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Living a lie: The truth behind *Isohydnocera curtipennis* (Newman) and other historically confused species of *Phyllobaenus* Dejean, with the description of the new genus *Neohydnocera* (Coleoptera: Cleridae: Clerinae: Hydnocerini: Hydnocerina)

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Abstract. Taxonomic changes in the New World Hydnocerina (Coleoptera: Cleridae: Clerinae: Hydnocerini) at the species and genus level are presented. *Phyllobaenus suturalis* (Klug, 1842) and *Hydnocera limbata* Spinola, 1844 are designated junior synonyms of *P. pallipennis* (Say, 1825), **new synonymy**. *Phyllobaenus nigrescens* (Schaeffer, 1909) is designated a junior synonym of *P. verticalis* (Say, 1835), **new synonymy**. *Isohydnocera curtipennis* (Newman, 1840), *P. lineaticollis* Spinola, 1844, and *Clerus brachypterus* Klug, 1842, are re-established as junior synonyms of *P. verticalis* (Say, 1835), **status reinstated**, and *I. curtipennis* is accordingly reassigned to *Phyllobaenus* Dejean as *P. curtipennis*, **new combination**. *Cephaloclerus* Kuwert, 1893 is removed from synonymy under *Phyllobaenus* and re-elevated to genus rank, **status resurrected**. The genus *Isohydnocera* Chapin, 1917 is designated a junior synonym of *Phyllobaenus* Dejean, 1833, **new synonymy**, and *I. liebecki* Wolcott, 1928 is designated a junior synonym of *I. tabida* (LeConte, 1849), **new synonymy**. The **new genus** *Neohydnocera* is described to accommodate species formerly known as *Isohydnocera* Chapin. *Hydnocera longicollis* Zeigler, 1844 is removed from synonymy under *I. curtipennis*, **status resurrected**, and recognized as *Neohydnocera longicollis*, **new combination**. The following new combinations for species previously considered *Isohydnocera* are presented: *Neohydnocera aegra* (Newman, 1840), **new combination**, *Phyllobaenus albocinctus* (Horn, 1871), **new combination**, *N. brunnea* (Chapin, 1917), **new combination**, *N. californica* (Barr, 1966), **new combination**, *N. chiricahuana* (Knull, 1949), **new combination**, *P. cryptocerinus* (Gorham, 1883), **new combination**, *N. gerhardi* (Wolcott, 1910), **new combination**, *N. mima* (Wolcott, 1928), **new combination**, *N. nigrina* (Schaeffer, 1908), **new combination**, *N. ornata* (Wolcott, 1908), **new combination**, *N. pusilla* (Schaeffer, 1909), **new combination**, *P. schusteri* (LeConte, 1866), **new combination**, *N. tabida* (LeConte, 1849), **new combination**, and *P. tricondylae* (LeConte, 1849), **new combination**.

Key words. *Hydnocera longicollis*, *Isohydnocera curtipennis*, *Phyllobaenus pallipennis*, *Phyllobaenus suturalis*, *Phyllobaenus verticalis*.

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Introduction

Colorful, intraspecifically variable, speciose groups of insects are especially vulnerable to being over-described, the unfortunate but all too common case in which a species is described more than once. The more times a species has been described, the number of different authors publishing the descriptions and diagnoses and, subsequently, the number of different depositories of the type series specimens for each described species, all contribute to reducing the likelihood that one will discover such errors in “over-description.”

In the case of checkered beetles (Coleoptera: Cleridae), the taxonomically perplexing historical issue of over-description runs rampant. When Mawdsley (2006) revised *Omadius* Laporte (Clerinae), 78 of 142 described species were synonymized, Gerstmeier (2009) synonymized four of the seven described species of *Diplocladus* Fairmaire (Tillinae), and Solervicens (1986) synonymized 60 of 83 described species of *Eurymetopum* Blanchard

(Hydnocerini: Lemidiina)—all prior to describing many new species. Over-description not only makes generic revisions more laborious, but propagates misinterpretations of behavior, distribution and, in the present case, taxonomy at the genus level. The species of *Phyllobaenus* Dejean (formerly *Hydnocera*) are no exception.

Over twenty years ago Dr. Michael C. Thomas (pers. corr.) had presented me a series of questions about the Florida “Hydnocerinae” that have stalemated the publication of ‘the Checkered Beetles of Florida’ (Leavengood 2008) ever since: **1**) Because Bill Barr (pers. corr. via M. C. Thomas) questioned if he had ever truly seen the type of *Hydnocera curtipennis* Newman, was our present-day concept of *H. curtipennis* accurate, or was *H. curtipennis* something else entirely? **2**) With all the apparent variation in *Phyllobaenus verticalis* (Say) as well as other *verticalis*-like species (e.g., *Phyllobaenus nigrescens* (Schaeffer, 1909) or published synonyms of *P. verticalis*), how many *verticalis*-like species actually occur in Florida and the eastern United States? **3**) And spawned from the latter question, what exactly is *Phyllobaenus suturalis* (Klug)? Is it a valid species, and if so, is it in Florida? What followed was two decades of exploration into the confoundingly diverse and variable species of *Phyllobaenus* and allied genera as the type material and thousands of specimens of the aforementioned taxa were exhaustively reviewed.

Presented is a literature review of the earliest described members of *Hydnocera* from description date to present day, including vying historical opinions on the synonymy of species and genera (e.g., LeConte 1849; White 1849), explanations to such disagreements, and taxonomic solutions. The gross taxonomic changes herein include the reassignment of all species of *Isohydnocera* to the altogether new genus *Neohydnocera* (described herein) or the taxonomic melting pot of *Phyllobaenus*. Some trends in the morphology within *Phyllobaenus* are also discussed.

Leavengood (2014), Leavengood and Garner (2014), and Leavengood et al. (2022; *Tarsobaenus* Leavengood) represent the first revisionary steps for the New World Hydnocerini. The present work lays a foundation for the subsequent revision of the eleven species of the genus formerly known as *Isohydnocera*, in addition to correcting a century-long confusion between available names and contested synonyms of common, over-described species of *Phyllobaenus*. Moreover, the present work answers all of the aforementioned questions posited by Dr. Michael C. Thomas regarding Florida’s hydnocerine fauna.

Materials and Methods

Descriptions follow the standards of Leavengood (2020), Leavengood and Rifkind (2020), and Leavengood et al. (2022). Specimens and primary types (at least photographs of primary types in some cases) of all described species of *Isohydnocera* and those species of *Phyllobaenus* assessed herein were examined during the preparation of this work.

Specimens were photographed in two separate laboratories. At the University of Kentucky, specimens were photographed with a JVC KY-F75 3 CCD digital camera mounted on a Leica MZ16 ZP0 stereomicroscope. Source images were stacked using Archimed v. 5.2.2 or Automontage[®] and montaged images were edited using Adobe Photoshop CS5. At the USDA laboratory, specimens were photographed with a Nikon Digital Sight DS-Fi2 imaging system mounted on a Nikon SMZ-18 stereomicroscope. Photograph layers were stacked using Helicon Focus 6 (www.heliconsoft.com/heliconsoftproducts/helicon-focus) and edited using Adobe Photoshop Elements 12 Editor (<https://www.adobe.com/products/photoshop-elements.html>), which was also employed for subsequent editing of images from the University of Kentucky, and to assemble figure plates.

Robert Finn (National Identification Services, USDA-APHIS-PPQ-PEIP) provided photographs of the lectotype of *Hydnocera nigrescens* Schaeffer and specimen labels. Charles Farnum (Museum of Comparative Zoology, Harvard University; <https://mcz.harvard.edu/permissions-copyright>) provided photographs of the holotype of *Hydnocera longicollis* Ziegler and specimen labels. These images were cropped and color-corrected by the author.

The depositories and collections of the type specimens and imaged specimens referenced are presented with the following museum codens:

BMNH Natural History Museum, London, United Kingdom

FSCA Florida State Collection of Arthropods, Gainesville, Florida, USA

JECC J. Eric Cronin, private collection (now deposited in the FSCA)

- JMLC** John M. Leavengood, Jr., private collection, Brandon, Florida, USA
MCZ Museum of Comparative Zoology, Cambridge, Massachusetts, USA
NMNH National Museum of Natural History, Washington, D. C., USA
RAAC Robert A. Androw, private collection, Gibsonia, Pennsylvania, USA
ZMHB Museum für Naturkunde, Berlin, Germany

Literature Review

The founding species of *Hydnocera*. When Newman (1840) described *Hydnocera curtippennis*, there were only seven other species (four of which are currently valid) that would subsequently be assigned to the New World Hydnocerina: *Clerus humeralis* Say, 1823 (Fig. 9–10), *Clerus unifasciatus* Say, 1825, *Clerus pallipennis* Say, 1825 (Fig. 17–18), *Phyllobaenus axillaris* Dejean, 1833 (*nomen nudum*) [*nec* Van Dyke], *Phyllobaenus quadrimaculatus* Dejean, 1833 (later synonymized under *pallipennis*), *Trichodes verticalis* Say, 1835, and *Hydnocera serrata* Newman, 1838 (later synonymized under *pallipennis*). Along with *curtippennis*, Newman (1840) also described *H. rufipes* Newman and *H. aegra* Newman.

Klug (1842) described *Clerus brachypterus*, *C. suturalis* (Fig. 25), and mentioned *Clerus* (*Hydnocera*) *verticalis* and *H. curtippennis* among others currently known as *Phyllobaenus* and *Isohydnocera*. Klug also indicated the alliance of *C. pallipennis* and *C. unifasciatus* to the others by listing them as *Clerus* (*Hydnocera*).

Zeigler (1844) described the elongate species *H. longicollis* (Fig. 11–12) and placed it dubiously in *Hydnocera* (with a “?”). Spinola (1844) described *H. limbata* and *P. lineaticollis* which, as with most Spinola species, would both later be synonymized.

A web of synonymy (Table 1). Spinola (1844) considered *P. quadrimaculata* = *H. serrata*; *Phyllobaenus transversalis* Dejean, 1833 and its variation *aequinotialis* Dejean, 1833 = *H. limbata*; provided an illustration of *H. suturalis* to compare to *H. limbata*, and an illustration of *H. brachyptera* to compare to *P. lineaticollis*. White (1849), in agreement and following up on Spinola’s aforementioned similar species pairs (i.e., via figures), agreed that *Hydnocera quadrimaculata* = *H. serrata*; and designated *H. limbata* (along with *Phyllobaenus transversalis* and its variation *aequinotialis*; both *nomina nuda*) = *H. suturalis*; and *H. lineaticollis* = *H. brachyptera*.

LeConte (1849) considered *H. serrata* = *H. pallipennis*; *H. limbata* = *H. verticalis*; and *H. brachyptera* and *H. lineaticollis* = *H. curtippennis*, but LeConte (1866) changed his mind about *H. limbata*, from *H. limbata* = *H. verticalis* to *H. limbata* = *H. suturalis*. He also considered that (in addition to *H. brachyptera* and *H. lineaticollis*) *H. curtippennis* = *H. verticalis*. This is the “most correct” synonymy scheme in the 1800s literature. Chevrolat (1874) and Schenkling (1906) agreed with LeConte regarding the junior synonyms of *H. verticalis*, and Lohde (1900) and Schenkling (1910) agreed with all of LeConte’s synonymies.

Chapin (1917b) apparently ignored the taxonomic work of LeConte and those who subsequently accepted his synonymies. Chapin presented *H. curtippennis* as a valid species, made no mention of past literature or reinstated species status, and was the first to consider *H. longicollis* a junior synonym (= *H. curtippennis*). Wolcott (1947), Corporaal (1950), Papp (1960), and Barr (1975) accepted Chapin’s synonymy of *H. longicollis*, but otherwise adhered to LeConte’s (1866) synonymies. However, Barr later had doubts about the species coleopterists recognized as *Isohydnocera curtippennis* and *P. verticalis* (*in litt.*, M. C. Thomas, J. Rifkind).

The miscreation of *Isohydnocera*. Erichson (1845) was the first to recognize that a group of species within *Hydnocera* had dentate claws (Fig. 1, 5, 9, 13) and included *H. brachyptera* and *H. suturalis* among them. *Hydnocera brachyptera* was synonymized under *H. curtippennis* (LeConte, 1849), and then both *H. brachyptera* and *H. curtippennis* under *H. verticalis* (LeConte, 1866).

Having synonymized *H. longicollis* and *H. curtippennis*, Chapin (1917b) described *Isohydnocera*, which is distinguished from members of *Hydnocera* (mostly today’s *Phyllobaenus*) by “simple, at most slightly thickened” tarsal ungues (i.e., not dentate/bifid) (Fig. 11). However, both type specimens of *H. curtippennis* possess well-developed, toothed ungues (Fig. 13). Chapin’s description also addressed the “very elongate” body whereas the type specimens of *H. curtippennis* are no more elongate in body form than most specimens of *H. verticalis*, the species from which Chapin unofficially removed *H. curtippennis* from junior synonymy. It is here revealed that

Table 1. Changes in synonym designations over time, by publication. All species prior to 1917 were in the genus *Hydnocera*. The “~” indicates that when describing the first-mentioned species, the second-mentioned species was used as an illustration, indicating a strong similarity.

Species	Spinola 1844	White 1849	LeConte 1849	LeConte 1866	Chapin 1917	This work
<i>pallipennis</i>			<i>pallipennis</i> = <i>serrata</i> = <i>quadrimaculata</i>	<i>pallipennis</i> = <i>serrata</i> = <i>quadrimaculata</i>		<i>Phyllobaenus pallipennis</i> = <i>serrata</i> = <i>quadrimaculata</i> = <i>suturalis</i> = <i>limbata</i> = <i>transversalis</i> = <i>t. aequinoctialis</i>
<i>serrata</i>	<i>serrata</i> = <i>quadrimaculata</i>	<i>serrata</i> = <i>quadrimaculata</i>				
<i>limbata</i>	<i>limbata</i> = <i>transversalis</i> = <i>t. aequinoctialis</i>					
<i>suturalis</i>	<i>suturalis</i> ~ <i>limbata</i>	<i>suturalis</i> = <i>limbata</i> = <i>transversalis</i> = <i>t. aequinoctialis</i>		<i>suturalis</i> = <i>limbata</i> = <i>transversalis</i> = <i>t. aequinoctialis</i>		
<i>lineaticollis</i>	<i>lineaticollis</i> ~ <i>brachyptera</i>					
<i>brachyptera</i>		<i>brachyptera</i> = <i>lineaticollis</i>				
<i>verticalis</i>			<i>verticalis</i> = <i>limbata</i> = <i>transversalis</i> = <i>t. aequinoctialis</i>	<i>verticalis</i> = <i>curtipennis</i> = <i>brachyptera</i> = <i>lineaticollis</i>		<i>Phyllobaenus verticalis</i> = <i>curtipennis</i> = <i>brachyptera</i> = <i>lineaticollis</i> = <i>nigrescens</i>
<i>curtipennis</i>			<i>curtipennis</i> = <i>brachyptera</i> = <i>lineaticollis</i>		<i>Isohydnocera curtipennis</i> = <i>longicollis</i>	
<i>longicollis</i>						<i>Neohydnocera longicollis</i>

Chapin either did not examine the *H. curtipennis* syntypes (but rather additional *H. longicollis* specimens) or simply assumed by the original descriptions that they represented the same species (again, having only examined specimens of *H. longicollis*).

Hydnocera curtipennis was rightfully designated a junior synonym under *H. verticalis*. As such, *Isohydnocera* is hereby designated a junior synonym of *Phyllobaenus*. The species which Chapin assigned to *Isohydnocera*, including *I. curtipennis* (but intending *H. longicollis*), *I. tabida* (LeConte, 1849), *I. schusteri* (LeConte, 1866), *I. ornata* (Wolcott, 1908), *I. gerhardi* (Wolcott, 1910), *I. pusilla* (Schaeffer, 1909), *I. aegra* (Newman, 1840), *I. brunnea* Chapin, 1917, and *I. albocincta* (Horn, 1871), and all others which followed are hereby reassigned to the new genus *Neohydnocera* (described herein) or *Phyllobaenus*.

Hydnocera serrata is the type species of *Hydnocera*. But because this species was synonymized under *H. pal-lipennis*, the genus was invalidated. Wolcott (1944) most thoroughly accounted for the junior status of *Hydnocera* (a synonym, in part, of *Phyllobaenus*), the seniority of *Phyllobaenus*, and recognized the validity of Hydnocerinae over Phyllobaeninae, which pertained to species of what is now *Madoniella* Pic.

What this means for the New World genera of Hydnocerini. While “true” specimens of *H. curtipennis* fail to agree with the generic description for which it (as *H. longicollis*) was named the type species, several other species do possess simple tarsal ungues and a rather elongate body form. Most species with notably more elongate body forms (e.g., *I. longicollis*, *I. aegra*, *I. tabida*, *I. brunnea*, *I. pusilla*) possess simple tarsal ungues. These species form a natural group in the new genus *Neohydnocera* (described herein).

Another genus to consider is *Wolcottia*, also described by Chapin (1917b), distinguished by “simple or but slightly thickened” tarsal ungues. There are only two species of *Wolcottia* (*H. pedalis* LeConte, 1866 and *H. sobrina* Fall, 1906) which, evidently, exhibit a range in tarsal unguis expression (Fig. 15). Chapin recognized the length of the third antennomere to distinguish *Wolcottia* from *Isohydnocera*. Chapin also considered the shape of the pronotum, a character which is somewhat intraspecifically variable within and between sexes, to be distinct in *Wolcottia*, *Isohydnocera* and *Phyllobaenus*.

Across the New World Hydnocerina (*Isohydnocera*, *Phyllobaenus*, *Tarsobaenus*, and *Wolcottia*) there are two general elytral types: **1)** dorsally rather flat and somewhat tegminal (sometimes flexible), with the apices more independently produced and often apically tumid, never carinate (Fig. 2, 6, 10, 12, 14, 16); and **2)** convex, coleopterous and rigid, the apices converging into a rounded edge and never tumid, sometimes carinate (Fig. 4, 8). The molecular phylogeny of Gunter et al. (2013) identified two distinct clades of New World Hydnocerina. Not only was *Isohydnocera* recovered “within” *Phyllobaenus* s. l. (then including *Tarsobaenus*), but *Phyllobaenus* + *Isohydnocera* formed two distinct clades, one including all analyzed taxa with somewhat flattened elytra and the other including all taxa with convex elytra. Chapin (1922) recognized that *I. cryptocerina* (Gorham, 1883) and *I. albocincta*, both placed in *Isohydnocera* by his discretion and both having convex elytra, appeared to represent “a type quite apart from *I. curtipennis* (Newman) [actually referring to *H. longicollis*] and will ultimately be separated as a distinct genus.” Wolcott (1927) agreed with this notion and added *H. corticina* Gorham, 1883 (the morphology and identity of which are discussed in Leavengood et al. (2012)) to the list of candidate species. Presently, several new genera are eventually expected, with *Tarsobaenus* being the first to be published (Leavengood et al. 2022).

Phyllobaenus and *Isohydnocera* both historically include species with both types of elytra. However, species were described or assigned to both genera with both types of tarsal ungues (simple and bifid) as well. This should come as no surprise since these species are the product of occasional descriptions by general coleopterists in a time when attention to systematic treatment and synapomorphy was grossly outweighed by the popularity and allure of describing new species and placing them in groups of “similar looking” species out of convenience while either “assuming” corresponding morphology or lacking the appropriate microscopy to recognize it. Recent erroneous associations confusing the two genera were recognized and corrected in Leavengood (2024) and are further corrected herein.

The majority of species recognized as *Isohydnocera* share several synapomorphies—simple tarsal ungues, somewhat flattened elytra, the more elongate 3rd antennomere, and elongate bodies. Similar are the species of *Wolcottia*, which have somewhat flattened elytra, modified but not distinctly bifid tarsal ungues, and otherwise look quite similar to several species of *Phyllobaenus* (e.g., *P. pubescens* LeConte).

The impact of *Isohydnocera curtipennis* on the literature, and *Wolcottia sensu* Kolibáč (1998). In most cases, solving issues of synonymy in literature is simple. The most confusing or uncertain taxa (e.g., *H. suturalis*) are often ignored or referenced anecdotally, and synonymy simply merits name substitutions with the scribbled annotation of a pen in one’s dated reprints. Chapin’s (1917b) error resulted in calling specimens of *H. longicollis* by the name *I. curtipennis*, the types of which indicate synonymy with *P. verticalis*. However, the effects of this error were consistently applied in the literature. Prior to Chapin’s synonymy of *H. longicollis*, all references to *H. curtipennis* (= *H. verticalis*) and *H. longicollis* were correct. After 1917, all (or nearly all) references to *I. curtipennis* were actually *H. longicollis* and all references to *H. verticalis* were presumably correct.

The disappointment arises in that one of the most common and easily recognized clerids of the eastern United States has been consistently misidentified for over 100 years in checklists (Wolcott 1947; Corporaal 1950; Papp 1960; Barr 1975; Gosling 1980; Peck and Thomas 1998) and books (Knull 1951; Dillon and Dillon 1972; Downie and Arnett 1996; Opitz 2002; Majka 2006; Evans 2014), and resulted in the common use of a genus which is herein rendered invalid, yet passed unrecognized from its very creation. It is especially shocking that Wolcott, who began publishing on Cleridae eight years before Chapin's 1917 synonymization, did not notice this error. However, Wolcott had seen specimens of *P. verticalis* and *H. longicollis*, but never *curtipennis* (according to his publications). And so began the era (1917–2024) of the misrepresented species *Isohydnocera curtipennis*.

Kolibáč (1998) examined *H. longicollis* and not “true” *H. curtipennis*. This had no effect on his analysis of the tribes of Hydnocerinae, but renders his synonymy of *Isohydnocera* under *Wolcottia* incorrect. This is because whereas Kolibáč (1998) considered *Isohydnocera* a junior synonym of *Wolcottia*, he also considered *Wolcottia* (+ *Isohydnocera*) and *Phyllobaenus* to be two distinct genera. So Kolibáč's (1998) synonymy is herein considered invalid, restoring *Isohydnocera*, **status resurrected**, from *Wolcottia* before subsequently synonymizing *Isohydnocera* under *Phyllobaenus*, **new synonymy**.

Wheeler and Stocks (2009) were the only authors to acknowledge Kolibáč's (1998) change. Opitz (2010) included “*Isohydnocera curtipennis*” in his subfamily treatise. However, the specimen examined was *H. longicollis*, which properly reflected the characteristics of the intended *Isohydnocera*. Opitz also analyzed *P. unifasciatus* (Say) and *W. pedalis* (LeConte). These three species reflect the three general character suites of the New World Hydnocerina and, thus, his subfamily-level analysis was not negatively affected. The key to the hydnocerine genera in Opitz (2002) remains correct for recognizing the species group with elongate bodies, simple claws, and somewhat flattened elytra. But the name *Isohydnocera* should be replaced in the literature with “*Phyllobaenus* (in part),” as should be the case for any key to the genera of Hydnocerinae published between 1917 and 2024, even if only for the confusion between *H. longicollis* and *I. curtipennis*.

Taxonomic Changes

Because of the complex combination of new synonymies, reinstated statuses and species, and generic designations, taxa are presented in the order of the nomenclatural acts performed.

Wolcottia Chapin

Discussion. Kolibáč (1998) synonymized *Isohydnocera* under *Wolcottia*. Most literature ignored this change and continued to refer to *Isohydnocera curtipennis* when, in fact, *Wolcottia curtipennis* was the correct status. I hereby resurrect *Isohydnocera*, **status resurrected**, from synonymy under *Wolcottia*. This change reduces the genus *Wolcottia* to two described species.

Phyllobaenus pallipennis (Say, 1825) (Fig. 17–26)

Clerus pallipennis Say, 1825: LeConte 1859.

Clerus (Hydnocera) pallipennis: Klug 1842.

Hydnocera pallipennis: LeConte 1849, 1866; Gorham 1877; Chittenden 1890; Hamilton 1895; Wickham 1895; Lohde 1900; Drury 1902; Felt 1906; Schenkling 1906; Wolcott 1909; Schenkling 1910; Wolcott 1910; Wickham 1911; Pierce et al. 1912; Wickham and Wolcott 1912; Chapin 1917a, b.

Phyllobaenus pallipennis: Wolcott 1947; Chapin 1948; Corporaal 1950; Knull 1951; Papp 1960; Ekis and Gupta 1971; Dillon and Dillon 1972; Ekis 1975; Barr 1975; Gosling 1980; Downie and Arnett 1996; Peck and Thomas 1998; Opitz 2002; Majka 2006; Leavengood 2008; Leavengood and Garner 2014.

= *Clerus suturalis* Klug, 1842 (Fig. 25): White 1849. (**new synonymy**)

Hydnocera suturalis: Spinola 1844, LeConte 1849; White 1849; LeConte 1866; Gorham 1882*, 1886* (wrong species); Schenkling 1910; Wickham and Wolcott 1912; Wolcott 1927.

Phyllobaenus suturalis: Wolcott 1947; Corporaal 1950; Papp 1960; Barr 1975; Ekis 1975; Peck and Thomas 1998; Leavengood 2008.

= *Hydnocera limbata* Spinola, 1844: White 1849. (**new synonymy**)

- = *Phyllobaenus quadrimaculatus* Dejean, 1833: White 1849.
- = *Hydnocera serrata* Newman, 1838: Newman 1840; Klug 1842; Spinola 1844; White 1849; Leavengood and Garner 2014.
- = *Phyllobaenus transversalis* Dejean, 1833: White 1849. (*nomen nudum*)
- = *Phyllobaenus transversalis* var. *aequinocialis* Dejean, 1833: White 1849. (*nomen nudum*)

Comments. Gorham (1882, 1886) referred to three specimens of a variation of *H. marginata* Gorham which he thought might be *H. suturalis*. I have seen two out of three of these specimens referenced in 1882 (those from San Gerónimo and Boquete) and two from Volcan de Chiriquí referenced in 1886. Lohde (1900), Schenkling (1910), Wolcott (1947), Papp (1960), and Barr (1975) also associated these specimens (or at least the reference) with *P. suturalis*. They are neither *P. suturalis* nor a variation of *P. marginata*. They are most similar to *H. testacea* Gorham, which includes radical variation of elytral form and color pattern in the type series (possibly more than one species) (Leavengood and Garner 2014). However, Gorham's aforementioned specimens have color patterns which do not appear to fall within the range of *H. testacea*. Wickham and Wolcott (1912) wrote "it is probable [that their Tampa, Florida specimen] will prove distinct" from the Central American specimens. However, their specimen was, in fact, distinct from the Central American specimens in that it was *P. pallipennis*. Wolcott (1927) later [correctly] considered that his Florida species truly was *H. suturalis*.

Notes on types. Ekis (1975) designated lectotypes for *H. limbata* and *P. aequinocialis*. Leavengood and Garner (2014) designated the lectotype for *H. serrata*.

Phyllobaenus verticalis (Say, 1835) (Fig. 27–40)

Trichodes verticalis Say, 1835: LeConte 1859.

Clerus (Hydnocera) verticalis: Klug 1842.

Hydnocera verticalis: LeConte 1849, 1866; Osten-Sacken 1861; Chevrolat 1874; Drury 1879; Chittenden 1890; Hamilton 1895; Drury 1902; Felt 1906; Schenkling 1906; Wolcott 1909; Schenkling 1910; Wolcott 1910; Wickham 1911; Wickham and Wolcott 1912; Chapin 1917a; Bøving and Champlain 1920; Wolcott 1927; Knull 1930; Bøving and Craighead 1931; Knull 1932; Sabrosky 1934; Beal and Massey 1945.

Phyllobaenus verticalis: Wolcott 1947; Corporaal 1950; Craighead 1950; Knull 1951; Papp 1960; Dillon and Dillon 1972; Barr 1975; Ekis 1975; Gosling 1980; Downie and Arnett 1996; Peck and Thomas 1998; Mawdsley 1999; Eliason and Potter 2000; Leavengood 2008.

= *Hydnocera nigrescens* Schaeffer, 1909. (**new synonymy**)

= *Phyllobaenus lineaticollis* Spinola, 1844: Ekis 1975. (**status reinstated**)

= *Clerus brachypterus* Klug, 1842: Spinola 1844. (**status reinstated**)

Hydnocera brachyptera: White 1849; Wolcott 1927.

= *Phyllobaenus lineaticollis* Spinola, 1844: White 1849.

= *Hydnocera curtipennis* Newman, 1840: Klug 1842; LeConte 1849; White 1849; Drury 1879; Chapin 1917b. (**status reinstated**)

Isohydnocera curtipennis: Leavengood and Garner 2014.

Comments. The status of *I. curtipennis* as a junior synonym results in the subsequent junior synonymy of *Isohydnocera* (= *Phyllobaenus*), **new synonymy**. Despite this synonymy, historic records and identifications of *I. curtipennis* should not be considered *P. verticalis* (see Conclusions section).

Notes on types. Leavengood and Garner (2014) designated and photographed the type series of *H. curtipennis* (type species of *Isohydnocera*) (Fig. 27). Ekis (1975) designated the lectotype for *P. lineaticollis*.

Phyllobaenus Dejean

= *Isohydnocera* Newman, **new synonymy**

Discussion. With the junior synonymy of *Isohydnocera curtipennis* under *Phyllobaenus verticalis*, *Isohydnocera* is rendered invalid. The inclusion of such species as *Phyllobaenus albocinctus* (Horn, 1871), *P. bituberculatus* (Chevrolat, 1874), *P. corticinus* (Gorham, 1883), *P. cryptocerinus* (Gorham, 1883), *P. cylindricollis* (Gorham, 1886), and many other species with a simple (or nearly so) tarsal unguis and coleopterous elytra, lacking apical tumescence or dehiscence, illustrates the long-overlooked need for a reassessment of the generic limits of the genus. Kolibáč (1998) synonymized *Cephaloclerus* Kuwert under *Phyllobaenus*, which Leavengood et al. (2022) has come to

recognize as a polyphyletic genus of putative genus-groups characterized by combinations of characteristics of the tarsal claw, elytral form, basal antennomeres, plical excavation, and modifications of the apical abdominal segments of males. Moreover, it appears that *Cephaloclerus* may, as well, contain more than one genus within. As such, herein the African genus *Cephaloclerus* is removed from synonymy and re-elevated to genus rank, **status resurrected**. Because no new research on *Cephaloclerus* has emerged since 1998, and subsequent references to the species diversity of *Phyllobaenus* have only been in the context of New World species, this has no impact on cataloging species.

Tentative redefinition of the genus. Tarsal unguis with well-developed bifidity (Fig. 1, 5, 9, 13) and elytra plank-like, somewhat flattened, with or without apical tumescence, dehiscent at about apical third (Fig. 2, 6, 10); or tarsal unguis simple (Fig. 3), or nearly so (Fig. 7), and coleopterous elytra, not flattened, lacking apical tumescence or dehiscence (Fig. 4, 8).

***Neohydnocera* Leavengood, new genus**

Type species. *Hydnocera longicollis* Ziegler, 1844, **here designated**.

Description. Hydnocerina. Antennae with ten antennomeres, terminating in a single-antennomere club; antennomere III elongate, about 2× as long as wide (antennomere III about as long as wide in *Wolcottia*); antennomeres VI and VIII smaller than antennomeres V, VII, and IX; pronotum weakly laterally produced (more so than in *Wolcottia*, notably less so than in *Phyllobaenus*); mesepisternum and metepisternum often vested in dense silvery setae; metasternum well-developed, with ventral surface semi-flattened, flattened surface with shorter setae, often with much longer setae at the ventro-lateral margins (in males of most species); elytra somewhat flattened, plank-like, often with apical tumescence, dehiscent at about apical third or fourth (as in *Wolcottia*, *Tarsobaenus*, and some *Phyllobaenus s. l.*) and bearing a concave plical foliation near the point of dehiscence, elytral length covering 50% (e.g., *N. pusilla*) to over 80% (e.g., *N. tabida*) of abdomen when extended; posterolateral and apical margins of elytra with small serrulations; body more elongate (than *Wolcottia* or *Phyllobaenus*) with legs simple, never with notably thickened femora (as in many *Phyllobaenus*); femora thicker than tibiae, with some femoral setae as long as greatest width of femur, tibial setae up to 3–4× greatest width of tibia; trochanters triangular; tarsal unguis simple or nearly so (tarsal claw with feebly developed basal denticle in *Wolcottia*, bifid with deeply acute internal angle in *Tarsobaenus*); abdominal ventrite V of males typically with a small, notched emargination to a broad, gradual, shallow emargination (simple to strongly modified in *Phyllobaenus*), abdominal ventrite VI of males divided and reduced to a pair of lateral, clasper-like appendages (simple to strongly modified in *Phyllobaenus*); abdominal tergite VI normally unmodified. Males (typically *N. longicollis* and *N. tabida*) often with face yellow, extending from clypeus variably upward as far as the top margin of the eyes, often complemented by denser silvery setae where eyes meet antennal insertions and variably extending inward and upward.

Distribution. Canada to Mexico. This distribution may be expanded with subsequent revision and descriptions of new species of *Neohydnocera*. There are several undescribed Neotropical species.

Remarks. With the exception of *Isohydnocera albocincta* (Horn, 1871), *I. cryptocerina* (Gorham, 1883), *I. schusteri* (LeConte, 1866), and *I. tricondylae* (LeConte, 1849), all species formerly considered in the genus *Isohydnocera* are now designated in *Neohydnocera*. Barr (2018) recognized *Phyllobaenus schusteri* (LeConte, 1866) without formally addressing the change in designation from *Isohydnocera*. The four aforementioned species of *Isohydnocera* share characteristics of the tarsal claws and elytral form consistent with *Phyllobaenus* as it is tentatively redefined above. The genus *Neohydnocera* includes eleven described species.

New combinations resulting from the junior synonymy of *Isohydnocera* and reassignments to *Neohydnocera* and *Phyllobaenus*

Neohydnocera aegra (Newman, 1840), **new combination**

Neohydnocera brunnea (Chapin, 1917), **new combination**

Neohydnocera californica (Barr, 1966), **new combination**

Neohydnocera chiricahuana (Knull, 1949), **new combination**

Neohydnocera gerhardi (Wolcott, 1910), **new combination**

Neohydrocera longicollis (Ziegler, 1844), **new combination**
Neohydrocera mima (Wolcott, 1928), **new combination**
Neohydrocera nigrina (Schaeffer, 1908), **new combination**
Neohydrocera ornata (Wolcott, 1908), **new combination**
Neohydrocera pusilla (Schaeffer, 1909), **new combination**
Neohydrocera tabida (LeConte, 1849), **new combination**
Phyllobaenus albocinctus (Horn, 1871), **new combination**
Phyllobaenus cryptocerinus (Gorham, 1883), **new combination**
Phyllobaenus schusteri (LeConte, 1866), **new combination**
Phyllobaenus tricondylae (LeConte, 1849), **new combination**

***Neohydrocera longicollis* (Ziegler, 1844), new combination, status resurrected (Fig. 41–53)**

***Hydrocera longicollis* Ziegler, 1844:** LeConte 1849, 1866; Chittenden 1890; Baker 1895; Hamilton 1895; Wickham 1895; Lohde 1900; Drury 1902; Wickham 1902; Schenkling 1906; Wolcott 1909; Schenkling 1910; Wolcott 1910; Wickham and Wolcott 1912; Chapin 1917a, 1917b; Sabrosky 1934.

***Isohydrocera curtipennis* Chapin, 1917b:** Chapin 1922; Wolcott 1927; Sabrosky 1934; Wolcott 1947; Corporaal 1950; Knull 1951; Papp 1960; Gosling 1980; Downie and Arnett 1996; Peck and Thomas 1998; Mawdsley 1999, 2002; Opitz 2002; Majka 2006; Leavengood 2008.

***Wolcottia curtipennis*:** Wheeler and Stocks 2009.

Comments. The description of *Isohydrocera* was based on *H. longicollis*, although Chapin (1917b) used the name *H. curtipennis*. *Hydrocera longicollis* is resurrected from synonymy under *Isohydrocera curtipennis* and designated the type species of *Neohydrocera*.

Notes on types. The types of *H. longicollis* (MCZ; Fig. 41–45) and *H. curtipennis* (Fig. 27; BMNH) were examined.

***Neohydrocera tabida* (LeConte, 1849), new combination**

= *Isohydrocera liebecki* Wolcott, 1928. (**new synonymy**)

Comments. Wolcott (1928) refers to the diagnostic characteristics of *liebecki*, e.g., a subtle degree of difference in elytral elongation, serrulation and dehiscence. Examination of the type of *I. liebecki* (FMNH) and comparison of the original description yield the conclusion that *I. liebecki* is conspecific with *I. tabida*, which expresses considerable variation for these “diagnostic” traits. Whereas most specimens of *N. tabida* have the body uniformly black to piceous (but pale legs), many misidentifications have been found based on confusion with dark forms of *N. longicollis* and maculate forms of *N. tabida*. Dorshorst (*in litt.*) contended that there is an additional, undescribed species among specimens he considered *I. tabida*. I agree, but liken the putative new species more to *N. longicollis*. This will be clarified in a revision of the genus.

Conclusions

The impact of *Isohydrocera curtipennis*, *Neohydrocera longicollis* and *Phyllobaenus verticalis* on determined specimens in museums in collections. Because the name *Isohydrocera curtipennis* was so consistently used in determinations of *Hydrocera longicollis* (now *Neohydrocera longicollis*), it can be assumed that any specimens identified as *Isohydrocera curtipennis* (but not necessarily *Hydrocera curtipennis*) should now be considered *Neohydrocera longicollis*. This applies even to identifications of *I. curtipennis* made by the author (Leavengood). Historic determinations of *Hydrocera curtipennis* specimens, particularly those before 1917, should be considered *Phyllobaenus verticalis*. Specimens of *P. verticalis* should remain as such. The exceptions to the aforementioned cases would be in the event of outright misidentifications, which would not be rare between these two species. When in doubt, the simple tarsal claw will distinguish *N. longicollis* from the bifid tarsal claw of *P. verticalis*.

Future directions. It is the author’s intention to continue with revisions of the genera *Neohydrocera* and *Wolcottia*. Undescribed species of *Neohydrocera* as far south as Peru and Bolivia have been discovered in museum loans. Potentially new species of *Wolcottia* have been found in southern Mexico, the two described Nearctic species lack

sufficient species delimitation, and some species of South American *Phyllobaenus* seem to share affinities with *Wolcottia*.

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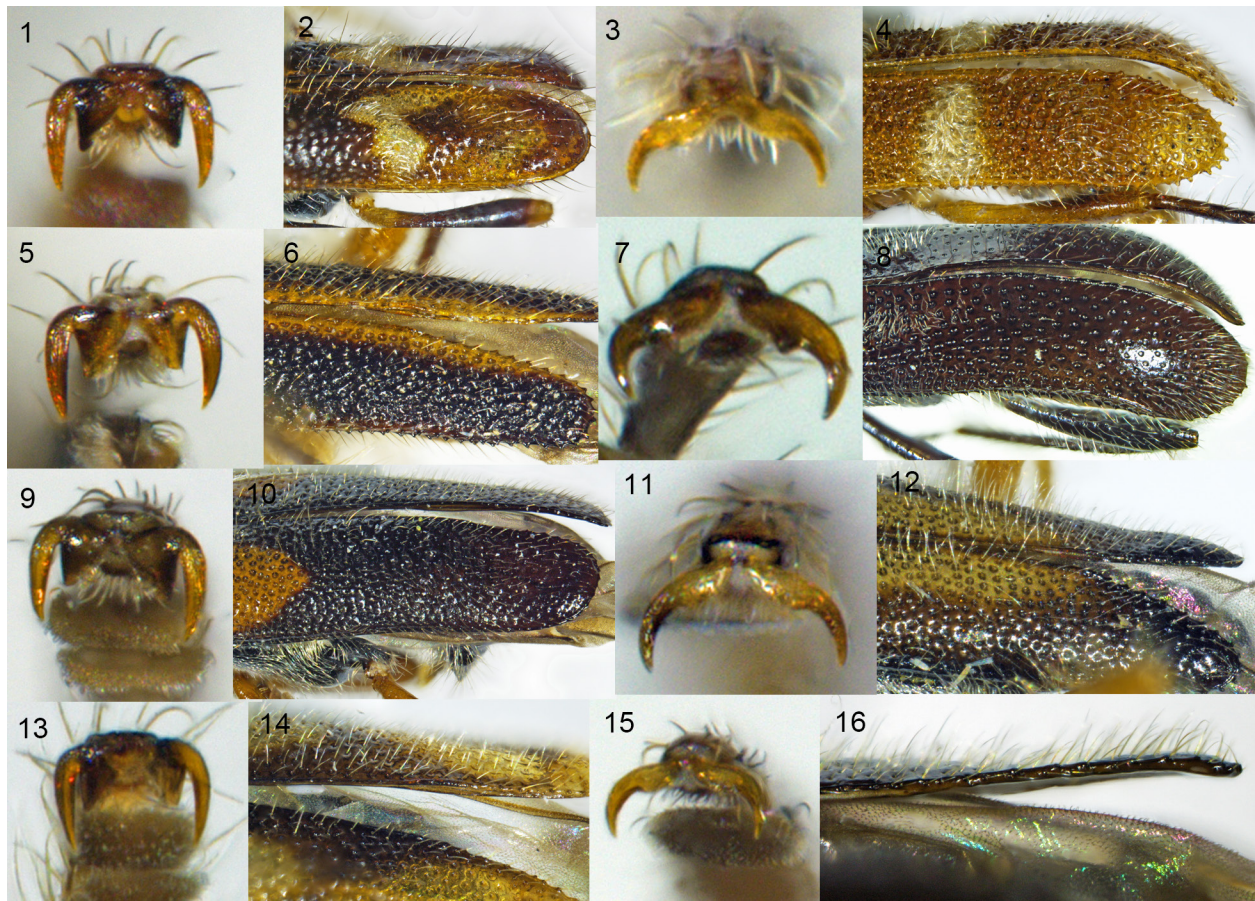
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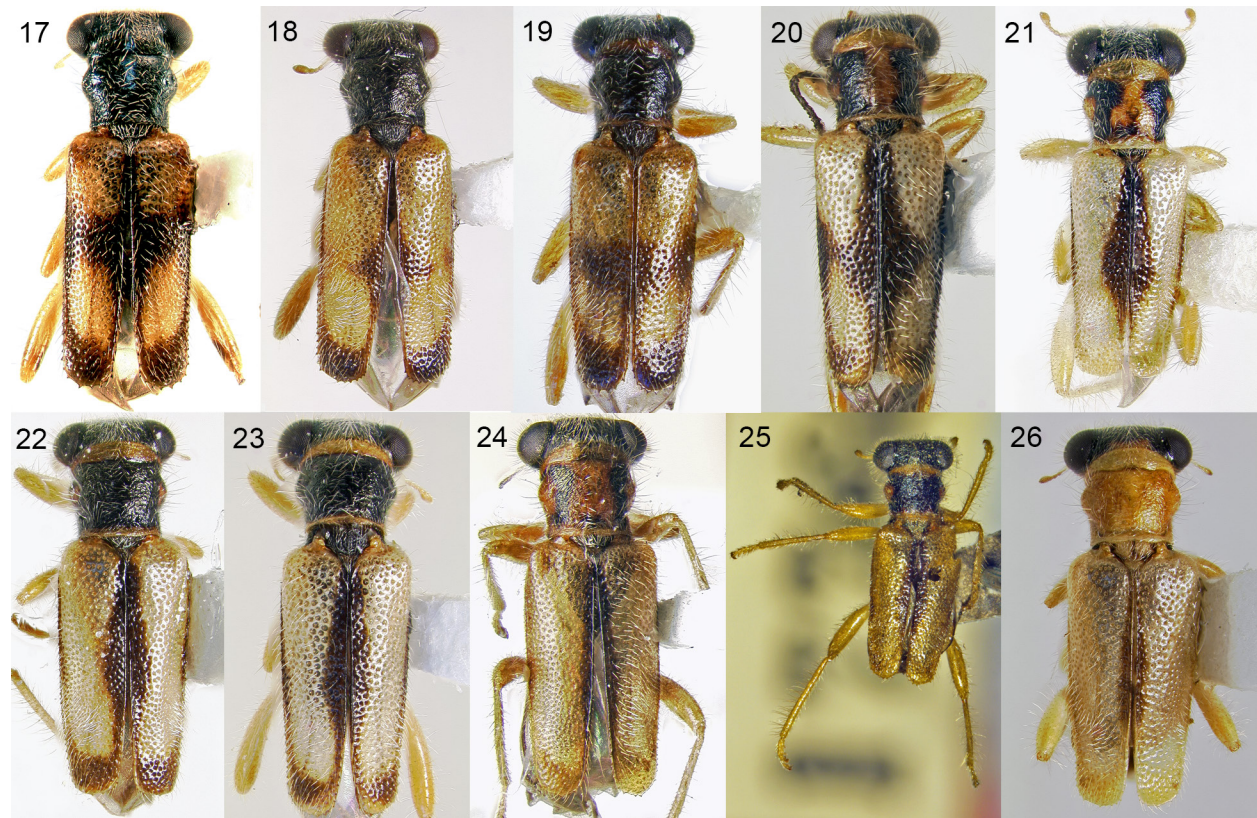
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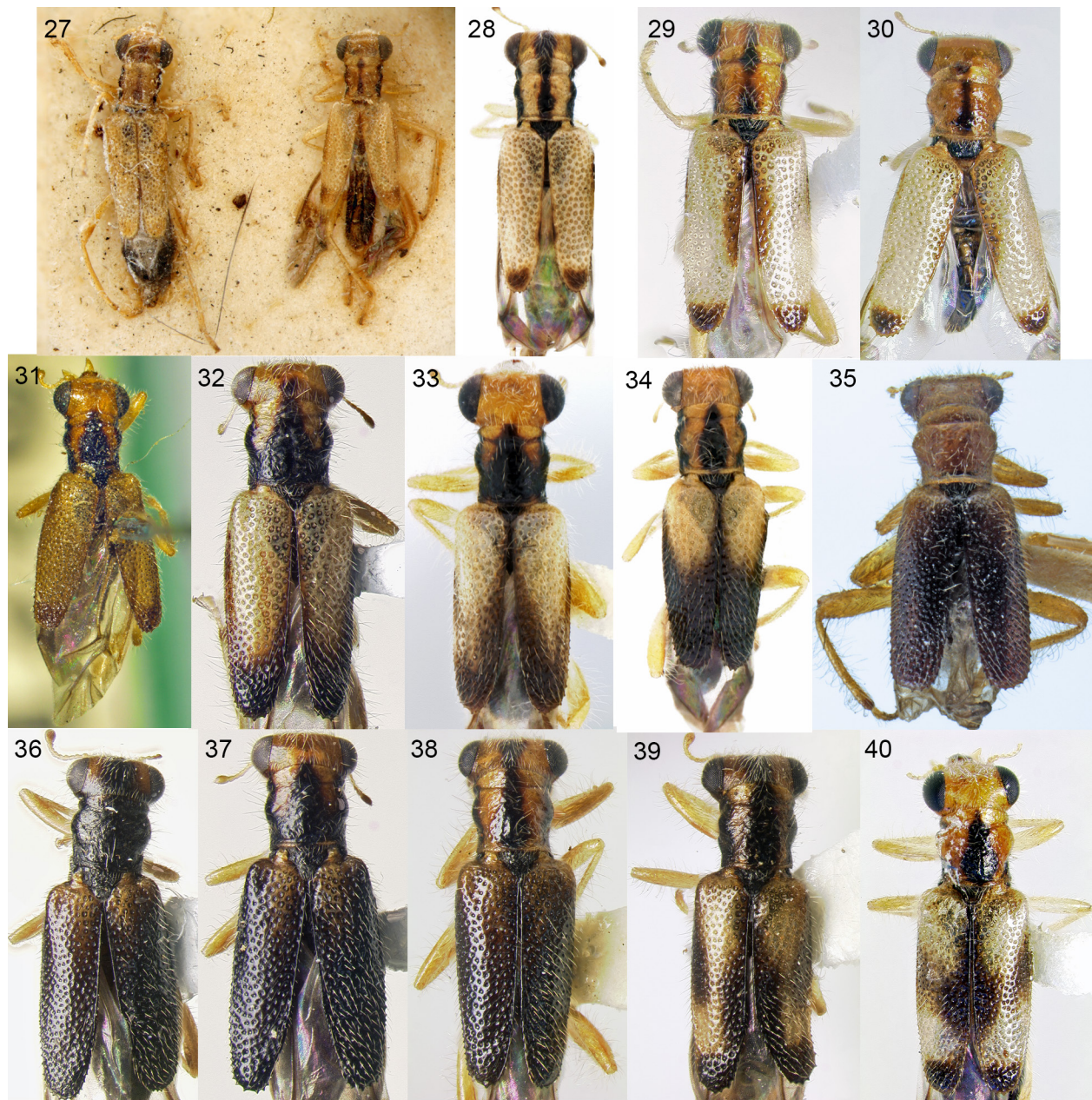
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Figures 1-16. Tarsal claws and elytra of Hydnocerina. 1-2) *Phyllobaenus aeneicollis* (JMLC). 3-4) *Phyllobaenus albocinctus* (JMLC). 5-6) *Phyllobaenus antillae* (JMLC). 7-8) *Phyllobaenus bituberculatus* (JMLC). 9-10) *Phyllobaenus humeralis* (JMLC). 11-12) *Neohydnocera longicollis* (JMLC). 13-14) *Phyllobaenus verticalis* (JMLC). 15-16) *Wolcottia pedalis* (JMLC)



Figures 17–26. *Phyllobaenus pallipennis* (Say). 17) Florida (FSCA). 18) Illinois (FSCA). 19) Maryland (FSCA). 20–22) Florida (FSCA). 23) Florida (JECC). 24) Georgia (RAAC). 25) Holotype of *Clerus suturalis* Klug (ZMHB). 26) Florida (FSCA).



Figures 27–40. *Phyllobaenus verticalis* (Say). 27) *Hydnocera curtipennis* Newman, Lectotype [left] and Paralectotype [right] (BMNH). 28) Florida (JMLC). 29–30) Oklahoma (FSCA). 31) *Clerus brachypterus* Klug, type (ZMHB). 32) Ohio (RAAC). 33–34) Florida (FSCA). 35) *Hydnocera nigrescens* Schaeffer, Lectotype (NMNH). 36) West Virginia (RAAC). 37) Texas (RAAC). 38–39) Florida (FSCA). 40) Missouri (FSCA).



Figures 41–53. *Neohydrocera longicollis* (Ziegler). **41–45** *Hydrocera longicollis* Ziegler, Holotype, Museum of Comparative Zoology, Harvard University; © President and Fellows of Harvard College. **46** Texas (JMLC). **47** Florida (UCFC). **48** Kentucky (JMLC). **49** Florida (JMLC). **50** Missouri (JMLC). **51–52** Kentucky (JMLC). **53** Florida (JMLC).

