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What we do and don’t know about New World pinhole borers (Coleoptera, Curculionidae, Platypodinae)

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Data for this paper include label information from over 6,600 specimen records for Platypodinae (Coleoptera, Curculionidae) from the Americas and come from two centuries of primary literature on Platypodinae of the world. The New World Platypodinae (pinhole borers) comprise 300 described and 225 undescribed species distributed among 15 genera in three tribes: Schedlariini, with one species; Tesserocerini, with 102 species distributed among three genera, and Platypodini, with 422 species in 11 genera. The material available for study has greatly increased in recent years, as Malaise traps, flight intercept traps, and light traps have become more widely employed in the Neotropics. However, species in this region are difficult to identify because there have been no genus-level revisions and there are no keys to species. We briefly summarize the combinations of characters used to identify tribes, genera and species; while tribes are easily distinguished, as are genera in the Tesserocerini, the boundaries separating Platypodini genera are in many cases vaguely defined and unclear.

We review the natural history of American platypodines: they are life-long monogamous wood-boring ambrosia beetles nearly all of which are found in tropical and subtropical forests, use long-distance attractant pheromones, have complex courtship behaviour, employ stridulation in (at least) courtship, and construct extensive tunnel systems that may produce offspring over several years. Larvae feed exclusively on the ambrosia fungi that grow on the tunnel walls. We discuss what little is known about social behaviour in the group. We briefly review the relationships between Platypodinae and their symbiotic ambrosia fungi: as far as is known, primary ambrosia fungi are all species of *Raffaelea* (Arx & Hennebert). Where known, fungal spores are transported in special small cavities in the exoskeleton (mycangia); these are usually pairs or clusters of tiny pores on the pronotum of females that in some species are also found on males. Mycangia have not been identified in several New World genera. Platypodinae are generally known to be host plant generalists, but host relations for New World species are poorly known: < 10% of described species have more than five host records, and 2/3 have no genus-level host records at all. Most Neotropical platypodines are restricted to lower elevations, with a few species clearly restricted to higher elevations, suggesting that the pinhole borer-ambrosia fungus symbiosis is sensitive to relatively small differences in temperatures. A wide range of natural enemies have been collected from Platypodinae in other regions, but nearly nothing is known about those of American species. Pinhole borers play an important role in decomposition of wood in temperate and tropical forests. Generally, the dark-stained tunnels from platypodine activity reduce the value of tropical timbers for some uses. Few Neotropical species are considered economically important for other reasons. We discuss the impacts that *Megaplatypus mutatus* (Chapuis, 1865), *Euplatypus parallelus* (Fabricius, 1801), and *E. segnis* (Chapuis, 1865) have on plantation forestry and agriculture. Our review concludes with a short summary of the data gaps in our knowledge of the biodiversity and natural history of Nearctic and Neotropical Platypodinae.

Spanish abstract. Información usada en este artículo incluye datos de rótulos de más de 6,600 ejemplares de Platypodinae de los Américas y recopilación de dos siglos de literatura primaria sobre Platypodinae del mundo. Los Platypodinae del mundo nuevo (barrenadores agujeriteros) abarcan 300 especies descritas y 225 especies inéditas distribuidas entre 15 géneros en tres tribus: los Schedlariini, con una especie; los Tesserocerini, con 102 especies en tres géneros, y los Platypodini, con 422 especies en 11 géneros. Material disponible para estudio se ha aumentado mucho en años recientes, ya que trampas “Malaise”, trampas de intercepción de vuelo, y trampas de luz se han empleadas más ampliamente en la región neotropical. Aún así, es difícil identificar especies en esta región porque no se han publicado claves a especies de ningún género. Resumimos las combinaciones de caracteres usados para identificar tribus, géneros y especies; aunque se distinguen tribus fácilmente, tal como géneros en los Tesserocerini, los límites separando géneros en los Platypodini en muchos casos imprecisos y faltan claridad. Revisamos la historia natural de los platipodinos americanos: son escarabajos de hábito ambrosial, barrenadoes de madera, de monogamia de toda la vida, los cuales se encuentran en bosques tropicales y subtropicales. Utilizan feromonas atrayentes de larga distancia, tienen comportamiento de apareamiento complejo, utilizan la estridulación (por lo menos) en el apareamiento, y construyen sistemas extensos de túneles que pueden producir progenie durante un lapso de varios años. Las larvas se alimentan exclusivamente de los hongos ambrosiales que crecen en las paredes de los túneles. Discutimos lo poco que se conoce de comportamiento social en el grupo. Tratamos brevemente las relaciones entre los Platypodinae y sus hongos ambrosiales simbióticos; en cuanto se sabe, las especies ambrosiales primarias son todas especies de *Raffaelea*. Cuando conocido, las esporas de hongos se transportan en cavidades pequeñas especiales en el exoesqueleto (micángios); generalmente consisten en parejas o agrupaciones de poros pequeños en el pronoto de hembras, en algunas especies en machos también. No se han identificado micángios en varios géneros americanos. Por lo general los Platypodinae son generalistas con respecto a sus plantas hospedantes, pero las relaciones con hospedantes para las especies americanas son poco conocidas: <10% de especies descritas tienen más de 5 registros de hospedantes, y 2/3 carecen completamente de registros de hospedantes al nivel genérico. La mayoría de los platipodinos neotropicales se limitan a altitudes menores, con unas cuantas limitadas a elevaciones mayores, sugiriendo que la simbiosis barrenador agujeritero-hongo ambrosial es sensible a diferencias relativamente pequeñas en temperatura. Un rango amplio de enemigos naturales se ha colectado en otras regiones, pero la información es muy escasa sobres especies americanas. Los barrenadores agujeriteros juegan un papels importante en la descomposición de madera en bosques templadas y tropicales. En general los túneles con mancha oscura de las actividades de platipodinos reducen el valor de maderas tropicales para ciertos usos. Discutimos los impactos de *Megaplatypus mutatus*. *Euplatypus parallelus* y de *E. segnis* en plantaciones forestales y agrícolas. Concluimos nuestra revisión con un resumen corto de los vacíos en nuestro conocimiento de la biodiversidad e historia natural de los Platypodinae neárcticos y neotropicales.

Key words: Coleoptera, Platypodinae, pinhole borers, saproxylic, biodiversity, Neotropics.

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Introduction

Platypodinae (Coleoptera, Curculionidae), commonly referred to as pinhole borers, are a clade of highly derived cylindrical weevils that spend nearly their entire lives deep in wood. Platypodinae are ambrosia beetles—beetles that cultivate symbiotic fungi—and their biology closely resembles that of ambrosia beetles in the weevil subfamily Scolytinae.

Worldwide, over 1,400 species of platypodines are known (Wood 1993, Jordal 2014), making up over 1/3 of all species of ambrosia beetles (Mayers et al. 2021). Nearly all species are found in the tropical regions of the Americas, sub-Saharan Africa, Asia south of the Himalayas and the archipelagos and landmasses of Oceania. There are a very small number of truly temperate species in the United States, Europe, Northeastern Asia, and Australasia. There are no species restricted to the austral temperate regions of South America.

A total of 300 Nearctic and Neotropical species were described between 1776 and 1978. Fully two-thirds of the American species were described in the monograph by Félicien Chapuis (1865: 77 species) and in 26 papers published over 46 years by Karl E. Schedl (1933a,b, 1935a,b, 1936, 1937, 1939, 1940, 1948, 1951, 1952, 1954, 1959, 1961, 1963, 1965, 1966, 1967, 1970a,b, 1971, 1972a,b, 1976, 1977, 1978: 135 species) (Table 1). The species-level taxonomy of American Platypodinae has not been reviewed since the 1865 monograph, which remains the most important reference for species from this region. No new species were described after 1978 by Schedl, who died the next year. Stephen L. Wood collected platypodines as well as scolytines on his trips to northern South America, Mexico and Central America and he described the new species he found in two bouts (Wood 1966, 1972). His subsequent work with Platypodinae involved cataloguing (Wood & Bright 1992) and his revision of genera (1993). There is no lack of species to describe: among the 6,600+ individuals we have identified are examples of 225 species we could not identify and nearly all of which we believe to be undescribed.

We have been identifying Neotropical Platypodinae along with Scolytinae for several decades now, and in recent years have started focusing more on Platypodinae than before. Having studied type material of most of the described species in the Americas, we have now begun to revise the New World fauna (Kirkendall 2017a,b, Kirkendall & Atkinson 2023, 2024). Here, we summarize our current knowledge about this understudied but important group of woodborers—what we do and don’t know about the New World Platypodinae—and we hope it will encourage further biodiversity and ecological research into these fascinating insects.

This is not intended to be an exhaustive review of all aspects of the biology, morphology or taxonomy and systematics of all Platypodinae. We chose to go into more detail on some aspects (such as host use or courtship and copulation) than others (morphology, life cycle, invasive species). Social behaviour, primarily studied in the eusocial species *Austroplatypus incompertus* Browne, is treated briefly here, but has been reviewed in Kirkendall et al. (2015) and is presented in detail in Smith et al. (2018). The interested reader will find information on topics we discuss cursorily here in the primary literature we cite as well as in some more general works (Beeson 1941, Browne 1961a, Schedl 1972a, Wood 1993).

Because of the direction of our own work, the central subject of this review is the Nearctic and Neotropical pinhole borer fauna. However, with respect to ecology and behaviour, we have had to lean heavily on studies from other parts of the world, where these topics have been investigated in much more detail.

TABLE 1. Numbers of species of Neotropical Platypodinae described by taxonomists working at least occasionally with this group. A total of 300 Neotropical species were described between 1776 (*Platypus flavicornis* Fabricius) and 1978 (*Platypus interponens* Schedl, *P. roppae* Schedl).

Karl E.Schedl (26 papers, publ. from 1933–1978)	135
Félicien Chapuis (1865 monograph)	77
Stephen L. Wood (1966, 1972)	35
Walter F. H. Blandford (1895, 1896)	20
Marian Nunberg (1939, 1959, 1963)	7
Hans Reichardt (1962, 1965)	3
+ 17 authors who described 1 or 2 species each.	

Methods

Database and Alpha Taxonomy

The core of this paper is a series of analyses of data in the relational database developed and maintained by THA that underlies the website "Bark and Ambrosia Beetles of the Americas" (Atkinson 2023). The database includes specimen and series-level information captured from specimens of Scolytinae and Platypodinae identified by both of us as well as species-level data such as type status, distribution, and host records. The information in the database also includes published data from such central works as the world catalogue for both taxa (Wood & Bright 1992), Wood's monographs for American Scolytinae (1982, 2007), the only monographs specifically about Platypodinae (Chapuis 1865, Schedl 1972a), and many research papers. Specimen data were captured over several decades by both authors, from repeated visits to museums in the USA, Mexico, Costa Rica and various European countries, and from loans from a wide variety of museums. The most important museums for American Platypodinae type material are those in Washington, DC (US National Museum, home to collections of both Eggers and Wood), London (many Blandford, Chapuis, and Schedl types), and Vienna (which houses Schedl's collection and some Eggers types), plus a few other museums which have numerous Chapuis syntypes or holotypes (primarily, Paris, Brussels, and Berlin). Data for this paper include label information from over 6,600 specimen records for Platypodinae from the Americas. The sources with the most identified specimens are INBio, the now-defunct national biodiversity institute of Costa Rica (27%); the Snow Entomological Museum Collection of the University of Kansas (9%), and US National Museum (8%). We also reviewed many specimens from the Florida State Collection of Arthropods, Texas A&M University, and the Field Museum (Chicago). Of these records, 84% are our own identifications while 16% are records captured from the literature. We emphasize that our species determinations in nearly all cases have been based on comparisons with type material, much of which we have on long term loans. LRK has worked with type material for about 90% of the 300 known species. We also have in our collections 225 unidentified species, most of which we believe will turn out to be undescribed.

Geographic coverage

Our review covers the taxa found in the Americas (the New World), including the Caribbean islands. Nearly all American species are Neotropical, as only seven species are found north of the Neotropics (in the Nearctic realm), all of which are apparently derived from tropical lineages. We use "Neotropics" in the sense of Holt et al. (2013), a combination of their Panamanian and Neotropical realms. Our Neotropical region then includes the lowland regions of Mexico (including both coasts), the Caribbean islands, Central America, and South America. The distinction between Neotropical and Nearctic breaks down when we consider species from Mexico to western Panama at higher elevations in montane forests. We use the term "Old World" as a useful umbrella term meaning all regions outside of the Americas.

Photographs by THA were taken with a Canon EOS camera with a Cannon MP–E 65 mm 1–5X macro lens mounted on a Cognisys Stackshot rail system (Cognisys Inc., Traverse City, MI). Images were stacked with Zerene Stacker (Zerene Systems LLC, Richland, WA). Unless otherwise indicated, all photographs in plates were taken by the junior author. Other photos by Sarah Smith were taken with a similar system by Visionary Digital Passport II (Dun Inc., Palmyra, VA). Montage images were assembled using Helicon Focus Mac Pro 6.7.1 (Helicon Soft, Kharkov, Ukraine). Photographs of specimens from the Smithsonian Institution include the barcoded catalog number (USNMENT…). Data associated with these specimens are available at https://collections.nmnh.si.edu/search/ento/ via a barcode search.

Trapping methods used for collecting Platypodinae

The main trapping methods that capture good numbers of Platypodinae are flight intercept traps, Malaise traps, and light traps. Our analyses give a general overview of the diversity of species captured by such methods and an idea of which taxa are caught in largest numbers. Label data does not always include how many days a given trap was run, so cannot be used for calculating trapping effort. Furthermore, little if anything is given about the exact type of trap used, trap placement, the materials used, size of the trapping surface, and so forth. Flight intercept traps and Malaise traps are a frequent choice for sampling specific insect groups or for insect biodiversity surveys because they can be run for long periods of time and collect large numbers of flying insects. Though often run for just one or a few nights, light traps can also sample over long time periods (Wolda et al. 1998). All types of traps can be mounted at different heights above ground, often using towers, but traps are usually employed just a meter or two above the ground.

Flight intercept traps (perhaps better denoted as "knock-down" traps) normally are composed of a vertical barrier that knocks down flying insects and a fluid-filled tray into which insects fall and from which they normally cannot extricate themselves and which preserves the insects until trays can be emptied. The barrier wall can vary from a small piece of glass or plexiglass (so-called windowpane traps) to a several meters long piece of fine-meshed cloth (such as the wall of a Malaise trap or of a Gressitt trap). Trap design variations (such as size or colour of trays used), height of placement, and whether or not the traps are baited (such as with ethanol) lead to significant differences in which insect taxa are captured and numbers of individuals that are caught (Masner & Goulet 1981, Campos et al. 2000, Chung 2004, Gerónimo-Torres et al. 2021). Further, for larger insects such as Cerambycidae (and presumably larger Platypodinae), lubricating a solid-material wall increases catches (Allison et al. 2014). Rarely is any of this variation in methods or materials detailed on insect labels.

Malaise traps are sometimes classified as flight intercept traps (Basset 1988, Souza et al. 2015, de Souza Amorim et al. 2022) However, Malaise traps capture different subsets of insect communities than do flight intercept traps (Basset 1988, Lamarre et al. 2012, LRK unpublished data), because insects fly upwards when encountering the porous cloth wall of a Malaise trap, while flight intercept traps capture insects knocked down by their solid wall. As with flight intercept traps, Malaise traps come in a variety of structures, varying especially in size of the vertical wall and colour of the cloth roof (Sheikh et al. 2016, de Souza Amorim et al. 2022, Uhler et al. 2022). Insects hitting the cloth wall bounce off and fly upwards, eventually being funnelled into a capture bottle in the upper corner of the trap. Importantly with respect to wood-boring insects (and differing in this regard from flight intercept traps), the collecting bottle normally is filled with 70% ethanol; the evaporating alcohol can be either an attractant or a repellent or neutral, depending on the taxon and the evaporation rate. All types of flight intercept traps, including Malaise traps, can be used to sample flying insects in tree canopies (Skvarla et al. 2020).

For a third mass trapping method, we include specimens collected "at light". It should be noted that light in different wavelength bands attracts different compositions of nocturnal insects (Ramamurthy et al. 2010, Infusino et al. 2017). Light trapping can involve the use of incandescent lamps (tungsten or mercury vapor), fluorescent lamps, or LED assemblages (or combinations of light sources). There are a variety of ways to use light to attract and capture insects, such as simply manually collecting specimens that come to building lights or to light sources at campsites, hanging light bulbs in front of white sheets, or suspending specialized light traps. Light trapping is most often at ground level using white sheets, collecting from white walls, or using specialized traps, but specialized traps can be hoisted to different heights and can be deployed in the canopy (Wolda et al. 1998, Brehm & Axmacher 2006, Stork et al. 2015).

There are other collecting methods specified in our specimen records, but none represent more than about 5% of all records and they are not discussed further here.

Results: Biodiversity

Systematics and evolutionary history

Similarities in morphology, ecology and behaviour have resulted in considerable evolutionary convergence between Platypodinae and Scolytinae. The striking similarities have led to a long history of disagreement regarding the systematic placement of Platypodinae relative to Scolytinae, with no consensus being reached until quite recently. Different viewpoints have included treating pinhole borers as:

- a separate family, its relationship to Scolytidae not stated, within the superfamily Curculionoidea (Wood 1993, Bright 2014);
- a separate family, not closely related to the family Scolytidae, though frequently treated together with bark beetles in faunistic or taxonomic papers (Browne 1961a, Schedl 1972a);
- a separate family, sister group to the family Scolytidae (Hopkins 1915, Swaine 1918, Kalshoven 1960, Reichardt 1962, Wood & Bright 1992, Wood 1993, Morimoto & Kojima 2004);
- a subfamily of weevils (of Curculionidae), closely related or not to subfamily Scolytinae (Marvaldi et al. 2002, Jordal et al. 2011);
- and even as a clade positioned within the subfamily Scolytinae (Kuschel et al. 2000).

A clear conclusion has emerged from recent analyses of molecular data—most recently, data from hundreds of genes—combined with re-examinations of morphology: the Platypodinae and Scolytinae are somewhat distantly related subfamilies of Curculionidae, Platypodinae most likely being the sister group to Dryophthorinae (McKenna et al. 2009, Haran et al. 2013, Gillett et al. 2014, Jordal et al. 2014, Jordal 2015, Shin et al. 2017, Mugu et al. 2018, Chamorro et al. 2021). (For a similar discussion of the systematic placement of Platypodinae see Hulcr et al. 2015.) We distinguish between Platypodinae broadly defined and "core Platypodinae" (*sensu* Schedl 1972a, Wood 1993, Jordal 2014: Table 2). Non-core Platypodinae are species whose systematic placement is unclear, and their inclusion in Platypodinae is questioned (Table 3). Wood (1993) treated pinhole borers as the weevil family Platypodidae, comprising three subfamilies (now demoted to tribes): **Coptonotinae** for the platypodine-like genera *Coptonotus* Chapuis, *Protohylastes* Wood, *Scolytotarsus* Schedl, *Mecopelmus* Blackman, *Protoplatypus* Wood, and *Schedlarius* Wood; **Tesserocerinae**, with 11 genera; and **Platypodinae**, with 22 genera, 11 of which were described as new in that work. Kato (1998) described an additional new genus (*Phylloplatypus* Kato, 1998) that he placed in Coptonotinae, for a pinhole borer-like species mining leaves of pandanus palms (*Pandanus* Parkinson) on the Bonin Islands.

Advances in our understanding of both morphology (Jordal 2014 and see references in Zarazaga & Lyal 2009) and genetics (Jordal et al. 2011, Jordal 2015, Shin et al. 2017, Mugo et al. 2018) have anchored Platypodinae firmly within Curculionidae and led to the removal of all but *Schedlarius* from this weevil subfamily. Tesserocerini plus Platypodini clearly form a monophyletic clade, the core Platypodinae. Zarazaga & Lyal (2009) chose to place Wood's entire Coptonotinae in Scolytinae (as tribe Coptonotini) but acknowledged the following proposed placements by other specialists of the coptonotine genera into the following Curculionidae subfamilies: *Coptonotus* into Scolytinae; *Protohylastes* into Cryptorrhynchinae; *Scolytotarsus* into Conoderinae; *Protoplatypus* and *Phylloplatypus* into Cossoninae. The genus *Mecopelmus* was placed by Zarazaga and Lyal in a newly erected platypodine tribe, Mecopelmini Thompson, 1992, while *Schedlarius* was placed in Schedlariini Wood & Bright, 1992. Subsequently, based on both multigene and morphological data, Jordal (2015: 305, see also Mugo et al. 2018) concluded that *Mecopelmus* is *not* a Platypodinae, though its exact placement within weevils is uncertain. Finally, the conclusion from the recent molecular and morphological investigations is that *Coptonotus* is likely a subfamily of weevils (Coptonotinae) that is more closely related to Scolytinae and Cossoninae than it is to Platypodinae (Jordal 2014, 2015, Smith & Cognato 2016). These recent suggested placements are summarized in Table 3 (see also Table 3.7.13.1 in Jordal 2014). Based on these considerations, we consider Platypodinae to include only *Schedlarius* in addition to the core Platypodinae, resulting in three tribes: Schedlariini, Tesserocerini, and Platypodini, all of which occur in the New World

TABLE 2. The tribes and genera of core Nearctic and Neotropical Platypodinae, with numbers of described and putative undescribed species per genus (as of March 2023). "[Species] *inquirendae*": nine species which cannot be identified because the type material is apparently lost (based on Schedl 1972, Wood and Bright 1992, and our own research). "*Platypus*" is in quotes because the genus *Platypus* Herbst is now considered to be strictly an Old World genus (Wood 1993); we expect that all native American species still in *Platypus* will eventually be transferred to New World genera. "Undescribed": morphospecies we cannot place in described species at this time and which we presume to be new to science.

Tribe	Genus	Described	Inquirendae	Undescribed	Total
Schedlariiini	*Schedlarius*	1	-	-	1
Tesserocerini	*Cenocephalus*	10	-	20	30
	Tesserocerus	26	4	41	71
	Tesserocranulus	1	-	-	1
Platypodini	*Costaroplatus*	16	-	14	30
	Epiplatypus	19	-	32	51
	Euplatypus	43	2	32	77
	Megaplatypus	92	1	52	145
	Myoplatypus	8	-	3	11
	Neotrachyostus	15	-	4	19
	Oxoplatypus	1	-	-	1
	Platyphysus	5	-	1	6
	"Platypus"	35	2	-	37
	Teloplatypus	17	-	24	41
	Treptoplatypus	2	-	-	2
	1st new genus	-	-	1	1
	2nd new genus	-	-	1	1
	Totals	**291**	**9**	**225**	**525**

TABLE 3. A summary of current ideas on placement within Curculionidae of species whose recent inclusion in subfamily Coptonotinae of Platypodidae by Wood (1993) or Kato (1998) is controversial. See text for details and literature sources.

Genus	Probably belongs in
Coptonotus Chapuis	own subfamily
Protohylastes Wood	Cryptorhynchinae
Scolytotarsus Schedl	Conoderinae
Mecopelmus Blackman	unclear, but not Platypodinae
Protoplatyus Wood	Cossoninae
***Shedlarius* Wood**	**Platypodinae, basal**
Phylloplatypus Kato	Cossoninae

(Table 2).

Wood's (1993) tribal and generic revisions within the core Platypodinae should be considered preliminary. Since 1993 there have been no other living systematists of the group that have made any significant comments, either in favor or in opposition. Since Wood's revision, the valid status of an Oriental genus that he overlooked has been clarified (*Carchesiopygus* Schedl: Beaver & Sanguansub 2015) and one new genus was subsequently added (*Pereioplatypus* Beaver, 2007).

Based on DNA sequencing of portions of one mitochondrial and four nuclear genes, Jordal (2015) concluded that the Neotropics were colonised by ancient long-distance dispersal a minimum of three times from the Afrotropical region, twice by species in the Tesserocerini and once (the most recent) by the ancestor of the Neotropical Platypodini genera (see also Mugo et al. 2018). There were two separate origins of the Neotropical tesserocerine genera. *Tesserocranulus* and *Tessserocerus* are closely related and arose from the earliest dispersal event (54–78 million years ago); these two genera are more distantly related to *Cenocephalus*, which represents the second long-distance dispersal. Jordal suggested that the Neotropical Platypodini clade could have originated from one ancestor, the most recent of the three postulated dispersal events. All Mexican amber and Dominican amber fossils discovered so far have been of species clearly belonging to the Tesserocerini clade (no Platypodini have been found), supporting the conclusion from molecular clock estimates that the Platypodini lineage must be quite young in an evolutionary time perspective (22–32 million years ago). Given Jordal's results, the two North American species of *Treptoplatypus* (not sequenced) either are unrelated to Asian and Australian species currently placed in *Treptoplatypus* or they represent a fourth dispersal event. Based on similarities of ecology and morphology, they could be closely related to the Eurasian fir specialist *T. oxyurus* (Dufour).

Morphology supports the hypothesis of a recent origin for American Platypodini, in that there are so few unambiguous characters that separate genera (Table 4). At the extreme, the genus *Platypus* as re-defined by Wood (1993) has no unique derived characteristics at all (Table 4), and molecular data shows the genus to be polyphyletic (Jordal 2015). Further, females of American Platypodinae can be difficult to identify even to genus much less to species (Wood 1993, Beaver 2004, and our personal experiences). In the older clades of Tesserocerini, by way of comparison, the genera are usually easy to separate for either sex and, though differences can be subtle, females can nearly always be identified to species.

Importance of modern insect trapping methods for species discovery

Prior to the widespread use of flight intercept traps and Malaise traps, Platypodinae accumulated very slowly in museum collections. As a result, many species are known only from one original collection (often, only one specimen), and we have registered a large number of undescribed species (Table 2). Pinhole borers spend more than 99% of their adult lives (and 100% of their juvenile existence) in wood, so are rarely encountered by non-specialists. Significant numbers do accumulate, on the other hand, in larger flight intercept traps and in Malaise traps, which are often run for anywhere from a few days to several weeks or months. Some Platypodinae can be captured at night using various types of lights (Perez de la Cruz et al. 2011, 2015, Geronimo-Torres et al. 2015, 2019, 2021, Kirkendall 2017b). The THA database contains identifications we have made of 3242 specimens caught by flight intercept traps (including window traps) or Malaise traps or taken at light (incandescent, flourescent, or LED) (Table 5). This total represents about half of all individuals we have identified. Nearly 40% of all species known to us were caught by these methods, including 101 described species and 100 undescribed species (data not shown). In early years, we had the impression that few species fly at night and would be found coming to light, and platypodines are generally considered to be diurnal fliers. We were surprised, then, to see that our database has accumulated records of 46 described and 17 undescribed species that were captured by some form of light trapping. The number of specimens collected at lights is an underestimate and highly biased: two very abundant and widespread species, *Euplatypus parallelus* (F.) and *E. segnis* (Chapuis), come in large numbers to light and (especially the former) can be abundant in collections. However, we often do not register all specimens of these two species that we come over, so they are under-represented

TABLE 4. Character states separating Neotropical genera of Platypodini (Wood 1993). Platypodini genera are separated by combinations of traits unique to a genus and traits shared with a subset of genera. The characters discussed here are best understood by careful study of identified specimens or of photographs (https://www.barkbeetles.info/). Character states usually apply to males, as females of many genera lack readily distinguishing features. The characters and character states are those used in Wood's key and in his genera descriptions in the text. Categorizations as autapomorphy (unique derived character state) or homoplasy (convergent character state) are by the authors. Some homoplasies are not given here (see Wood 1993). Quotation marks indicate words or phrases used by Wood (1993). M-m: impression at the distal end of the metanepisternum and metaventrite (see text and Fig. 5). OW, NW: Old World, New World (American).

Taxon	**Autapomorphies**	**Diagnostic homoplasies**	**Comments**
Costaroplatus (Nunberg)	Paired spines on ventrite 5	M-m with spines on anterior margin; no pores on pronotum, either sex; discal interstriae carinate posterior half of disc; declivity short and steep, ventrolateral angles poorly developed.	As *Platyscapulus* Schedl, removed from synonymy with *Platypus*. We have discovered a few species in other genera that have spines or carinae on ventrite 5 but these do not otherwise resemble species placed in *Costaroplatus*.
Epiplatypus Wood	Distinct elytral declivity: two pairs of serrations on the ventrolateral margin of the male elytral declivity, "usually" connected by a carina.	m-m with spines on anterior margin; "usually" a pair of mycangial pores on pronotum of female or of both sexes.	Very similar to *Teloplatypus* and some species without pores could go in either genus.
Euplatypus Wood	Male ventrolateral processes well developed, long, exceeding sutural apex, never with serrations or denticles on the apical margin between these processes.	M-m with spines on anterior margin; female or both sexes "often" with a pair of mycangial pores.	*Euplatypus* and *Megaplatypus* can be difficult to separate based on Wood's characters (see text).
Megaplatypus Wood	"Poorly formed and much less strongly produced posterolateral angles of the male elytra"; apical margin between angles "sometimes" with one or two pairs of small denticles.	M-m in many species with spines on anterior margin, but some with none; mycangial pores "uncommon" (females) or "rare" (males), may consist of a pair or a cluster of pores.	"...distinguished with some difficulty [from *Euplatypus*]".
Myoplatypus (Wood)	Paired spines on ventrite 3	pronotum usually with one pair mycangial pores in the female, sometimes present in the male.	One species, *M. flavicornis*, is only found in temperature forests.
Neotrachyostus Browne	Posterior face of protibiae sexually dimorphic, that of females being mostly granulate. Female with pair of tiny mycangial pores on pronotum.	M-m impression having no spines on anterior margin, surface with some setae.	Not clear that the sexually dimorphic protibiae alone clearly defines a monophyletic group: some species currently in *Euplatypus* have this.

TABLE 4. *continued*

Taxon	Autapomorphies	Diagnostic homoplasies	Comments
Oxoplatypus Wood	Pair of large spines on ventrite 4 (and none on other ventrites).	M-m with spines on anterior margin. Female pronotum with pair of large pores.	Genus contains one temperate species. Wood considered the genus to be similar to *Costaroplatus*, but the females are quite different.
Platyphysus Wood	Ventrite 5 moderately to strongly inflated, posterior 1/4 ascending abruptly to meet elytral apex.	M-m with spines on anterior margin. Mycangial pores never present on pronotum. Declivity steep, strongly convex, unarmed or with small denticles on odd interstriae.	The genus probably should be combined with *Costaroplatus*. Females of the two genera are indistinguishable (e.g. Kirkendall 2017).
Platypus Herbst	(None.)	M-m impression having no spines on anterior margin, surface with some setae. Mycetangial pores on pronotum numerous when present ("mostly" in females). Apical margin of declivity at suture not "dehiscent" (the processes not splitting apart from each other).	Wood made this an OW genus but it is included in this table because he transferred the Neotropical species *quadrilobus* Blandford from *Neotrachyostus* to *Platypus*. Most similar to *Treptoplatypus* among NW genera. In Wood's text and key, *Platypus* is defined by absence of the features that distinguish similar Platypodini genera.
Teloplatypus Wood	Male elytral declivity with one pair of serrations on the ventrolateral margin, with a carina connecting these to a spine on interstriae 3 at the base of the declivity	M-m with spines on anterior margin. Declivity descends only slightly. No mycetangial pores.	Very similar to *Epiplatypus* and some species could go in either genus.

in our database.

We have very few records of pinhole borers collected by sweeping, in pitfall traps, from flowers, or by other methods commonly used by general insect collectors.

Biodiversity of the American fauna

The American fauna comprises 15 genera distributed among three tribes: Schedlariini, for *Schedlarius mexicanus* (Duges); Tesserocerini, with 3 genera; and Platypodini, with 11 genera (Table 2). All Nearctic and Neotropical genera but *Treptoplatypus* Schedl are found only in the Americas. After Wood's revision of the world genera, there has been steady progress in revising the genera in the Afrotropical, Palearctic, Indomalayan Oceanic and Australasian realms (Beaver 1995, 1998a,b, 2000, 2002, 2004, 2005, 2007, 2011, 2013, Beaver & Sanguansub 2015, 2020, Beaver & Liu 2018, Bickerstaff et al. 2020). However, our knowledge of the taxonomy of American species remains quite poor. We have a key for identifying all world genera (Wood 1993), but for only the small genus *Myoplatypus* do we have a key to species of any Neotropical genus that includes more than one species (Kirkendall & Atkinson 2023).

The total of 525 known species of Platypodinae

TABLE 5. For described and undescribed species of each genus, the numbers of specimens in our database which have been collected by the main mass trapping methods. The database comprises 6632 records as of 15 Mar. 2023, and 3242 specimens were collected by one of these three methods. Note that flight intercept traps can vary considerably in dimensions, and light trapping can involve the use of incandescent, ultraviolet, or mercury bulbs (or combinations). Further, flight intercept and Malaise traps could have been run for up to two or three weeks before a collection was made. See text for other important considerations, for understanding these data.

			Flight intercept traps		**Light trapping**		**Malaise traps**	
Tribe	**Genus**	**Species status**	**Nr species**	**Nr individuals**	**Nr species**	**Nr individuals**	**Nr species**	**Nr individuals**
Tesserocerini	*Cenocephalus*	described	3	13	4	29	3	12
		undescribed	6	22	2	2	2	12
	Tesserocerus	described	11	121	6	278	11	206
		undescribed	15	52	6	68	9	65
	Tesserocranulus	described	1	9	1	16	0	0
Platypodini	*Costaroplatus*	described	4	7	4	59	2	20
		undescribed	6	8	0	0	2	6
	Epiplatypus	described	3	34	0	0	4	21
		undescribed	13	32	0	0	4	27
	Euplatypus	described	12	236	8	318	11	134
		undescribed	13	61	5	7	2	15
	Megaplatypus	described	18	193	10	28	22	289
		undescribed	15	103	1	1	10	75
	Myoplatyus	described	5	14	1	16	3	0
		undescribed	2	3	0	0	7	0
	Neotrachyostus	described	3	23	0	0	2	11
		undescribed	1	0	0	0	0	0
	Oxoplatypus	described	1	4	1	6	1	1
	new genus 1	undescribed	1	47	0	0	1	17
	new genus 2	undescribed	1	0	1	0	1	1
	Platyphysus	described	1	20	1	12	1	28
		undescribed	0	0	0	0	0	0
	Platypus	described	4	5	2	30	2	8
	Teloplatypus	described	6	103	5	37	6	269
		undescribed	4	5	2	2	0	0
Schedlariini	*Schedlarius*	described	0	0	1	1	0	0
		undescribed						
		Totals	**149**	**1115**	**61**	**910**	**106**	**1217**

comprises 102 Tesserocerini that have evolved from a minimum of two long-distance dispersals from the Afrotropical region and 422 species of Platypodini from possibly as few as one long-distance dispersal from the Afrotropical region plus a colonization of *Treptoplatypus* which could have been via a land bridge from northeastern Asia. (The 525th species is *Schedlarius mexicanus*, which has no clear Old World antecedents). Four genera have more undescribed than

described species: *Cenocephalus, Tesserocerus, Epiplatypus, Teloplatypus*. At the other end of the scale, *Schedlarius*, *Tesserocranulus* and *Oxoplatypus* remain monotypic, and relatively few new species have been discovered for *Platyphysus* or *Neotrachyostus*.

If the Neotropical Platypodini are indeed only 22–32 million years old (Jordal 2015), then it is striking that they have radiated into over 400 species, a speciation rate of ca 12–18 species per million years. The clade of *Tesserocerus* + *Tesserocranulus* comprises at least 72 species (Table 2) and was estimated to have originated 54–78 million years ago, 0.9–1.3 species per million years, a much more modest evolutionary rate. Similarly, the clade of *Cenocephalus* contains at least 30 species and was estimated to have originated 30–44 million years ago, 1.0–1.6 species per million years.

The striking difference in evolutionary rates between each of these Tesserocerini clades compared with the Platypodini clade suggests that there must be important differences in behavior or ecology between Tesserocerini and Platypodini that our current knowledge is missing.

Overall, 225 of 525 known species are currently believed to be undescribed (43%) (Table 2). We have not yet carefully studied all species in the two most species rich genera, *Megaplatypus* and *Euplatypus*, many of which are known only from types. It is likely that a very small number of species which we have not been able to identify will in the end turn out to be described species. However, at the same time, with each new large collection that we study we find additional unidentified species. So, we expect that the estimate of the proportion of species that are undescribed may increase in the near future.

Collection effort has been very uneven geographically, as reflected by data on numbers of species currently known for American countries (including the Caribbean region) (Figure 1). Of the countries in the Americas, the only countries where the known number of species (described plus undescribed) is likely to be close to the actual number of species are Canada and Chile (1 species each), the continental United States (7 species) and Mexico (56 species). In Mexico, THA and associates have collected extensively over the last several decades, and both S. L. Wood and D. E. Bright made several collection trips to the country. Even so, a large number of the known species have never been recorded from Mexico in publications and there is good reason to expect that the number of species, especially in the southern states of Veracruz, Oaxaca and Chiapas will rise with further collecting. It is no surprise that Brazil has the largest number of known species. The similarly high numbers known from Peru are due to several large sampling projects in the Amazonian region that were not specifically oriented towards Platypodinae. Despite the large numbers of specimens from Peru that were available for study, higher elevations are under-represented and further collecting should discover even more species (Kirkendall 2017b). We suspect that many of these species also will be found in Brazil. Finally, the very high number of species known from Costa Rica highlights the lack of sampling in neighbouring countries, rather than any unique conditions there. The main difference is sampling effort due to a long sabbatical residence by S. L. Wood there and mass sampling of flying insects by INBio and by the ALAS project (https://ants.biology.utah.edu/ALAS/).

Interestingly, only 6 of 137 species known from Brazil are undescribed (4%). In other words, those specimens that were collected from Brazil and ended up in American or European museums were identified and new species described from them long ago, and that little material has made its way out of Brazil to North American or European museums in recent decades. We would expect there to be roughly 40% undescribed species in Brazil (as is the case overall), so the Platypodinae fauna of Brazil must be severely undercollected. Supporting this inference, recent large collections of Platypodinae from trapping projects in the neighbouring Peruvian Amazon rainforest generated hundreds of new specimen records (Kirkendall 2017b), with the result that 54 of 109 currently known species (50%) are undescribed in that fauna. We expect that a similar influx of new specimens from Brazil would greatly increase the number of undescribed species found in that country.

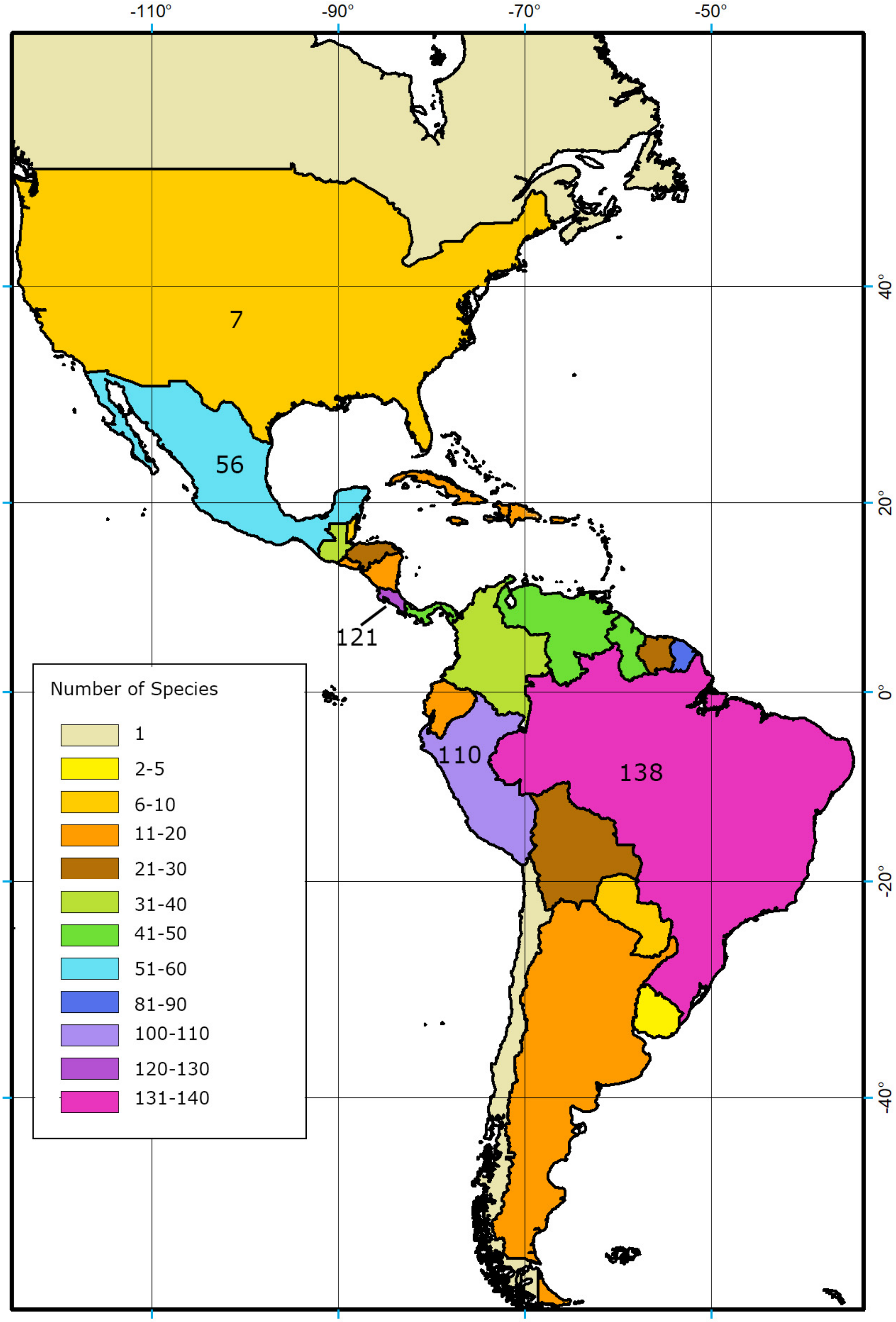

FIGURE 1. Map showing numbers of described Platypodinae for countries in the Nearctic and Neotropical realms. Exact numbers are shown for the USA, Mexico, Costa Rica and Peru, countries for which the fauna is relatively well known, and for Brazil, which is undercollected.

Of 300 described species, 9 cannot be identified because the types are known or believed to be lost. In addition to this, 70 species are known from either a female holotype (or lectotype) or from a syntype series that is just females. Many of these are probably not identifiable.

There are 37 American species currently in the genus *Platypus* Herbst in Table 2. Except for *P. quadrilobus* Blandford, Wood (1993) transferred all Neotropical species out of *Platypus*, such that the genus is now nearly exclusively Old World. These 37 New World *Platypus* species were either described in papers that Wood overlooked or are species which he could not readily move out of *Platypus* without seeing them. We have studied type material for nearly all these species and will be able to transfer them to current genera in future papers. None appear to fit into the current concept of *Platypus*.

Morphology of adults

For a comprehensive description of general Platypodinae morphology see Jordal (2014). New World species vary in length from less than 2 to about 11 mm in length. The core genera have an elongate cylindrical shape (most species 3x or more as long as wide), the head partly concealed by the pronotum and no rostrum (snout), with few setae and no scale-like setae. The eyes are relatively large, round or slightly elongate, and are weakly to strongly protruding from the head. The antenna is short, elbowed, and terminates in a large, flattened club formed by fusion of the last three antennal segments. The legs have long "feet", with a very long first tarsal segment that is longer than the other four segments combined. Mature Neotropical Platypodinae are usually reddish to blackish brown but can be dirty yellow in colour; some species (including most species of *Teloplatypus*) are bicolored, the central portion of the elytra being lighter in colour than the base and apex.

Tesserocerini

In general males have more pronounced apical projections on the elytra. This character is generally valid for distinguishing sexes if both are present but varies so widely among species that males of some groups have apical projections shorter than females of others. In the genus *Tesserocerus*, males typically lack any vestiture on the face of the declivity. In females of many species there is a band of dense setae along the central line of the declivity.

Platypodini

For a given species, males have much more pronounced apical projections of the elytra; females often have no projections at all. This can be somewhat difficult to detect in the genus *Teloplatypus* and certain *Epiplatypus* where male declivital armature is much reduced, and apical projections are lacking in males of *Platyphysus* and many *Costaroplatus*. The face of the male declivity is often vertical or nearly so, and may be concave. In various genera, we have seen that the female mouthparts (labial and maxillary palpi) are much expanded by comparison with conspecific males, but this character has not been studied over a wide range of species.

Sexual dimorphism

The seminal taxonomic work for Platypodinae is the 1865 world monograph by the prolific Belgian doctor and coleopterist Félicien Chapuis (1824–1879), in which he described 77 new Neotropical species (1/4 of all currently described New World species). Although Chapuis consistently switched the sexes, describing males as females and females as males, this mix-up has been implicitly corrected by all subsequent taxonomists (explicitly by Smith 1935 and Schedl 1960). Generally, males are the sex with simple to elaborate developments of the elytral declivity such as single or multiple spines or other sculpturing (most often, on the lower corners of the declivity) and the sex having a near-vertical or vertical declivity that is often slightly or distinctly concave. Males usually have a frons (forehead) without special setae and that is weakly to strongly convex, though it is not uncommon for males to have a weakly concave frons when the female frons is deeply concave (Figure 2). Males in some genera have paired strong ventral spines on one or two abdominal segments (Figure 3); these

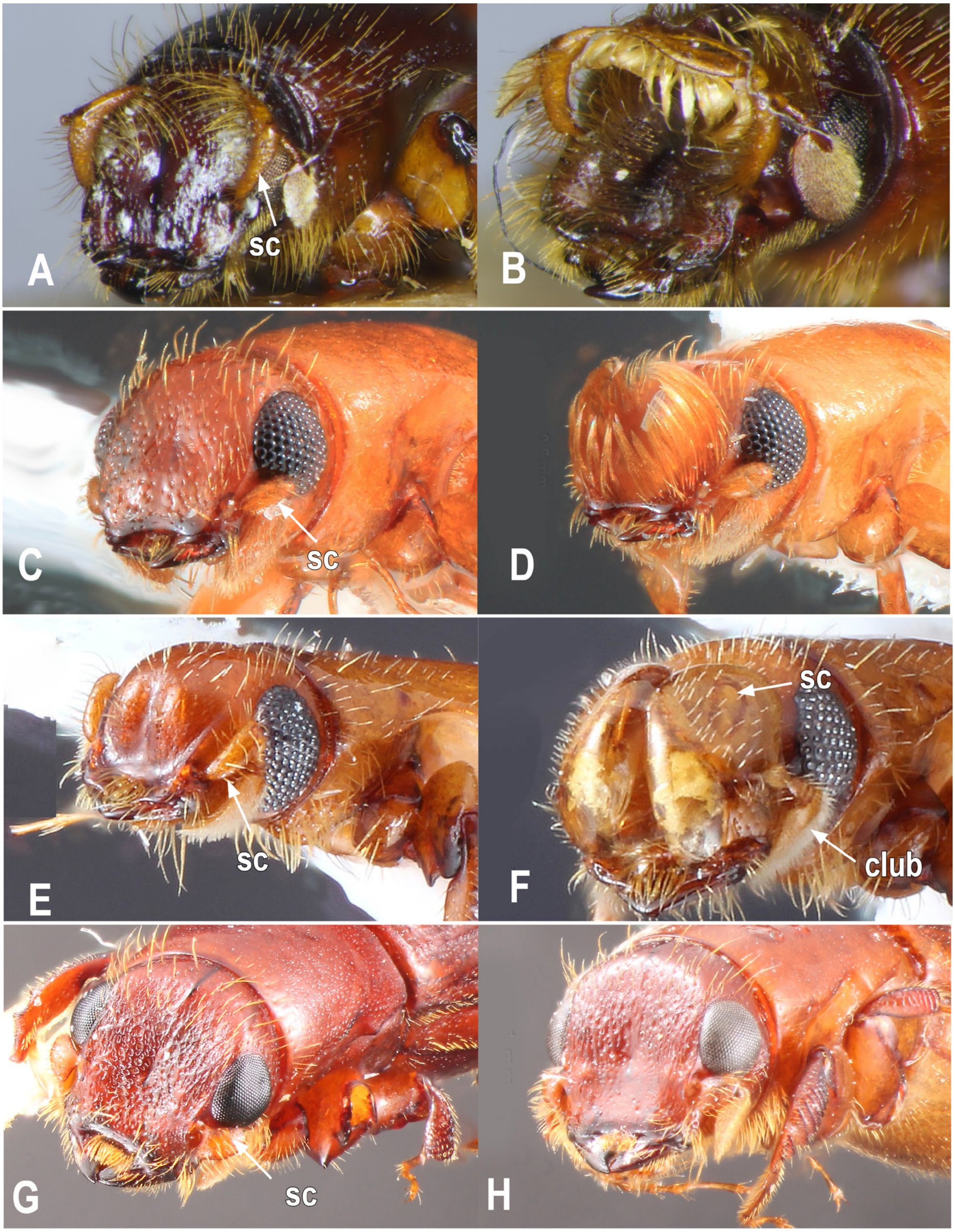

FIGURE 2. Features of the frons (forehead) and antennal scape: examples of differences between males (left side) and females (right side) of the same species, and differences among genera. **A, B**. *Tesserocerus insignis* (Saunders, 1836). The long extensions of the scape and the sexual dimorphism in scape setation ("hairiness") are typical for this group of *Tesserocerus* species. **C, D.** *Cenocephalus lalolaensis* Nunberg, 1963. Females of most species have a more concave frons and dense patches of setae on the sides of the frons. **E, F.** *Tesserocranulus nevermanni* Schedl, 1933. The female antennal club is greatly expanded and concave. **G, H.** *Megaplatypus exaratus* (Blandford, 1895). Sex differences in the frons are usually quite minimal, as seen in this example. Photos by T.H. Atkinson.

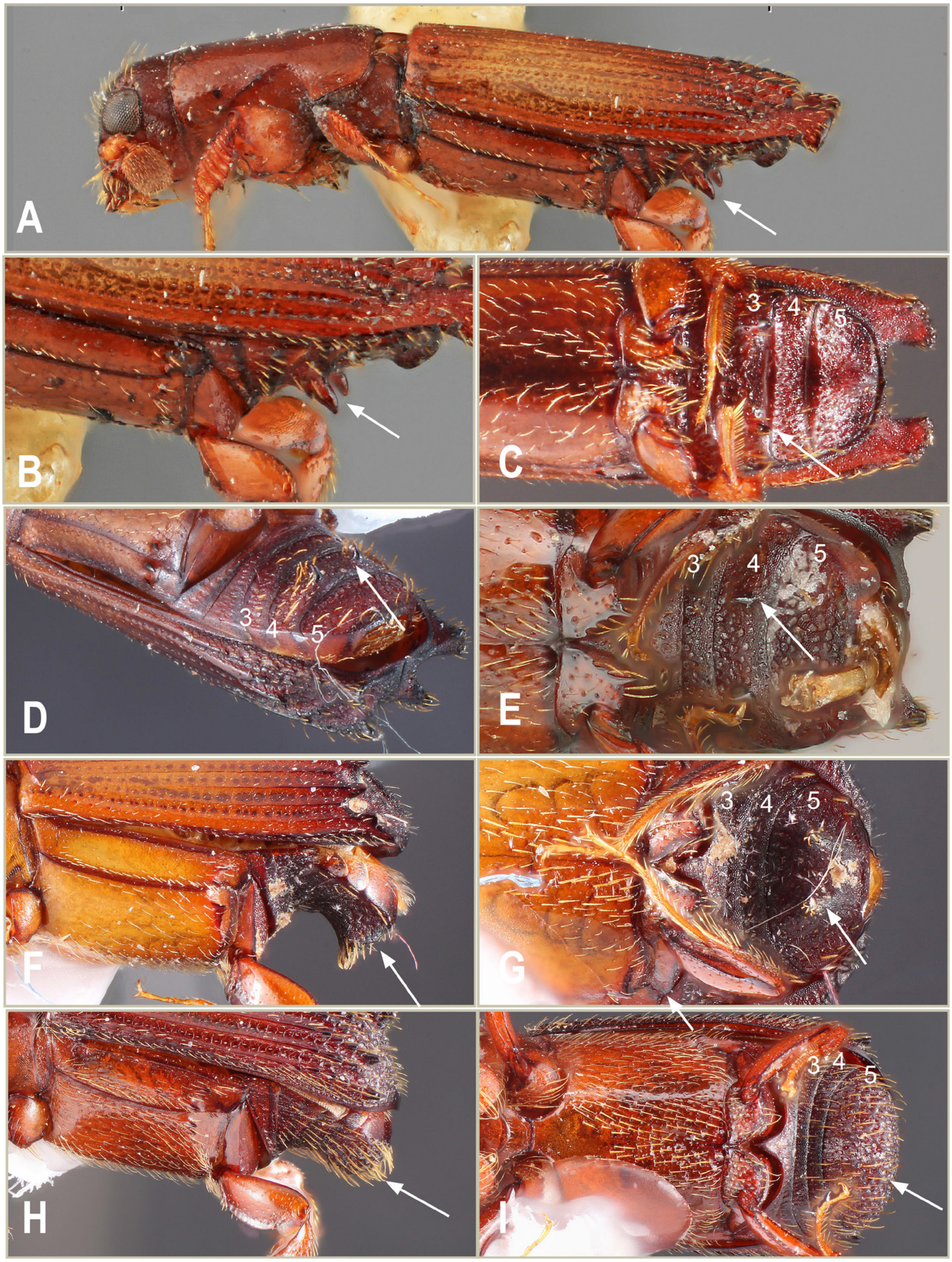

FIGURE 3. Lateral, posterolateral and ventral views of male Platypodini showing modifications of the last three sternal segments (ventrites 3, 4 and 5), important characters for separating Platypodini genera. Conspecific females do not share these sternal modifications. **A–C**. *Myoplatypus biprorus* (Blandford, 1896) (USNMENT00912032) with a transverse pair of spines on ventrite 3. **D, E**. *Oxoplatypus quadridentatus* (Olivier, 1795) with a transverse pair of spines on ventrite 4. **F, G**. *Costaroplatus manus* (Schedl, 1936) with a transverse pair of spines on ventrite 5. **H, I**. *Platyphyusus obtusus* (Chapuis, 1865) with an inflated ventrite 5. Photos of *M. biprorus* (specimen USNMENT00912032) by S.M. Smith, all others by THA.

are absent in conspecific females. Females in most genera have simple, gently rounded declivities. In many cases, females have a frons that is weakly to strongly concave (in part, or entirely so) and they may have dense long setae arising from the bottom, sides, or top of the frons (Figure 2). The hind legs of males may be more strongly developed (Browne 1961a). As far as is known, females always have mycangia for transporting the ambrosia fungi on which all stages depend for food. Mycangia frequently take the form of pairs of pores or patches of pores found on either side of the median line on the pronotum (Figure 4; discussed in more detail later in this review). Males may or may not have mycangia.

The M-m character in Platypodini.

A useful character for grouping species into genera or species groups in Platypodini (but not in Schedlariini or Tesserocerini) is the presence of a vertical row of small spines or short carinae (or their absence) on the anterior margin of the impression that receives the femur of the third leg (metafemur) when it is folded into the body (Table 4, Figure 5). This impression is found towards the posterior end of the uppermost visible thoracic segments, the metanepisternum and metaventrite (which we will refer to as “m-m”). Wood (1993: 271) discusses the potential usefulness of this character and in several couplets in his key to genera he employs presence or absence of the tiny spines. The m-m character was subsequently used in several taxonomic works by Roger Beaver and his colleagues (Beaver 2007, Beaver & Liu 2007, 2018, Beaver & Sanguansub 2015) and in our revision of *Myoplatypus* (Kirkendall & Atkinson 2023).

For the genera present in the Americas, Wood characterizes the m-m impression as being absent or weak in *Neotrachyostus*, *Treptoplatypus* and the group of species related to *Euplatypus longulus* (Chapuis). The impression is never absent in Platypodini, but in some it is only weakly concave.

Comments on taxonomy of tribes, genera and species

In this section we comment on tribes and genera as currently defined. Separating tribes is not problematic, and the genera of Tesserocerini are well delimited. Problems arise when placing species into Platypodini genera.

New World tribes: Schedlariini, Tesserocerini, Platypodini

Schedlarius differs in several external and internal characters from core Platypodinae (Wood 1993, Jordal 2014), reflecting its presumed basal position in Platypodinae. The only species, *Schedlarius mexicanus,* is easily identified from photos (Figure 6). The split between Tesserocerini and Platypodini is old enough (> 80 million years ago: Jordal 2015) that the two tribes can be fairly easily separated by differences in the underside of the head (Wood 1993, our Figure 7). Three features of the underside of the head in particular are relatively easily seen with good lighting and good magnification: (1) the cleft (gap) between the pregula (prementum)—the central segment to which the maxillary and labial palps are attached—and the rest of the underside of the head (“cleft” in Figure 7); (2) the form of the maxillary palps (“mxp” in Figure 7); and (3) the form of the pair of labial palps (“lp” in Figure 7). In the Tesserocerini, the cleft is shorter, extending less than halfway to the base of the pregula (to the bottom of the inverted triangle formed by that segment); the maxillary palps each form a conical pyramid of three segments; and the labial palps form adjacent conical pyramids with the basal segments clearly separated from each other. In the Platypodini, there is a longer cleft, extending more than halfway to the base of the pregula; the maxillary palps appear “squashed” with the upper segment strongly flattened (truncated); and the paired labial palps have the basal segments fused. A second difference between Tesserocerini and Platypodini is the form of the indentation in the side of the thorax that receives the profemur when the legs are folded into the body—the femoral groove (Figure 8). This impression is broader and more widely rounded above in Tesserocerini but

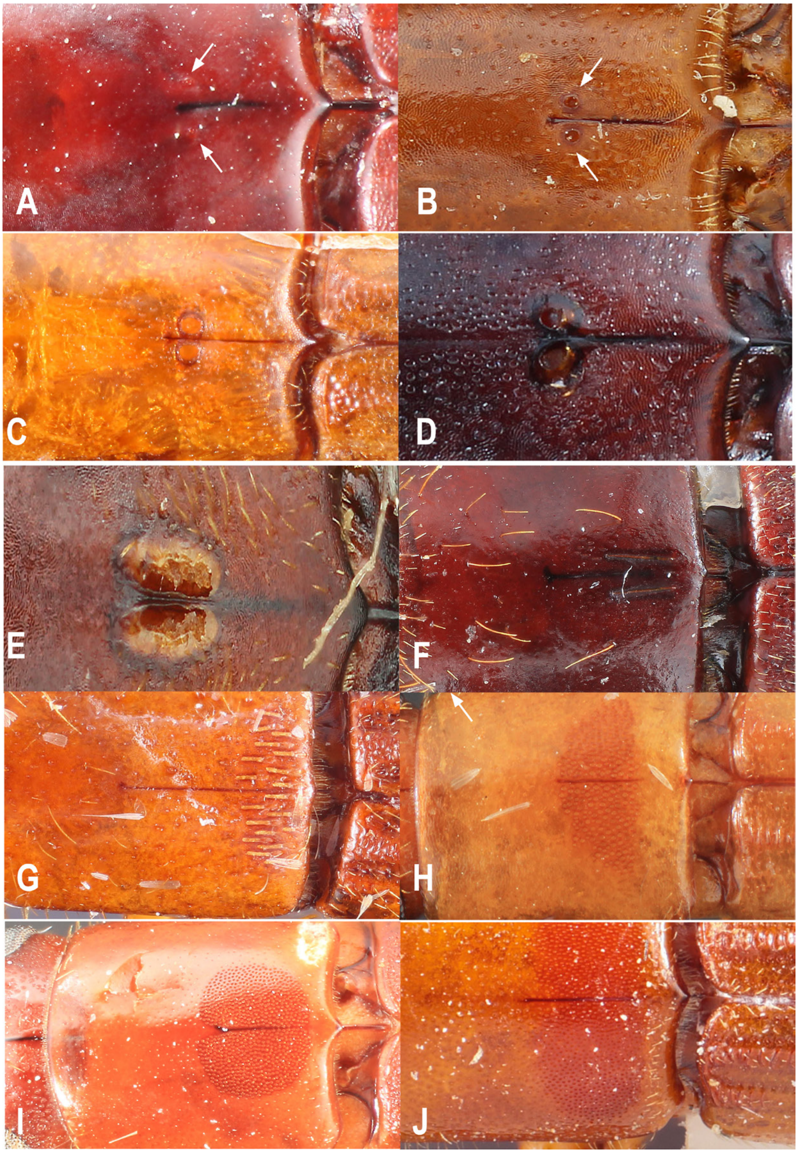

FIGURE 4. Examples of pronotal pores in females. The numbers, sizes, and positions of mycangial pores on the pronotum can aid in identifying females to species. **A.** *Neotrachyostus obliquus* Wood, 1966. There are several tiny pores on either side of the midline in females of *Neotrachyostus*, scarcely visible in the photo. **B.** *Euplatypus compositus* (Say, 1823). **C.** *Euplatypus* sp., from Chiapas, Mexico. **D.** *Euplatypus pini* (Hopkins, 1905). The position relative to the midline and to the mucro as well as the spacing between the pores differentiate this species from the previous two. **E.** *Euplatypus otiosus* (Schedl, 1936). The oblong shape and relatively large, subcontiguous pores of this species are unique. **F.** *Tesserocerus simulatus* (Schedl, 1936). Though the species is generally quite similar to other *Tesserocerus* species, these parallel long slits are quite unique. **G.** *Tesserocerus spinax* Blandford, 1896. The patterns of short slit-like pores in *Tesserocerus* are species-specific for both sexes. **H.** *Cenocephalus lalolaensis* Nunberg, 1963. **I.** *Cenocephalus* sp., the female of an undescribed species from Mexico. The patterns of dense tiny pores on the female pronotum in *Cenocephalus* are species-specific, though females of this genus can usually be easily separated by a variety of characters. **J.** *Cenocephalus robustus* Schedl, 1966. Photos by T.H. Atkinson.

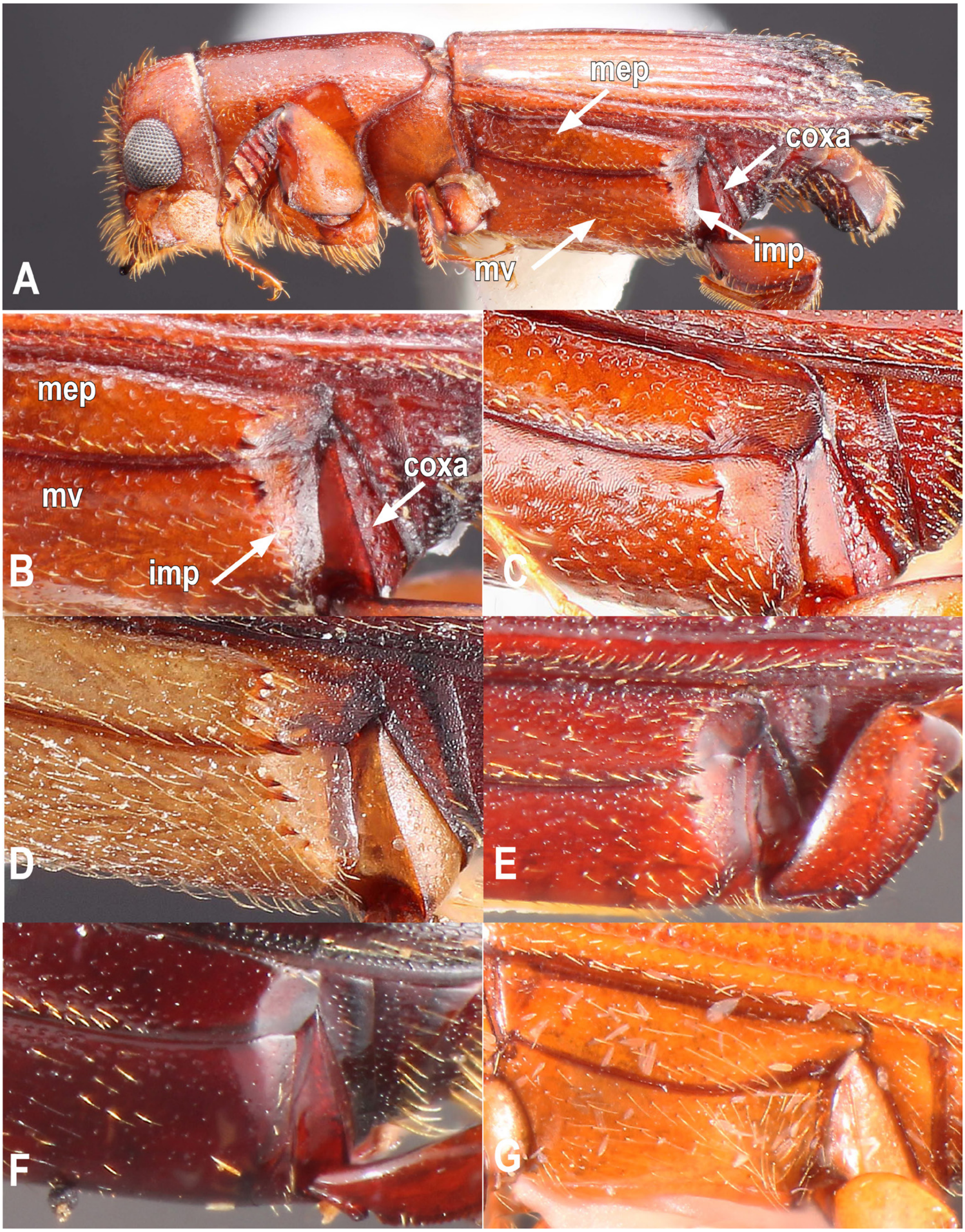

FIGURE 5. Variability of the metanepisternum-metaventrite (m-m) character: Lateral views of the thorax showing the metanepisternum (mep), metaventrite (mv), metacoxa (coxa) and impression (imp). The m-m character is the number of teeth or small carinae on the anterior margin of the impression. The figures are of males; any teeth or carinae are usually smaller and indistinct or absent in conspecific females. **A.** *Euplatypus parallelus* (Fabricius, 1801), lateral view. **B.** Same *E. parallelus,* closer view. **C.** *Euplatypus trispinatus* (Schedl, 1952). **D**. *Megaplatypus discicollis* (Chapuis, 1865). **E**. *Megaplatypus ramali* (Schedl, 1940). **F**. *Megaplatypus occipitalis* (Chapuis, 1865), an example of a Platypodini species with no bordering teeth or carinae. **G**. *Tesserocerus dewalquei* Chapuis, 1865: no Tesserocerini have teeth or carinae on the border of the impression, in either sex. Photos by T.H. Atkinson.

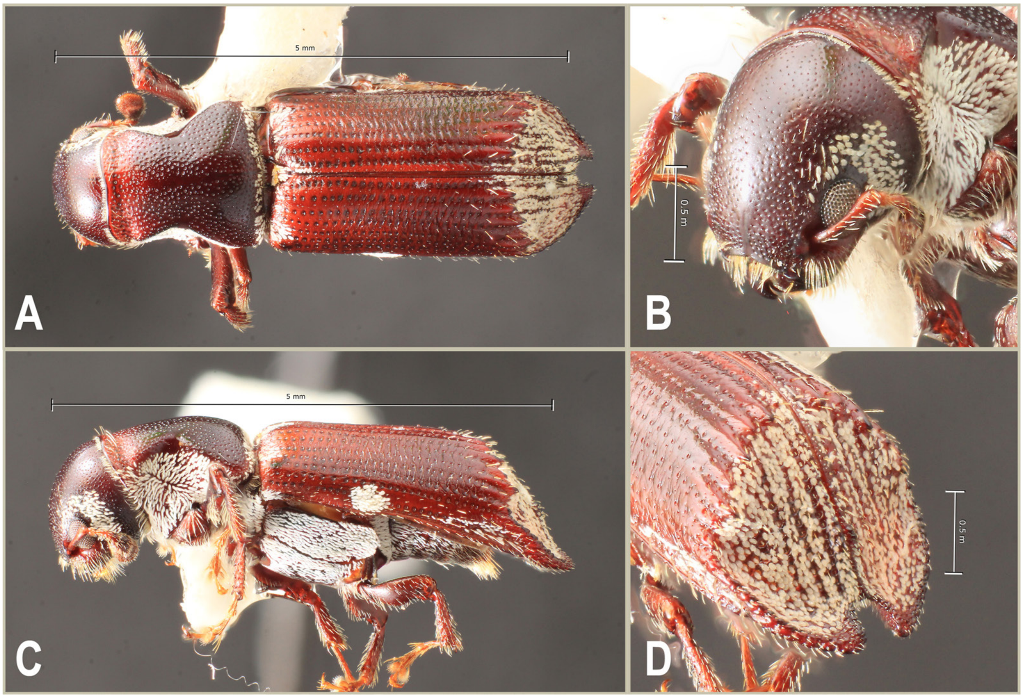

FIGURE 6. *Schedlarius mexicanus* (Duges, 1885). Male habitus (**A–D**). **A**. Dorsal view. **B**. Lateral view. **C**. Frontal view, illustrating frons and antenna. **D**. Declivity. Photos by T.H. Atkinson.

narrower, more narrowly rounded above, and more distinct in Platypodini. Further, in Platypodini, the impression formed by the femoral groove results in a notch in the side of the pronotum when viewed from above (Figure 8C, "fg"). In all *Tesserocerus* and most *Cenocephalus* the lateral margins of the pronotum appear straight when viewed from above (Figure 8A). For more details on the morphological differences between Tesserocerini and Platypodini, see Wood (1993) and Jordal (2014).

In our experience, the only genera an inexperienced researcher is likely to confuse with respect to tribal placement are *Cenocephalus* (Tesserocerini) and *Costaroplatus* (Platypodini). The mouthparts, m-m character (small teeth on the margins of the impression in *Costaroplatus*), shape of the scape, and shape of the femoral groove should allow proper assignment.

Schedlariini genera

The only genus in the tribe, *Schedlarius*, was established for the quite unique species *Schedlarius mexicanus* (Figure 6). This species breeds exclusively in *Bursera* (Burseraceae) in seasonally dry tropical forests and has only been collected in Mexico and Central America (south to Costa Rica). No similar species have yet been found, and we have not seen remarkable morphological variation in this species.

Tesserocerini genera

The three current Neotropical genera in Tesserocerini are quite distinct from one another and from their African counterparts (Wood 1993). *Tesserocerus* and *Cenocephalus* each consist of several species groups separable by adult morphology, groups that perhaps should be considered separate genera.

Tesserocranulus Schedl is monotypic, and *T. nevermanni* Schedl is readily identified from photographs (Figure 9). The extremely elongate form reminds one of brood parasites of ambrosia beetles, but the biology of *Tesserocranulus* is unknown. It is often collected at lights or in light traps (Table 5), so it may be nocturnal.

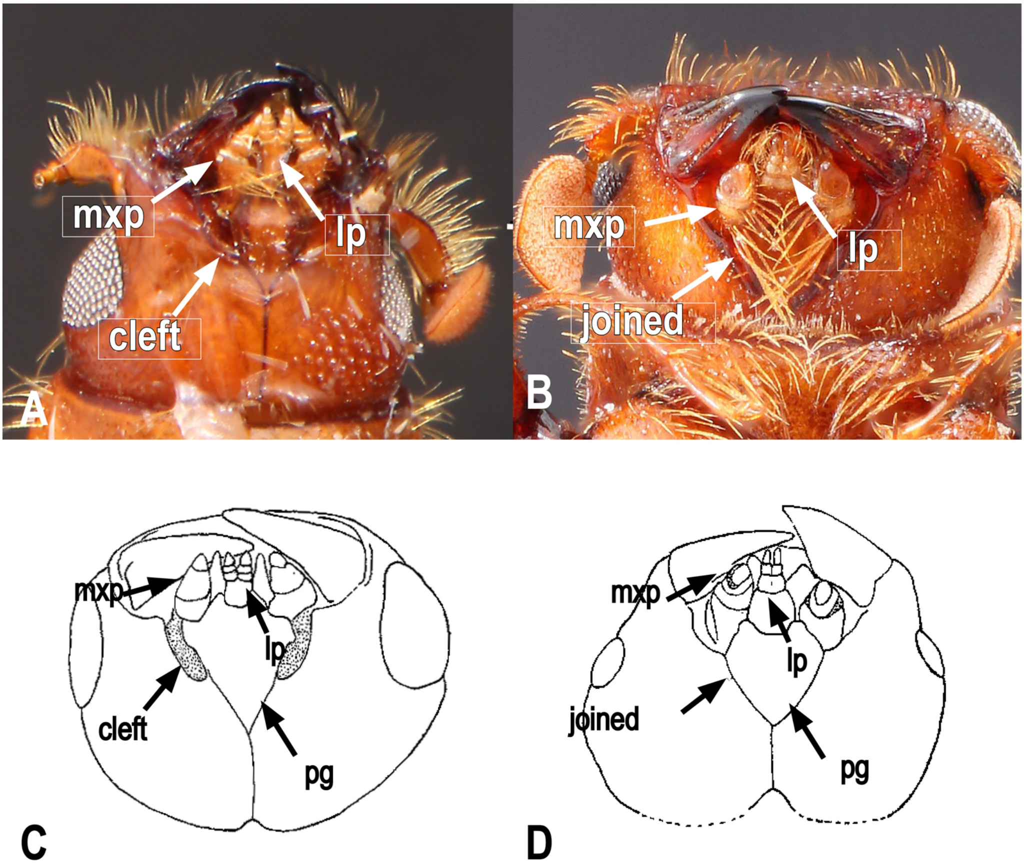

FIGURE 7. Characters of the underside of the head that are used in separating the Tesserocerini and Platypodini tribes: mouthparts, *lp* = labial palp, *pg* = pregular sutures; *cleft*, an elongate opening that is larger in Tesserocerini than Platypodini. **A.** *Tesserocerus dewalquei* Chapuis, 1865) female; **B.** *Euplatypus parallelus* (Fabricius, 1801, male; **C.** *Tesserocerus dewalquei*, female; **D.** *Euplatypus parallelus*, male. **C** and **D** modified from Wood (1993, Figs. 4 and 5). See text for details.

Tesserocerus Saunders is the largest of the three genera in the Neotropics, with 26 described species and 41 species we believe to be new (Table 2). There are three distinct groups of species in the genus: the *dewalquei* species group, with quite distinct sexes (Figure 10); the *belti* group, with female-like males (Figure 11); and the *spinax* group, with male-like females (Figure 12). Most species are in the *dewalquei* group, including the type species of the genus *T. insignis* (Saunders). The *belti* group comprises only four described and possibly five undescribed species, the *spinax* group three described and three undescribed species. The sexes in the *dewalquei* and *spinax* groups are dimorphic but in a consistent manner, and conspecific males and females can usually be matched when both are present in a collection. They are different enough, though, that early in his career Karl Schedl described the female of *Tesserocerus spinax* Blandford as a separate species, *T. forficula* Schedl. Species in these two groups differ especially in characters of the male declivity and the female head and antennal scape, but also in body size. Males and females of the species in the small *belti* group are extremely similar; species differ in head and declivity characters, as well as body size. In all three groups, species and sexes differ in the shape of the patterns formed by patches of tiny mycangial pores on the pronotum. Interspecific differences

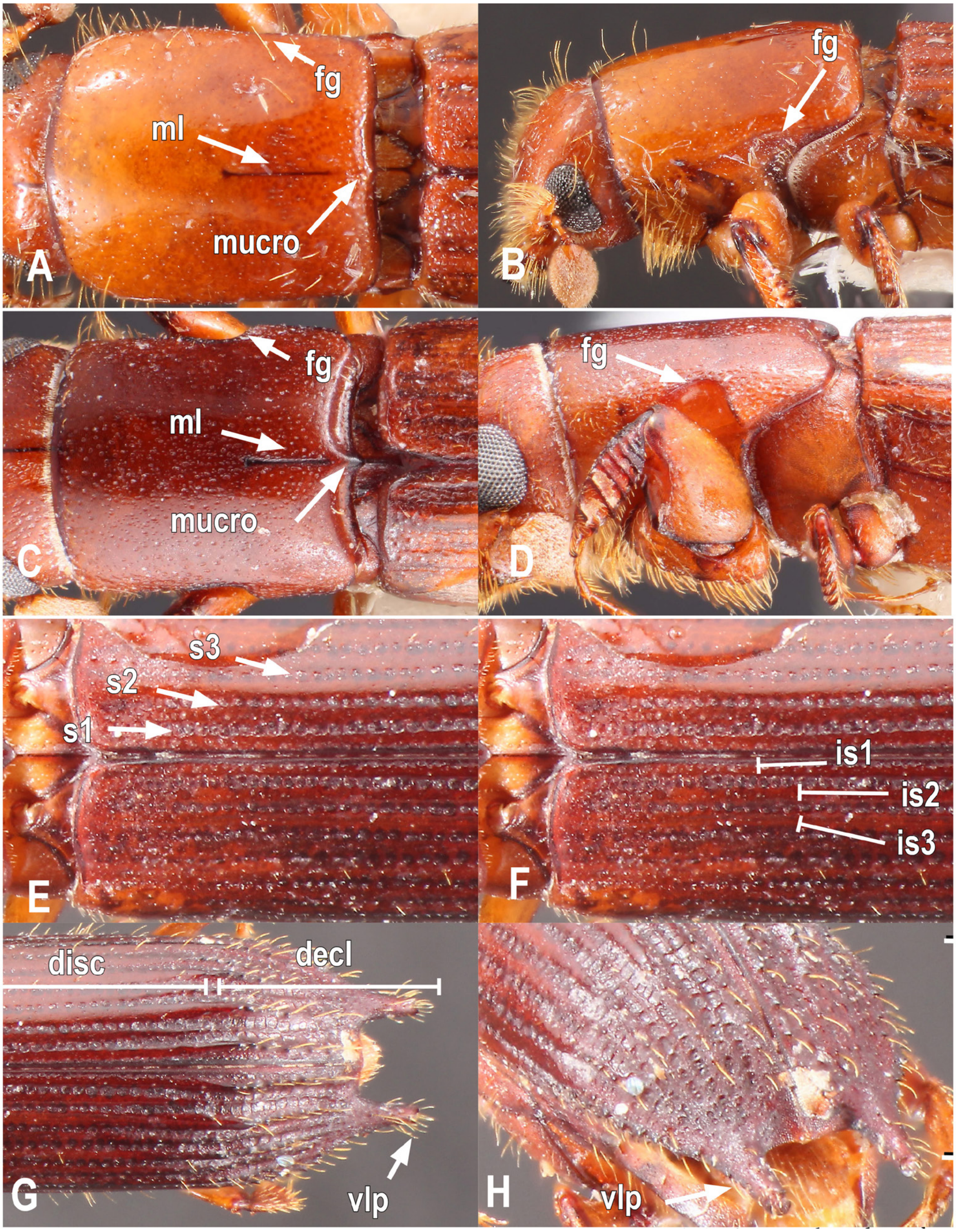

FIGURE 8. Terminology for characters useful for separating taxa. **A–D.** Features of the pronotum: *ml* = midline, which marks a central sulcus on the distal portion of the pronotum; *mucro* = the obtuse point in the middle of the posterior margin; *fg* = femoral groove, a large impression on the side of the pronotum that receives the femur of the first pair of legs. **E–F.** Features of the elytral disc: s*1*, s*2* and *s3*, striae 1, 2 and 3 (lines of shallow punctures); *is1*, *is2* and *is3*, interstriae 1, 2 and 3, the spaces between striae. **G–H.** Features of the elytra: *disc*, the flat portion of the elytra; *decl* = declivity, the sloping ends of the elytra; *vlp* = ventrolateral projection, referring to variously shaped protruding features arising from the corners of the apex of the declivity. **A–B.** *Tesserocerus dewalquei* Chapuis, 1865, male; **C–D.** *Euplatypus parallelus* (Fabricius, 1801, male; **E–H.** *Euplatypus alternans* (Chapuis, 1865), male. Photos by T.H. Atkinson.

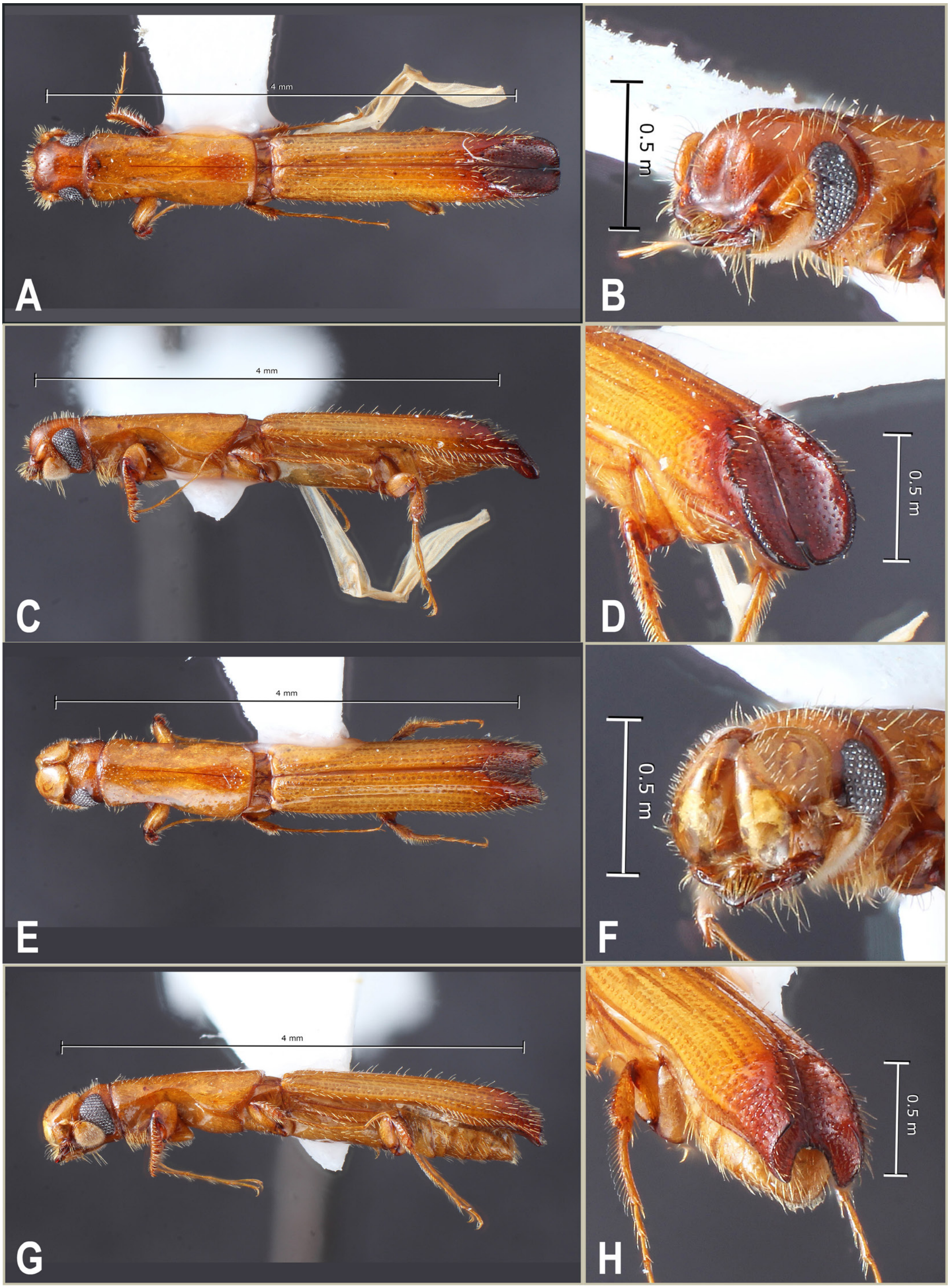

FIGURE 9. *Tesserocranulus nevermanni* Schedl, 1933. Male habitus (**A–D**). **A**. Dorsal view. **B**. Lateral view. **C**. Frontal view, illustrating frons and antenna. **D**. Declivity. Female habitus (**E–H**). **E**. Dorsal view. **F**. Lateral view. **G**. Frontal view, illustrating frons and antenna. **H**. Declivity. Photos by T.H. Atkinson.

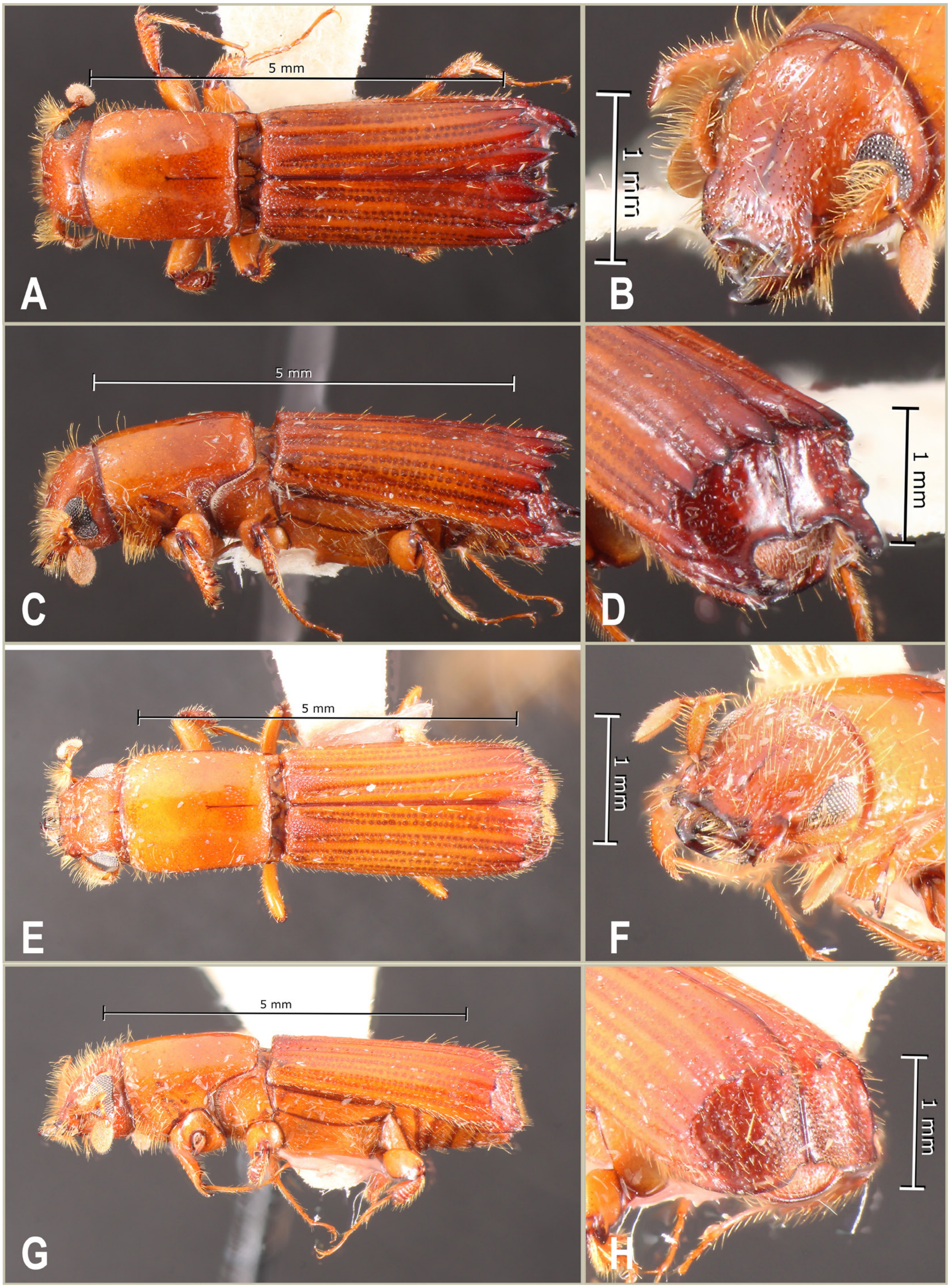

FIGURE 10. *Tesserocerus dewalquei* Chapuis, 1865. Male habitus (**A–D**). **A**. Dorsal view. **B**. Lateral view. **C**. Frontal view, illustrating frons and antenna. **D**. Declivity. Female habitus (**E–H**). **E**. Dorsal view. **F**. Lateral view. **G**. Frontal view, illustrating frons and antenna. **H**. Declivity. Photos by T.H. Atkinson.

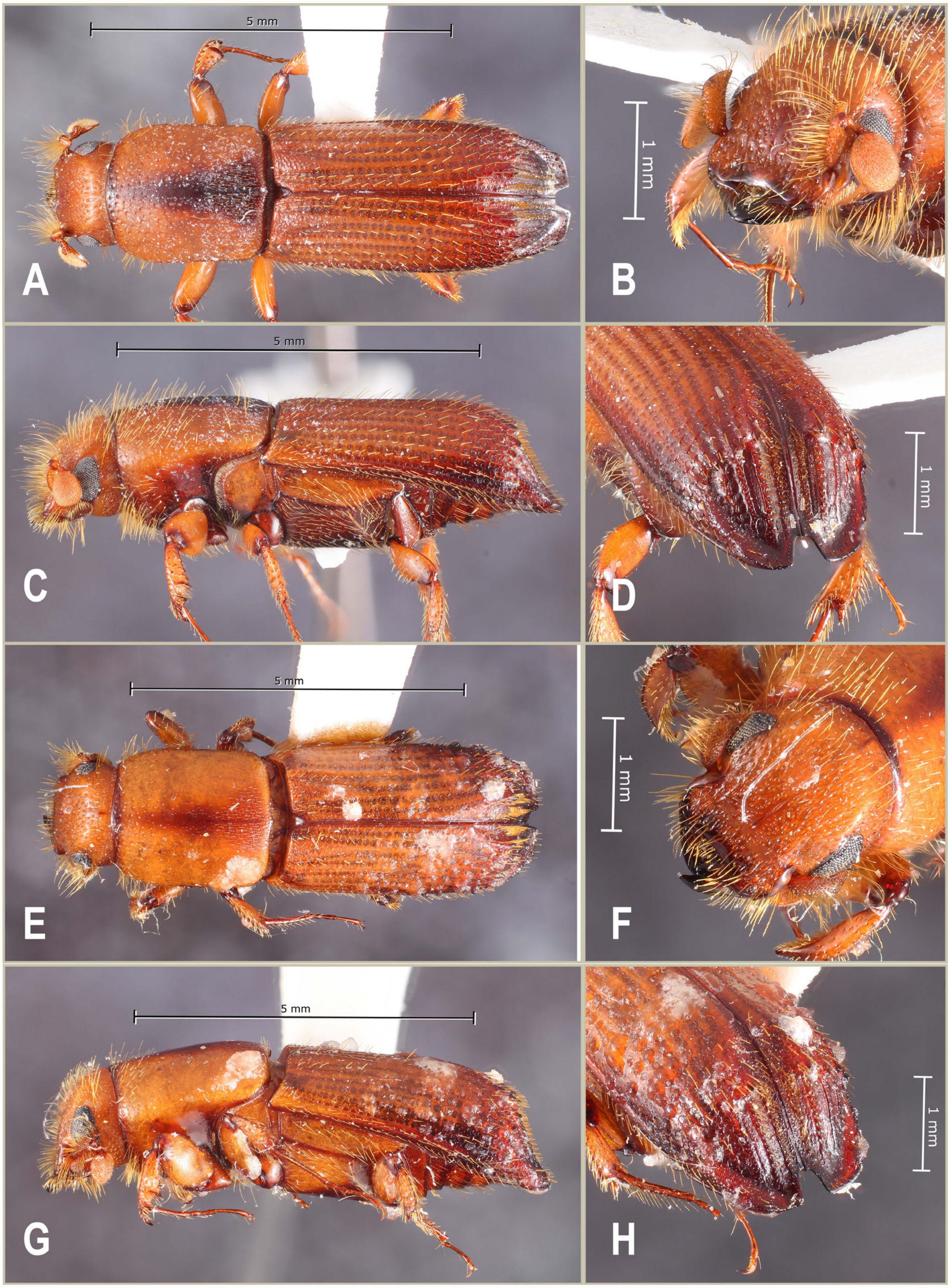

FIGURE 11. *Tesserocerus inermis* Guérin-Méneville, 1838. Male habitus (**A–D**). **A**. Dorsal view. **B**. Lateral view. **C**. Frontal view, illustrating frons and antenna. **D**. Declivity. Female habitus (**E–H**). **E**. Dorsal view. **F**. Lateral view. **G**. Frontal view, illustrating frons and antenna. **H**. Declivity. Photos by T.H. Atkinson.

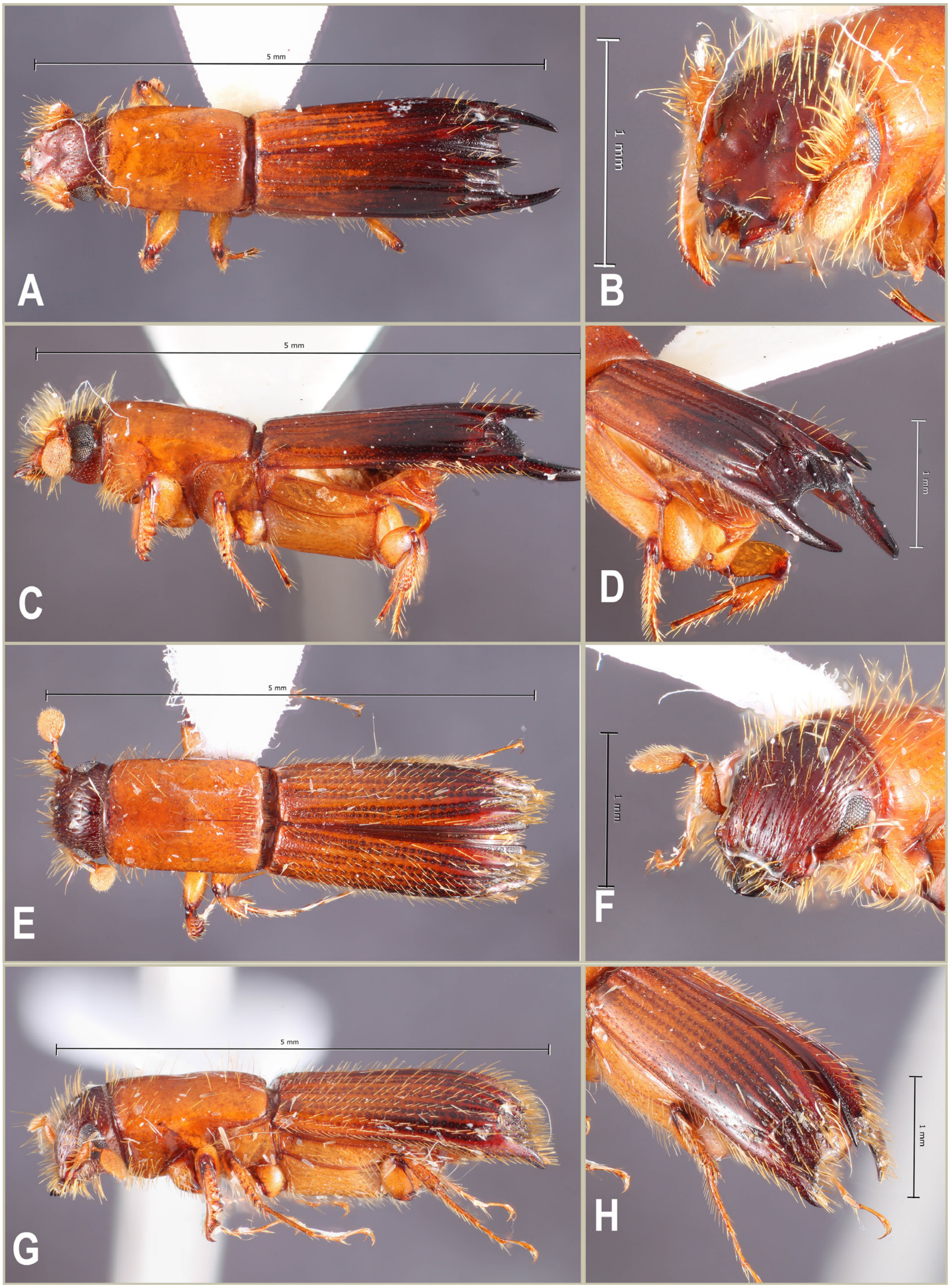

FIGURE 12. *Tesserocerus spinax* Blandford, 1896. Male habitus (**A–D**). **A**. Dorsal view. **B**. Lateral view. **C**. Frontal view, illustrating frons and antenna. **D**. Declivity. Female habitus (**E–H**). **E**. Dorsal view. **F**. Lateral view. **G**. Frontal view, illustrating frons and antenna. **H**. Declivity.

among females in the *spinax* and *belti* groups are large enough that females can be identified to species and new species of *Tesserocerus* can be safely described from females when males are not known. We are not sure if describing new species only from females is possible for the *dewalquei* group, however, where interspecific differences other than body size can be quite small.

Cenocephalus Chapuis is a fairly large genus, comprising 10 described and 20 undescribed species (Table 2). Sexes are strongly dimorphic. Males differ in features of the declivity; females differ in head characters—most species have long golden setae arising from the epistoma or borders of the frons, and have a concave frons, but species differ in details. For both sexes, the pattern of mycangial pores is also species specific. As a consequence, *Cenocephalus* species can be safely described from females alone, when males are absent, and females can be safely identified to species. We currently divide them into three species groups: species similar to *C. pulchellus* Schedl (Figure 13); species similar to *C. lalolaensis* Nunberg (Figure 14), and a few species similar to *C. thoracicus* Chapuis (not illustrated here, but see photos on Atkinson 2023).

Platypodini genera

Current boundaries among American genera of the young tribe Platypodini were drawn by Wood in his 1993 revision of world genera. Characters delimiting these genera (Table 4) were described in the brief discussions of each genus and in the key to genera. The descriptions of genera include a mixture of character traits only shown by species of that genus (autapomorphies) and traits that have developed similarly in unrelated genera (homoplastic or plesiomorphic traits). As we have gradually familiarized ourselves with the entire breadth of variation in Neotropical platypodines, More and more cases of homoplasy have appeared, creating difficulties for Wood's conceptions of these genera. Wood (1993) separated genera primarily by the armature of the male declivity and by the presence and arrangement of spines on the male venter. We have encountered a disturbingly large number of species (including some already described) with sets of character states that do not fit within Wood's genera as defined. Likewise, limits between some of his genera become blurred when larger numbers of species are considered. A further problem is that females of Neotropical Platypodini are remarkably uniform in general habitus and lack the characters used in males to separate genera. Most cannot be identified to genus if collected alone. In geographically localized areas with low diversity, it can be possible to associate females with males.

We present in Table 4 brief summaries of the key characteristics of the Platypodini genera recognized by Wood. Future revisionary work likely will lead to considerable restructuring of genera. What is needed is integrated taxonomy when molecular data from a broad sampling of species becomes available (Jordal 2015). In Table 4 one can readily see some of the difficulties with Wood's delimitations of American genera of Platypodini. In particular, the frequent usage in his key of caveats such as "usually", "often" or "uncommon" can make identification to genus tricky or impossible using his key. As with certain genera of Xyleborini (Smith et al. 2020, Smith & Cognato 2021), some of Wood's Platypodini genera are defined by combinations of homoplastic and apomorphic character states—and in the case of *Platypus*, solely by homoplastic character states. It should be noted, however, that character states which have evolved more than once within the tribe nonetheless delimit small groups of genera and even can define species within small groups of genera. As is the case with the Xyleborini, a robust generic classification probably cannot be established based on external morphology alone, without molecular support.

Costaroplatus and ***Platyphysus*** were established by Wood (1993) for tiny to medium-sized species with a pair of spines on male ventrite 5 (*Costaroplatus*, as *Platyscapulus* Schedl at the time: Figure 15B) or an inflated male ventrite 5 (*Platyphysus*: Figure 16B). The ventrite 5 character in *Platyphysus* males varies, and in *P. convexus* (Schedl) the ventrite is actually flat. In other features, we can see no consistent differences between these genera, and suspect that more rigorous analysis would result in merging them (see also Kirkendall 2017a). Among other

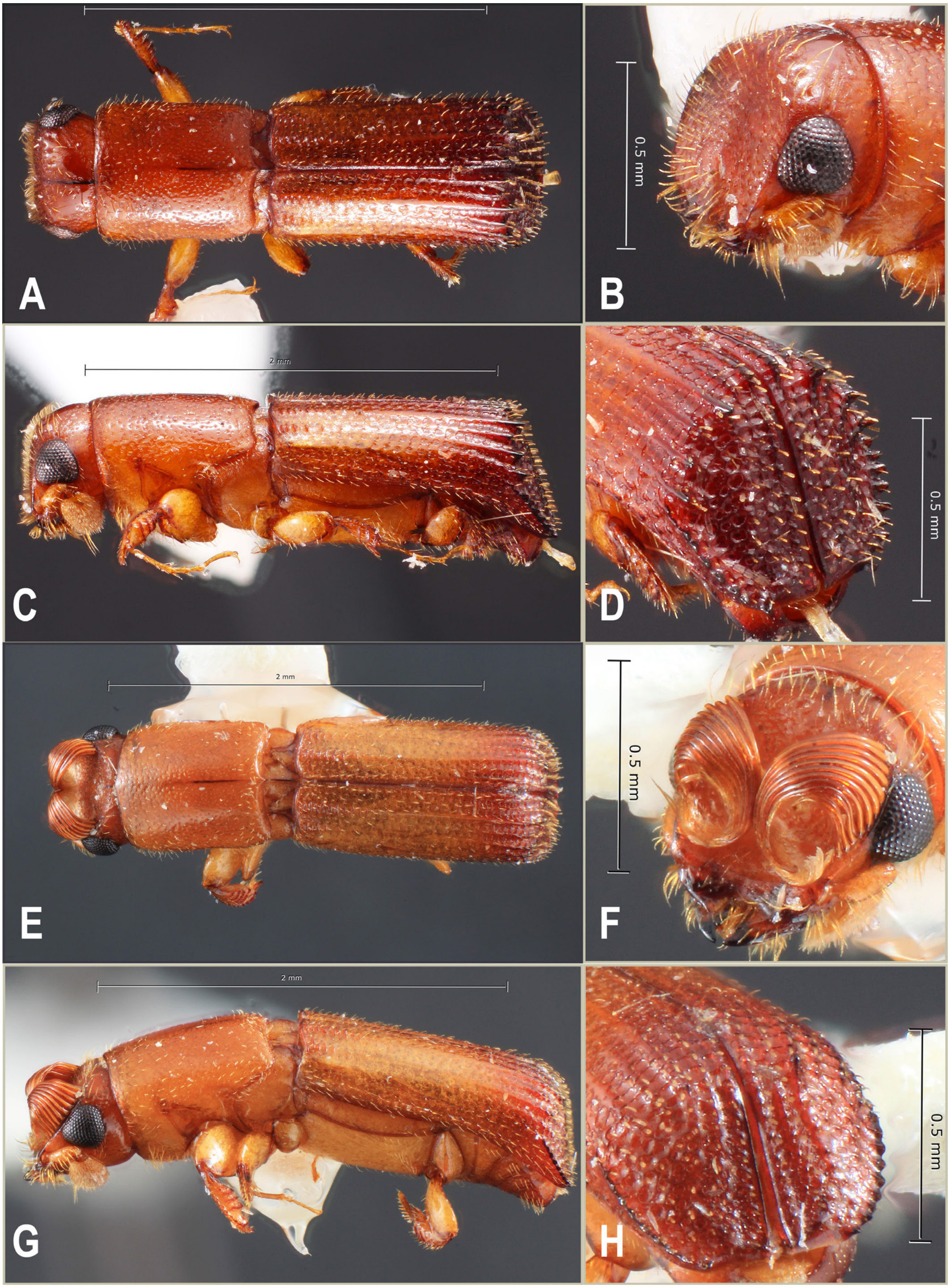

FIGURE 13. *Cenocephalus pulchellus* Schedl, 1935. Male habitus (**A–D**). **A**. Dorsal view. **B**. Lateral view. **C**. Frontal view, illustrating frons and antenna. **D**. Declivity. Female habitus (**E–H**). **E**. Dorsal view. **F**. Lateral view. **G**. Frontal view, illustrating frons and antenna. **H**. Declivity. Photos by T.H. Atkinson.

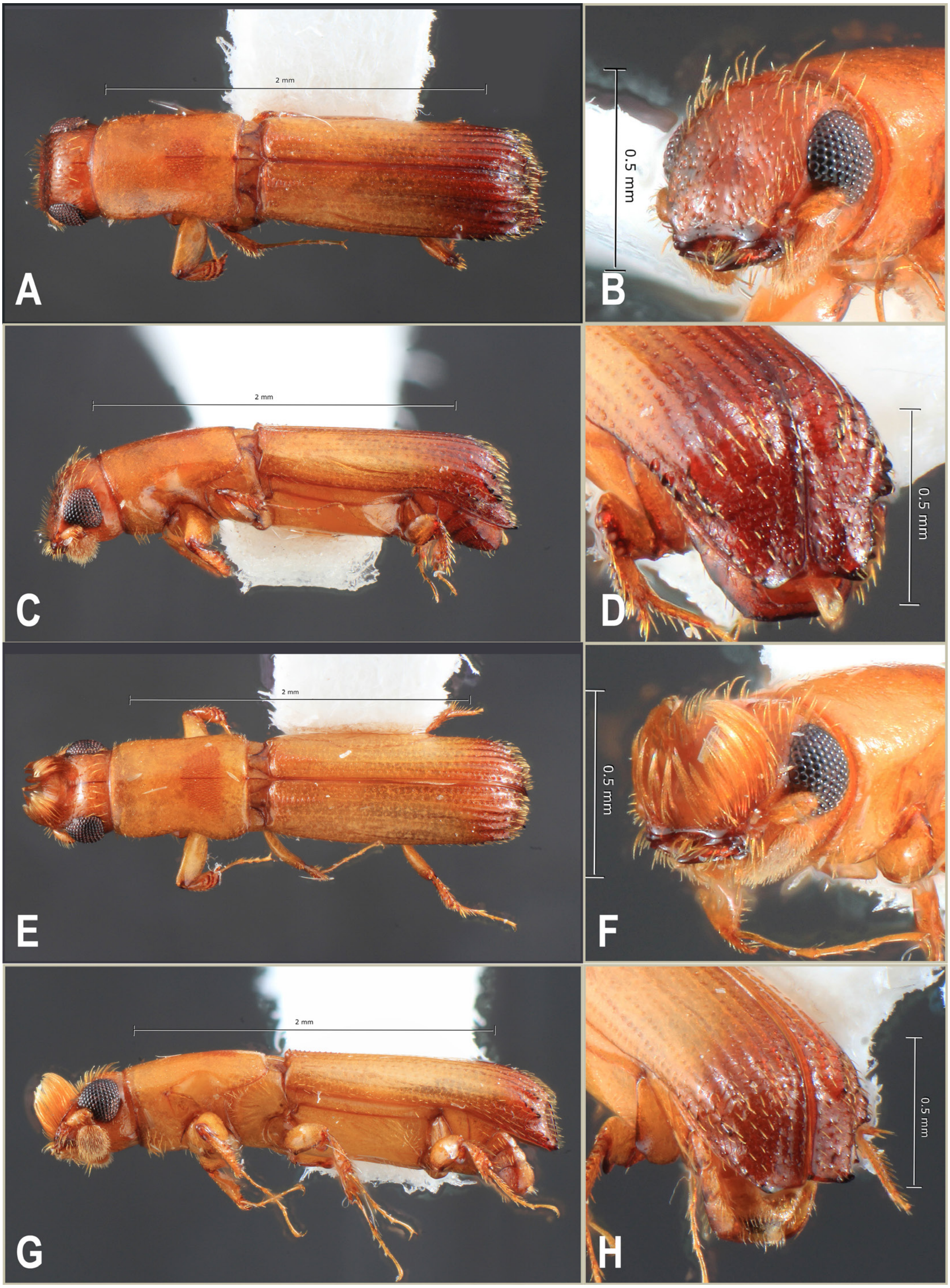

FIGURE 14. *Cenocephalus lalolaensis* Nunberg, 1963. Male habitus (**A–D**). **A**. Dorsal view. **B**. Lateral view. **C**. Frontal view, illustrating frons and antenna. **D**. Declivity. Female habitus (**E–H**). **E**. Dorsal view. **F**. Lateral view. **G**. Frontal view, illustrating frons and antenna. **H**. Declivity. Photos by T.H. Atkinson.

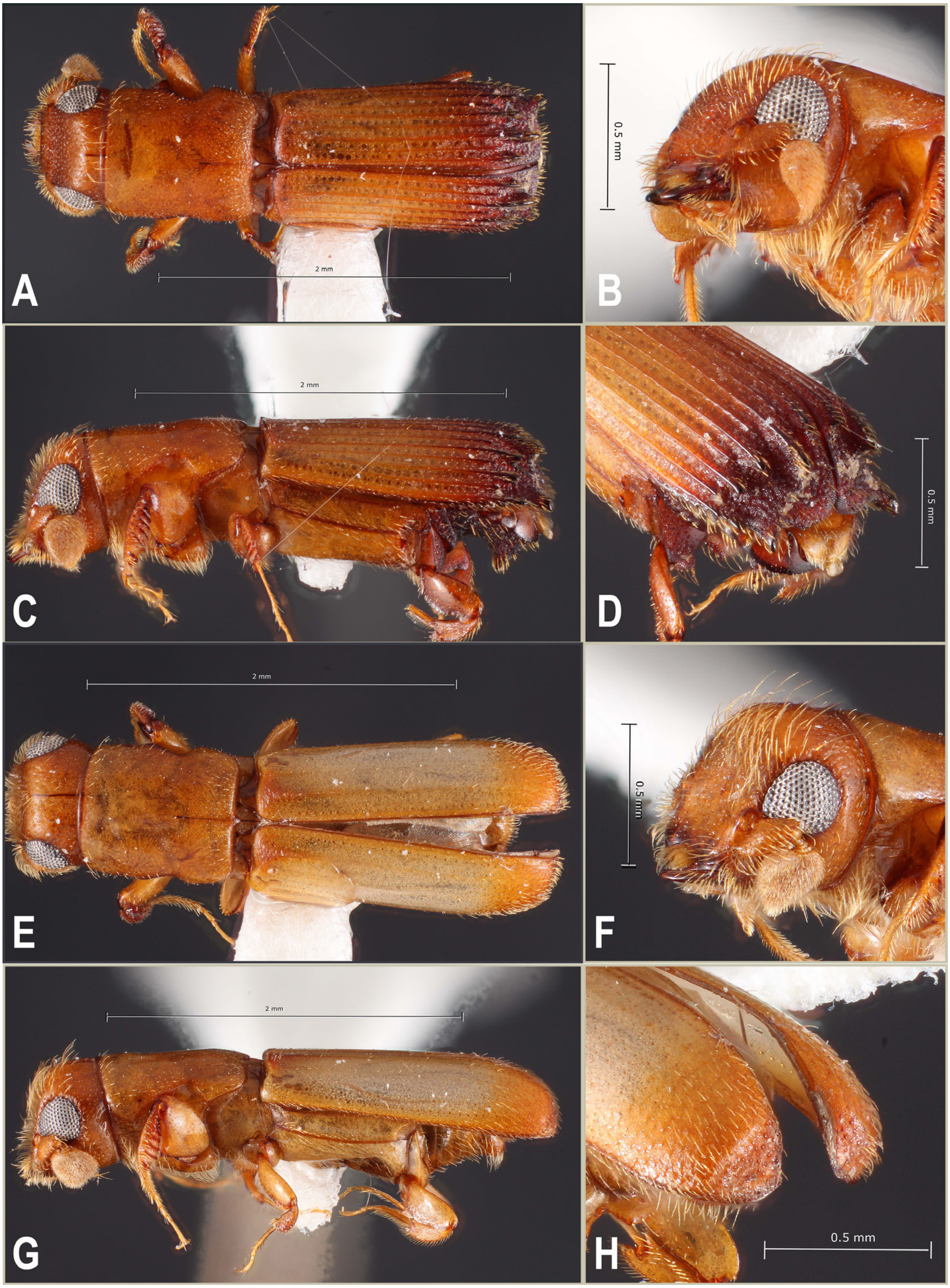

FIGURE 15. *Costaroplatus carinulatus* (Chapuis, 1865). Male habitus (**A–D**). **A**. Dorsal view. **B**. Lateral view. **C**. Frontal view, illustrating frons and antenna. **D**. Declivity. Female habitus (**E–H**). **E**. Dorsal view. **F**. Lateral view. **G**. Frontal view, illustrating frons and antenna. **H**. Declivity. Photos by T.H. Atkinson.

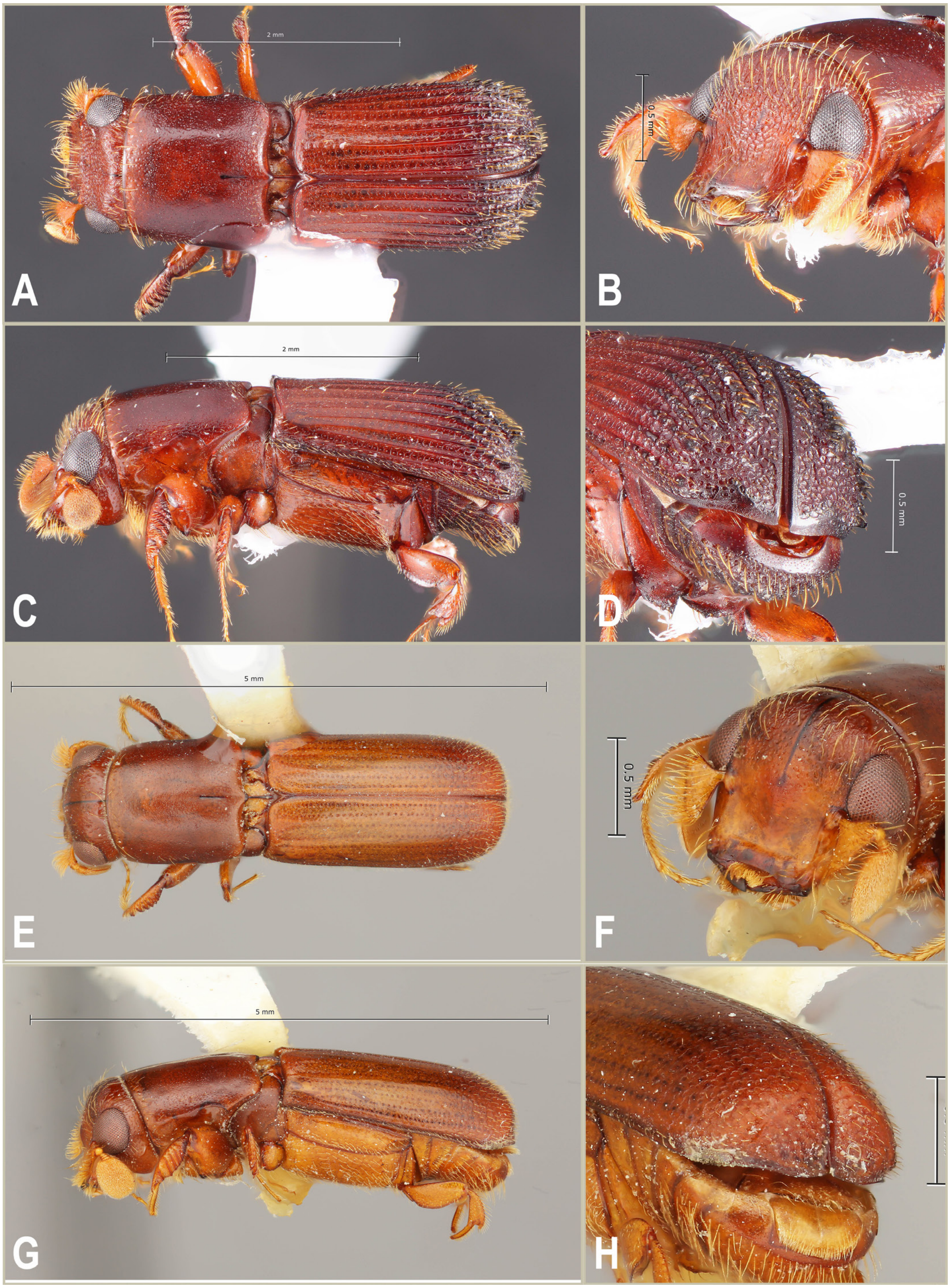

FIGURE 16. *Platyphysus obtusus* (Chapuis, 1865). Male habitus (**A–D**). **A**. Dorsal view. **B**. Lateral view. **C**. Frontal view, illustrating frons and antenna. **D**. Declivity. Female habitus (**E–H**). **E**. Dorsal view. **F**. Lateral view. **G**. Frontal view, illustrating frons and antenna. **H**. Declivity. Photos by T.H. Atkinson.

similarities, the species in these genera have a distinctive combination of a concave lower frons in both sexes (less concave in males) and a triangular to subquadrate, relatively large scape.

Epiplatypus Wood contains small, slender species and is one of two Platypodini genera with with considerably more undescribed than described species (Table 2). Small or large paired mycangial pores on the pronotum are common for females but found on males as well in some species (see Figure 17A,E). There are a few species that seem to be intermediate between *Teloplatypus* and *Epiplatypus*, and *Epiplatypus spectus* (Wood) is quite similar to *T. concinnulus*, so these genus boundaries require further study. Most species have an m-m formula of 1 / 0, while most species of *Teloplatypus* have a formula of 2 / 1.

The large genus ***Euplatypus*** is found throughout the Neotropical region, including montane areas of Mexico. *E. pini* (Hopkins) is associated with pines in the mountains of Central America and Mexico, reaching its northernmost extension in southern Arizona and western Texas. As currently understood, *E. compositus* (Say) may be restricted to the southeastern United States but may be conspecific with populations from Mexico and northern South America. Species in this genus are generally medium to large in size. In many species the females have paired tiny mycangial pores on the pronotum which are usually absent in males. The genus can be tentatively divided into two groups. Males of species resembling *E. longulus* (Figure 18A–D) have odd numbered elytral interstriae continuing down the declivity and have peg-line projections from the ventrolateral angles (the lower corners). The m-m formula for this species group is 0 / 0. Males of species like *E. parallelus* (Figure19A–D) have elytral interstriae 1 ending in a knob or short blunt spine at the top of the declivity; the anterolateral projections usually have three teeth. The m-m impression has teeth or short carinae, at least one in total, usually no more than 2 on either segment, the most frequent formula being 2 / 1. The two groups also differ consistently in the shape of the antennal funicle.

Megaplatypus Wood is the most speciose Platypodinae genus in the Americas and includes the largest species within the tribe Platypodini, though the size range overlaps considerably with that of *Euplatypus*. There is considerable variation in the morphology of species Wood assembled into this genus, including in the m-m character. Two quite different forms are exemplified by *M. discicollis* (Chapuis) (Figure 20) and *M. quinquecostatus* (Chapuis) (Figure 21). In the former, the male declivity is quite simple, nearly female-like in its lack of features. The latter is typical of a large group of species in which the odd interstriae of the elytra end in strong knobs or teeth atop the declivity, while the ventrolateral angles are modified into strong protrusions. While *M. quinquecostatus* and closest relatives typically have an m-m formula of 1 / 0, the m-m formula for the *discicollis* species group is (3-4) / (3-4). Deeper study will likely result in breaking this genus up into several more coherent genera.

Myoplatypus Wood comprises a small number of what are mostly rarely collected species that are largely found at elevations above 1000 m (Kirkendall & Atkinson 2023). Several seem to be restricted to breeding in oaks (*Quercus* species). *Myoplatypus* are slender pinhole borers that superficially resemble *Epiplatypus* but have males that have a transverse pair of large spines on ventrite 3 (Figure 22B). With one exception, females of *Myoplatypus* lack the paired mycangial pores found on the pronotum of *Epiplatypus* species.

The genus ***Neotrachyostus*** was established by Browne (1962b) for two Chapuis species groups that were then in the Afrotropical genus *Trachyostus* Schedl. Unlike most other Platypodini, *Trachyostus* and *Neotrachyostus* have sexually dimorphic protibiae, with the typical strong transverse rugae on the outer (posterior) surface largely replaced by numerous small granules or irregular short, low rugae in females (compare Figures 23B,G). The phylogenetic value of having sexually dimorphic protibiae is unclear, as it is shared with the unrelated Old World genus *Crossotarsus* and with some Neotropical species currently in *Euplatypus*. Browne (1962b) and Wood (1993) also state that females of *Neotrachyostus* have tiny mycangial pores on either side of the upper (anterior) end of

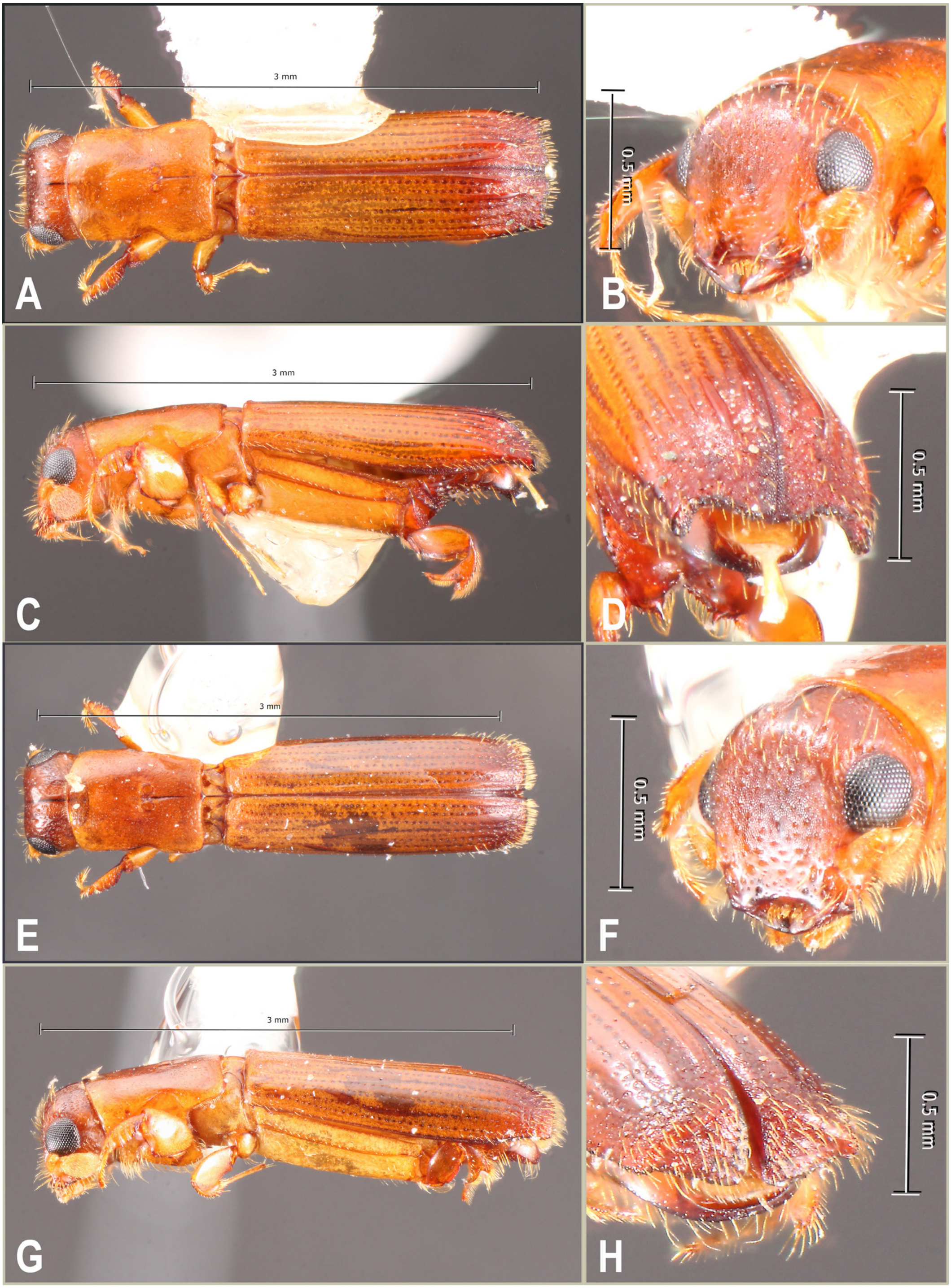

FIGURE 17. *Epiplatypus annexus* (Wood, 1966). Male habitus (**A–D**). **A**. Dorsal view. **B**. Lateral view. **C**. Frontal view, illustrating frons and antenna. **D**. Declivity. Female habitus (**E–H**). **E**. Dorsal view. **F**. Lateral view. **G**. Frontal view, illustrating frons and antenna. **H**. Declivity. Photos by T.H. Atkinson.

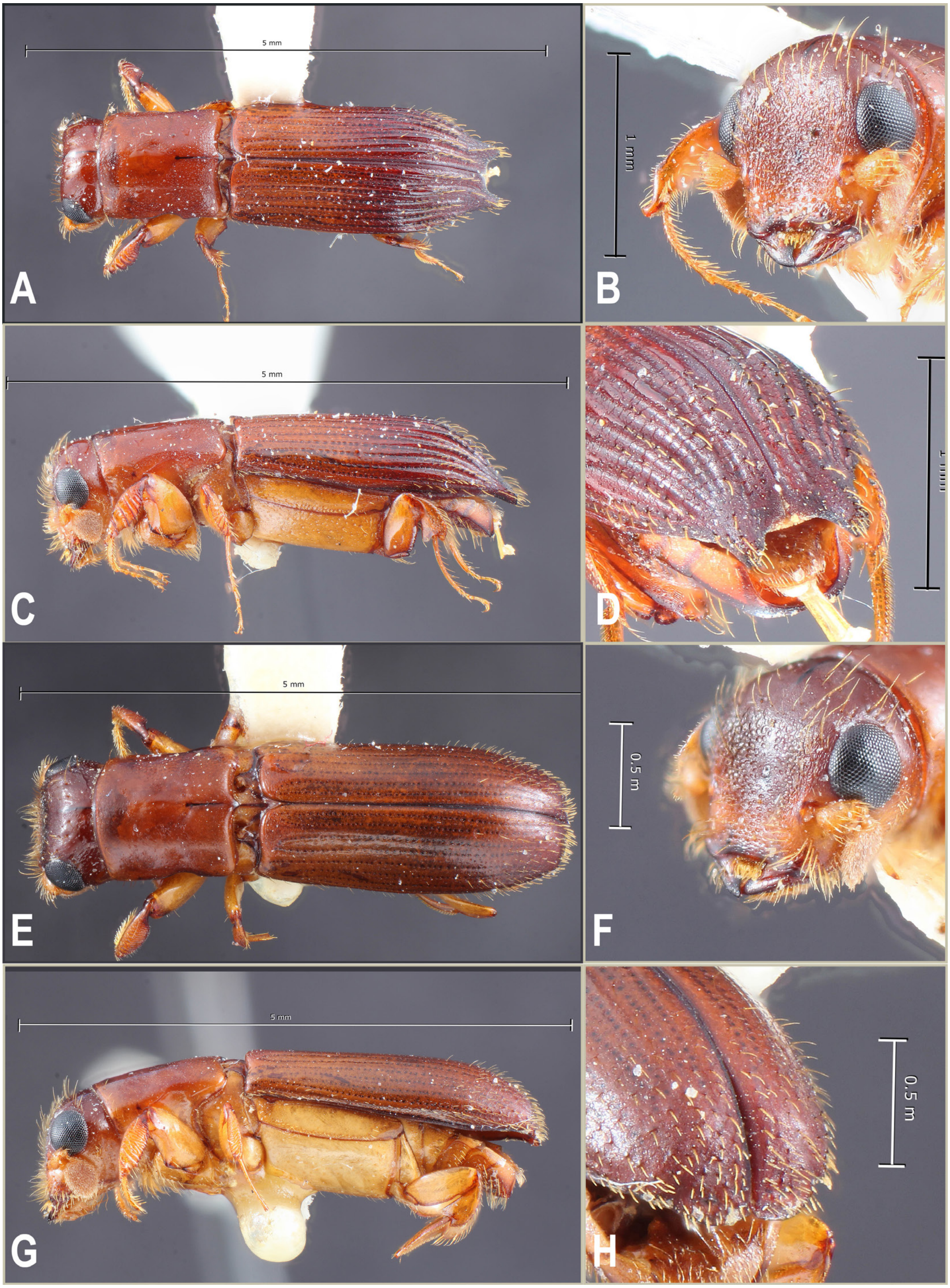

FIGURE 18. *Euplatypus longulus* (Chapuis, 1865). Male habitus (**A–D**). **A**. Dorsal view. **B**. Lateral view. **C**. Frontal view, illustrating frons and antenna. **D**. Declivity. Female habitus (**E–H**). **E**. Dorsal view. **F**. Lateral view. **G**. Frontal view, illustrating frons and antenna. **H**. Declivity. Photos by T.H. Atkinson.

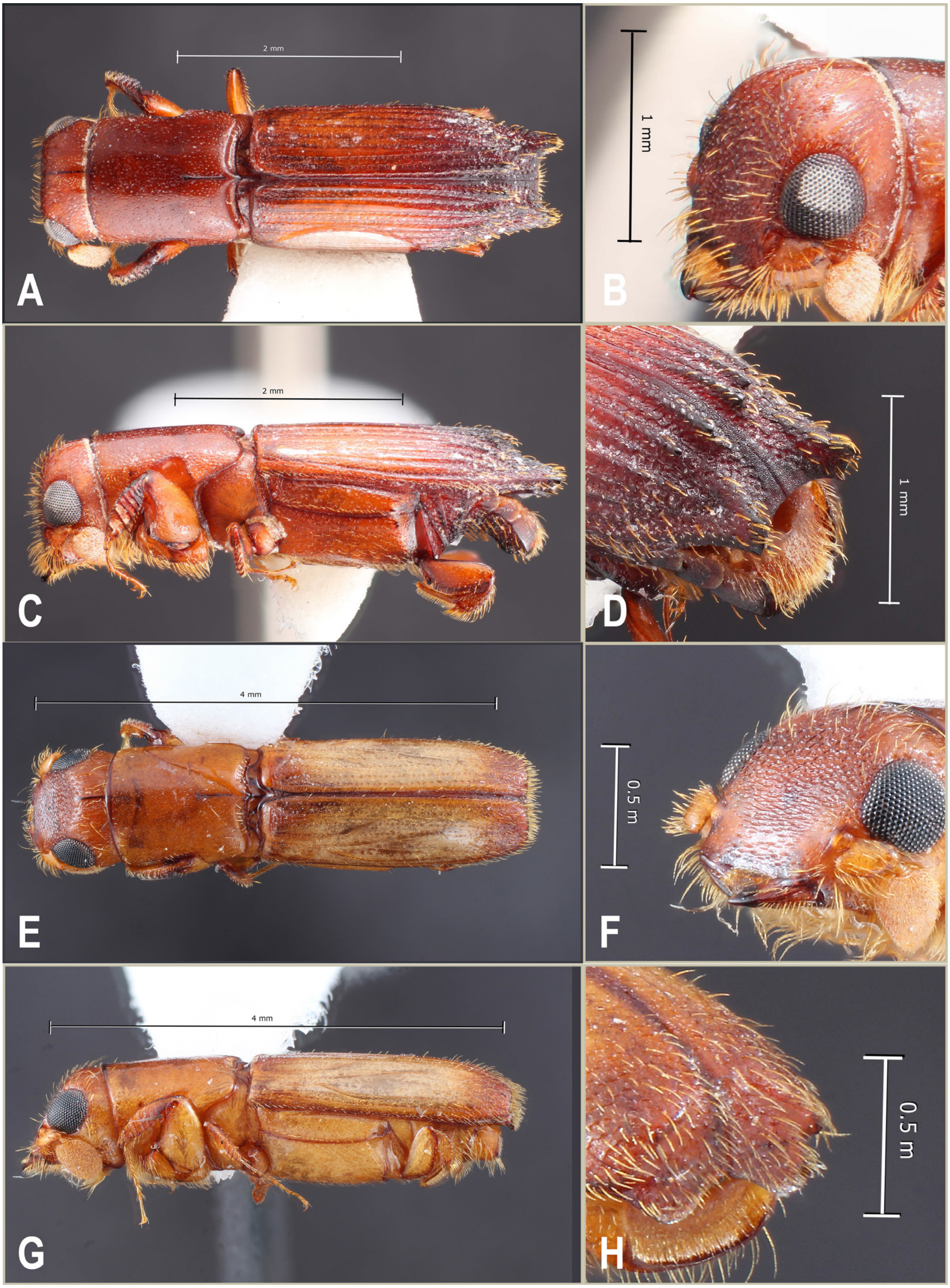

FIGURE 19. *Euplatypus parallelus* (Fabricius, 1801). Male habitus (**A–D**). **A**. Dorsal view. **B**. Lateral view. **C**. Frontal view, illustrating frons and antenna. **D**. Declivity. Female habitus (**E–H**). **E**. Dorsal view. **F**. Lateral view. **G**. Frontal view, illustrating frons and antenna. **H**. Declivity. Photos by T.H. Atkinson.

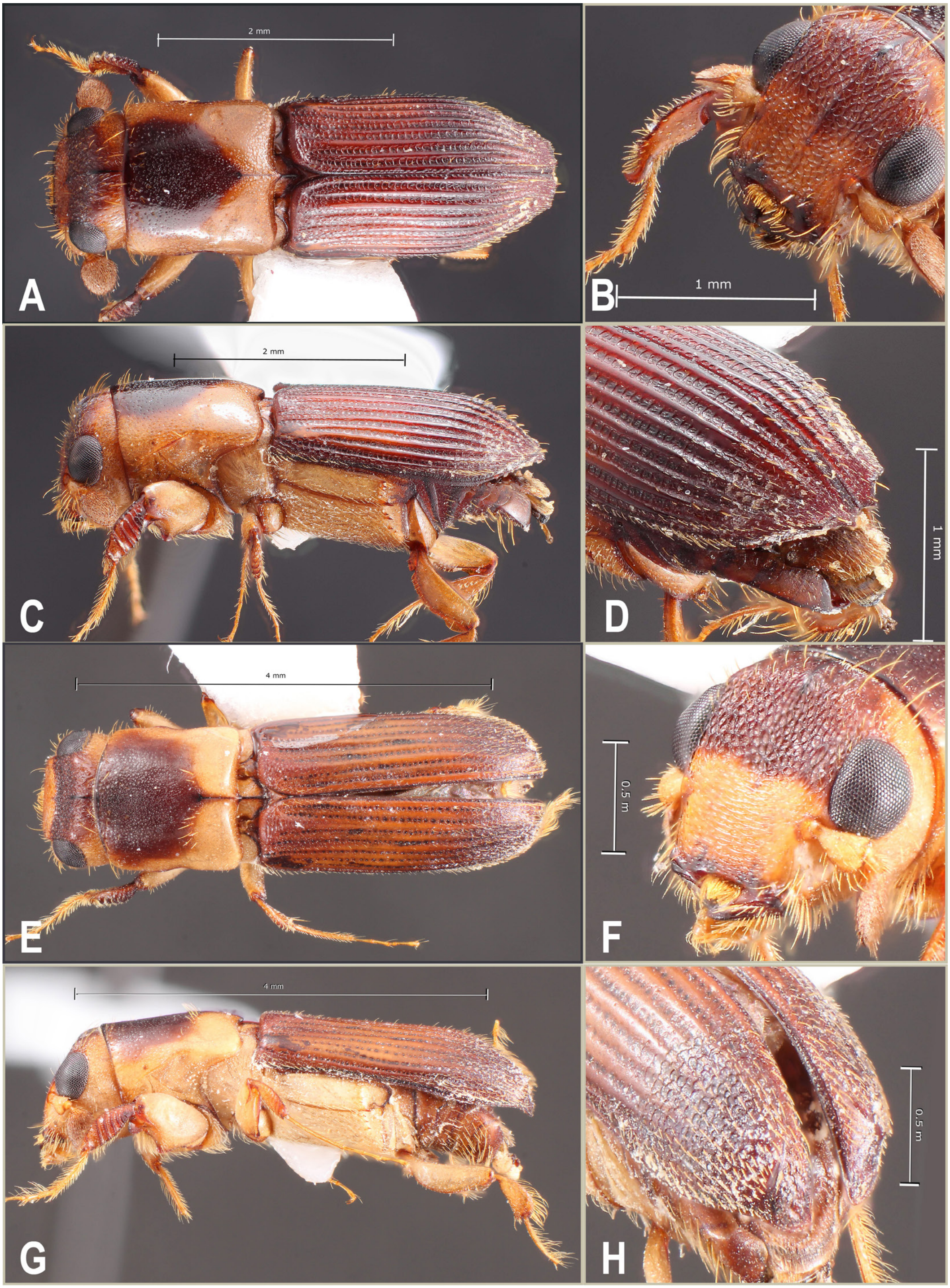

FIGURE 20. *Megaplatypus discicollis* (Chapuis, 1865). Male habitus (**A–D**). **A**. Dorsal view. **B**. Lateral view. **C**. Frontal view, illustrating frons and antenna. **D**. Declivity. Female habitus (**E–H**). **E**. Dorsal view. **F**. Lateral view. **G**. Frontal view, illustrating frons and antenna. **H**. Declivity. Photos by T.H. Atkinson.

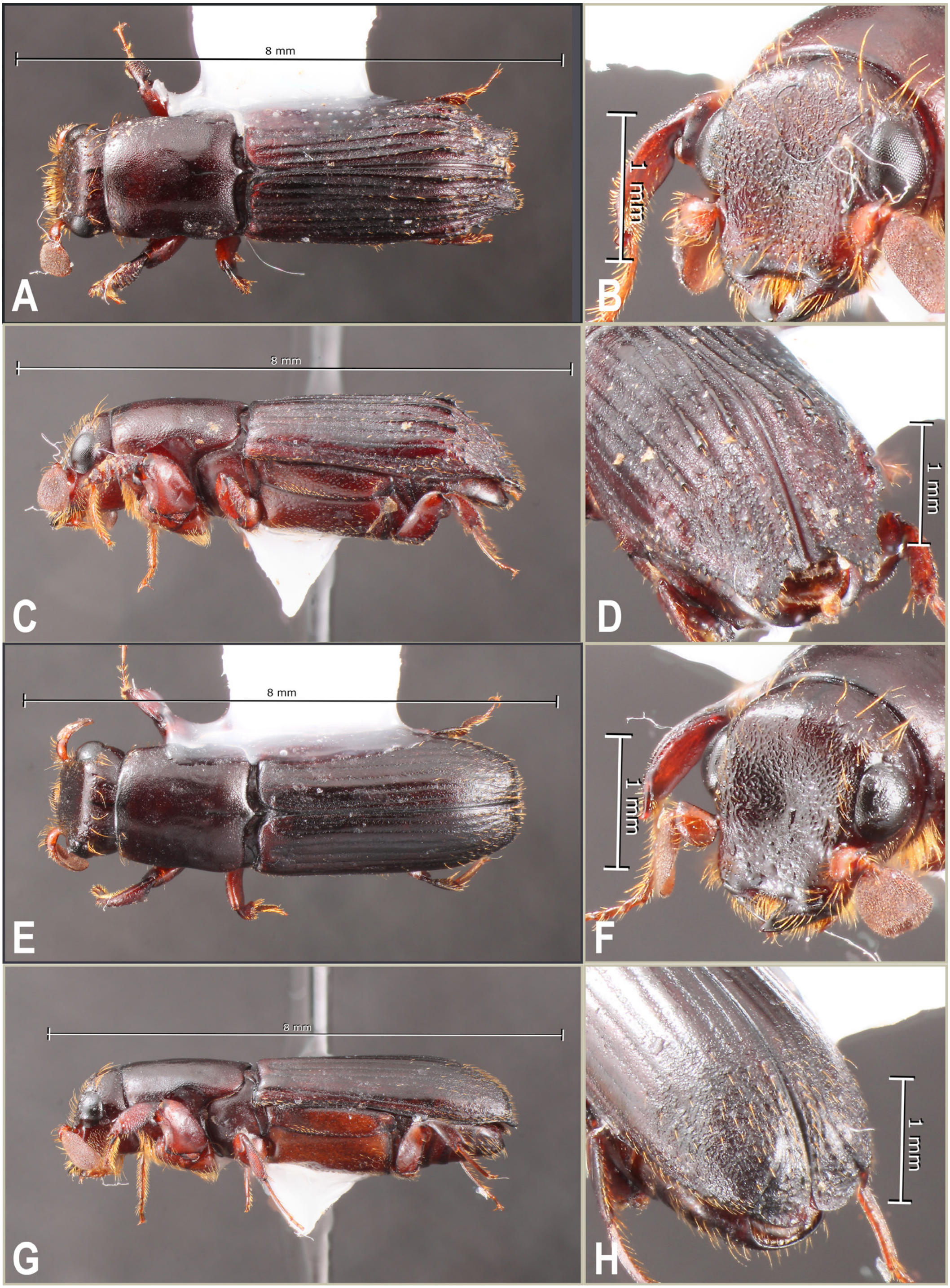

FIGURE 21. *Megaplatypus quinquecostatus* (Chapuis, 1865). Male habitus (**A–D**). **A**. Dorsal view. **B**. Lateral view. **C**. Frontal view, illustrating frons and antenna. **D**. Declivity. Female habitus (**E–H**). **E**. Dorsal view. **F**. Lateral view. **G**. Frontal view, illustrating frons and antenna. **H**. Declivity. Photos by T.H. Atkinson.

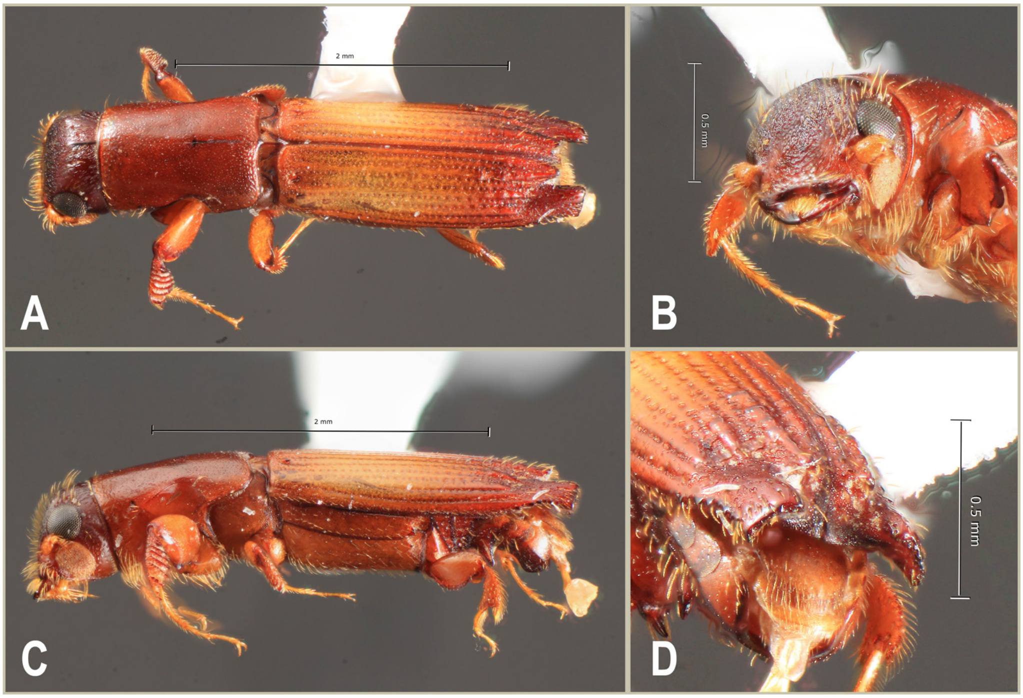

FIGURE 22. *Myoplatypus biprorus* Blandford, 1896. Male habitus (**A–D**). **A**. Dorsal view. **B**. Lateral view. **C**. Frontal view, illustrating frons and antenna. **D**. Declivity. Photos by T.H. Atkinson.

the median line on the pronotum (the pores are not visible in Figure 23E); this character trait is not found only in *Neotrachyostus*, however, and some females in *Neotrachyostus* have small clusters of tiny pores rather than single pores on either side of the median sulcus.

Wood (1993) erected the genus ***Oxoplatypus*** for *Oxoplalypus quadridentatus* (Olivier), a species breeding in oaks in the southern USA and northern Mexico (Figure 24). The genus is distinguished by the combination of a pair of large spines on ventrite 4 of the male and a pair of large mycangial pores on the female pronotum (Table 4). Only one other American platypodine has spines on male ventrite 4, *Myoplatypus brevicornis* (Wood), which is otherwise a typical *Myoplatypus* species (a genus in which spines on ventrite 3 is a diagnostic character: Table 4). Paired large pores on the female pronotum is otherwise a typical feature of the *filiformis* species group of *Epiplatypus*. *Oxoplatypus quadridentatus* has only been collected in oaks (*Quercus*) and has a disjunct distribution: It is widely and generally distributed in the mixed hardwood-conifer forests of the southeastern United States, the high mountains of northeastern Mexico, and along the western ranges from southern Arizona to Oaxaca. The disjunction in Mexico is probably due to the breakup of more generally distributed mesic forests in the post Pleistocene in southwestern North America.

The genus ***Teloplatypus*** Wood includes many of the smallest species in the tribe. Species in the genus are most commonly collected from leguminous hosts. Though some are unicolorous, both sexes of many species have bicolored elytra as in *T. ratzeburgi* (Chapuis) (Figure 25). In general, bodies of Neotropical Platypodinae are different shades of uniform black, reddish brown or brown. *Teloplatypus* is one of only two Platypodini genera that has more undescribed than described species (Table 2). Unfortunately, while most species placed in *Teloplatypus* are quite uniform in external morphology, the species chosen by Wood as type species of the genus, *T. concinnulus* Blandford, has a declivity that does

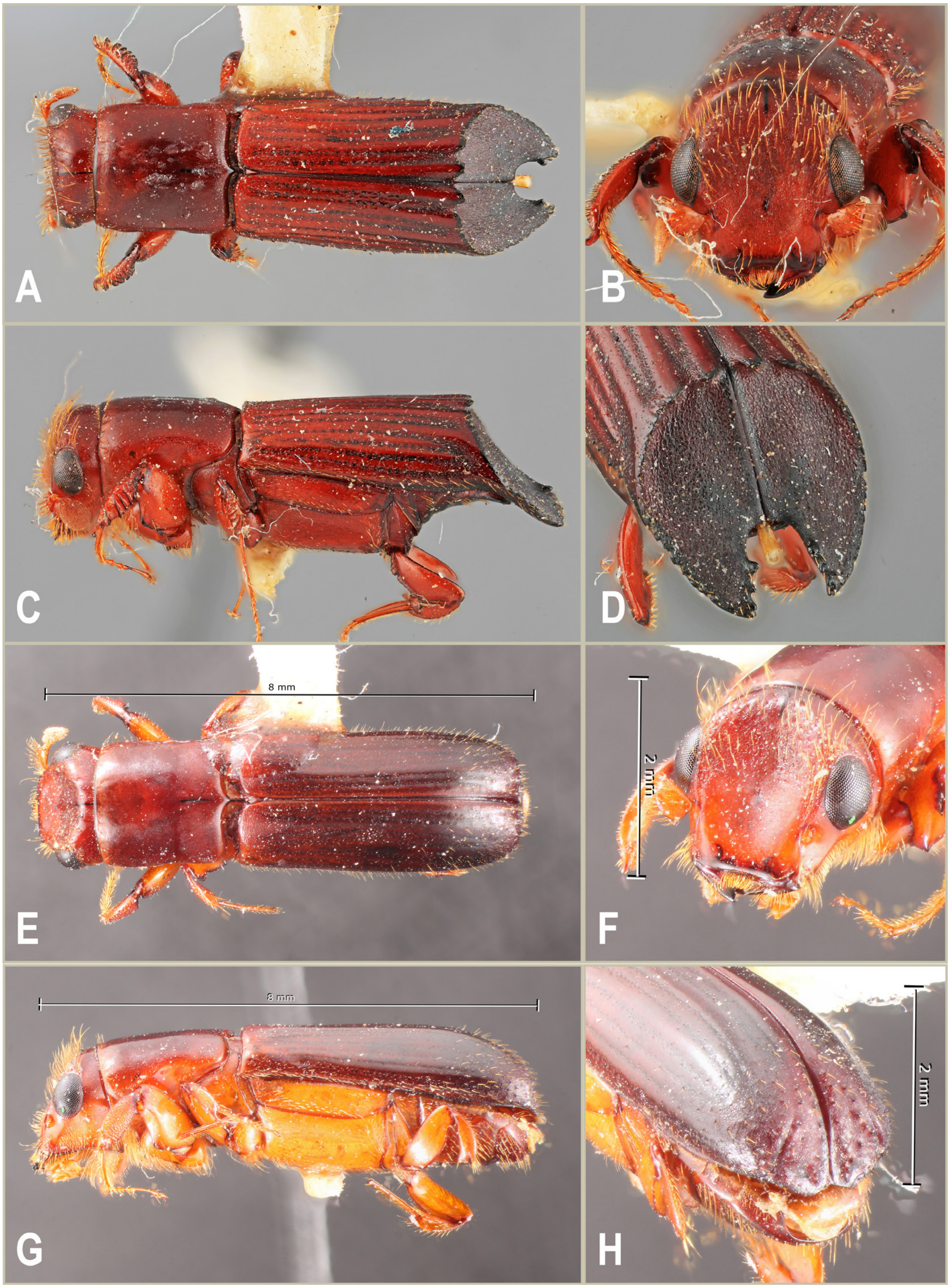

FIGURE 23. *Neotrachyostus obliquus* Wood, 1966. Male habitus (**A–D**). **A**. Dorsal view. **B**. Lateral view. **C**. Frontal view, illustrating frons and antenna. **D**. Declivity. Female habitus (**E–H**). **E**. Dorsal view. **F**. Lateral view. **G**. Frontal view, illustrating frons and antenna. **H**. Declivity. Photos by T.H. Atkinson.

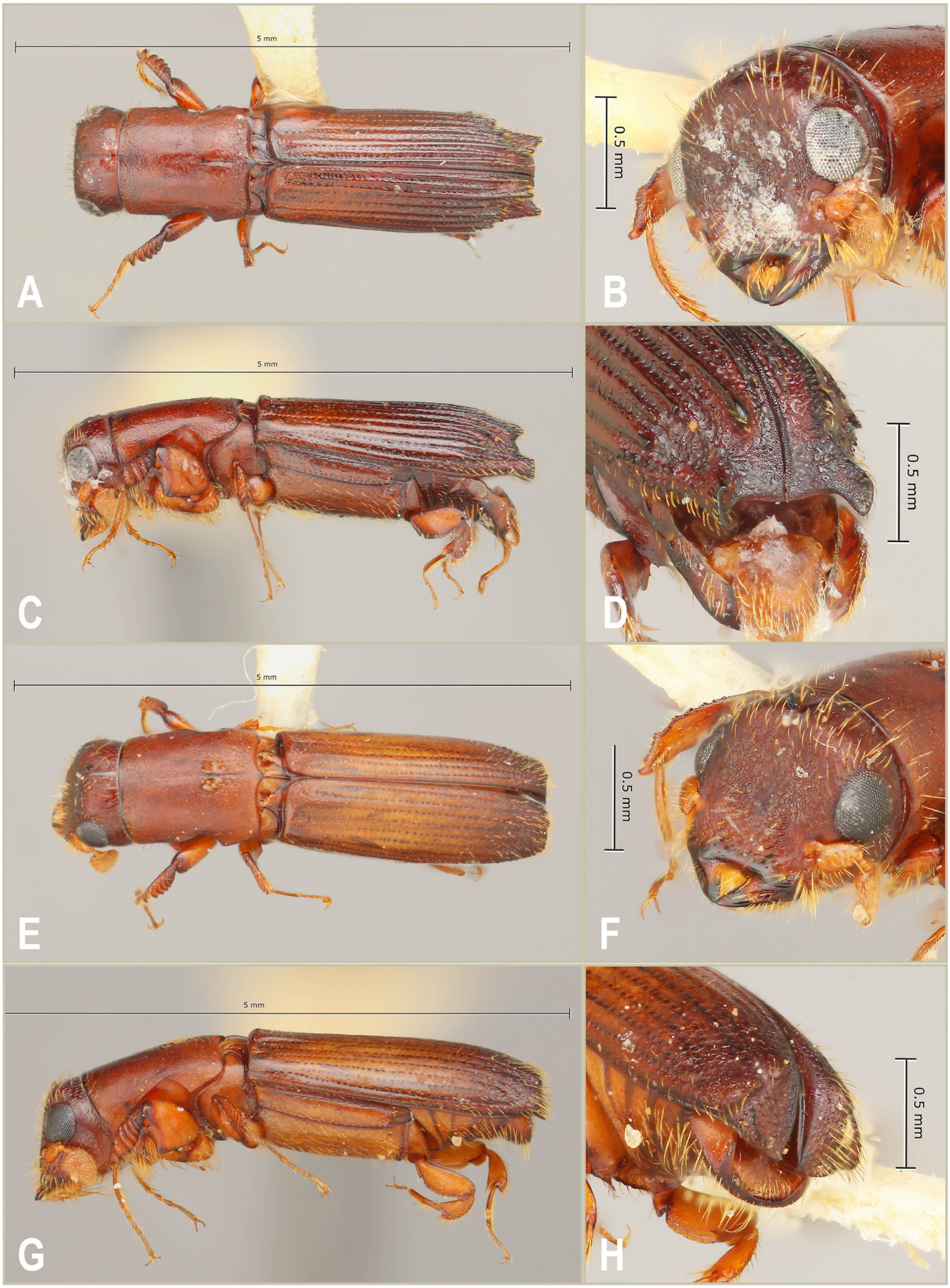

FIGURE 24. *Oxoplatypus quadridentatus* (Olivier, 1795). Male habitus (**A–D**). **A**. Dorsal view. **B**. Lateral view. **C**. Frontal view, illustrating frons and antenna. **D**. Declivity. Female habitus (**E–H**). **E**. Dorsal view. **F**. Lateral view. **G**. Frontal view, illustrating frons and antenna. **H**. Declivity. Photos by T.H. Atkinson.

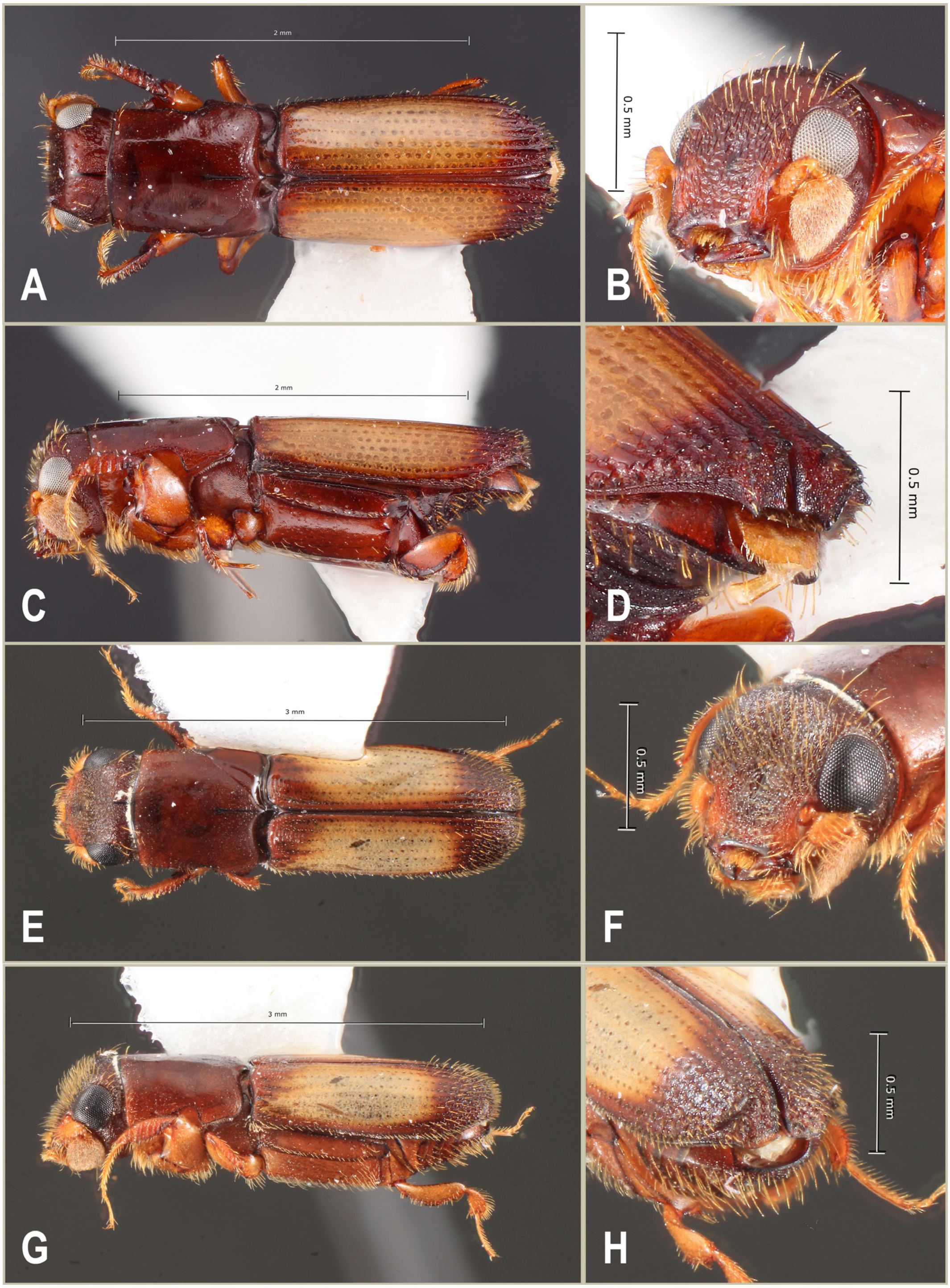

FIGURE 25. *Teloplatypus ratzeburgi* (Chapuis, 1865). Male habitus (**A–D**). **A**. Dorsal view. **B**. Lateral view. **C**. Frontal view, illustrating frons and antenna. **D**. Declivity. Female habitus (**E–H**). **E**. Dorsal view. **F**. Lateral view. **G**. Frontal view, illustrating frons and antenna. **H**. Declivity. Photos by T.H. Atkinson.

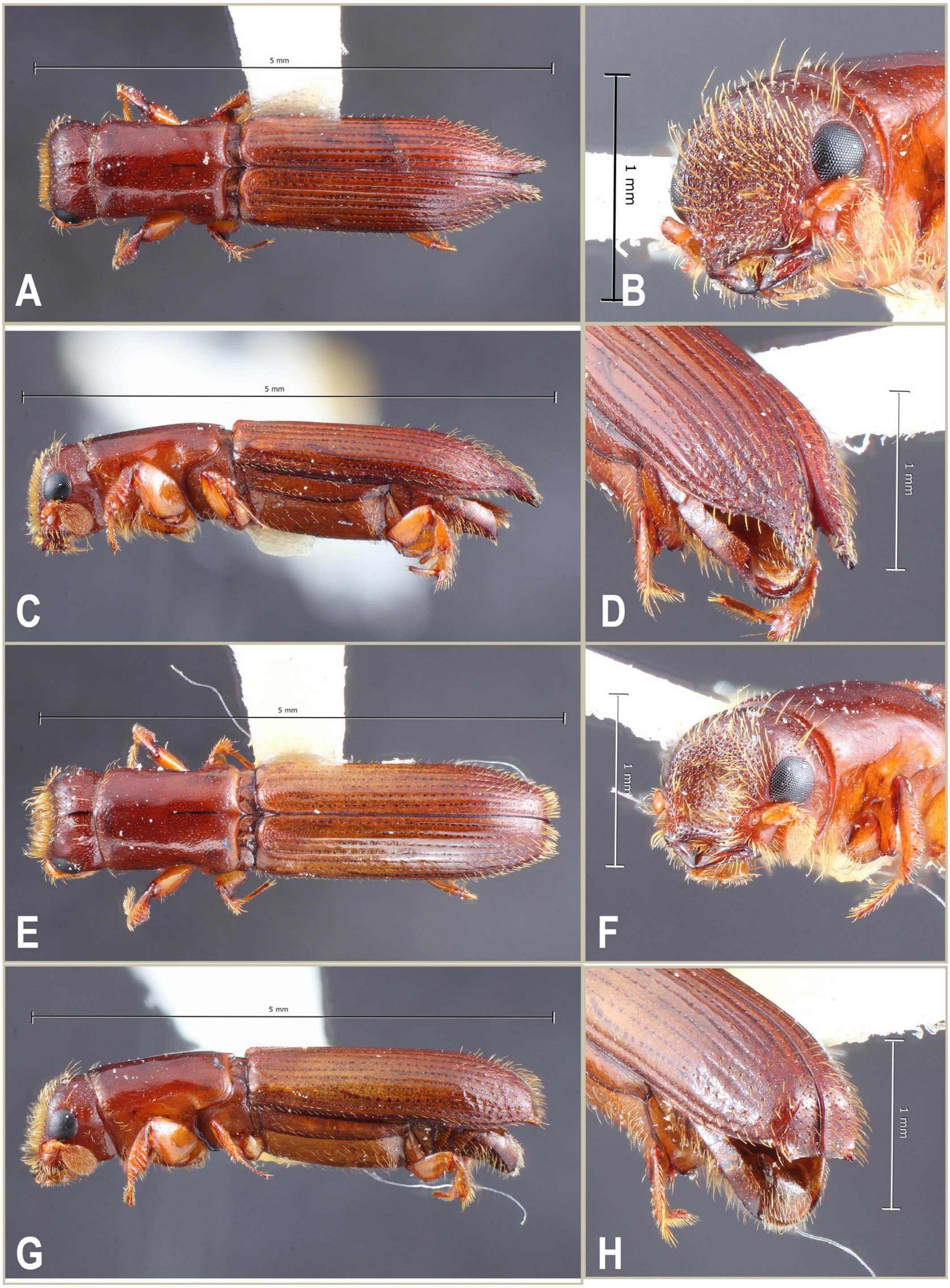

FIGURE 26. *Treptoplatypus abietis* (Wood, 1958). Male habitus (**A–D**). **A**. Dorsal view. **B**. Lateral view. **C**. Frontal view, illustrating frons and antenna. **D**. Declivity. Female habitus (**E–H**). **E**. Dorsal view. **F**. Lateral view. **G**. Frontal view, illustrating frons and antenna. **H**. Declivity. Photos by T.H. Atkinson.

not correspond to the description of the genus and would not key out to *Teloplatypus*. All species (including *T. concinnulus*) have an m-m formula of 2 / 1.

Two very similar American species were transferred to ***Treptoplatypus***: *T. abietis* (Wood) (Figure 26) which breeds in firs (*Abies*) and *T. wilsoni* (Swaine) which breeds primarily in firs but occasionally in related genera (*Picea, Pseudotsuga, Tsuga*). Males have a strongly narrowed, obliquely truncate male declivity; females have clusters of tiny mycangial pores on either side of the midline on the pronotum (Farris & Funk 1965). The genus is otherwise largely tropical, with species distributed from India to Japan and Australia (Wood 1993).

Results: Natural History

Platypodinae are adapted to warm, humid conditions, with relatively few species that have adapted to temperate climates; Schedl (1972) estimated that 98% of the world fauna is found in tropical and subtropical forests. In the southern parts of North America, only seven species occur: *Treptoplatypus abietis* (Wood), *T. wilsoni* (Swaine), *Oxoplatypus quadridentatus* (Olivier), *Myoplatypus flavicornis* (F.), *Euplatypus parallelus (*F.), *E. pini* (Hopkins), and *E. compositus* (Say). The remaining species are found in forest ecosystems of Mexico, Central America, and South America.

Schedlariini: Biology and behavior of *Schedlarius*

Schedlarius mexicanus, the only species in the genus, is of particular interest because it could be either the sister group of Platypodinae or phylogenetically basal within Platypodinae (Jordal 2014, 2015). Knowing more about the behavior, ecology, and evolutionary history of *Schedlarius* would greatly help us to understand both the evolution of obligatory fungus farming in beetles as well as illuminating the morphological and behavioral evolution of Platypodinae.

This species has been collected from several states in Mexico and from Costa Rica and Guatemala. Though the species was described well over a century ago, its natural history is only sketchily known. All host records are from *Bursera*. Wood (1957) excavated galleries in a 20 cm diameter broken branch of an unknown host species, in a dry tropical forest site at 1,200 m elevation. Long tunnels ran in the sapwood, up and down the branch (longitudinally). Most of the wood was slightly discoloured by fungi, but there was no evidence of the sort of fungal grown on tunnel walls that we associate with true ambrosia beetles, so larvae were apparently feeding on a combination of wood and fungi. From one to five tunnels branched off from a short entrance tunnel. Unlike other platypodines, eggs were laid singly in niches in the tunnel walls and the niches plugged with boring dust, as they are in most bark beetles. There are additional notes on this species from Atkinson et al. (1986), who collected *Schedlarius* from discoloured wood of various species of *Bursera* at elevations ranging from 1000 m to 1,700 m. They categorized *Schedlarius* as monogynous (one reproducing female per tunnel system) because several collections were of male-female pairs. They noted that larvae mined away from the egg tunnels and pupated terminally in larval mines. Given Wood's observations, however, it is also possible that the species is either harem polygynous or that monogynous pairs at least sometimes share a common entrance. Finally, Burgos Solorio & Hernández (2020) collected *Schedlarius* in host material ranging from 10–30 cm in diameter and noted that initial entries were generally at wounds where the bark had been displaced.

Biology and behaviour of core Platypodinae

General life history

What we know about the behaviour and ecology of pinhole borers is nearly exclusively drawn from studies of a few species in Africa, Asia, and Europe, though there is a recent, thorough review of the biology of the South American species *Megaplatypus mutatus* (Chapuis) (Ceriani-Nakamurakare et al. 2022). There has been detailed research on those temperate Old World species that cause economic losses or that are associated with forest decline due to spread of pathogens. Eurasian species include *Platypus cylindrus* F. in Europe (Chapman 1870, Strohmeyer 1906, 1907, Husson 1955, Belhoucine et al. 2011, Bellahirech et al. 2016, Nones et al. 2021) and the two Asian species *Platypus quercivorus* Murrayama (Soné et al. 1998, Ohya & Kinuura 2001, Kobayashi et al. 2002, Kinuura & Kobayashi 2006, Ueda & Kobayashi 2014, Saito et al. 2016, Nakajima 2019, Kuma et al. 2021, Pham et al. 2021) and *P. koryoensis* (Murryama) (Hong et al. 2006, Kim et al. 2009, Lee et al. 2011, Nam et al. 2013, 2014, Lee et al. 2019). There has also been research into the biology and behavior of platypodines causing economic losses in tropical forests of in West Africa (Jover 1952, Roberts 1960, 1962, Browne 1961b, 1962a, Roberts 1968, 1969b, Wagner et al. 1991) and temperate rain forests of New Zealand (Smith 1935, Neumann & Harris 1974, Milligan 1979, Elliot et al. 1983, Ytsma 1988). One Australian species, *Austroplatypus incompertus*, is particularly well known because of its advanced social behaviour (Smith et al. 2018). Detailed biological investigations have not been carried out for any American species (temperate or tropical) other than the aforementioned *Megaplatypus mutatus* (de Silva et al. 2013, Ceriani-Nakamurakare et al. 2022).

In addition, as far as we know, the general life cycle seems to be quite uniform (Beeson 1917, 1941, Smith 1935, Hogan 1948, Browne 1961a,b, 1962, Roberts 1960, 1968, Soné et al. 1998, Whitehead & Zack 2003, de Silva et al. 2013, Ceriani-Nakamurakara et al. 2022). Males emerge earlier than females and seek out suitable host material, orienting initially by host odours or ethanol or both. Once established in a short tunnel into the wood, they release pheromones that attract females and, in most cases, males as well. Females run rapidly over the bark surface looking for unmated males. Courtship involves a rapid exchange of physical, chemical, and acoustic signals, and as described seems to involve mate selection on the part of both sexes (see below).

Having found a receptive male, after a brief copulation, females tunnel further into the wood, constructing a long curving gallery in the end of which they begin laying a small number of eggs (often less than 10); once this first batch of eggs has hatched, the female begins extending the curving tunnel further, laying more batches of eggs in the main tunnel or in short branches; these later batches are often said to be larger and can be 30 or more. Oviposition takes place over several to many months, producing cohorts of progeny that overlap developmentally with each other. Secondary branches in at least *Doliopygus* Schedl are partly or possibly entirely the work of 5th instar larvae (Browne 1961b). Secondary branches in most genera lie in the same horizontal plane, but short secondary branches can lead to new large transverse tunnels such as in *Euplatypus parallelus* (de Silva et al. 2013) and *M. mutatus* (Figure 27; Ceriani-Nakamurakare et al. 2022). In the unrelated genera *Trachyostus* and *Crossotarsus* the secondary branches are long and vertical (Roberts 1960, Browne 1962, Schedl 1962, Beaver 1988); we have reproduced the excellent illustrations from Roberts' study of *Trachyostus ghanaensis* Schedl (Figure 28A–D), showing the progression of gallery system construction in a species with vertical secondary branches. In older gallery systems there can be much cross-linkage of tunnels, sometimes both vertically and horizontally (see illustrations in Smith 1935, Beeson 1941, Schedl 1962, Paullier & Núñez 1991, Soné et al. 1998, Smith et al. 2018, Ceriani-Nakamurakara et al. 2022), and the work of several females can coalesce (Beeson 1917). Platypodinae pupate in pupal cells (also called pupal cradles) chewed out by the last instar larvae (Figures 27A, 28C–D).

Young (teneral) adults may remain for some time to feed and mature, before finally exiting via the one entrance hole. In warm, moist, fresh wood, the life cycle can be completed in a couple of months, but in some circumstances one, two, or more years go by before young beetles begin to emerge (e.g. two years in *Platypus gracilis* Broun in New Zealand: Milligan 1979), and both the colonization and emergence processes can stretch over several years (Hogan 1948, Roberts 1960, 1968, Neumann & Harris 1974, Soné et al. 1998, Whitehead & Zack 2003).

The numbers of progeny emerging from a

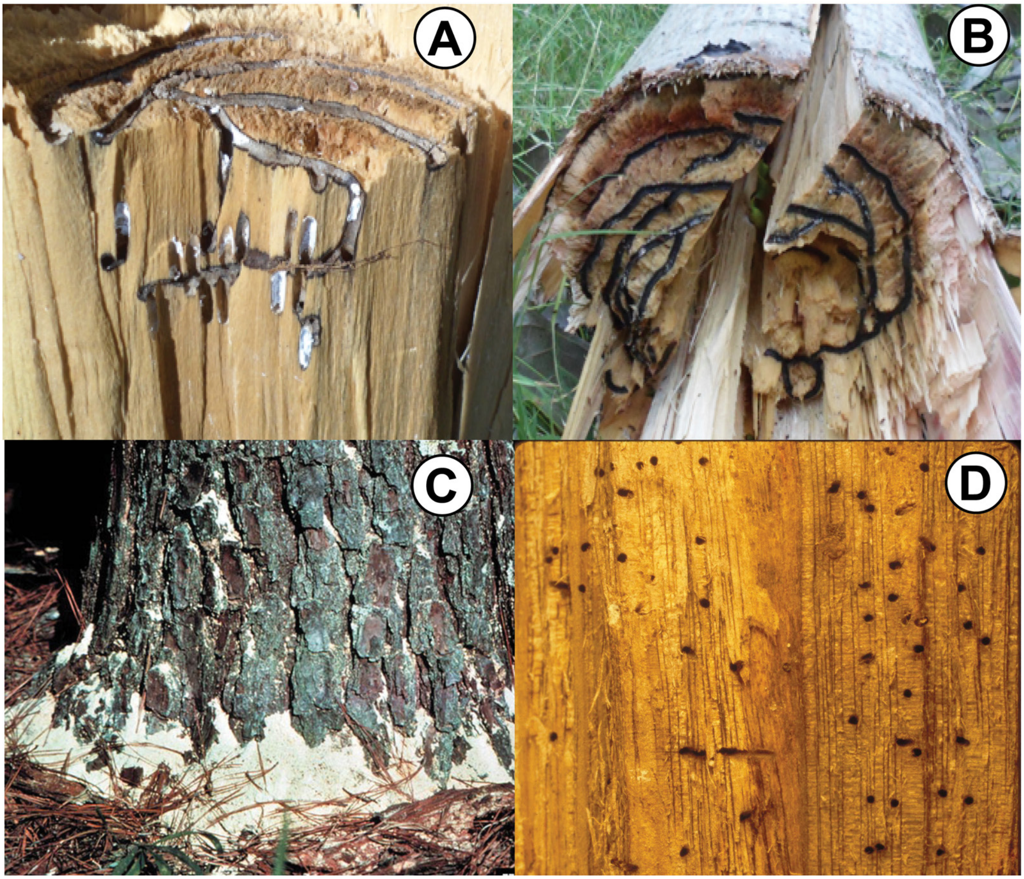

FIGURE 27. Horizontal galleries of single families of *Megaplatypus mutatus* (Chapuis, 1865) in a poplar (*Populus* sp.). **A**. Lateral view of a tunnel system, with whitish fungal growth on tunnel walls and showing a typical branch tunnel with pupal cells. Photos of A and B by Ceriani-Nakamurakare. **B**. Tunnel system in a fallen poplar trunk that had been snapped by strong winds. **C.** Boring frass ejected by *Myoplatypus flavicornis* (Fabricius, 1776) from infested pine. Photo by Ronald F. Billings, Texas A&M Forest Service, from Bugwood.org; **D.** Damage to pine wood from galleries of *Myoplatypus flavicornis*. Photo by T.H. Atkinson.

single tunnel system seems to vary considerably among species and can be surprisingly large. At the low end, Hogan (1948) noted that he never found more than six to ten eggs in a gallery system of the Australian endemic *Platypus subgranosus* Schedl and that a maximum of 34 young adults emerging from a single entry hole. Chapman reports that *Platypus cylindrus* females lay 60–100 eggs, and Swaine (1918) states that *Treptoplatypus wilsoni* (Swaine) produces a hundred or more. Similarly, Soné et al. studied the oak borer *Platypus quercivorus* over two years in Japan and reported average brood sizes of 50 (max. 161) and 60 (max. 136) respectively. Browne (1961b) estimated that 80 to 90 eggs is usual for a female *Doliopgygus dubius* (Sampson), with a maximum of 150 to 160, and Beeson (1917) estimated that the number of eggs laid by a *Genyocerus tallurae* (Stebbing) female “exceeded 100”. For *Megaplatyus mutatus,* Paullier & Núñez (1991) reported an average of 391 (range 157–968) emerging per entrance hole.

Use of pheromones

The production of attractant odours (pheromones) that can attract potential mates over long distances is widespread in weevils (Ambrogi et al. 2009, Tewari et al. 2014, Symonds & Gitau-Clarke 2016, Scheepers et al. 2020, Bandeira et al. 2021),

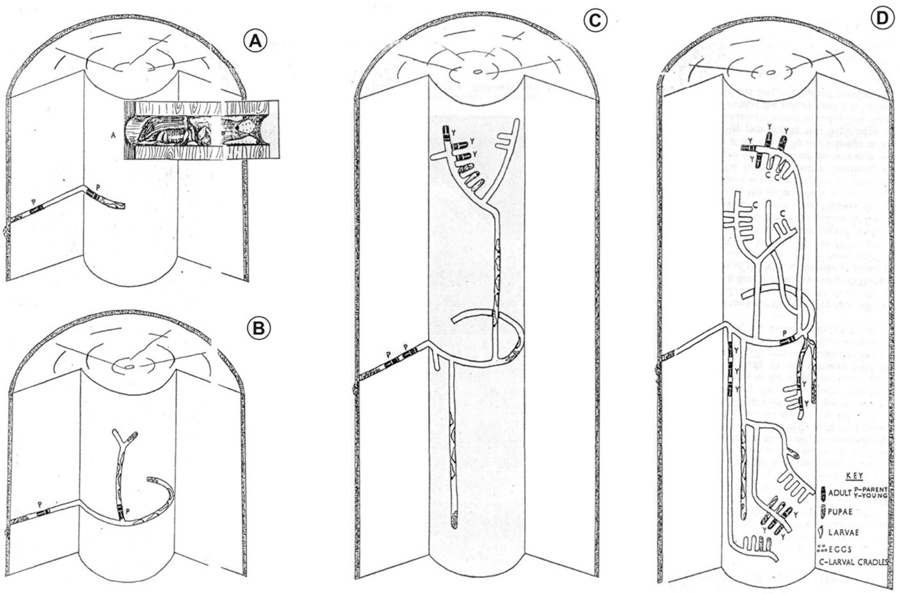

FIGURE 28. Tunnel system construction by a single family of *Trachyostus ghanaensis* Schedl, 1959. **A.** Female (innermost parent beetle) beginning the primary circumferential tunnel; eggs and a larva can be seen in the far end of the tunnel. The male (outermost) remains in the entryway. **B.** The circumferential tunnel has been extended by the parent female, who has laid two further batches of eggs, one represented by four large larvae in the middle and the next by three eggs in the end of a short branch tunnel. The first-produced offspring, now last (fifth) instar larvae, have bored a vertical branch tunnel; the parent female has layed eggs in a short branch. **C.** Pupal cells can be seen in the ends of the bifurcating first vertical tunnel; last instar larvae have added a second vertical tunnel. **D**. After several months, there is complete overlap of generations, though the parent male has died; the entryway is now tightly blocked by frass (boring dust and feces). **Source**: Roberts (1960).

and has been recorded in species of *Platypus* (Hogan 1948, Milligan & Ytsma 1988, Algarvio et al. 2002, Kashigawa et al. 2006, Kamata et al. 2008, Kim et al. 2009), *Euplatypus* (Rainho et al. 2021), *Megaplatypus* (Audino et al. 2005, Gatti et al. 2011), *Myoplatypus* (Madrid et al. 1972, Renwick et al. 1977) and *Treptoplatypus* (Ytsma 1989). All these genera are in the tribe Platypodini: notably absent is any research on *Schedlariini* or *Tesserocerini* looking for pheromone-based attraction or use of pheromones in courtship. Given that long-distance pheromones have been found in such a variety of weevils, it seems likely that pheromone usage is ancestral in Platypodinae and will also be found in other tribes of the subfamily. In the Neotropics, the use of pheromones has only been demonstrated for *Euplatypus parallelus* (Rainho et al. 2021) and *Megaplatypus mutatus* (Audino et al. 2005). In the Nearctic, we know that at least *Myoplatypus flavicornis* uses pheromones (Madrid et al. 1972).

Details of courtship and copulation

Courtship and copulation, along with males blocking the tunnel opening and ejecting frass, are the only pinhole borer activities that are usually visible. Nonetheless, there are few descriptions of mating behaviour, including one of a Neotropical species. We summarize the general components here based nearly entirely on reports for African and Asian species. The only lengthy descriptions of mating behaviour are a generalized description of behaviour in several species by Jover (1952) and quantitative studies of courtship and copulation in *Platypus quercivorus* by Ohya and Kinuura (2001) and Kobayashi and Ueda (2002).

In the paper on the biology of Ivory Coast

Platypodinae (published posthumously), it is unclear which species Jover observed with respect to courtship and mating, though it may have been all of those that were the subject of his study: 12 species from the Platypodini genera *Doliopygus*, *Platypus* and *Triozastus* Schedl, and one species of *Periommatus* from the Tesserocerini (Jover 1952). Introducing the text on their behaviour, he writes that (our translation from the French) "After our observations, from a biological point of view, all these species have important characters in common."

Males of all species arrive at a new host first and bore a short tunnel that is at least two body lengths in length. Males then wait in this short tunnel with the tip of the abdomen flush with the bark surface. Females land on the host and search for male tunnels. Jover then divided the courtship process into five rapidly completed phases which were well illustrated by line drawings (his Figures 1–6):

a. The female finds a male and pushes him inside, and both then disappear from view.
b. The male pushes the female back out and exits himself.
c. The female enters the tunnel, followed by the male.
d. The male grips the apex of the abdomen [the elytra?] of the female and tries to pull her out; this can take several seconds, as the female is sometimes "reluctant". Eventually the female is pulled nearly entirely out, with her head and thorax still in the tunnel.
e. The male copulates with the female while atop her, coupling taking "a fraction of a second", followed by both disappearing into the tunnel (the female first). Following the same pattern, Jover adds, coupling can take place several times. Copulation is not seen again.

At some point soon after mating, it is has been reported for both Tesserocerini and a variety of Platypodinae genera that both sexes lose their tarsal claws, something which enforces life-long monogamy and full commitment to the current gallery system, since the beetles can no longer cling to surfaces (Chapman 1870, Strohmeyer 1907, Beeson 1917, Roberts 1960, Browne 1961a; reviewed and discussed in Kirkendall et al. 1997 and Smith et al. 2018 which cites additional sources), though this does not impede their ability to move within their tunnels. The female now devotes her efforts to enlarging the tunnel, tending to ambrosia fungus growth, and, eventually, egg laying. The male remains in the tunnel entrance and ejects the wood fibers and frass resulting from the female's activities; by plugging the entrance males keep out predators and parasites, regulate the humidity of the system, and prevent free-wandering larvae from falling out (Milligan 1979, Kirkendall et al. 1997, 2015, Smith et al. 2018).

There has been a series of investigations by several research groups into the ecology and behaviour of *Platypus quercivorus* because of its role in the mass mortality of oaks in coastal Japan. Ohya & Kinuura (2021) used video and sound recordings to elucidate the nature and role of sound production during courtship. Kobayashi and Ueda (2002) used video recordings of 19 successful matings to quantify courtship and copulation. Their findings supported the general description of Jover that was presented above, that the mating sequence involves a tug-of-war between the male and the female before copulation occurs (see their Figure 1). Ohya and Kinuura found both sexes stridulate regularly during the courtship sequence and that female stridulation was required in order to elicit male exit (Jover's "b"). They also report that the female uses her mandibles to attempt to pull the male out of the tunnel. Kobayashi and Ueda found that in 15 of 19 successful matings the courtship sequence was carried out without repetition of any of the behaviours and took on average about 1-1/2 minutes. There were six unsuccessful matings; in these cases, either males refused to back out or females left voluntarily, suggesting that mate selection might be mutual.

Other descriptions of courtship and copulation are not as detailed but fill out the picture of the general procedure outlined by Jover or confirm that other species behave in roughly the same way, though variations may occur. Husson (1955) and Menier (1976) reported the occurrence of stridulation during courtship in *Platypus cylindrus,* for example, and Ytmsa (1988) showed experimentally that, for *P. apicalis* White, *P.*

gracilis and *Treptoplatypus caviceps* (Broun), female stridulation was necessary for male acceptance. Browne (1962a) described courtship of *Doliopygus conradti* (Strohmeyer) as a tug-of-war, where the female must forcibly drag the male out of his tunnel, and where courtship can go quickly (as described by Jover) or go on for hours, sometimes ending with the male kicking the female so strongly that she is thrown from the log.

In the only paper we found in which courtship is described for a Neotropical species, *Megaplatypus mutatus,* the sequence seems to be very similar. Ceriani-Nakamurakare et al. (2022) mention female stridulation, females "nudging" males, and females attempting to pull males out of their tunnels by grasping and pulling on the third pair of legs. They also observed that females sometimes chose to leave even when a male did exit his tunnel, again suggesting the possilbity that both sexes exercise mate choice in pinhole borers.

All the above species are in the Platypodini. In the only mentions of courtship in a species in the Tesserocerini, Roberts (1993) reported that, for the New Guinea species *Diapus robustu*s Schedl, female courtship included drumming on the protruding male abdomen with the hirsute antennae, and both Smith (1935, *D. pusillimus* Chapuis) and Roberts noted that females deploy the large, deciduous mandibular appendages characteristic of *Diapus* females to attempt to lever males out of their tunnels.

Use of sound

As is thought to be commonly the case in beetles (Darwin 1877, Wessel 2006), stridulation by Platypodinae is used mainly in the contexts of mating and of competition for mates. Roberts (1960) mentions that guarding *Trachyostus ghanaensis* males also stridulate when contacted by predators trying to gain entrance to the gallery system, and Chapman (1870) reports that one can elicit "a chorus of squeaking" by shaking a log with galleries of *Platypus cylindrus*. As with pheromone production, stridulation is widely distributed in weevils, particularly elytral-tergal stridulation which is the form found in Platypodinae (Menier 1976, Lyal & King 1996). Stridulation, then, is likely ancestral in Platypodinae and has been witnessed in a wide variety of genera (Chapman 1870, Roberts 1960, Browne 1961b, Menier 1976, Ytsma 1988, Del Tio et al. 1995, Ohya & Kinuura 2001, Bedoya et al. 2019).

Mating system

Core platypodines are uniformly life-long monogamous (Schedl 1972a, Wood 1993, Kirkendall et al. 2015, Smith et al. 2018). Given that the Platypodinae subfamily is likely at least 100 million years old (Jordal 2015), comprises multiple genera and over 1400 species, and has spread around the world, it would seem that life-long monogamy has been evolutionarily stable in Platypodinae.

Social behaviour

Ambrosia beetles, including Platypodinae, have been the subject of research into the biology and evolution of social behaviour. Social behaviours that are common in Platypodinae include investment by both mothers and fathers in parental care, gregarious larval feeding, larval cooperation in extending tunnel systems, and alloparental care (aiding offspring that are not one's own) (reviewed by Kirkendall et al. 1997, Kirkendall et al. 2015). At least *Trachyostus ghanaensis* can be classified as "facultatively eusocial" (Boomsma 2009), in that at least some young females delay leaving and instead work in their natal nest (Roberts 1960); this behaviour is likely to be much more common than we currently know.

Years of research into the behaviour of *Austroplatypus impertus* in Australia has resulted in that species being added to the rather short list of "obligate eusocial" animals in the world (highly social animals in which there are permanently sterile workers). The extraordinary life cycle of this pinhole borer has been elucidated in a series of papers by Deborah S. Kent and colleagues (Kent & Simpson 1992, Kent 2002, 2008a, 2008b, 2010, Smith et al. 2009, 2018; see also Harris et al. 1976, and reviews in Kirkendall et al. 1997, 2015). Nests of this species are constructed in healthy, live *Eucalyptus* trees, and successful colonies can be active for over 30 years (Harris et al. 1976, Kent & Simpson 1992). Using microsatellites, Smith et al. genotyped over 500 individuals from a total of 33 different colonies. Their analyses showed that the species is indeed strictly monogamous and derived from one core family, and that young daughter workers do not mate and do not leave the colony (other daughters and the sons do disperse to mate elsewhere).

Social behavior in Platypodinae and Scolytinae is reviewed Kirkendall et al. (2015), but for recent advances in our understanding of the evolution of social behaviour in ambrosia beetles and other fungus cultivating insects see Biedermann & Rohlfs (2017), Smith et al. (2018), Nuotclà et al. (2019), Biedermann (2020), and Biedermann & Vega (2020). Biedermann & Rohlfs (2017) provide excellent discussions of the evolutionary feedbacks between insect sociality (including examples from ambrosia beetles) and microbial management, and of evolutionary feedbacks between insect sociality and pathogens. The importance of pathogens in social evolution of ambrosia beetles is further developed in Nuotclà et al. (2019).

Ecology

Relations with ambrosia fungi

The Platypodinae are believed to be the oldest group of insect farmers (Vanderpool et al. 2017). Platypodinae transport ambrosia fungi in so-called mycangia, cuticular invaginations of exoskeleton (Farris & Funk 1965, Nakashima 1975, Cassier et al. 1996, Beaver 1998, Kent 2008a, Moon et al. 2012, Belhoucine et al. 2013; see Table 7.1 in Mayers et al. 2021 for a summary). In most genera these take the form of smaller or larger pores (also referred to as pits) on the pronotum, which occur as pairs of smaller or larger patches. The number of such pores on a pronotum varies from two to hundreds (Nakashima et al. 1975, Mayers et al. 2021). Pronotal mycangial pores are known in many cases to be connected to gland cells. Pores are often accompanied by several or many stiff setae that presumably aid in funneling spores into the mycangia, and in some cases may help hold spores in place (Kent 2008a). Coxal mycangia are known from a few species of *Platypus*, and *Crossotarsus* have a mycangium in the head. As far as is known, in species for which mycangial transport of fungi is known, females do have mycangia but males most often do not. Transport of spores in the digestive system is also known for Platypodinae but for species that also have mycangia (Mayers et al. 2021). The primary ambrosia fungi of all Platypodinae are from the polyphyletic genus *Raffaelea* of the Ophiostomatales (Vanderpool et al. 2017). However, Platypodinae probably transport on or inside their bodies a variety of fungi, yeasts and bacteria as do scolytine ambrosia beetles, sometimes including pathogenic fungi (Platypodinae, Belhoucine et al. 2011, Alvidrez-Villereal 2012, Tarno et al. 2016, Nones et al. 2021, Ceriani-Nakamurakare et al. 2020, 2022, Inacio et al. 2022; Scolytinae, Hulcr et al. 2012, Hulcr et al. 2020, Rassatti et al. 2019, Ibarra-Juarez et al. 2020).

In Neotropical species, both sexes of Tesserocerini genera have pronotal pores (Figure 4F–J). In Platypodini, pronotal pores can be seen in at least females of *Epiplatypus, Euplatypus*, *Megaplatypus*, *Myoplatypus*, *Neotrachyostus*, *Oxoplatypus*, and *Treptoplatypus* though in most genera they are not universally present [Figure 4A–E]. How ambrosia fungi are transported is simply not known for species in the aforementioned genera that do not have pronotal pores, or for any species in the genera *Costaroplatus*, *Platyphysus*, and *Teloplatypus*.

Choice of plant hosts

Most ambrosia beetles in Scolytinae and Platypodinae are host generalists, capable of breeding in tree species from unrelated plant families (Beeson 1941, Browne 1958, 1961a, 1971, Kalshoven 1960, Schedl 1962b, 1972, Roberts 1968, Beaver 1976, 1979, Atkinson & Equihua-Martinez 1986, Beaver & Shih 2003, Burgos & Equihua 2007, Hulcr et al. 2007, Beaver & Liu 2013). As early as 1941, the forest entomologist C. F. C. Beeson, writing about the forest insects of India, noted that *Crossotarsus externedentatus* Fairmaire could colonize over 100 tree species (Beeson 1941), and for the same species Roberts (1977) recorded 69 host species from 42 families just on the Fijian islands. For *Euplatypus hintzi* (Schaufuss), nearly 200 host plants have been reported, distributed among no less than 43 plant families (Schedl 1972a). Although many species seem to be completely nonselective (Browne 1961a), in a survey of the Platypodinae of Zambia, Beaver & Löyttyniemi (1985) found that some species that have been collected from several to many host families do seem to have more taxonomically restricted preferences; preferences can be for related families, one host family, several related genera, or a single genus. Roberts (1962) reported that *Trachyostus aterrimus* (Schaufuss) in West Africa can be collected from many host families but has a strong preference for the genus *Celtis* (Cannabaceae). *Trachyostus ghanaensis,* the borer of wawa, attacks only live trees of one species, *Triplochiton scleroxylon* (Malvaceae) (Roberts 1960). The Malayan *Dendroplatypus impar (*Schedl) breeds only in *Shorea* species (Dipterocarpaceae) (Browne, 1965), and the Eurasian species *Treptoplatypus oxyurus* only in *Abies* (Pinaceae) (Whitehead & Zack 2003). The eusocial Australian species *A. incompertus* is also restricted to one genus, live trees of *Eucalyptus* (Kent, 2002). It was believed earlier (Beeson 1917, 1941) that *Genyocerus talurae* (Stebbing) (cited as *Diacavus furtivus* Sampson) breeds only in one host, *Shorea robusta* (Dipterocarpaceae), but more recent studies have revealed that this species breeds successfully in at least five genera of trees belonging to that same family (Beaver & Liu 2007). Several other species of *Genyocerus* also seem to be restricted to Dipterocarpaceae (Beaver & Liu, op. cit.). Other platypodines have also been reported to largely breed in just one family. Several Fijian *Platypus* species are restricted to Myrtaceae (Beaver 2000a), and in Zambia, 15/42 Platypodinae species seem to prefer Fabaceae (Beaver & Löyttyniemi 1985). Where some degree of host specificity has been found, it seems to have evolved for one of two reasons. Species in forests with few tree species often specialize on the most abundant family or genus of trees (Beaver 1989, Beaver & Browne 1979, Whitehead & Zack 2003). Species that regularly attack healthy standing trees and breed in them without causing apparent harm breed locally in only one genus (Beaver 1989, Kirkendall et al. 2015).

Such nuanced knowledge of host use and host preferences is largely lacking for Neotropical pinhole borers and consequently it difficult to generalize about host breadth of American pinhole borers by using label data from museum specimens and the few papers that contain host records. There is much better host breadth data for Neotropical Scolytinae than there is for the pinhole borers of the same region (Wood 1982, 2007). Most of the records in our database (which include records captured from publications) lack host information, in part because so many of those we have identified were taken in in traps or at light. Table 6 gives an overview of proportions of described species in a genus that have how many genus-level host plant records, while Table 7 summarizes what we know about degree of host selectivity for those 27 Neotropical species that have been collected from a host identified at least to genus on more than five occasions (more than five collecting events).

From Table 6 we can see that few Neotropical species have more than a handful of host records; 2/3 of described species (204/300) have no genus-level host records at all, though three of these do have at least one family-level host record. Only 10% have more than five such host records, and two genera have no described species at all with that many host observations. There are 22 records that have family-level but not genus-level information (data not shown).

Table 7 presents what little we can say about host preferences in American species, based on specimen label data captured in our database (noting that the database includes host data from publications as well). Three of the temperate species are clearly highly selective, breeding in just pines or just oaks. The tropical species *Schedlarius mexicanus* breeds only in *Bursera*. A few other tropical taxa may turn out to be selective to some degree: *Euplatypus cribricollis* (Blandford) thus far has only been collected from Lecythidaceae, and the genus *Teloplatypus* seems to at least have a strong preference for Fabaceae, a hypothesis that is supported by observations in Kalshoven (1963), Atkinson & Equihua M.

TABLE 6. On the lack of good host data for New World species of Platypodinae. Without good genus-level host data, and data from multiple collecting events, host plant breadth cannot be determined for a species. Numbers are numbers of species for a genus with 0, 1–5, or more than 5 host records (as of March 2023). Note that a species can have multiple host genus records, but all or most could have been from just one collecting event or from a study of just one tree family. The majority of records for most genera do not have host records because the beetles came from trapping or canopy fogging samples (see Table 5). "Described": number of described species in that genus. "genus records": genus-level plant host records.

Tribe	Genus	Described	No genus records	1–5 genus records	> 5 genus records
Schedlariiini	*Schedlarius*	1			1
Tesserocerini	*Cenocephalus*	10	8	1	1
	Tesserocerus	30	14	10	2
	Tesserocranulus	1	0	0	1
Platypodini	*Costaroplatus*	16	13	3	0
	Epiplatypus	19	10	9	0
	Euplatypus	45	27	8	8
	Megaplatypus	93	68	18	6
	Myoplatypus	8	1	6	1
	Neotrachyostus	15	11	3	1
	Oxoplatypus	1	0	1	1
	Platyphysus	5	2	2	1
	"Platypus"	37	33	2	0
	Teloplatypus	17	9	4	4
	Treptoplatypus	2	0	0	2
	Totals	**300**	**196**	**67**	**29**

(1986, 1988), Thunes (1998), and Burgos & Equihua (2007). The tropical species in the genus *Myoplatypus* have mainly been collected from oaks (Kirkendall & Atkinson 2023).

It seems likely that the ambrosia fungi upon which pinhole borers and scolytine ambrosia beetles feed can flourish in most sources of dead xylem tissues—tissues which do not differ much biochemically or structurally among woody species. Rather than specificity based on host plant taxonomy, it is more likely that ecological specialisations (ecological niche differences) will be found in breeding material diameter (trunks vs branches), use of heartwood vs sapwood, conditions of temperature and humidity, and wood moisture content (Beeson 1941, Fisher 1952, Bletchly 1961, Browne 1958, 1961a, Jover 1952, Roberts 1969b, Beaver 1976, 1989, Ytsma 1988, Noblecourt et al. 1995, Hulcr et al. 2008a,b, Iidzuka et al. 2014, 2016, Peng et al. 2022). Hints as to such niche differences can be gleaned from data on arrival sequences for species coming to a given host. Jover (1952), studying 13 species that colonized logs of *Turraeanthus africana* (Meliaceae), observed that *Doliopygus serratus* Strohmeyer, *D. vegrandis* Sampson, and *Platypus hintzi* Schaufuss came in large numbers the same day that trees were cut down, while the latest arriving species, *Triozastus propatulus* Schedl, did not colonize logs until well after a month had gone by since they were cut. Two abundant species on the Fijian islands also differ in when they colonize newly cut *Swietenia* (mahogany) logs: *Crossotarsus externedentatus* begins to colonize nearly immediately after felling, while *Platypus gerstaeckeri* Chapuis does not come to these logs until over a month later (Roberts 1977). In species colonizing southern beech (*Nothofagus*

TABLE 7. Breadth of host records for the 27 described species of New World Platypodinae that have more than 5 independent collections from hosts that were identified at least to genus (as of March 2023). The columns indicate whether a species has been collected from just one genus, just one family, or more than one host plant family. This table and Table 6 both illustrate how little is known about host usage for New World species (< 10% of described species have more than 5 indepent host records). Nonetheless, it is clear that most species are at least slightly polyphagous (breed in woody plants from more than one plant family). "Coll." = collection(s). A collection event includes all specimens that have the same collection data on their labels (same locality, same date or date range, same host plant). In Comments, "families" = plant families.

Species	Coll. events	1 genus	1 family	>1 family	Comments
Cenocephalus epistomalis Wood	3			+	
Tesserocerus dewalquei Chapuis	7			+	
Tesserocerus spinax Blandford	7			+	
Tesserocranulus nevermanni Schedl				+	
Euplatypus compositius (Say)	> 10			+	
Euplatypus cribricollis (Blandford)	2		+		Lecythidiaceae
Euplatypus longius (Wood)	10			+	
Euplatypus longulus (Chapuis)	7			+	7 coll., 7 families
Euplatypus otiosus (Schedl)	10			+	
Euplatypus parallelus (F.)	> 10			+	
Euplatypus pini (Hopkins)	> 10	+			Pine specialist
Euplatypus segnis (Chapuis)	9			+	
Megaplatypus dentatus (Dalman)	6			+	6 coll., 5 families
Megaplatypus deyrollei (Chapuis)	6			+	6 coll., 6 families
Megaplatypus exaratus (Blandford)	> 10			+	
Megaplatypus godmani (Blandford)	6			+	
Megaplatypus mutatus (Chapuis)	7			+	7 coll., 5 families
Myoplatypus flavicornis (F.)	> 10				
Neotrachyostus lobatus (Chapuis)	4			+	
Oxoplatypus quadridentatus (Olivier)	> 10	+			Oak specialist
Platyphysus obtusus (Chapuis)	8			+	2 families
Teloplatypus enixus (Schedl)	8			+	Most from Fabaceae
Teloplatypus excisus (Chapuis)	> 10			+	Most from Fabaceae
Teloplatypus ratzeburgi (Chapuis)	9			+	8/9 coll. from Fabaceae
Teloplatypus ustulatus (Chapuis)	> 10			+	13/14 coll. from Fabaceae
Treptoplatypus abietis (Swaine)	> 10	+			Pine specialist
Treptoplatypus wilsoni (Wood)	> 10		+		Pinaceae specialist
Schedlarius mexicanus (Duges)	> 10	+			*Bursera* specialist

species), *Treptoplatypus caviceps* survives in drier material than similar platypodines in the same forests (Ytsma 1988), while *Platypus gracilis* can establish gallery systems in logs or stumps that are 20 or more years old (Milligan 1979). Another possible niche dimension is host diameter; it seems likely that the largest species cannot breed in small branches. There are undoubtedly similar niche differences among Neotropical species that await discovery.

Elevational specialization

Another niche dimension for Platypodinae is adaption to temperature; in some cases, this would be in connection with specialization to host plants that grow at higher elevations such as neotropical *Quercus* or temperate Eurasian *Abies*. Species restricted to higher elevations (which elevations in the tropics are in or above cloud forest) must be adapted to cooler temperatures than are species from the lowlands. Presumably (and this is a testable hypothesis), it is the coevolving ambrosia fungi cultivated by cloud forest species that are adapted to the lower temperatures.

Most Neotropical Platypodinae are found in lowland wet tropical forest species. For the records in our database for which we have an elevation or elevational range, a small number of species seem to be specialized to higher elevations and are found primarily in cloud forests or even above them. In the Tesserocerini, one undescribed species of *Cenocephalus* seems to be a cloud forest species (23/25 specimens collected at elevations > 1000 m). *Tesserocerus rudis* Chapuis has primarily been collected at elevations greater than 1000 m (52/59 specimens), and one undescribed *Tesserocerus* species has only been collected at higher elevations (N = 39). The elevational range of *Tesserocranulus* extends into the cloud forest, having been collected at elevations ranging from near sea level to 1300 m. A handful of *Cenocephalus* and *Tesserocerus* species also seem to extend into the lower cloud forest. In Platypodini, most species in the genus *Myoplatypus* have been collected at higher elevations. There are no known cloud forest specialists in *Costaroplatus* or *Platyphysus*. In other genera, most individuals have been collected from lower elevations, though each genus has one or a few species restricted to higher elevations. In *Euplatypus*, most of the cloud forest species are in the *longulus* species group, which includes lowland and highland species as well (Table 8).

Natural enemies of Neotropical Platypodinae

Nearly nothing is known about predators, parasites, or parasitoids of Neotropical Platypodinae, though we know much about the natural enemies of African and Asian species. We can surmise that flying and newly landed pinhole borers are taken by insect-eating birds and by lizards, as witnessed by Roberts on Fiji (Roberts 1977). Once landed, they must also be vulnerable to ants and predatory beetles such as carabids and clerids, and once inside the wood can be attacked by specialized predators from families such as Borthrideridae, Brentidae and Histeridae.

We have found only 3 papers mentioning predators or parasites of Neotropical Platypodinae. Lewis (1911) points out that the histerid beetle *Trypaneus torpedo* Lewis was discovered by Thomas Belt in Nicaragua at the same time as specimens of *Tesserocerus belti* Sharp and given its size and the known habits of the genus, Lewis surmises that the histerid is a predator of the tesserocerine.

Clarke and Menard (2006) discovered that the checkered beetle *Thanasimius dubius* (F.) that had been drawn to pines attacked by the bark beetle *Dendroctonus frontalis* (Zimmermann) subsequently preyed upon the later-arriving

TABLE 8. An example of elevational zoning of very similar species of *Euplatypus*—the group of species related to *E. longulus* (Figure 18). Most records are from the elevational gradient of the ALAS project in Costa Rica. Numbers are numbers of individuals collected, most of which were caught by Malaise traps. (Numbers as of March 2023).

	<1000 m	**1000-2000 m**	**≥ 2000 m**
E. alternans (Chapuis)	0	37	9
E. dimidiatus (Chapuis)	14	1	0
E. longior (Wood)	0	2	1
E. longius (Wood)	0	9	2
E. longulus (Chapuis)	71	12	0
E. otiosus (Schedl)	0	0	7

pinhole borer *Myoplatypus flavicornis*. In a study or *Euplatyus parallelus* reported in a short congress proceedings paper, de Silva et al. (2013) mention finding Colydiidae (now in Zopheridae) and *Trypaneus* Godet inside the galleries they had dissected. Finally, Rainho et al. (2021) trapped two *Sosylus* Erichson species (Bothrideridae, but Colydiidae in early papers) in a field trial of *Euplatypus parallelus* pheromone; *Sosylus* are well known to be both parasites (as larvae, on platypodine pupae) and predators (as adults) of Platypodinae in the Old World (Browne 1962a,c, Roberts 1969a). Literature from outside the Americas documents a wide variety of predators: swallows, lizards, Brenthidae, Bothrideridae, Carabidae, Cerylonidae, Cleridae, Colydiidae, Cucujidae, Curculionidae, Histeridae, Nitidulidae, Reduviidae, Tenebrionidae, and Zopheridae (Hogan 1948, Jover 1952, Cachan 1957, Browne 1962a,c, Shedl 1962a, 1972, Roberts 1968, 1969a,b, 1977, 1980, Iidzuka et al. 2016). The 48-page catalog by Karl Schedl (1962a) is a compilation of all insect predators and commensals found with bark beetles or pinhole borers in the Belgian Congo and includes many records for Platypodinae. What is known about the natural enemies of platypodines from this work is summarized in Schedl (1972). In addition, wasps in the Old World genus *Monacon* Waterston in the chalcidoid family Perilampidae are known parasitiods of Platypodinae (Boucek 1980, Darling & Roberts 1999, Darling & Tatarnic 2020). We can expect to find an equally rich mix of predators, inquilines, and parasites of New World platypodines.

Results: Ecological and socioeconomic importance of Platypodinae

Ecological importance

Scolytinae and Platypodinae are important agents of nutrient recycling in forest ecosystems. Phloem feeders (phloeophages) and ambrosia beetles are among the first organisms to colonize dead and dying woody plants. They bring with them a community of symbiotic and opportunistic fungi, yeasts, bacteria, and mites, and their tunnelling create entry points for a wide variety of dead-wood (saproxylic) organisms (Schedl 1962a, Kirkendall et al. 2015). The effects of bark beetles and pinhole borers are amplified by the fact that they often colonize single hosts in large numbers, either because they utilize pheromones in their communication systems or because they are concentrated by host attractants such as ethanol (Elliot et al. 1983, Rainho et al. 2021). Pinhole borers penetrate deeply into larger diameter trunks and branches, and their tunnel systems can be quite extensive (Figures 27, 28). Because of differences among local species in moisture and other requirements, colonization of dead trees or woody debris can be spread out over years, and because the older sapwood of larger stumps or tree trunks in less tropical climates provide a voluminous and relatively stable habitat for years, they can be continuously utilized by even the same species over several years (Hogan 1948, Neumann and Harris 1974, Peng et al. 2022).

Economic damage

Although a handful of species regularly attack healthy trees (Kirkendall et al. 2015), it is well established that most Platypodinae species normally colonize only weakened or moribund trees (Beeson 1941, Browne 1961, Roberts 1968, Wagner et al. 1991). In some cases, attacks on live trees by Platypodinae can kill or weaken trees, primarily in conjunction with pathogenic fungi they carry (Elliot et al. 1983, Kinuura & Kobayashi 2006, Qi et al. 2011, Beaver 2013, Ploetz et al. 2013, Inacio et al. 2022, and see below). However, the most common economic damage due to pinhole borer colonization is loss of value (degrading) for wood with many tunnel holes (Figure 27D) and with discoloration from symbiotic fungi, what in North America is sometimes called "pinworm" damage to lumber (Graham & Boyes 1950, McMullan 1956, Bletchly 1961, Roberts 1968, Elliot et al. 1983, Carpenter et al. 1989, Noblecourt et al. 1995, Wagner et al. 1991). Loss of value is to wood destined for veneer, plywood or panelling and for some uses of pulp, but not to lumber used for construction (McMullan 1956, Carpenter et al. 1989, Daterman & Ovenhulser 2002). The loss due to degrade can be especially high for large, high-value logs; furthermore, wood with ambrosia beetle damage may be rejected for export (Daterman & Ovenhulser 2002).

There are very few examples from the Americas of single pinhole borer species that are clearly associated with economic losses. In the Neotropics, only *Megaplatypus mutatus* is considered a serious perennial threat to plantation trees in the tropics (Alfaro et al. 2007, Ceriani-Nakamurakare et al. 2022). *Megaplatypus mutatus* (*Platypus sulcatus* Chapuis or *P. plicatus* Brethes in early literature) is apparently found throughout South America, likely excluding only Chile, in forests ranging from tropical to cool temperate (Ceriani-Nakamurakare et al. 2022). The species breeds in native and exotic trees from a broad range of plant families, both gymnosperms as well as angiosperms (Giménez & Etinnot 2003, Alfaro et al. 2007, Ceriani-Nakamurakare et al. 2022). *Megaplatypus mutatus* is one of the very few ambrosia beetle species that mainly colonize live standing trees that are apparently healthy (Giménez & Etinnot 2003). This large species is considered a major pest of plantation trees of non-native species such as *Eucalyptus* and *Populus* in Argentina, Uruguay, Paraguay and Brazil (Alfaro et al. 2007). The extensive, large-diameter (5 mm) tunnel systems weaken trees to the point that they break from strong winds (Figure 27B). In addition to the structural damage, as with pinhole borer galleries generally, tunnelling reduces the number of potential uses for the wood and hence its market value (Ceriani-Nakamurakare et al. 2022). For orchard species, fruit set of attacked trees is lowered (Carella & Spigno 2003). As is likely the case with platypodines generally, but largely uninvestigated, *M. mutatus* is associated with a wide variety of microbes other than the primary *Raffaelea* species ambrosia fungi (reviewed in (Ceriani-Nakamurakare et al. 2022). *Megaplatypus mutatus* is one of very few Platypodinae known to have established self-sustaining populations outside of their native range; it is well established in Italy, where it causes economic losses to fruit and nut crops as well as to poplar plantations (Pasiecznik et al. 2005 and references in Ceriani-Nakamurakare et al. 2022).

Euplatypus parallelus is the most numerous Neotropical pinhole borer in many museum collections, due to its abundance, wide distribution in Central and South American forests, and to the fact that it comes to light in large numbers and hence is often sampled by general collectors. It is another of the very few Platypodinae that have become successful invasive species, now being found at lower elevations in tropical Africa, warmer parts of Asia, and oceanic islands such as the Seychelles and Hawaii, islands in Indonesia and the Philippines, and New Guinea (reviewed in Beaver 2013, see also Li et al. 2018, Barnouin et al. 2020). In addition to reducing the value of timber, this species can colonize weakened and stressed plantation trees in large numbers, and vectors pathogenic fungi in a variety of countries, such as rubber plantations in Brazil, Thailand, and China (Sittachiya and Beaver 2009, Beaver 2013, de Silva et al. 2013, Lai et al. 2020). While attacks on stressed trees may usually be secondary, they likely contribute to tree mortality (Kirkendall & Islam 2003, Boa & Kirkendall 2004).

Euplatypus segnis is abundant throughout Latin America (Kirkendall 2017a,b) where it is highly polyphagous, colonizing native and introduced trees from a wide variety of plant families (Atkinson et al. 1986, Burgos & Equihua 2007). Attacks to pecan trees (*Carya illinoensis*) by the platypodine in combination with fungi lead to significant yield losses in many plantations (Alvidrez-Villereal et al. 2012). Along with *E. parallelus*, this pinhole borer is also one of a complex of ambrosia beetle species that attack sick or dying avocado trees (*Persea americana*) in Mexico, and a species that could potentially spread the disease laurel wilt (*Raffaelea lauricola*) should it be introduced there (Àngel-Restrepo et al. 2019, 2022). Alvidirez-Villareal et al. (2012) found that *E. segnis* in pecan orchards spread pathogenic fungi.

Research gaps: What we don’t know about New World Platypodinae

Biodiversity

The Americas host about 300 described species but we have in our respective current collections well over 200 species that are currently unidentified, nearly all of which are certainly undescribed. With the increase in material becoming available from Malaise and flight intercept traps being deployed in the tropics we are getting a better idea of the distributional ranges of at least some taxa (Kirkendall 2017b), but we still don't know if there are species with very restricted ranges or declining populations that would deserve the attention of conservation biologists. As more and more specimens are identified, patterns of elevational limits to distributions of species will become clearer. Most pressing is the need for integrated taxonomy, as the alpha taxonomy of species in this region has thus far been based solely on external morphology. DNA investigations would not only aid in establishing species boundaries but are essential for the establishment of better generic bounds.

Morphology

Males of closely related species can usually be told apart by external morphology, and taxonomists working with Neotropical Platypodinae have seldom examined internal features such as the proventriculus (Nobuchi 1969) or genitalia (Roberts 1961, Calder 1990, Epila-Otara & Triplehorn 1990, Belhoucine et al. 2013). Perhaps comparative studies of platypodine genitalia could contribute to grouping species taxonomically, as well as to separating closely related species. We do not know how the Neotropical species lacking mycangial pores on the pronotum transport spores of ambrosia fungi. Old World genera often differ in larval characters (Browne 1972), knowledge of which could aid in delineating New World genera. Broad DNA studies could tell us the degree to which certain morphological characters are informative about higher level relationships in the Platypodini in particular: characters such as sexually dimorphic protibiae, structure and location of mycangia, the small teeth or carinae bordering the metanepisternal-metaventrite impression (the m-m character), modifications of ventrites in males.

Behaviour and ecology

That so much of this review necessarily draws from studies done in other regions emphasizes what little we know about the natural history of Platypodinae from the Nearctic and Neotropical realms. While many Neotropical species are undoubtedly host generalists, we know that polyphagous species from other regions can have host preferences. Further, there are likely to be species in the American tropics that specialize to one family or possibly groups of genera in one family; we suspect this might be the case, for example, for many species in *Myoplatypus* (oaks) and most species of *Teloplatypus* (Fabaceae) but often we have too few good host records to be certain. We know almost nothing about preferences for other aspects of host plants that might contribute to niche differences among co-occurring species: living vs dead, large vs small diameter material, higher vs lower moisture content, standing vs fallen, exposed vs shaded, and so forth. We know that these types of differences occur among scolytine ambrosia beetles, so we can expect that pinhole borers differ in such resource quality aspects as well.

The effects of Platypodinae colonization on wood decomposition, nutrient cycling, and successional dynamics and on the economics of forestry and woody plant crops are little known for the Neotropics.

Based on knowledge of the behaviours of studied species from other parts of the world, we can draw broad generalizations about communication by pheromones and acoustic signalling, about male and female reproductive behaviours, and about gallery construction, but there are certainly important variations among tribes, genera or species that we know little or nothing about. Most of what we know about social behaviour comes from a very few studies of African and Australian species: do Nearctic and Neotropical communities also harbour species with advanced forms of sociality?

Finally, we are likely to see major impacts of climate change on the plant and animal communities of tropical forests. We know very little about how climate or forest changes will affect wood-boring beetle communities.

Concluding words

We initiated this review in the hopes of informing and perhaps inspiring future research into Nearctic and especially Neotropical Platypodinae. We are in the process of revising the genera of these biotic realms, but currently our taxonomic research is based solely on external morphology, the limitations of which we are keenly aware. Nonetheless, we believe we can produce tools (keys, illustrations, databases) that, in combination with this review, will lower the learning curve for newcomers to the group. Neotropical Platypodinae are fascinating for many reasons, but understudied in part simply due to the complete lack of means for identifying them. Research using Platypodinae could contribute to fields such as biodiversity patterns; sexual selection (mutual sexual selection in monogamous species); signalling evolution (pheromones, stridulation); or many facets of tropical ecology.

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Notes added in proof

Our review paper was written in the spring and summer of 2023. Since then, the senior author has written a paper on Neotropical Platypodinae that comprises 49 new generic assignments and 22 new synonymies. These taxonomic changes slightly alter the numbers of species per genus given in Table 2. In particular, all but six Neotropical species still in *Platypus* were transferred to their proper genera. See: Kirkendall, L. R. 2024. Taxonomic changes for Neotropical pinhole borer ambrosia beetles (Coleoptera: Curculionidae: Platypodinae). *Zootaxa* 5410 (2), 199-221.

In Table 5, “new genus 1” is now described: Kirkendall, L. R. 2024. A new genus and species of Platypodini pinhole borers from South America (Coleoptera, Curculionidae, Platypodinae). *Zootaxa* 5432 (1), 83–95.

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