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ON THE TAXONOMIC PLACEMENT OF *PENICHRUS* CHAMPION, 1885 AND A SYNOPSIS OF NORTH AMERICAN OPATRINI (COLEOPTERA: TENEBRIONIDAE: BLAPTINAE)

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Abstract.— The taxonomic position of *Penichrus blapstinoides* Champion, 1885 (type species of *Penichrus* Champion, 1885) within Tenebrionidae is discussed based on the analysis of both type material and comprehensive internal and external morphology. The species was formerly classified within Opatrini (subfamily Blaptinae); however, this hypothesis is hereby rejected as this species does not share any of the diagnostic characteristics proposed for that tribe. A detailed analysis of other phylogenetically crucial features (including male and female terminalia, defensive glands, antennae, and abdominal ventrites) places *Penichrus* within Tenebrioninae. However, a more detailed assignment is not currently possible given the present circumscriptions of tenebrionine tribes. The genus is hereby placed as incertae sedis within Tenebrioninae. A morphological analysis and discussion of current tribal concepts is presented, which exposes the weakness of the currently accepted classification system, and highlights a need for extensive comparative morphological studies within Tenebrioninae and related subfamilies. A lectotype for *Penichrus blapstinoides* is designated. *Distolinus impressicollis* Fairmaire, 1892 is reinstated as a junior synonym of *Penichrus blapstinoides*. A revised checklist and key to the genera of Opatrini known from mainland North America are provided.

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Key words.— *Penichrus blapstinoides*, lectotype, Tenebrioninae, darkling beetles

Introduction

The genera comprising the New World subtribe Blapstinina Mulsant and Rey, 1853 (Tenebrionidae Latrielle, 1802: Blaptinae Leach, 1815: Opatrini Brullé, 1832) have seen a modern resurgence of taxonomic and phylogenetic study (*e.g.*, Hart and Ivie 2016, Ivie and Hart 2016, Kamiński *et al*. 2019a, 2019b, 2020, Lumen *et al*. 2019, 2020). This work is far from complete with many constituent genera last revised over a century ago. However, the current species-level nomenclature of the group was recently catalogued (Bousquet *et al*. 2018)

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and natural history collections and online identification tools (*e.g.*, http://www.bugguide.net)) contain authoritatively identified material at least for most taxa from the United States and Canada. Nevertheless, several questions remain about the generic composition of Blapstinina and there is no synopsis of significant recent works, which are scattered throughout the literature.

The genus *Penichrus* Champion, 1885 was erected for a single species, *Penichrus blapstinoides* Champion, 1885, in what was then considered the tribe Pedinini Eschscholtz, 1829, though its placement was noted as uncertain (Champion 1885: 134). This placement was continued through later works (*e.g.*, Blackwelder 1945) until the genus was placed into the 'opatrina group' of Opatrini by Iwan (2004) along with the rest of the North American genera it had been historically associated with. The subtribal classification was subsequently refined resulting in the majority of the North American genera classified into Blapstinina (Iwan and Kamiński 2016, Lumen *et al*. 2020).

Penichrus has not been investigated or mentioned in any of the works subsequent to Iwan (2004) except for a study on the Blapstinina of the West Indies (Ivie and Hart 2016). Ivie and Hart (2016) reviewed the species described as *Diastolinus impressicollis* Fairmaire, 1892, which had later been transferred to *Penichrus* (Marcuzzi 1977: 31) and ultimately synonymized with *P. blapstinoides* (Marcuzzi 1998a: 157). Recognizing that *Diastolinus impressicollis* did not belong in Blapstinina, and based on advice from other Neotropical tenebrionid authorities, it was transferred to the genus *Goniadera* Perty, 1832 which belongs to the subfamily Lagriinae Latrielle, 1825 (Ivie and Hart 2016: 452). It is worth noting that they followed the advice for "placement in the subgenus *Anaedus* Blanchard, 1845" (Ivie and Hart 2016: 454). This is problematic because the genus *Anaedus* has long been, and remains distinct from *Goniadera* (Bousquet *et al*. 2018), but perhaps was intended for the subgenus *Aemymone* Bates, 1868. In either case, their treatment was only meant for the type of *Diastolinus impressicollis* and they specifically state that "the status of the actual *P. blapstinoides* is unknown to us and beyond the scope of this paper" (Ivie and Hart 2016: 452).

In the present study, we review the internal and external morphology of *Penichrus blapstinoides* to assess its subfamilial and tribal placement. We also provide an updated checklist of the genera of Opatrini known from North America along with a key to the genera known from the mainland.

MATERIALS AND METHODS

This study was based on material from the Natural History Museum in London (BMNH), United Kingdom, the M. Andrew Johnston Research Collection in Tempe, Arizona (MAJC), the Canadian Museum of Nature in Ottawa, Ontario (CMNC), and the Museum and Institute of Zoology of the Polish Academy of Sciences in Warsaw (MIZ PAS), Poland. The original label data for the specimens is given in quotation marks and separated by a comma. Each line of the original label data is separated by a forward slash. Morphological terminology follows that of Doyen (1966), with additional specialized terms used for the male and female terminalia (Iwan & Kamiński 2016). Terminalia were investigated using standard methodologies (see Iwan & Kamiński 2016). Morphological measurements were recorded using a filar micrometer. Images of morphological details were taken using a Leica M165C system in Purdue University, and with a Hitachi S-3400N SEM in MIZ PAS.

SYSTEMATICS

Genus ***Penichrus*** Champion, 1885

Penichrus Champion, 1885: 135. Type species: *Penichrus blapstinoides* Champion, 1885: 135, by monotypy.

Diagnostic redescription. Body small, < 6 mm, oblong-ovate, somewhat flattened (Fig. 1A). Head prognathous, strongly constricted just behind eyes (Fig. 2A). Labrum transverse, labroclypeal membrane concealed. Apical maxillary palpomere securiform (Fig. 2B), lacinia bearing uncus. Mentum simple, subquatrate (Fig. 2C). Antennae 11-segmented, weakly clavate, extending just beyond base of pronotum, antennomere 3 only slightly longer than 2, stellate compound sensoria present on apical 4 or 5 antennomeres (Fig. 2D). Eyes bulging, reniform, weakly emarginate anteriorly by epistoma. Tentorial bridge apparently absent.

Prothorax transverse; pronotum flat, margined laterally, very slightly explanate. Procoxal cavities closed internally and eternally; prosternal process narrower than coxal diameter, declivous behind coxae. Scutellar shield triangular, clearly visible. Elytra each with scutellary striole and nine complete striae; humeri well developed; epipleuron distinct from base to apex. Mesocoxal cavities broadly closed laterally by mesepimeron. Hind coxae transverse. Metathoracic wings present, well-developed, recurrent cell relatively large, apical membrane about one third of total wing area. Metendosternite with narrow elongate base and narrow elongate furcae; laminae absent; anterior tendons inserted apically; furcal apices with flattened muscular attachment sites. Legs bearing scattered golden setae; all femora weakly clavate, profemora more clavate than others; tibiae simple, subcylindrical, more densely setose near inner apical surface; tarsi not lobed, all bearing golden setae beneath, protarsi of males dilated and bearing dense pads of golden setae beneath basal 4 tarsomeres; tarsal claws not pectinate, widened in basal third, sickle-shaped in apical two thirds.

Abdomen with five visible ventrites (Fig. 2G); ventrites 1–3 connate; membranes visible between ventrites 3–5. Paired defensive glands present between sternites VII–VIII; saccate; approximately as long as sternites VI and VII combined; with common volume; membrane simple, lacking pleating or annulations (Fig. 1F, G).

Ovipositor well developed, paraprocts subequal in length to coxites; baculi of paraproct longitudinal in basal half, apical half bent medially, oblique. Coxite four-segmented, bearing gonostyle subapically (Fig. 1C). Vagina elongate, bearing long, narrow duct proximally (anteriorly), which in turn bears a coiled globular spermatheca near mid-length (Fig. 1E). Spiculum ventrale with relatively short base (Fig. 1D).

Adeagus simple, evenly sclerotized. Tegmen curved roughly 90° in basal two thirds. Parameres simple, apparently fused along entire length of mesal longitudinal suture (Figs 1H, 2F).

Penichrus blapstinoides Champion, 1885

Penichrus blapstinoides Champion, 1885: 135.
=*Diastolinus impressicollis* Fairemaire, 1892: 81 **Synonymy Reinstated.**

Material Examined. **Lectotype,** here designated (BMNH): „Panama. / Champion.", „88", „Godman-Salvin / Coll., Biol. / Centr.-Amer.", „♂", „Penichrus / blapstinoides, / ♂ Champ.", QRcode"NHMUK 011520738" (Fig. 1A, B). **Additional specimens: Guatemala:** "Guatemala: Peten, / Ixpanpajul Nature Park / 16.8728°, -89.8149° 210m / 10.VIII.2016 M. A. Johnston / Leaf Litter Sifting" (1 MAJC). **Nicaragua:** "Nicaragua: Grenada / Volcan Mombacho Res. Nat. / 1150 m, N11°50.0' W85°58.8' / 2-5.VI.2002, R. Anderson / elfin cloud for. Litter, 2002-033B" (2 CMNC). **Panama:** "Panama: Colon Prov., / Gamboa, bldg 183 lights / 9.116202,-79.698124 / 186ft. 5-12.III.2014, at / night, leg. S. S. Anzaldo" (4 MAJC); "Panama: Colon Pr. Gamboa / STRI bldg 183 lights @ night, / 9.1162616, -79.698145 / v.5-7 2015 leg S. S. Anzaldo" (1 MAJC); same data, 8.v.2015 (18 MAJC); same data, 14-17.V.2015 (18 MAJC). **Venezuela:** "Venezuela: Bolivar / 20km S Tumeremo, / 12.VIII.1987, S.&J. Peck / seas. Humid for. On sand, / fungus sifting. 87-12" (1 CMNC); "Venezuela: Guarica / Guatopo NP, S Border, / 24km N Altagracia, 10. / VI.1987, 300m. S.&J. / Peck, forest leaf litter" (2 CMNC); "Venezuela: Merida / Tovar, 100m, / 25.VI.1989, S.&J. Peck / coffee forest litter, 89-233" (5 CMNC); "Venezuela: Miranda / Guatopo NP, El Lucero, / 28km N Altagracia, 8.VI. / 1987, 700m, S.&J. Peck / rotted log litter, 87-12" (1 CMNC); same data, 14.VI.-5.VIII.1987, forest ravine f.i.t. Malaise trap (1 CMNC); "Venezuela: Sucre / 26km SE Rio Caribe, 50m / 28.VII.1987, S.&J. Peck / forest over cacao tree / base litter, 87-101" (2 CMNC).

Specimens are also known from **Trinidad** (Ivie and Hart 2016) and **Costa Rica** (records published online by GBIF 2020).

Diagnosis. As genus, 4.5–6mm long, reddish brown to black, slightly shining and aeneus, covered in short, scattered, decumbent golden setae. Head and pronotum densely and fairly finely punctate. Elytral striae distinct, comprised of moderate punctures, slightly impressed; elytral intervals minutely punctured. Antennae bearing short golden decumbent setae interspersed with scattered longer, suberect setae.

Remarks. Ivie and Hart (2016: 452) give the full taxonomic history of *Diastolinus impressicollis* and ultimately treated it as *Goniadera (Anaedus) impressicollis*. We hereby recognize it as a synonym of *P. blapstinoides* based on examination of specimens from across its range and the type images given by Ivie and Hart (2016). This synonymy was also previously recognized by Marcuzzi (1998a), as discussed in the introduction.

Penichrus nanus Marcuzzi, 1998

Penichrus nanus Marcuzzi, 1998b: 223.

Remarks. This species was described from two specimens (type locality: Curapoa, Guarenas, E. do Miranda, Venezuela) and was named in reference to an unavailable name which was mentioned by Champion (1885: 135) for a species known from Colombia and Brazil. Putatively extremely similar to *P. blapstinoides*, this species is characterized by the antennae bearing "knobbed hairs" (Marcuzzi 1998b: 224). We have not seen the type or any specimens referable to this species.

DISCUSSION

Placement of *Penichrus* within Tenebrionidae

The presence of compound antennal sensoria, paired defensive glands, and a non-opatrine protrochanter-femoral joint preclude the previous placements within the Lagriinae (sensu Bouchard *et al.* 2005) and Blaptinae (sensu Kamiński *et al.* 2020), and place the genus firmly within the 'tenebrionoid-group' of tribes generally constituting the subfamilies Diaperinae Latreille, 1802, Tenebrioninae Latreille, 1802,

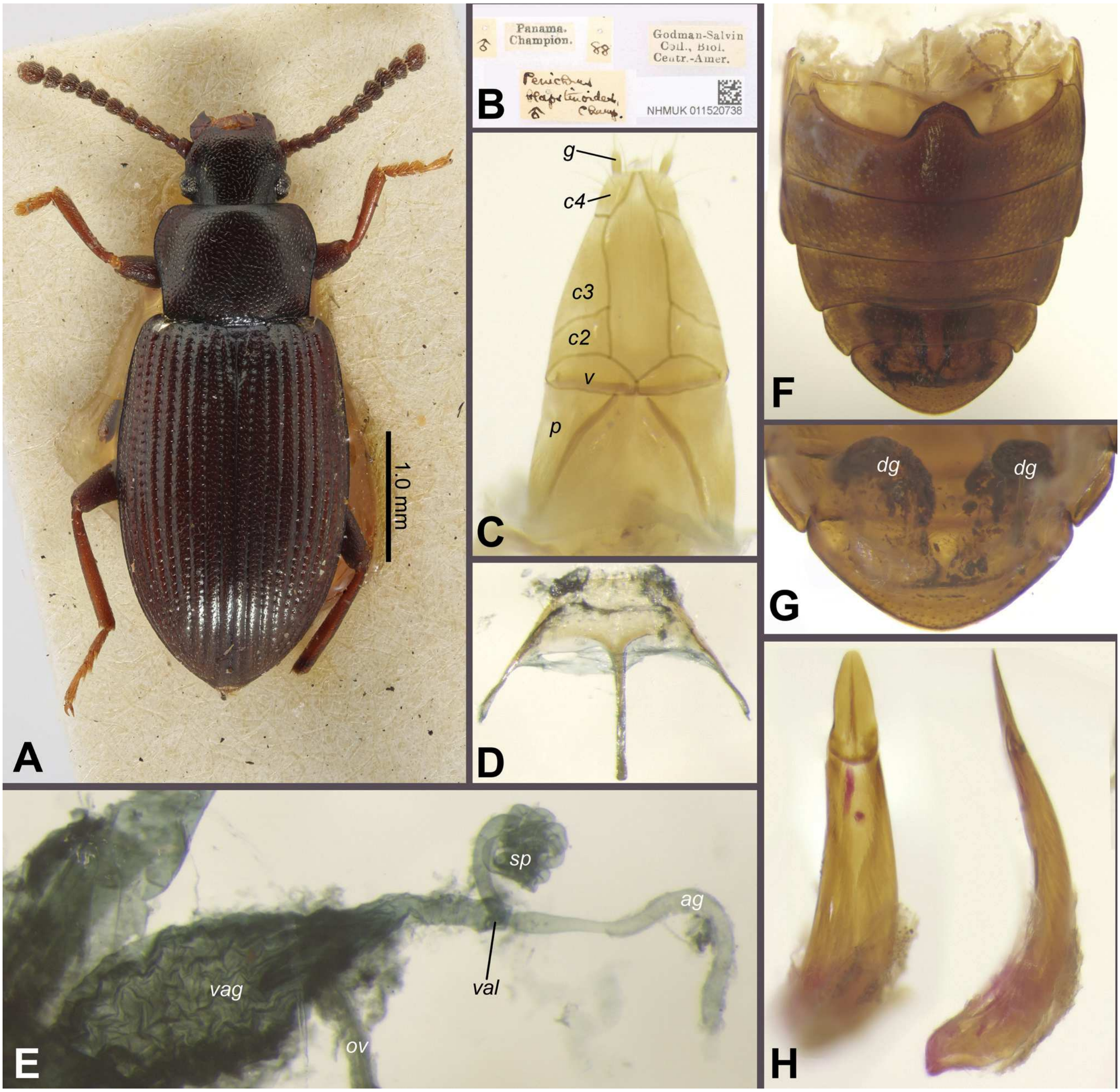

Figure 1. Morphology of *Penichrus blapstinoides*: (A) newly designated lectotype with (B) labels; (C) ovipositor (ventral side); (D) spiculum ventrale; (E) female genital tubes; (F, G) abdominal ventrites and defensive glands; (H) aedeagal tegmen. Abbreviations: *ag* – accessory gland, *c2-c4* – subsequent coxites, *g* – gonostylus, *dg* – defensive gland, *p* – paraproct, *ov* – oviduct, *sp* – spermatheca, *v* – valvifer, *vag* – vagina, *val* – valve

and Stenochiinae Kirby, 1837 (Doyen and Tschinkel 1982, Matthews and Bouchard 2008, Kanda 2017).

Adult morphological characters that have been used to classify higher level groups within the tenebrionidae include antennal sensoria, female reproductive tract, and abdominal defensive glands (*e.g.*, Medvedev 1977, Tschinkel and Doyen 1980, Doyen 1989, Flores 2000, Matthews and Bouchard 2008, Johnston 2019, Kamiński *et al*. 2020). Molecular phylogenetic studies suggest that these character systems are important and useful at the tribal level, but also strongly suggest that most subfamilies and some tribes, particularly Tenebrioninae and Tenebrionini Latrielle, 1802 respectively, are polyphyletic as currently circumscribed (Kergoat *et al*. 2014, Kanda 2017, Kamiński *et al*. 2020). Each system is discussed below to consider tribal placement of *Penichrus* in relation to the current morphological conception of tenebrionid tribes.

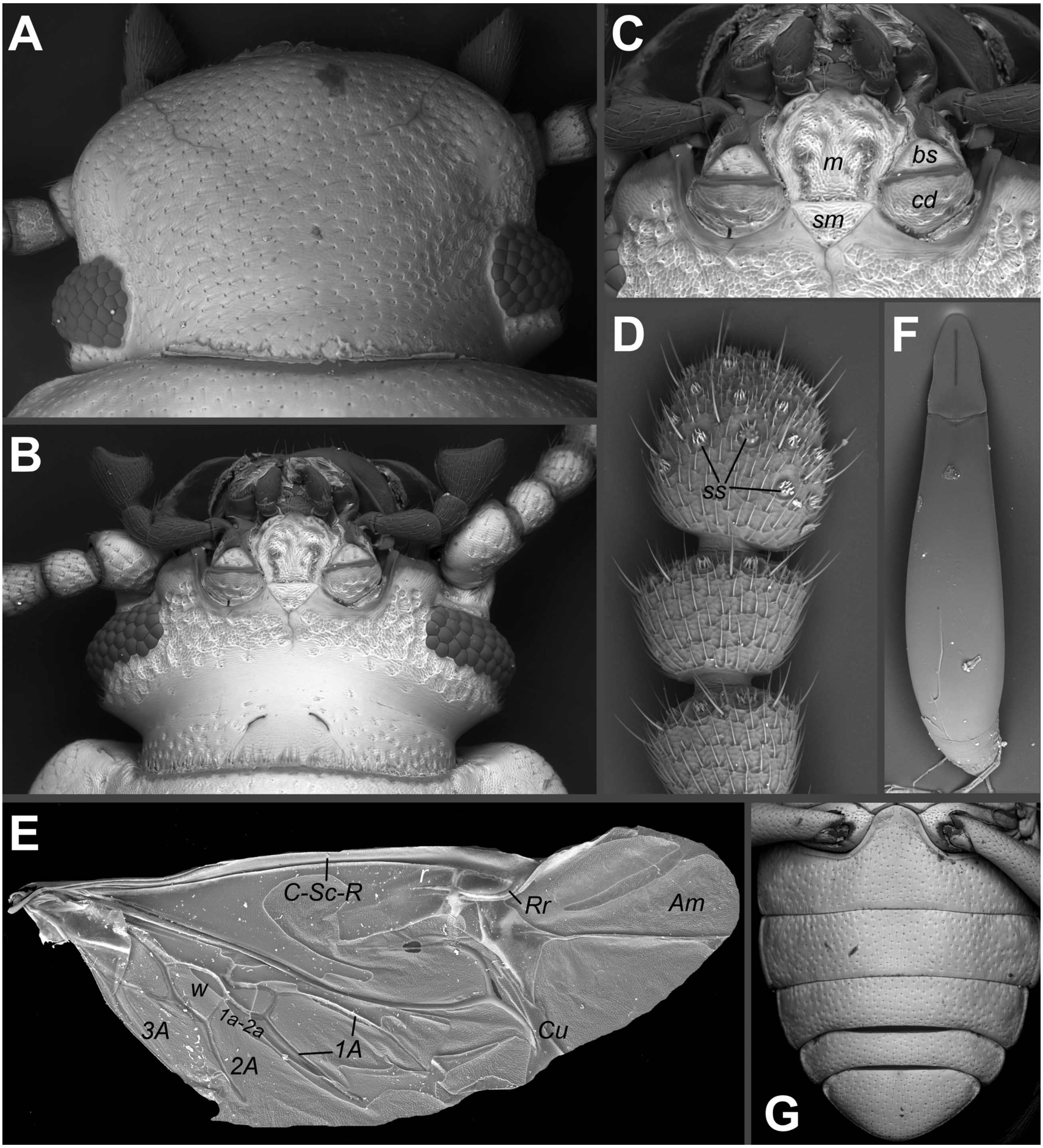

Figure 2. Morphology of *Penichrus blapstinoides*: (A) dorsal and (B) ventral views of head; (C) mouthparts; (D) apical antennomeres; (E) metathoracic wing (nomenclature after Doyen 1966); (F) aedeagal tegmen; (G) abdominal ventrites. Abbreviations: *bs* – basistipes, *cd* – cardo, *m* – mentum, *sm* – submentum, *ss* – stellate sensoria.

The presence of compound sensoria preclude the inclusion of *Penichrus* in Helopini Latrielle, 1802, Tenebrionini (strict sense, including *Tenebrio* Linnaeus, 1758 and *Idiobates* Casey, 1891 in the New World), or any of the members of Blaptinae (Kanda 2017, Kamiński *et al*. 2020). They instead show similarity to the subfamilies Diaperinae, Stenochiinae, and some remaining Tenebrioninae tribes, particularly the tenebrionine tribes Alphitobiini Reitter, 1917, Metaclisini Steiner, 2016, Ulomini Blanchard, 1845, and the genus *Neatus* LeConte, 1862 (Tenebrionini) (Doyen 1989, Kanda 2017). Emerging evidence suggests that compound antennal sensoria arose once within the tenebrionoid-group, though this remains to be thoroughly investigated (Kanda 2017, Kamiński *et al*. 2020).

The *Penichrus* ovipositor is the standard tenebrionine form (sensu Tschinkel and Doyen 1980) and itself does not further preclude additional tribal placements other than potentially groups characterized with apomorphic modifications (Tschinkel and Doyen 1980, Doyen 1989, Steiner 2016). Similarly, the internal reproductive tract, bearing a single coiled spermatheca attached at mid-length of a duct inserted to the bursa proximally (anteriorly), is similar to many tenebrionine tribes and the enigmatic Australian diaperine tribe Ectychini Doyen, Matthews, and Lawrence, 1990, as well as some members of the already precluded Blaptinae and Helopini. The spermatheca precludes inclusion in the tribes Stenochiini, Kirby, 1837 and Cnodalonini Oken, 1843, which are characterized by an enlarged spherical spermatheca at the end of the spermathecal duct (Tschinkel and Doyen 198, Doyen 1989). *Penichrus* is similarly precluded from a lineage containing Alphitobiini and *Neatus,* which possess a strongly sclerotized capsular spermatheca which is reniform or w-shaped (Doyen 1989, Steiner 2016, Kanda 2017).

The paired saccate defensive glands (Fig 1G), which share common volume are considered to be the pleisiomorphic state for the tenebrionoid-group (Tschinkel and Doyen 1980, Doyen and Tschinkel 1982, Kanda 2017). *Penichrus* is precluded from most New World tenebrionoid-group tribes that possess compound antennal sensoria, which are characterized as having annulated or pleated defensive glands (*e.g*., Cnodalonini, Metaclisini, Centronopini Doyen, 1989, Cerenopini Horn, 1870, Eulabini Horn, 1870, Scotobiini Solier, 1838, some Tenebrionini including *Zophobas* Dejean, 1834 and *Rhinandrus* LeConte, 1866) (Tshinkel and Doyen 1980, Doyen and Tschinkel 1982, Doyen 1989). The defensive glands and compound sensoria of *Penichrus* are together consistent with the tenebrionine tribes Alphitobiini and Ulomini, and the diaperine tribe Ectychini.

From these observations, three tribes merit a closer comparison with *Penichrus*, namely: Alphitobiini, Metaclisini, and Ulomini. Alphitobiini possesses similar antennal sensoria and defensive glands to *Penichrus*, but the apomorphic spermatheca seems to strongly preclude placement therein (Doyen 1989, Steiner 2016). In a similar manner, *Penichrus* and Metaclisini are united by the spermatheca and antennal sensoria yet differ in the simple as opposed to pleated defensive glands, respectively. Lastly, Ulomini and *Penichrus* are not definitively separated by any of the three character systems discussed. This similarity is likely due to sympleisiomorphy or convergence because *Penichrus* lacks the other morphological characteristics which define Ulomini (Doyen 1985), namely: fore tibiae expanded, fossorial (simple in *Penichrus*); tergite VII generally exposed beyond elytra as a pygidium (elytra covering abdomen completely in *Penichrus*); mesocoxal cavities fully or very nearly closed laterally by mesosternum and metasternum (closed broadly by mesepimeron in *Penichrus*). We also note that, while we consider this less important than the characters discussed above, *Penichrus* in no way fits into the fairly recognizable gestalt that the three discussed tribes each portray.

Penichrus can be further excluded from other New World tribes of Tenebrioninae not already discussed above. Members of the Amarygmini Gistel, 1848 are generally characterized by a hypognathous head, an inner sclerotized prong on abdominal sternite VII, elongate defensive glands, and typically possess vaginal sclerites (Tschinkel and Doyen 1980, Matthews and Bouchard 2008, Bremer and Lillig 2014), none of which are present in *Penichrus*. Similarly, Palorini Matthews, 2003 are distinguished from *Penichrus* by possessing only simple antennal sensoria, lacking a lacinial uncus, the presence of a spherical spermatheca, and mesocoxal cavities closed by the mesosternum and metasternum (Matthews 2003, Matthews and Bouchard 2008). The tribe Triboliini Gistel, 1848 is likely a heterogeneous and non-monophyletic group (Doyen 1985, Kanda 2017). *Tribolium* MacLeay, 1825 and closely related genera bear only simple antennal sensoria, have the mesocoxae closed by the mesosternum and metasternum, and possess a tentorial bridge (Doyen 1985), all of which preclude an association with *Penichrus*. Other New World Triboliini genera that possess compound antennal sensoria, including *Hypogena* Dejean, 1834 and *Mycotrogus* Horn, 1870, need to be reexamined at the tribal level (Kanda 2017, MAJ personal observation) but still differ from *Penichrus* by having strongly reduced coxites of the female ovipositor and the mesocoxal cavities closed by the mesosternum and metasternum (Spilman 1963, Grey and Smith 2020).

The final set of tribes to consider from the 'tenebrionoid-group' belong to the subfamily Diaperinae, which is almost certainly polyphyletic (Doyen *et al*. 1990, Kergoat *et al*. 2014, Kanda 2017). *Penichrus* can be excluded from the following tribes based on their female internal tract not being a strongly differentiated spermatheca but instead an elongated and apically enlarged accessory gland and their ovipositor bearing short and reduced coxites: Crypticini Brulle, 1832; Hyociini Medvedev and Lawrence, 1982; Phaleriini

Blanchard, 1845; and Trachyscelini Blanchard, 1845 (Tschinkel and Doyen 1980, Doyen and Tshinkel 1982, Doyen *et al*. 1990, Matthews and Bouchard 2008).

Penichrus appears to be somewhat similar to the Australian tribe Ectychini, which was erected in 1990 (Doyen *et al*. 1990) for two small Australian genera based on the morphology of the female internal tract, ovipositor, defensive reservoirs, the presence of antennal sensoria and an uncus on the lacinia. Doyen *et al*. (1990) noted that this tribe shared characteristics of both the subfamilies Diaperinae and Tenebrioninae, and placed it within Diaperinae pending future work. While the characters listed above are similar between Ectychini and *Penichrus*, there are also differences, including the presence of a flat tentoral bridge (absent in *Penichrus*) and internal vaginal sclerites on some Ectychini taxa. The uncertain placement of Ectychini mirrors that of *Penichrus* in many ways. However, without larval morphology, molecular phylogenetic analyses, or the presence of diagnosable morphological apomorphies, we do not feel justified in placing *Penichrus* within Ectychini.

The remaining tribes classified within Diaperinae have well-developed ovipositor coxites, yet additional characters of the respective tribes preclude the inclusion of *Penichrus*. The enigmatic tribe Mymechixenini Jacquelin du Val, 1858 has clubbed antennae, an exposed pygidium, an arched tentorial bridge and an elongate apically enlarged accessory gland (Doyen *et al*. 1990, Matthews and Bouchard 2008). Scaphidemini Reitter, 1922 and Hypophlaeini Billberg, 1820 are characterized by a strongly sclerotized T-shaped spermatheca (Tschinkel and Doyen 1980, Matthews and Bouchard 2008). The tribe Diaperini latreille, 1802 is readily characterized by the highly modified globular 'check-valve' spermatheca (Tschinkel and Doyen 1980, Doyen 1984, Matthews and Bouchard 2008). Leiochrinini Lewis, 1894 typically have reduced coxites, defensive glands with constricted exit ducts connected by a tubular commissure, and a large spherical spermatheca (Doyen *et al*. 1990, Matthews and Bouchard 2008). Gnathidiini Gieben, 1921 lacks a spermatheca (Matthews and Bouchard 2008) and all known New World genera are in the subtribe Anopidiina Jeannel and Paulian, 1945 which are further characterized as having a 4-4-4 tarsal formula and lacking hind wings.

Penichrus exhibits a number of derived yet also ambiguous adult morphological characteristics and does not fit into the current concepts of any New World tenebrionid tribes. In the same manner, the lack of any convincing synapomorphies leaves us with little justification to expand any other tribal concepts further to accommodate *Penichrus*. As such, we hereby place *Penichrus* as *incertae sedis* within Tenebrioninae until such time as tribal concepts can be further understood and a placement can be well justified. It is worth noting that future studies on the tribal status of *Penichrus* should also consider the species *Diastolinus brevicollis* Fairmaire, 1892, which was similarly removed from the Blapstinina and speculatively placed as *incertae sedis* within Stenochiini by Ivie and Hart (2016: 454). The latter species, though unexamined by us, is externally similar to *Penichrus* (cotype specimen imaged in Ivie and Hart 2016: 454) and the shared historical and uncertain current tribal placements warrant internal morphological investigation.

The above discussion also highlights how the current subfamilial and tribal classifications seem to be inadequate to differentiate and diagnose monophyletic groups, at least in the New World. We are hopeful for and look forward to a new era of tenebrionid systematics building from molecular phylogenetic insights where subfamilies and tribes will be reevaluated and morphologically redefined.

Synopsis of North American Opatrini

The Opatrini of North America were very recently catalogued by Bousquet *et al.* (2018), which remains a reliable source for nomenclature and distributional information. However, multiple synonymies and subtribal concepts have been clarified since (Iwan and Kamiński 2016, Kamiński *et al*. 2019b, Lumen *et al*. 2019, 2020). A reliable and recent key exists for the genera of the West Indies (Ivie and Hart 2016), but the most recent generic key for mainland North America (Aalbu *et al*. 2002) is outdated due to new taxonomic studies and recent introductions (Aalbu e*t al*. 2009, Steiner and Swearingen 2015).

The following generic checklist and key summarize these recent changes as an update to Bousquet *et al*. (2018). For each genus, the most relevant recent work is given as reference for diagnoses, illustrations, and species keys. The biogeographic breaks, generic concepts, and species distributions of the West Indies Opatrini are thoroughly summarized in Ivie and Hart (2016), and here the genera known only from the islands and not the mainland are identified in the checklist as [WI] and are not included in the following key.

Subtribe **Opatrina** Brullé, 1832

Ephalus LeConte, 1862
=*Pseudephalus* Casey, 1924 (Synonymy: Lumen *et al*. 2020)
    2 species, Lumen *et al*. 2020
Gonocephalum Solier, 1834
    1 species [adventive], Steiner and Swearingen 2015
Opatroides Brullé, 1832
    1 species [adventive], Aalbu *et al*. 2009

Subtribe Blapstinina Mulsant and Rey, 1853

Aconobius Casey, 1895
    3 species, Casey 1914
Ammodonus Mulsant and Rey, 1859
    4 species, Fall 1912
Blapstinus Dejean, 1821
=*Mecysmus* Horn, 1870 (Synonymy: Lumen *et al.* 2020)
    78 species, Davis 1970, Lumen *et al.* 2020
Cenophorus Mulsant and Rey, 1859 [WI]
    1 species, Ivie and Hart 2016
Conibiosoma Casey, 1890
    1 species, Casey 1890
Conibius LeConte, 1851
    11 species, Casey 1895
Cybotus Casey, 1890
    1 species, Casey 1890
Diastolinus Mulsant and Rey, 1859 [WI]
    19 species, Hart and Ivie 2016
Hummelinckia Marcuzzi, 1954 [WI]
    1 species, Marcuzzi 1954
Nevisia Marcuzzi, 1985 [WI]
    1 species, Ivie and Hart 2016
Nocibiotes Casey, 1895
    4 species, Casey 1895
Notibius LeConte, 1851
    2 species, Casey 1890
Platylus Mulsant and Rey, 1859 [WI]
    1 species, Ivie and Hart 2016
Tonibiastes Casey, 1895
    1 species, Casey 1895
Tonibius Casey, 1895
    1 species, Casey 1895
Trichoton Hope, 1841
=*Bycrea* Pascoe, 1868 (Synonymy: Kamiński *et al.* 2019b)
    6 species, Kamiński *et al.* 2019b
Ulus Horn, 1870
    7 species, Lumen *et al.* 2019
Xerolinus Ivie and Hart, 2016
    31 species, Ivie and Hart 2016

Key to the Opatrini genera of mainland North America

Adapted in large part from Aalbu *et al.* (2002). The tribe can be recognized from all other tenebrionids by the combination of elongate base of protrochanter (see Fig. 17A, 18A-F in Iwan & Kamiński 2016), visible membranes between abdominal ventrites III–V, and presence of defensive glands.

1. Eyes whole or divided by epistomal canthus (see Fig. 15E–H in Iwan & Kamiński 2016) . . . . **2 (Opatrina)**
–. Eyes completely divided by expanding temples (see Fig. 15A–D in Iwan & Kamiński 2016) . . . . **4 (Blapstinina)**
2. Five apical antennomeres transverse; antennae short (reaching 0.5 of pronotal length) . . . ***Ephalus***
–. Apical antennomeres elongate; antenne elongate (reaching pronotal base) **3**
3. Eyes completely divided by epistomal canthus; elytra glabrous . . . . ***Opatroides***
–. Eyes not divided into ventral and dorsal parts; elytra densely covered with setae . . . ***Gonocephalum***
4. Mentum with visible median keel and exposed lateral wings; ovipositor with two visible coxites, gonostyli absent, bent baculi of paraprocts, sac-like spermatheca (see Lumen *et al.* 2020) . . . . ***Ammodonus***
–. Mentum flat, covering lateral wing; ovipositor with four coxite lobes distributed in single axis, gonostyli well developed, spermatheca elongate and coiled (see Lumen *et al.* 2020) **5**
5. Scutellar shield very broad and short, metathoracic wings absent; protarsus of male not dilated **6**
–. Scutellar shield triangular to subtriangular, metathoracic wings usually well developed; most with protarsus of male distinctly dilated **11**
6. Pronotum densely fimbriate laterally **7**
–. Pronotum not fimbriate laterally **8**
7. Protibiae broadly triangular, compressed; body stout, oblong-oval . . . . ***Notibius***
–. Protibiae narrow, non-fossorial; body narrow, parallel-sided . . . . ***Conibiosoma***
8. Elytral intervals distinctly elevated on disc **9**
–. Elytral intervals not elevated, elytra either smooth or with striae slightly impressed . . . . ***Conibius***
9. Elytral intervals acutely costiform (peninsular Baja California) . . . . ***Tonibiastes***
–. Elytral intervals more evenly rounded (widespread) **10**
10. Elytra, pronotum distinctly narrowed at base; basal width of pronotum narrower than basal width of elytra, widest anterior to middle; elytral intervals moderately convex with serial rows of aspirate punctures or tubercles on crest . . . . ***Nocibiotes***
–. Elytra subparallel, not narrowed at base; pronotum with lateral margins subparallel, basal width of pronotum equal to basal width of elytra; elytral intervals strongly convex, minutely punctured along crest . . . . ***Tonibius***
11. Protibiae simple, not acutely expanded or modified apically **12**
–. Protibiae modified, either bent or expanded apically, either acutely expanded apically or broadly triangularly expanded from base **14**
12. Elytral striae 7 and 8 merging anteriorly, not reaching elytral base; ventrite 1 bearing groove immediately bordering the metacoxa . . . . ***Xerolinus***

–. Elytral striae 7 and 8 not converging anteriorly, reaching elytral base; ventrite 1 without grooves behind metacoxae **13**

13. Surface and sides densely fimbriate; basal pronotal margin evenly arcuate; body in dorsal view narrow, convex . . . . ***Aconobius***

–. Not fimbriate laterally, dorsal surface more or less uniformly setose; basal pronotal margin usually noticeably bisinuate . . . . ***Blapstinus***

14. Body glabrous or very indistinctly setose; protibiae narrowly triangular from base to apex . . . ***Cybotus***

–. Body distinctly setose; protibiae strongly modified **15**

15. Protibiae with outer apical angle produced into triangular projection; body generally evenly setose; basal angles of fifth abdominal ventrite not depressed; apical part of tegmen base with membranous region (see Lumen *et al*. 2019a) . . . . ***Ulus***

–. Protibiae strongly modified apically, either distinctly bent or with apical margin greatly elongate and transverse; elytral vestiture generally noticeably patchy; basal angles of fifth abdominal ventrite glabrous and depressed (Kamiński *et al*. 2019b); apical part of tegmen base without membranous region . . . . ***Trichoton***

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