile" and, if correctly labeled, is a result of inadvertent commercial transport from Asia to Chile. *Chiliphileurus* was removed from the list of American phileurines by Ratcliffe *et al.* (2021).

Moraguesia Dechambre, 2008

Moraguesia Dechambre 2008b: 155.

Dechambre (2008b) described *Moraguesia* as a monotypic genus of Phileurini from French Guiana. Dupuis and Perrin (2020) transferred its species, *M. champenoisi* Dechambre, 2008, to *Oxyligyrus* Arrow in the Pentodontini.

Platyphileurus Ohaus, 1910

Platyphileurus Ohaus 1910: 684.

Ohaus (1910) created the genus *Platyphileurus* to accommodate a single species, *P. felscheanus* Ohaus, 1910. This species has an unusually flattened and posteriorly widened body form that may have suggested to Ohaus its phileurine affinities. After examining type specimens, Grossi *et al.* (2010) placed *Surutu jelineki* Endrödi, 1975 (Cyclocephalini) in junior synonymy with *P. felscheanus* and documented its occurrence in the Brazilian Atlantic Coastal Forest and Restinga biotopes in the Brazilian states of Bahia, Espírito Santo, Minas Gerais, Rio de Janeiro, Paraná, and Santa Catarina.

In a detailed study, Albertoni *et al.* (2014) described the immature stages and life history of *P. felscheanus*. They repeatedly collected and reared larvae and pupae in bromeliad phytotelmata in Santa Catarina in southern Brazil. Based on a detailed analysis of larval and adult characters, they transferred *Platyphileurus* from the Phileurini to the Oryctini and remarked that the flattened body shape was probably related to the beetle's unique habitat among tight bromeliad leaves, where larvae pupated and adults concealed themselves. Dupuis and Perrin (2020) suggested that the characters of *Platyphileurus* are closer to Cyclocephalini rather than Oryctini, and so definitive placement of this genus remains under study.

AUTHOR CONTRIBUTIONS

Each author participated equally in preparation of the manuscript. Second author Cave provided the Spanish translation.

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