

**Dangerous Liaisons:
From cryptic female choice to medieval battlefields
in genital evolution of the Galerucini
(Coleoptera, Chrysomelidae, Galerucinae)**

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Dangerous Liaisons: From cryptic female choice to medieval battlefields in genital evolution of the Galerucini (Coleoptera, Chrysomelidae, Galerucinae)

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ABSTRACT

Copulatory damage during mating has been found in nine orders of Arthropoda, including beetles: in Carabidae Latreille, 1802, Meloidae Gyllenhaal, 1810, and two subfamilies of Chrysomelidae Latreille, 1802. Traumatic mating has been intensively studied in the genus *Callosobruchus* Pic, 1902 (Chrysomelidae, Bruchinae Latreille, 1802), in which males have sharp genital spines that damage the female bursa copulatrix. A single instance of traumatic mating has been demonstrated in the subfamily Galerucinae Latreille, 1802, in *Monolepta elongata* Jacoby, 1888, in which the male has long needle-like spines that penetrate the female bursa copulatrix. In this study I examined the endophalli of males, and the bursae of associated females, of 46 genera across all five subtribes of the tribe Galerucini Laboissiere, 1921. Of these 46 genera, 32 had sclerotized structures on the endophallus whereas in 14 genera the endophallus was a simple membranous sac. In males with modified endophalli, sharp spurs, cornuti, and elongate spiculae were most commonly encountered; some species also bore sclerotized bars that deployed upon everting the endophallus. Some species had sclerites bearing small knobs that suggested a stimulatory function in copulation. Species with spines that could potentially damage the females were encountered across the largest subtribes, as were females showing puncture scars on their bursae. However, individual cases were encountered in which males had dangerous-appearing endophalli, but females had no corresponding damage. Development of bursal sclerites in females was most evident in the Monoleptites Chapuis, 1875 (Luperina Wilcox, 1973), in which male endophallic spines were exceptionally numerous and elaborate. *Pyrrehalta maculicollis* (Motschulsky, 1853) is transferred to *Xanthogaleruca* Laboissiere, 1934 under the name *Xanthogaleruca maculicollis* (Motschulsky, 1953) n. comb., and *Metrioidea blakae* (Wilcox, 1965) is transferred to *Monolepta* Chevrolat, 1837 under the name *Monolepta blakae* (Wilcox, 1965) n. comb. Some preliminary speculations are offered on how these structures might fit into current theories of copulatory behavior.

KEY WORDS

Endophallus,
bursa,
spicula,
cornuti,
traumatic mating,
leaf beetle,
male/female genitalia;
new combinations.

RÉSUMÉ

Liaisons dangereuses : du choix cryptique de la femelle aux champs de bataille médiévaux dans l'évolution génitale des Galerucini (Coleoptera, Chrysomelidae, Galerucinae).

Des lésions copulatoires durant l'accouplement ont été observées chez neuf ordres d'arthropodes, dont les coléoptères : chez les Carabidae Latreille, 1802, Meloidae Gyllenhaal, 1810, et chez deux sous-familles de Chrysomelidae Latreille, 1802. L'accouplement traumatique a été principalement étudié pour le genre *Callosobruchus* Pic, 1902 (Chrysomelidae, Bruchinae Latreille, 1802), chez lequel les mâles possèdent des épines génitales acérées qui endommagent la bursa copulatrix des femelles. Un cas unique d'accouplement traumatique a également été démontré pour *Monolepta elongata* Jacoby, 1888, appartenant à la sous-famille Galerucinae Latreille, 1802, chez lequel le mâle possède des longues épines en forme d'aiguilles qui pénètrent dans la bursa copulatrix des femelles. Dans cette étude, j'ai examiné l'endophallus des mâles et la bursa des femelles associées de 46 genres, appartenant aux cinq sous-tribus de la tribu Galerucini Laboissière, 1921. Parmi ces 46 genres, 32 présentaient des structures sclérifiées sur l'endophallus; tandis que dans 14 genres, l'endophallus était un simple sac membraneux. Chez les mâles présentant un endophallus modifié, on observe le plus souvent des éperons pointus, des cornutis, et des spicules allongés; alors que d'autres espèces présentent des barres sclérifiées qui se déploient lors de la copulation. Certaines espèces présentaient également des sclérites portant des petits bossés suggérant une fonction stimulante lors de la copulation. Des espèces dotées d'épines susceptibles d'endommager les femelles ont été rencontrées dans les sous-tribus les plus nombreuses, tout comme des femelles présentant des cicatrices de perforation sur la bursa. Cependant, des cas exceptionnels ont été observés dans lesquels les mâles présentaient des endophallus dangereux, alors que les femelles ne présentaient aucun dommage correspondant. En ce qui concerne les femelles, le développement de sclérite dans la bursa était plus évident chez les Monoleptites Chapuis, 1875 (Galerucini, Luperina Wilcox, 1973), chez qui les épines endophalliques mâles étaient exceptionnellement nombreuses et élaborées. *Pyrrhalta maculicollis* (Motschulsky, 1853) est transféré à *Xanthogaleruca* Laboissière, 1934 sous le nom *Xanthogaleruca maculicollis* (Motschulsky, 1853) n. comb., et *Metrioidea blakae* (Wilcox, 1965) est transféré à *Monolepta* Chevrolat, 1837 sous le nom *Monolepta blakae* (Wilcox, 1965) n. comb. Des hypothèses préliminaires sont proposées sur la façon dont ces structures pourraient s'intégrer aux théories actuelles sur le comportement copulatoire.

MOTS CLÉS

Endophallus,
bursa copulatrix,
spicule,
cornuti,
accouplement
traumatique,
combinaisons nouvelles.

INTRODUCTION

Some of the more puzzling phenomena in the study of evolutionary biology are cases in which a male appears to harm a female during copulation. This seems to fly directly in the face of dogmas about the paramount importance of maximizing individual reproductive fitness to ensure the species survival from one generation to the next. As Darwinian theory would predict, such damaging male behavior is quite rare (Reinhardt *et al.* 2015). However, it is not nonexistent. Lange *et al.* (2013) found that copulatory damage (which they have termed “traumatic mating”) occurs in nine phyla, and commonly occurs in certain groups within six phyla. However, the majority of cases they list are based on observations of only one or a few species. In the Arthropoda, they list traumatic mating as occurring in nine orders, but that only in some scorpions, the bedbug clade Cimiciformes Scuh & Štys, 1991, and one genus of Miridae Hahn, 1831 (Hemiptera) is it a routine occurrence. In addition, traumatic mating has been described in spiders (Řezáč 2009; Hosken & Price 2009), and even in *Drosophila melanogaster* (Meigen, 1830) (Kamimura 2010). In Coleoptera, traumatic mating has been observed only in Carabidae Latreille, 1802 (Sota & Kubota 1998; Okuzaki *et al.* 2012) and in the Chrysomelidae Latreille, 1802 subfamilies Bruchinae Latreille, 1802 and Galerucinae Latreille, 1802 (Lange *et al.* 2013). The Carabidae studies found that only interspecific matings resulted in damage to females. Recently, Eberhard (2023) found that

in *Lytta eucera* (Chevrolat, 1834) (Meloidae Gyllenhaal, 1810) the male has sclerotized teeth on the aedeagus that snag the female vagina, leaving small scars.

In the Bruchinae, mating studies of several species in the genus *Callosobruchus* Pic, 1902 have established that during copulation the male everts a spiny structure of the endophallus, which resembles a medieval spiked mace, inside the female bursa (Crudgington & Siva-Jothy 2000). Spines penetrate slightly through the wall of the bursa and subsequently leave permanent scars in the female. The entire process has been studied in detail in *Callosobruchus maculatus* (Fabricius, 1775) (Edvardsson & Tregenza 2005; Eady *et al.* 2007; Hotzy *et al.* 2012) and in lesser detail in some allied species of *Callosobruchus* (Rönn *et al.* 2007; Van Haren *et al.* 2017).

Studies of copulatory behavior in arthropods and other animals generally support a theory of sexual fitness that identifies different selection pressures for males and females. Fitness in a male is promoted by his ability to mate with multiple females, whereas female fitness depends on her ability to select the best possible male to contribute sperm to her offspring. The resulting conflictive coevolutionary selection does not necessarily stop with the onset of physical mating, but can continue to affect actual intromission, and even post-copulatory behavior. There are several scenarios that could drive antagonistic coevolution into traumatic mating territory. In *Callosobruchus*, females attempt to limit male copulation time by kicking to dislodge

overly persistent males. Evolution of endophallic spines in the males has been shown to enable them to anchor themselves for longer copulations, at the expense of the later health of the females (Crudginton & Siva-Jothy 2000; Edvardsson & Tregenza 2005). In some insects, the function of spines on the male endophallus is related to the male passing seminal fluids into the female body, as has been demonstrated in *Drosophila melanogaster* (Kamimura 2010), and some blow flies (Caliphoridae Brauer & Bergenstamm, 1889; Eberhard 1996). Another avenue that could select for traumatic mating is male sperm competition. Among arthropods such as dragonflies, earwigs, and spiders, mating behavior of the male involves removing sperm of other males from his current partner (Fincke 1997; Kamimura 2015; Aisenberg *et al.* 2015), or removing spermatophore plugs left in females by previous males.

Eberhard (2015) has argued that cryptic female choice may play an important evolutionary role even in cases of traumatic mating. In such cases females could benefit even from damaging males through the increased competitiveness of their sons (Hosken & Price 2009). Females could also develop strategies to thwart or modify traumatic male mating behaviors. It is now generally accepted that cryptic female choice is one of the drivers of selection for the enormous diversity found in male internal and external genitalia. Cryptic female choice would also imply active selection for, and diversity of, internal female structures in response to the diversity of endophalli. Spines and denticles in the female bursae are a widespread occurrence in insects (e.g. the numerous signa observed in species of female Lepidoptera Linnaeus, 1758 [Cordero 2005]). It has generally been assumed that these structures assist in opening or cutting up the male spermatophores. This could also be a site of active coevolution, with males investing in “tough” spermatophores to limit females ability to later mate, and with females investing in structures to more rapidly dispose of hardened spermatophores so that she can more quickly mate with other males (Cordero & Baixeras 2015). Sánchez *et al.* (2011) found a statistical correlation between thick spermatophores and development of signa in a lepidopteran family in which polyandrous species were more likely to have these traits than monandrous species.

Matsumura *et al.* (2017) published a detailed morphology of the genitalia of *Pyrrhalla maculicollis* (Motschulsky, 1853) (Chrysomelidae: Galerucinae: Galerucini Latreille, 1802), describing a chitin band bearing a row of snake-like curved teeth inside the male endophallus, and dark scars on the female bursa that they inferred were haemocyte plugging wounds caused by the males endophallic teeth. Similar wounds have been described as haemocyte plugs in female *Callosobruchus* (Crudginton & Siva-Jothy 2000), and as melanized patches in *Drosophila* (Kamimura 2010). During a study of how genital structures are deployed during copulation in Costa Rican Chrysomelidae, Flowers & Eberhard (2006) reported a case in which the female bursa was penetrated by long, needle-like spines of the male (Fig. 1A-C). This case was discovered in a copulating pair of a very small, nondescript galerucines that attracted attention by their frenetic somersaulting about the beating net while still staying firmly stuck together. The

pair was “quick frozen” *in copula* in the field, fixed in alcohol, and dissected. They were tentatively identified as *Monolepta elongata* Jacoby, 1888 (Galerucinae: Luperina Wilcox, 1965: Monoleptites Chapuis, 1875). An everted male endophallus is shown in Figure 1D. Everted endophalli of several other unidentified male Costa Rican *Monolepta* Chevrolat, 1837 were observed to have similar armaments of needles and/or blade-like structures; a related female also had apparent scar tissue similar to that described in *Callosobruchus* and *Pyrrhalla* de Joannis, 1865 (Flowers & Eberhard 2006).

Documentation of likely traumatic mating in two distantly related subtribes of the Galerucinae opens up the question of whether similar behavior is found elsewhere in this subfamily. The only way to establish with absolute confidence that traumatic mating occurs in a species is to study copulating pairs. However, finding a pair *in copula* in the field is a rare occurrence, at least in the author’s experience of many years of Neotropical fieldwork. The possibility for traumatic mating might be inferred indirectly, however, by the presence of genital structures on the male capable of damaging the largely membranous female genital tract. Nevertheless, few studies have attempted to evert or dissect the male endophallus to determine what structures may be present. A notable exception is Tracy & Robbins (2009), who used structures on the everted endophallus to help separate closely related species of *Diorhabda* Weise, 1883 (Galerucinae, Galerucini).

The present study attempts to determine if traumatic mating occurs more widely in Galerucini, through a study of the morphology of male and female genitalia. If males of a given species have aedeagal structures capable of penetrating a female bursa, and if the females show scar tissue in portions of their internal genitalia accessible to male genitalia, that species would be a strong candidate for traumatic mating behavior.

MATERIAL AND METHODS

This study was conducted across a broad spectrum of the Galerucini, including all five subtribes, and 13 sections (Seeno & Wilcox 1982). Representatives of 46 genera of galerucines were dissected and the male endophalli were artificially everted, or in some cases extracted if everting was not possible. Taxonomic coverage was somewhat opportunistic, being limited to identified specimens in the Florida State Collection of Arthropods (FSCA), the Florida A&M University teaching collection, and my own small personal collection. Vouchers of specimens dissected in this study are deposited in FSCA.

Previously determined museum specimens were used where possible. Neotropical species were determined by Shawn Clark, Brigham Young University, and by the key in Viswajothi & Clark (2022); Asian species were determined at least to genus using keys in Kimoto (1989) and Yang *et al.* (2015), as well as specialized publications that are noted in Table 1. Genitalia of both males and females were prepared by placing the abdomens in cold solutions of approximately 10% potassium hydroxide, for several hours to overnight (longer for larger specimens). For the males, the aedeagi were removed and the endophallus

was everted through the median lobe orifice. Clamping the base of the median lobe with fine forceps and gently squeezing and sliding a second pair of forceps forward along the median lobe, starting behind the retracted endophallus and moving toward the orifice could usually accomplish this. Even in some very small species with relatively large sclerotized structures on the endophallus, this technique worked surprisingly well.

In some cases, the endophallus had to be extracted by pulling structures out with very finely hooked insect pins.

Females were dissected and cleared in a similar manner. The bursa was examined for the presence or absence of scar tissue; dark sclerotized spots in the bursal tissue were considered to be scars produced by genital damage (e.g. as in Fig. 2F, H). Any sclerotized structures in the bursa were noted, if present,

TABLE 1. — Evidence for traumatic mating in genera of Galerucini. **Type of endophallic structure:** **A**, hooks, spines, cornuti, or spiculae present; **B**, sclerotized bars present. **Evidence of trauma:** **y/n**, scars or abrasions visible/not visible on the bursa; **–**, female not examined. **Bursa with sclerotized structures, Spermatophore material present?:** **y/n**, present/absent; **–**, female not examined. **Identification:** identifier, or literature reference to appropriate key.

Species	Specimens examined	Type of endophallic structure	Evidence of trauma	Bursa with sclerotized structures	Spermatophore material present?	Origin	Identification
OIDINA							
<i>Oides</i> nr. <i>duodecimpunctata</i> (Clark, 1866)	1 ♂, FSCA00081600	none	–	–	–	Sarawak	Lee & Beenen 2017
GALERUCINA							
Coelomerites							
<i>Coelomera</i> sp.	1 ♂, FSCA00081133 2 ♀, FSCA00081701 FSCA00081099	none	n	n	n	Costa Rica	S. M. Clark
<i>Dircema</i> sp.	1 ♂, FSCA00081687	none	–	–	–	Brazil	S. M. Clark
<i>Caraguata</i> sp.	1 ♂, FSCA00081735 2 ♀, FSCA00081734 FSCA00081700	A	n	n	?	Brazil	Viswajyothi & Clark 2022
<i>Neophaestus</i> sp.	1 ♂, FSCA00081122 1 ♀, FSCA00081699	B	y	n	n	Ecuador	S. M. Clark
<i>Nestinus viridis</i> Jacoby, 1888	2 ♂, FSCA00081526 FSCA00081685 2 ♀, FSCA00081097 FSCA00081527	none	n	n	y	Costa Rica	S. M. Clark
<i>Polysastra</i> sp.	1 ♂, FSCA00081686	spicules	–	–	–	New Guinea	Shute 1983
<i>Trirhabda bacharidis</i> (Weber, 1801)	6 ♂, FSCA00081682 FSCA00081683 FSCA00081703 FSCA00081704 FSCA00081705 FSCA00081121 2 ♀, FSCA00081104 FSCA00081107	A	n	n	y		Wilcox 1965
Atysites							
<i>Galerucella nymphae</i> (Linnaeus, 1758)	1 ♂, FSCA00081137 1 ♀, FSCA00081136	none	n	n	n	United States	Epler 2010
<i>Xanthogaleruca luteola</i> (Müller, 1766)	2 ♂, FSCA00081736 FSCA00081702 3 ♀, FSCA00081107 FSCA00081737 FSCA00081678	A	y	n	y	United States	Wilcox 1965
Schematizites							
<i>Monoxia angularis</i> (LeConte, 1859)	1 ♂, FSCA00081726 1 ♀, FSCA00081126	none	n	y	n	United States	Wilcox 1965
<i>Ophraella sexvittata</i> LeConte, 1865	1 ♂, FSCA00081676 1 ♀, FSCA00081675	none	n	n	n	United States	Wilcox 1965
<i>Schematiza</i> sp.	1 ♂, FSCA00081723 1 ♀, FSCA00081103	none	n	n	n	Bolivia	S. M. Clark
METACYCLINA							
<i>Byblitea jansonii</i> (Baly, 1864)	1 ♂, FSCA00081132 2 ♀, FSCA00081131 FSCA00081684	A, B	y	n	y	Costa Rica	S. M. Clark
<i>Chthoneis</i> sp. 1	1 ♂, FSCA00081525 1 ♀, FSCA00081140	A, B	y	n	n	Costa Rica	S. M. Clark
<i>Chthoneis</i> sp. 2	1 ♂, FSCA00081692 1 ♀, FSCA00081102	B	y	n	n	Costa Rica	S. M. Clark
<i>Exora encaustica</i> (Germar, 1823)	1 ♂, FSCA00081130 1 ♀, FSCA00081116	B	n	y	y	Panamá	S. M. Clark

Table 1. — Continuation.

Species	Specimens examined	Type of endophallic structure	Evidence of trauma	Bursa with sclerotized structures	Spermatophore material present?	Origin	Identification
<i>Hecataeus</i> sp.	1 ♂, FSCA00081727 1 ♀, FSCA00081127	B	y?	y	n	Ecuador	S. M. Clark
<i>Malacorhinus</i> sp.	1 ♂, FSCA00081728 2 ♀, FSCA00081125 FSCA00081618	B	y?	y	n	México	S. M. Clark
<i>Masurius</i> sp.	1 ♂, FSCA00081141 1 ♀, FSCA00081089 FSCA00081142	A, B	y	y	y	Costa Rica	S. M. Clark
HYLASPINA							
<i>Aplosonyx albicornis</i> (Wiedemann, 1821)	1 ♂, FSCA00081084 1 ♀, FSCA00081082	B	n	n	y	Malaysia, Sabah	Kimoto 1989
<i>Aplosonyx monticola</i> Bowditch, 1925	2 ♂, FSCA00081115 FSCA00081083 1 ♀, FSCA00081082	none	n	n	y	Malaysia, Sabah	Kimoto 1989
<i>Aplosonyx javana</i> (Wiedemann, 1821)	1 ♂, FSCA00081095 1 ♀, FSCA00081096	A	n	n	y	Indonesia, W. Sumba Is.	Kimoto 1989
<i>Dicertina collina</i> (Weise, 1924)	1 ♂, FSCA00081738 1 ♀, FSCA00081739	A	n	n	n	India	FSCA ident.
<i>Sermylassa halensis</i> (Linnaeus, 1767)	1 ♂, FSCA00081722 1 ♀, FSCA00081721	none	n	n	n	Italy	FSCA ident.
LUPERINA							
<i>Aulacophorites</i>							
<i>Agetocera similis</i> Chen, 1997	2 ♂, FSCA00081667 FSCA00081145 3 ♀, FSCA00081668 FSCA00081146 FSCA00081669	A	n	y	y	Laos	Lee <i>et al.</i> 2010
<i>Aulacophora antennata</i> Baly, 1886	1 ♂, FSCA00081742 1 ♀, FSCA00081741	A	y	y	y	Malaysia, Sabah	Kimoto 1989
<i>Aulacophora bicolor</i> (Weber, 1801)	1 ♂, FSCA00081696	A	–	–	–	Laos	Kimoto 1989
<i>Aulacophora cornuta</i> Baly, 1879	1 ♂, FSCA00081695 1 ♀, FSCA00081694	A	y	n	y	Indonesia, W. Sumba Is.	Kimoto 1989
<i>Aulacophora</i> sp.	1 ♂, FSCA00081744	A	n	n	y	New Guinea	Kimoto 1989
<i>Aulacophora luteicornis</i> (Fabricius, 1801)	1 ♂, FSCA00081732 1 ♀, FSCA00081733	A	n	n	n	Indonesia, Sumatra	Kimoto 1989
<i>Diabroticites</i>							
<i>Acalymma</i> sp. [in copula]	FSCA00081529	A	n	y	y	Dominica	FSCA ident.
<i>Acalymma subaeneum</i> (Jacoby, 1887)	1 ♂, FSCA00081674 1 ♀, FSCA00081673	A	n	n	n	Costa Rica	S. M. Clark
<i>Amphelasma decoratum</i> (Jacoby, 1887) [in copula]	FSCA00081124	none	n	n	n	México	Viswajyothi & Clark 2022
<i>Diabrotica undecimpunctata howardi</i> Barber, 1947 [in copula]	FSCA00081528	A	y	n	y	United States	FSCA ident.
<i>Gynandrobrotica ventricosa</i> (Jacoby, 1878)	1 ♂, FSCA00081718 1 ♀, FSCA00081731	A	y	n	y	Costa Rica	R. W. Flowers
<i>Isotes dilatata</i> (Jacoby, 1887)	1 ♀, FSCA00081129	–	y	n	n	Costa Rica	Rodríguez & Mermudez 2016
<i>Isotes rubripennis</i> (Erichson, 1847)	2 ♂, FSCA00081128 FSCA00081730 1 ♀, FSCA00081729	A	y	y	n	Ecuador	Rodríguez & Mermudez 2016
<i>Paranapiacaba</i> sp.	1 ♂, FSCA00081724 2 ♀, FSCA00081725 FSCA00081656	A	n	y	n	Argentina	Viswajyothi & Clark 2022
<i>Zischkaita</i> sp.	1 ♂, FSCA00081657	none	–	–	–	Ecuador	Viswajyothi & Clark 2022
Phyllethrites							
<i>Luperosoma subsulcata</i> (Horn, 1893) [males and females pinned in pairs]	FSCA00081109 FSCA00081110 FSCA00081111	A	y	n	n	United States	FSCA ident.
<i>Phyllethris dorsalis</i> (Olivier, 1808) [pairs in copula]	FSCA00081101 FSCA00081108	A	y	n	y	United States	FSCA ident.

Table 1. — Continuation.

Species	Specimens examined	Type of endophallic structure	Evidence of trauma	Bursa with sclerotized structures	Spermatophore material present?	Origin	Identification
Scelidites							
<i>Pteleon brevicornis</i> (Jacoby, 1887)	1 ♂, FSCA00081708 1 ♀, FSCA00081707	A	y	n	y	United States	FSCA ident.
<i>Amplioluperus cyanella</i> (Horn, 1895)	1 ♂, FSCA00081711 1 ♀, FSCA00081712	A	n	n	n	United States	FSCA ident.
<i>Scelida flaviceps</i> (Horn, 1893)	2 ♂, FSCA00081740 FSCA00081662 2 ♀, FSCA00081706 FSCA00081661	A	n	n	y	United States	FSCA ident.
<i>Scelida nigricornis</i> (Jacoby, 1888)	1 ♂, FSCA00081709 2 ♀, FSCA00081710 FSCA00081655	A	n	n	n	United States	FSCA ident.
<i>Scelolyperus leontii</i> (Crotch, 1873)	2 ♂, FSCA00081715 FSCA00081663 1 ♀, FSCA00081716	A	y	n	y	United States	FSCA ident.
<i>Synetocephalus bivittatus</i> (LeConte, 1859)	1 ♂, FSCA00081713 1 ♀, FSCA00081714	A	y	n	n	United States	FSCA ident.
<i>Triarius trivittatus</i> Horn, 1893	1 ♂, FSCA00081717	none	—	—	—	United States	FSCA ident.
Phyllobroticites							
<i>Phyllobrotica costipennis</i> Horn, 1893	1 ♂, FSCA00081720 1 ♀, FSCA00081719	none	n	n	n	United States	Wilcox 1965
Exosomites							
<i>Cneorane femoralis</i> Jacoby, 1888	4 ♂, FSCA00081144 FSCA00081670 FSCA00081671 FSCA00081672 7 ♀, FSCA00081094 FSCA00091143 FSCA00081654 FSCA00081698 FSCA00081666 FSCA00081664 FSCA00081665	A	y	y	y	Laos	Kimoto 1989
<i>Coeligenes borneensis</i> Mohamedsaid, 1994	1 ♂, FSCA00081697 2 ♀, FSCA00081123 FSCA00081658	A	y	y	n	Sabah	Mohamedsaid 1994
Monoleptites							
<i>Candezea semiviolacea</i> (Fauvel, 1862)	1 ♂, FSCA00081088 1 ♀, FSCA00081089	A	n	n	y	New Caledonia	Beenen 2013
<i>Eusattodera</i> sp.	1 ♂, FSCA00081118 2 ♀, FSCA00081119 FSCA00081117	A	y	n	y		
<i>Monolepta elongata</i> Jacoby, 1888	pair copulating in field (see Flowers & Eberhard 2006)	A	y	y	y	Costa Rica	Jacoby 1888-1892
<i>Monolepta irazuensis</i> (Jacoby, 1888)	1 ♂, FSCA00081534 1 ♀, FSCA00081533	A	y	y	y	Costa Rica	Jacoby 1888-1892
<i>Monolepta blakeae</i> (Wilcox, 1965) n. comb.	1 ♂, FSCA00081536 3 ♀, FSCA00081134 FSCA00081536 FSCA00081660	A	y	y	y	United States	R. W. Flowers
<i>Monolepta</i> sp.	1 ♂, FSCA00081091 1 ♀, FSCA00081092	A	y	n	y	Honduras	Viswajothi & Clark 2022
<i>Monolepta</i> sp.	1 ♂, FSCA00081093	A	—	—	—	Ecuador	Viswajothi & Clark 2022
<i>Monolepta</i> sp.	1 ♂, FSCA00081138 2 ♀, FSCA00081105 FSCA00081106	A	y	y	y	Nigeria	Wagner 2007
<i>Monolepta</i> sp.	1 ♂, FSCA00081530	A	—	—	—	Sumatra	Kimoto 1989
<i>Monolepta laosensis</i> Kimoto, 1989	1 ♂, FSCA00081139 1 ♀, FSCA00081100	A	y	y	y	Laos	Kimoto 1989
<i>Monolepta</i> sp.	2 ♂, FSCA00081532 FSCA00081537 1 ♀, FSCA00081531	A	y	y	y	Vietnam	Kimoto 1989
<i>Paleosepharia truncata</i> Laboissière, 1936	1 ♂, FSCA00091693	A	—	—	—	Laos	Kimoto 1989



FIG. 1. — Copulation in *Monolepta elongata* Jacoby, 1888, Costa Rica, reproduced with permission (Flowers & Eberhard 2006): **A**, dissection of copulating pair, **circles** show penetration of male spiculae through the bursa, spermatophore is the opaque white mass at left; **B**, aedeagus of *M. elongata* with endophallus everted; **C**, cleared dissection of copulating organs of *M. elongata*, showing needle-like spiculae of the male endophallus, and the saw-like sclerites of the female bursa; **D**, enlarged view of endophallus and female toothed sclerites. Abbreviations: see Material and methods. Scale bars: 0.5 mm.

as was the presence of spermatophore material (recognizable by its opaque white appearance, e.g. Fig. 1C) in the bursa. Dissected genitalia specimens were photographed either with a Spectroscopy Automontage system at FSCA, or with an objective-mounted Nikon Coolpix995, and stored in glycerin in genitalia vials pinned below the beetle specimens.

Wagner (2007) used the term “spicula” to generally describe spine-like structures on the endophalli of African *Monoleptites*, whereas Cordero (2010) used the term “cornuti” to describe dense patches of needle-like spines on the endophalli of some Lepidoptera. These terms are used in this paper; descriptions of other forms of sclerites of endophalli are based on physical appearance and relative position. In some cases, sclerites on the apex of the endophallus are referred to as apical sclerites when they are different in appearance from other sclerites. They may function in transferring the sperm to the spermatheca, inducing the female to transport sperm to the spermatheca,

or in forming the spermatophore in the female. None of the taxa studied had a flagellum in the males that could reach the spermatheca, as is found in many Eumolpinae Hope, 1840 (Flowers & Eberhard 2006) and in some Cassidinae Gyllenhaal, 1813 (Rodríguez *et al.* 2004).

ABBREVIATIONS

Male genitalia

As	apical sclerite;
Cti	cornuti;
MML	male median lobe;
spa	spicula;
Spf	spermatophore.

Female genitalia

B	bursa copulatrix;
spt	spermatheca;
vp	vaginal palpi.

RESULTS

Observations of the male endophalli, with any associated structures, as well as associated damage to internal female structures, are described below, and summarized in Table 1. While the larger endophallic structures showed a high level of variability across and within genera, they fell into two general categories: sharp sclerites such as spiculae and cornuti, described above, designated type A; and elongate bars or stout hooks that often rotated backwards as the endophallus everted, designated type B. Evidence of trauma to the bursa and/or vagina, are noted, as well as sclerotized structures in the female bursa, if present, and presence of spermathecal material in the female tract (evidence that the female has mated). The classification below follows Viswajyothi & Clark (2022)

Subtribe Oidini Chapuis, 1875

A single male specimen of *Oides* nr. *duodecimpunctata* (Clark, 1866) (not illustrated) had a completely membranous endophallus.

Subtribe Galerucini Latreille, 1802

Section Schematizites Chapuis, 1875

The simplest pattern of male genitalia in the Galerucini was a membranous sac-like endophallus with a long flexible sclerite along its length. Examples were *Monoxia angularis* (LeConte, 1859) (Fig. 2A [male], Fig. 2B [female]); *Ophraella sexvittata* LeConte, 1865 (not shown); and *Schematiza* Chevrolat, 1836 species (Fig. 2C).

Section Coelomerites Chapuis, 1875

Genera studied from this section had sac-like endophalli, either broad (a species of *Coelomera* Chevrolat, 1836), or narrow with a weakly sclerotized band along one side (*Nestinus viridis* Jacoby, 1888). A male *Dircema* Clark, 1865 (not shown) had a sac-like endophallus with a weak Y-shaped sclerotized area on the upper side, and membranous striae on the lower side. A male *Polysastra* Shute, 1983 (not shown) had a membranous endophallus lobed at the base, and covered with minute denticles. Shute (1983) illustrated the endophallus of a different species of *Polysastra*, in which the denticles at the apex of the endophallus were much longer and more needle-like.

In *Trirhabda bacharidis* (Weber, 1801) (Fig. 2D) the endophallus was very long with a sclerotized lobe at the base, this lobe bearing small teeth along its distal margin (Fig. 2D, inset). The female bursa showed no signs of scarring. A species of *Caraguata* Bechyně, 1954 from southwestern Brazil showed a similar but more elaborate

development of this pattern in the male endophallus. The median lobe has a robust lateral sclerotized strap with a basal lobe tipped with minute spines (Fig. 3A, inset), and a heavily sclerotized terminal bar (Fig. 3B). The bursa of the female (Fig. 3C) had an area of thick scars on the side of the vagina, and a smaller area of apparent abrasions on the rear of the bursa. Two pairs of *Neophaestus* Hincks, 1949 were collected from two nearby mountains in the Ecuadorian Andes. In one pair, the male had a membranous endophallus with a single sclerotized bar attached at one end (Fig. 2E). The female (Fig. 2F) displayed a pair of apparent puncture scars despite the lack of obvious sharp structures in the male. In the second pair the male lacked the sclerotized bar, and the female bursa was unmarked. *Neophaestus* is currently known from one species in Central America (Viswajyothi & Clark 2022); these data suggest that at least two more are found in South America.

Section Atysites Chapuis, 1875

The condition of a narrow endophallus with a lateral sclerotized band was found in *Galerucella nymphae* (Linnaeus, 1758). However, in *Xanthogaleruca luteola* (Müller, 1766) the male endophallus had a longitudinal flexible sclerite with a row of long, sharp, recurved teeth (Fig. 2G). Matsumura *et al.* (2017) described an almost identical structure on the endophallus of *Pyrrhalla maculicollis* (*Xanthogaleruca* was until recently considered a subgenus of *Pyrrhalla*). Bursae of several females of *X. luteola* were dissected and all except one showed signs of puncture damage (Fig. 2H, I).

Subtribe Metacyclini Chapuis, 1875

Seven genera from this tribe were studied from the Neotropical region. The median lobes of all studied males had elongate lateral endophallic sclerites that, when pushed out through the orifice, rotated either to a perpendicular position relative to the rest of the aedeagus, or rotated backward almost a full 180° with the former apical part now facing toward the base of the median lobe. *Byblitea jansonii* (Baly, 1864) demonstrates the latter case (Fig. 3D, E). The narrow lateral sclerite in the everted position has a row of small hooked teeth on its apex (Fig. 3E), now facing the basal part of the median lobe. The apex of the endophallus bears a complex sclerotized structure that includes a needle-like central spine and a lateral spine with a crochet-hook tip (Fig. 3D). The bursa of the female (Fig. 3F) shows an area with apparent abrasion scars.

An unidentified species of *Chthoneis* Baly, 1864 (sp. 1) had two backward-facing rotating sclerites with a sharp tooth on the median lobe: they are shown (Fig. 3G) in the process of being everted, and are fully extended in Figure 3H. An associated female (Fig. 3I) had a pair of possible puncture marks at a corresponding site, near the basal end of the bursa, but no other evidence of genital damage. A second undescribed



FIG. 2. — Genitalia of Galerucini: **A, B**, *Monoxia angularis* (LeConte, 1859): **A**, male median lobe, right side, endophallus everted; **B**, female; **C**, *Schematiza* sp., male median lobe, right side, endophallus everted; **D**, *Tirrhabda bacharidis* (Weber, 1801), male median lobe, right side, endophallus extruded. **Inset**: spiny lobe at base of endophallus; **E, F**, *Neophaestus* sp.: **E**, male median lobe, left side, endophallus everted; **F**, female, **arrows** point to scars at opening of the bursa; **G, I**, *Xanthogaleruca luteola* (Müller, 1766): **G**, male median lobe, right side, endophallus extruded; **H**, female, **arrows** point to scars at opening of the bursa; **I**, uninjured female. Scale bars: A, B, F, 0.5 mm; C-E, G-I, 1 mm.

species of *Chthoneis* (sp. 2) (Fig. 3J) differed in detail from *Chthoneis* sp. 1 in having a single sharp tooth, but both species show two reversing lateral sclerites, and a short endophallus

bearing a relatively large complex apical sclerite. In the case of *Chthoneis* sp. 2, the everted endophallus did not align along the axis of the median lobe, but this may be an artifact of

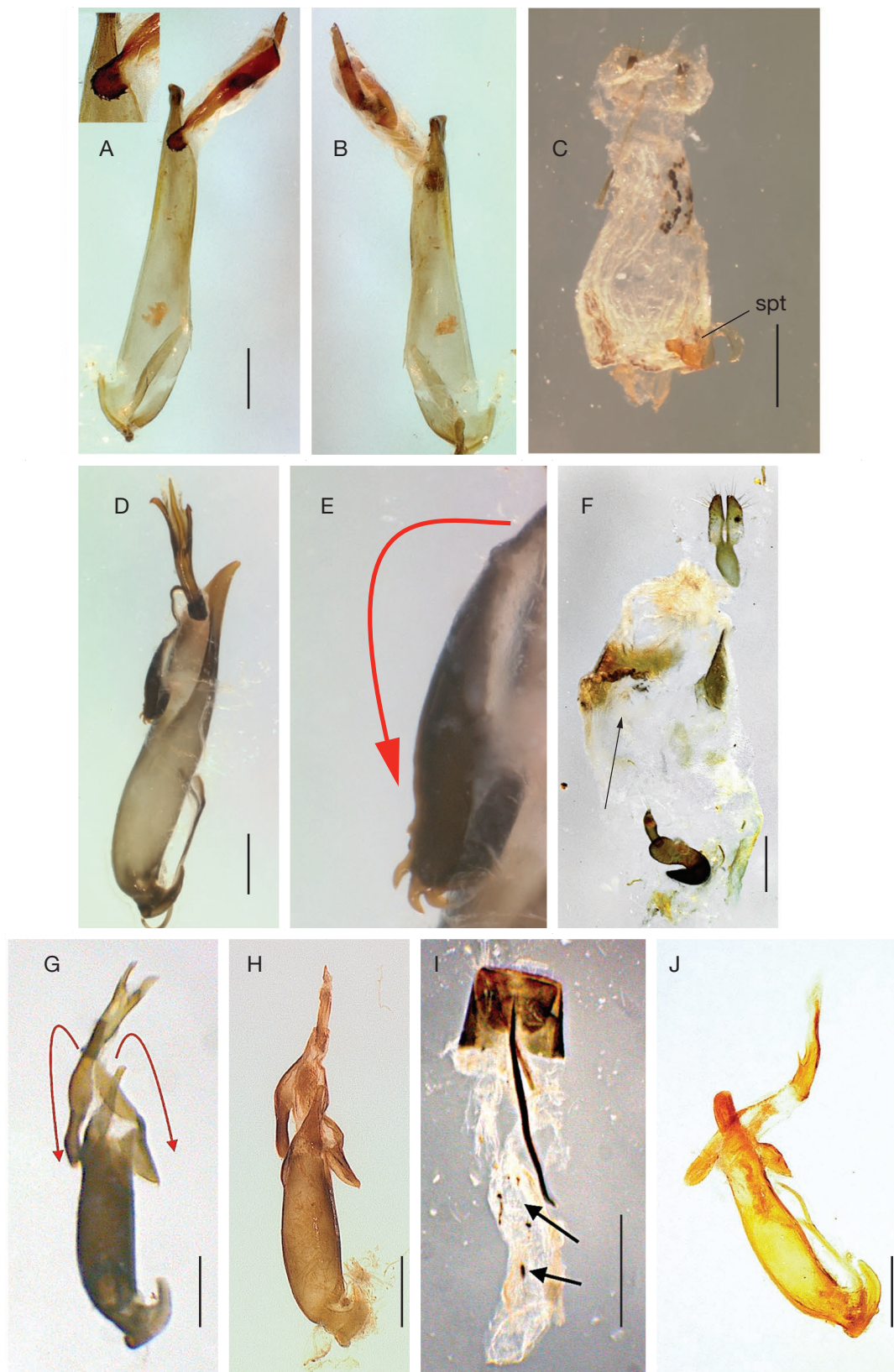


FIG. 3. — Genitalia of Galerucini (A–C) and Metacyclini (D–J): A–C, *Caraguata* sp.: A, male median lobe, left side. Inset: spiny lobe on base of sclerotized strap; B, male median lobe, right side; C, female internal genitalia; D–F, *Byblita jansoni* (Baly, 1864): D, male median lobe, right side; E, endophallic sclerite, **red arrow** shows motion as it everts from median lobe; F, female internal genitalia, **arrow** indicates abraded region; G–I, *Chthoneis* sp. 1: G, male median lobe, partly everted, **red arrows** indicate motion of lateral endophallic sclerites; H, male median lobe fully everted; I, female internal genitalia, puncture scars indicated by **arrows**; J, *Chthoneis* sp. 2, male median lobe, right side. Abbreviation: see Material and methods. Scale bars: A–D, G–J, 0.5 mm; F, 1 mm.

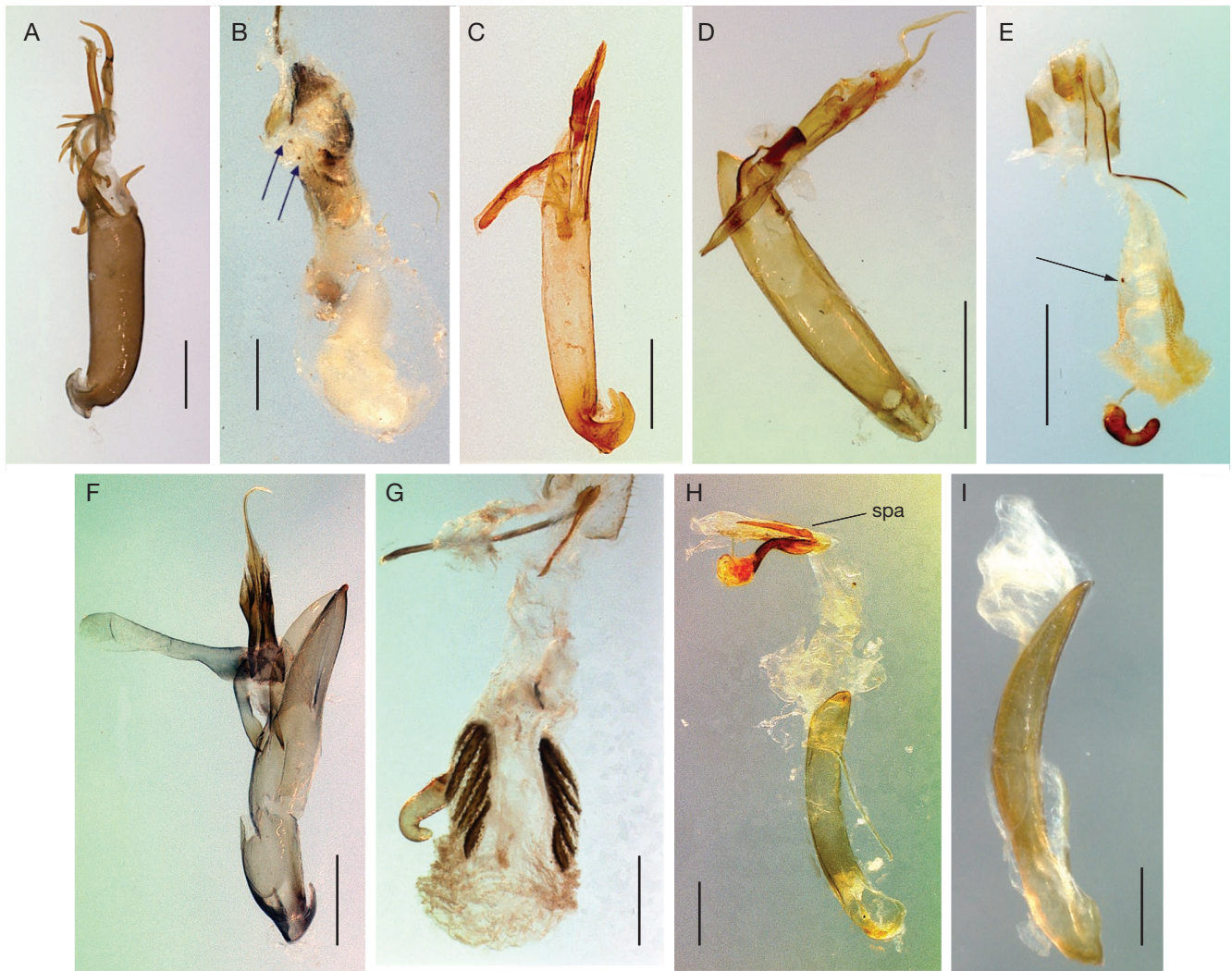


FIG. 4. — Genitalia of Metacyclini (A–G) and Hylaspini (H, I): **A, B**, *Masurius* sp., **A**, male median lobe, left side, endophallus everted; **B**, female, cleared genitalia with vaginal palpi at top, **arrows** indicate scars on vagina; **C**, *Exora encaustica* (Germar, 1823), male median lobe, right side, endophallus everted; **D, E**, *Hecataeus* sp.: **D**, male median lobe, top view, endophallus everted; **E**, female, internal genitalia, bursa showing minute internal sclerites and a puncture scar (**arrow**); **F, G**, *Malacorhinus* sp.: **F**, male median lobe, right-ventral view, endophallus everted; **G**, female, internal genitalia, bursa with heavy internal sclerites and possible abraded area above; **H**, *Dicertina collina* (Weise, 1924), male median lobe, right side; **I**, *Sermylassa halensis* (Linnaeus, 1767), male median lobe, right side. Abbreviation: see Material and methods. Scale bars: 0.5 mm.

preparation. A single female of this species had no convincing evidence of bursal damage.

An undescribed Costa Rican *Masurius* Jacoby, 1888 (Fig. 4A) displayed a complex endophallus displaying sclerites in the form of recurved spikes, a row of long spines, an elongate hook, and an elongate apical sclerite. Despite the impressive armature of the males, a female with a spermatophore collected along with the males had only a few possible scars (Fig. 4B). A second female that lacked a spermatophore had no signs of punctures in the bursa.

Endophalli of *Exora encaustica* (Germar, 1823) (Fig. 4C), *Hecataeus* Jacoby, 1888 species (Fig. 4D), and *Malacorhinus* Jacoby, 1887 species (Fig. 4F) all have lateral sclerites that lack sharp points (although apical sclerite complexes have them) but deploy at various angles to the main axis of the endophallus. The lateral sclerites of *Exora* Chevrolat, 1837

and *Malacorhinus* rotate to right angles to the endophallus, whereas in *Hecataeus* (Fig. 4D) the sclerite rotated a full 180°. The female of *Hecataeus* (Fig. 4E) shows a possible puncture scar, whereas the females of *Malacorhinus* (Fig. 4G) and *Exora* (not shown) do not show signs of puncture or other tissue damage. The female of *Malacorhinus* sp. has a pair of large branched sclerites on the inner surface of the bursa (Fig. 4G); the female of *Exora* has a similar arrangement of bursal sclerites.

There is a pair of curved spurs at the base of the median lobe in males of the Galerucina and Metacyclina (as in Figs 2A, C–E; 3A, D, G, H, J; 4A, C, F). This is an important taxonomic character that distinguishes Galerucina and Metacyclina from the remainder of the Galerucini (Viswajothi & Clark 2022) but is also found elsewhere in the Chrysomelidae (e.g. Eumolpinae; Flowers 1999); these spurs are not known to actively participate in copulation.



FIG. 5. — Genitalia of Hylaspiini: **A, D**, *Aplosonyx albicornis* (Wiedemann, 1821): **A**, male median lobe, top view, everted; **D**, female, internal genitalia; **B, E**, *Aplosonyx javana* (Wiedemann, 1821): **B**, male median lobe, top view, everted; **E**, female, internal genitalia, **arrows** indicate puncture scars; **C, F**, *Aplosonyx monticola* Bowditch, 1925: **C**, male median lobe, ventral view, everted with “retracting tendon” lying next to membrane; **F**, female, internal genitalia. Scale bars: 0.5 mm.

Subtribe Hylaspini Chapuis, 1875

Only three genera could be sampled from this largely Old World tribe. *Dicertina collina* (Weise, 1924) (Fig. 4H) had a membranous, elongate endophallus bearing a complex apical structure consisting of a tube-like central part, and a pair of sharp lateral spines. An associated female showed no signs of scarring. *Sermylassa halensis* (Linnaeus, 1767) (Fig. 4I) had an entirely membranous endophallus lacking any sclerotized structures. Three species of *Aplosonyx* Chevrolat, 1836 were studied. *Aplosonyx albicornis* (Wiedemann, 1821) (Fig. 5A) showed a long, tubular, membranous endophallus with the apical sclerite flanked by two elongate curved sclerites, and an endophallic membrane densely studded with minute spines or teeth. When the endophallus was everted, these lateral sclerites spread apart once clear of the membrane tube. A species from Indonesia, *A. javana* (Wiedemann, 1821) (Fig. 5B), had an apical sclerite arrangement similar to *A. albicornis*, except that the lateral sclerites were pointed and hook-shaped. In *A. monticola* Bowditch, 1925 (Fig. 5C), the endophallus was large and completely membranous, except for a small, sclerotized T-shaped apical sclerite. This species also had very long thin sclerite with a round plate on the base, running inside the endophallus to the apical sclerite (perhaps a retracting device). In both available specimens, everting the endophallus caused the sclerite to spring laterally through the endophallic membrane as shown in Figure 5C. Females of *A. albicornis* and *A. monticola* had no scars on the bursa or vagina (Fig. 5D, F). The female of *A. javana*, the species in which the male has sharp endophallic sclerites, had a pair of possible scars near the entrance of her bursa (Fig. 5E).

Photos of aedeagi in a recent revision of the Chinese *Aplosonyx* (Feng *et al.* 2023) show paired curved sclerites similar to those of *A. albicornis* lying inside the median lobes of 21 species.

Subtribe Luperini Gistel, 1848

Section *Aulacophorites* Chapuis, 1875

Five species of the large Asian genus *Aulacophora* Chevrolat, 1836 were examined. *Aulacophora antennata* Baly, 1886 had a short, robust, lightly sclerotized endophallus with a pair of curved sclerotized horns on the dorsal side at the base, and a large, heavily sclerotized apical sclerite (Fig. 6A) and a complex apical structure with brushes of fine setae. A female had a vagina with a relatively thick membrane with a pair of small spurs in the vagina and two small abraded areas at the rear wall of the bursa (Fig. 6B). This suggests male stimulation rather than traumatic penetration during mating.

Four other species of *Aulacophora* all had a different basic pattern in the male aedeagus: relatively short membranous endophalli with patches of small spines or denticles, ending in relatively long, heavily sclerotized apical sclerites. In *A. bicolor* (Weber, 1801) the endophallus had only very small patches of denticles along with a strong hook-shaped apical sclerite (Fig. 6C). *Aulacophora cornuta* Baly, 1879 (Fig. 6E),

an unidentified New Guinea species (Fig. 6D), and *A. luteicornis* (Fabricius, 1801) (Fig. 6G) all had apical sclerites in the form of elongate tubes. A female of *A. cornuta* (Fig. 6F) had numerous apparent scars or abrasions on the bursa; the sizes and numbers did not correspond in any obvious way with the male tube or hook; however, females of *A. luteicornis* showed no signs of bursal damage.

In *Agetocera similis* Chen, 1997 the male has a membranous, branched endophallus with each branch terminating in a sharp spike (Fig. 7A). Despite the impressive armature of the male, the female available for study showed no signs of damage, and she had a large sclerotized structure in the bursa (Fig. 7B). Lee *et al.* (2010), in their revision of the *Agetocera* Hope, 1831 of Taiwan, give line drawings of male median lobes with tracings of internal sclerites. It appears that their species also have “three-spike” endophalli similar to those of *A. similis*.

Section *Diabroticites* Chapuis, 1875

A pair of *Diabrotica undecimpunctata howardi* Barber, 1947, mounted *in copula*, was dissected with the male and female genitalia in position (Fig. 8A). The male endophallus had robust spines (Fig. 8A, B), and the female vagina bore scars a short distance away from the male organ (arrows in Fig. 8A). Although not obvious in the photo due to KOH clearing, the bursa also contained a large spermatophore. Derunkov *et al.* (2013) have published an electronic identification tool, which includes photos of everted endophalli for most of the species of *Diabrotica* Chevrolat, 1836 of North and Central America. These endophalli show a similar pattern of a relatively short membranous tube with from three to five robust sclerites variously developed as spikes, hooks, or serrated pads in different combinations. Copulation in *D. undecimpunctata* was also studied in flash-frozen beetle pairs by Tallamy *et al.* (2002). They found that the female has a fold in the vagina that she can use to exclude the entrance of the male median lobe. Male courtship activities can induce the female to relax the fold and permit entrance. However, the authors did not mention either the endophallus or the endophallic spines in their study.

A pair of *Acalymma* Barber, 1947 specimens from Dominica, preserved *in copula* was dissected, although the pair separated during this process. The female (Fig. 8F) showed some puncture wounds in the vagina, and the male endophallus (Fig. 8E) was a small, membranous lobe with a small curved spine and a very small knob at the apical end. *Acalymma subaeneum* Jacoby, 1887 (not shown) had two small sclerites in the endophallus, similar to the Dominica male; in the female, the vagina had no evidence of scarring.

The male *Isotes rubripennis* (Erichson, 1847) had a pair of backward-facing hooks at the base of the endophallus, reminiscent of similar structures found in the Metacyclini, and a spike-like apical sclerite (Fig. 8C). The female (Fig. 8D) had a few scar-like dots at the entrance of the bursa. Behind these, there was a transverse band of small black sclerites, arranged



FIG. 6. — Genitalia of Luperini: Aulacophorina: **A, B**, *Aulacophora antennata* Baly, 1886: **A**, male median lobe, right side; **B**, female genitalia, **arrows** indicate puncture scars; **C**, *Aulacophora bicolor* (Weber, 1801), male median lobe, right side; **D**, *Aulacophora* sp. (New Guinea), male median lobe, left side; **E, F**, *Aulacophora cornuta* Baly, 1879: **E**, male median lobe with endophallus everted, left side; **F**, female genitalia, bursa (in center) is heavily scarred and abraded; **G**, *Aulacophora luteicornis* (Fabricius, 1801), male median lobe, left side. Abbreviations: see Material and methods. Scale bars: 0.5 mm.

in a scale pattern. These are presumably structures related to processing the spermatophore. The vagina of *Isotes dilatata* (Jacoby, 1887) (not shown) had several apparent scars but lacked the sclerotized band of *I. rubripennis*. No males of this species were available.

In a *Paranapiacaba* Bechyně, 1958 species from Argentina, the male had a pair of sharp spines at the base of the endophallus and a long spiraling sclerite bearing a line of small bumps (Fig. 8G, H). A dissected female had an unequal pair of small

plate-shaped bursal sclerites, and some very small possible scars near the opening of the bursa (Fig. 8I).

A pair of *Amphelasma decoratum* (Jacoby, 1887) were found dried and *in copula*. When dissected (Fig. 9A, B), the male had the endophallus covered with fine denticles, similar to that described for the bruchid genus *Acanthoscelides* Schilsky, 1905 (Schmitt *et al.* 2023) and the Eumolpinae tribes Bromiini Baly, 1865 and Typophorini Baly, 1865 (Flowers 1999). The female *Amphelasma* had no sclerotized modifications on the

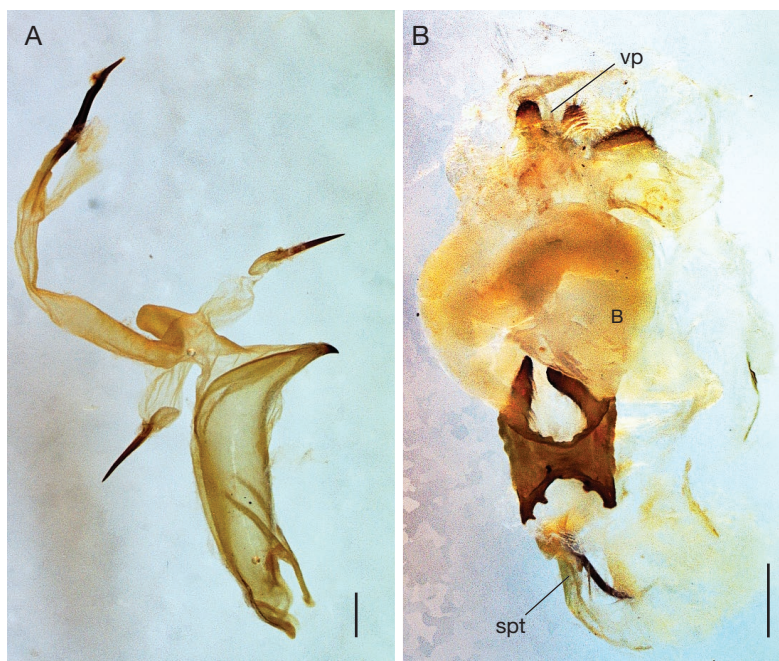


FIG. 7. — Genitalia of Luperini: Aulacophorina: *Agetocera similis* Chen, 1997: **A**, male median lobe, endophallus everted; **B**, female genitalia showing heavy saddle-shaped sclerite in bursa. Abbreviations: see Material and methods. Scale bars: 0.5 mm.

bursa. A species of *Zischkaiia* Bechyně, 1956 (not illustrated) also had a completely membranous male endophallus; a female was not dissected for this genus.

In *Gynandrobrotica ventricosa* (Jacoby, 1878), the endophallus was mostly membranous with a dorsal crest that has a sclerotized crenulate ridge along its length (Fig. 9C), and with a long tubular apical sclerite flanked by a pair of plates terminating in long spines (Fig. 9C, inset). A female showed a single possible scar near the entrance of the vagina (Fig. 9D).

Section Phyllethrines Horn, 1892

Several *Luperosoma subsulcata* (Horn, 1893) were examined. Males had flat arrowhead-shaped plates at the tip of the endophallus; these plates had trailing, curved, spine-like projections (Fig. 9E). Two females were dissected; one had bursal scars (Fig. 9F), whereas the other had no damage.

Two copulating pairs of *Phyllethriss dorsalis* (Olivier, 1808) were studied. Both were dry mounted on points, and both broke apart during specimen preparation. Rupture was at the point where the tip of the male median lobe entered the female, leaving the entire endophallus intact inside the bursa. The endophallus was membranous, tipped with a thin chevron-shaped sclerite with a moveable pointed spike (Fig. 9G, J). During copulation, the spike is deployed at an angle to the main axis of the median lobe. In one of the pairs dissected, the spike penetrated the bursa (Fig. 9I); however, in the other pair the spike remained inside the bursa, which was uninjured. In both dissected pairs there was evidence of spermatophore material in the bursae.

Section Scelidites Chapuis, 1875

Most genera in this group are found in Africa, Madagascar, and western North America (Seeno & Wilcox 1982). Six genera from the southwestern United States were examined in this study. *Triarius trivittatus* Horn, 1893 (not shown) had a long membranous endophallus with a thin flexible sclerite running along its length similar to the male *Monoxia* (Fig. 2A) and *Schematiza* (Fig. 2C). *Ampliolyperus* Viswajyothi & Clark, 2022, *Scelida* Chapuis, 1875, and *Scelolyperus* Crotch, 1874 all had a similar form of an endophallus that consisted of a thin membranous sac bearing rows or fields of small sharp spines or hooks. *Ampliolyperus cyanella* (Horn, 1895) (not shown) and *Scelida nigricornis* (Jacoby, 1888) (Fig. 10A) both had simple tubular median lobes with endophalli densely covered with short, sharp spines; the females of these species showed no signs of scarring.

Scelida flaviceps (Horn, 1893) (Fig. 10B), however, had a very different form of the median lobe from *S. nigricornis*, but a similar endophallus with a membranous tube bearing a field of spines. The female of this species also had no evidence of puncture scarring in the vagina. In *Scelolyperus leontii* (Crotch, 1873) the male has a pair of large blade-like sclerites at the tip of the median lobe, and the endophallus is almost entirely membranous with two lines of small, hooked sclerites (Fig. 10C). In the dissected female, there was a line of scars in the vagina (Fig. 10D) corresponding in size to the line of hooks found in the male.

In *Synetocephalus bivittatus* (LeConte, 1859), the male had a very large and complicated apical sclerite, as well as



FIG. 8. — Genitalia of Luperini: Diabroticites: **A, B**, *Diabrotica undecimpunctata howardi* Barber, 1947: **A**, in copula, **arrows** indicate puncture scars; **B**, median lobe of male shown in **A**, removed from female; **C, D**, *Isotes rubripennis* (Erichson, 1847): **C**, male median lobe, right side, with endophallus everted; **D**, female genitalia, **arrows** indicate puncture scars; **E, F**, *Acalymma* sp., **E**, male median lobe and endophallus, separated; **F**, female genitalia, **arrow** indicates puncture scars; **G, H, I**, *Paranapiacaba* sp.: **G**, male median lobe, left side, with endophallus everted; **H**, endophallus enlarged; **I**, female genitalia. Abbreviations: see Material and methods. Scale bars: 0.5 mm.

basal spines (Fig. 10E, inset); the female examined had markings in the vagina that could be abrasion damage (Fig. 10F). *Pteleon brevicornis* (Jacoby, 1887) had an endophallus covered with long cornuti (Fig. 10G), while the female (Fig. 10H) showed clear evidence of bursal tissue scar damage. In a revision of *Charaea* Baly, 1878 from Taiwan, Bezděk & Lee (2014) illustrate several everted endophalli that show strikingly similar patterns of cornuti to *Pteleon*, although *Charaea* is currently placed in a different section of the Luperina, the Eumelepitia Wilcox, 1973 (Seeno & Wilcox 1982).

Section Phyllobroticites Chapuis, 1875

In *Phyllobrotica costipennis* Horn, 1893 the male had a simple membranous endophallus without any trace of sclerotized structures (Fig. 11A). The female (not shown) had no scars or sclerotized structures in the vagina or bursa.

Section Exosomites Wilcox, 1973

This is a diverse African and Southeast Asian group with varied examples of endophallic sclerites found in the few genera so far investigated. In *Cneorane femoralis* Jacoby, 1888 the endophallus was elongate and bore a dense field of long, sharp cornuti on the apical third, as well as a blade-like apical sclerite at the tip (Fig. 11B). The female (Fig. 11C) had a field of sharp, black sclerites on the inside of the vagina adjacent to the bursa, presumably involved with processing the spermatophore. Behind this were small scarred areas, possibly due to contact with the male cornuti.

One of the stranger modifications of the male endophallus was found in the genus *Coeligetes* Jacoby, 1884, and apparently occurs in several allied genera. The endophallus in *Coeligetes borneensis* Mohamedsaid, 1994 was heavily sclerotized and lies along a depression in the dorsal side of the median lobe. The apex of the endophallus was curved up into a head-like structure capped with a dense brush of hair-like setae and bearing a pair of down-curved horns on the leading edge (Fig. 11D, E). The endophallus is capable of extending a short distance, as shown in Figure 11E, whereas in the drawings in Mohamedsaid (1994) and Bezděk (2016) it is shown in the retracted position. The female vaginal structure of *C. borneensis* is also unusual in that it is clearly broader than long (in all other species examined in this study the female internal structure was longer than broad, even if the bursa was distended by a spermatophore). In *C. borneensis* the bursa bears a pair of short spines just behind the lobe-like vaginal palpi, and a pair of probable scars on the rear wall of the bursa (Fig. 11F). Besides *Coeligetes*, four other East Asian genera show a similar development of the endophallus as a long sclerotized tube: *Coeligetoides* Bezděk, 2016 (Bezděk 2016), *Liroetis* Weise, 1889 (Bezděk 2021), *Luperogala* Medvedev & Samoderzhnikov, 1989 (Bezděk 2017), and *Siemsenius* Weise, 1922 (Lee 2016).

Section Monoleptites Chapuis, 1875

Representatives of this group of principally Old World genera have some of the most complex and potentially damaging endophalli yet found in Coleoptera. One North American Monoleptites in this study is currently listed under *Metrioidea* Fairmaire, 1881, i.e., *M. blakeae* (Wilcox, 1965), but Beenen (2008, 2013) has determined that the genus *Metrioidea* should be limited to a small group of species from Fiji and New Caledonia. *Metrioidea blakeae* is consequently transferred here to the genus *Monolepta*, with the new combination *Monolepta blakeae* (Wilcox, 1965) n. comb.

The case of *Monolepta elongata* (Fig. 1A-D), introduced above, represents a confirmed case of female damage during copulation. Everted male endophalli from three species of Costa Rican *Monolepta* were figured in Flowers & Eberhard (2006: figs 22, 23, 25). A female Monoleptites (without an associated male) from Costa Rica showed scar points on the bursa (Flowers & Eberhard 2006: fig. 24). In this study, similar structures and presumed damages for both sexes were found in other species: *Monolepta blakeae* n. comb. (male, Fig. 12A; female, Fig. 12B, C), *Monolepta irazuensis* (Jacoby, 1888) (male, Fig. 12D; female, Fig. 12E); unidentified *Monolepta* from Ecuador (Fig. 12F) and Honduras (male, Fig. 13A; female, Fig. 13B).

Endophallic spiculae (Wagner 2007) appeared to be differentiated into larger basal spines or hooks, and a more apical area of cornuti (very fine needles) and ranks of short, curved spiculae. The apical sclerite area (where fully everted) consisted of a thin curved tube flanked by a pair of leaf-like sclerites (as in Fig. 12A, D). The unidentified *Monolepta* from Ecuador (Fig. 12F) differed from other New World species in the structure of its median lobe. Characteristic scar points were present in females (Fig. 12B, C, E), but in *Monolepta blakeae* n. comb., for which a series of females was available, only one (Fig. 12B) of six specimens presented scar points.

In three examined species of Old World *Monolepta*, the various spiculae on the endophalli were more morphologically subdivided than was the case in the New World species. A *Monolepta* sp. from Nigeria (Fig. 13C) had basal spines as long and almost as slender as the apical spiculae; the female (Fig. 13D) had characteristic puncture scars. In a Sumatran species the endophallus had a whorl of needle-like spiculae and several paddle-shaped apical sclerites (Fig. 13E). Large *Monolepta laosensis* Kimoto, 1989 (male, Fig. 13F; female, Fig. 13G) and an unidentified species from Vietnam (male, Fig. 13I; female, Fig. 13J) show the organization of the different spicula types in discrete endophallic regions. Scarring was evident in females of both these species.

A single male of the monoleptine *Palaosepharia truncata* Laboissière, 1936 (Fig. 13H) showed a similar diversity and arrangement of spiculae to *Monolepta* (no female was available). Lee (2018) in a revision of *Palaosepharia* Laboissière, 1936 of Taiwan illustrates retracted spines of five species, all showing at least the potential of penetrating the female bursa. Rizki *et al.* (2016) redescribed and illustrated the type specimen of *P. truncata*, including a drawing of the median lobe with the



FIG. 9. — Genitalia of Luperini: Diabroticites (A–D) and Phyllethrites (E–J): A, B, copulating pair of *Amphelasma decoratum* (Jacoby, 1887): A, male genitalia on the left; B, same, male and female genitalia separated; C, D, *Gynandrobrotica ventricosa* (Jacoby, 1878): C, male median lobe with endophallus everted. Inset: dorsal view of endophallus and tip of median lobe; D, female genitalia, arrow indicates puncture scar; E, F, *Luperosoma subsulcata* (Horn, 1893): E, male median lobe, right side, with endophallus everted; F, female genitalia, arrows indicate puncture scars; G–J, *Phyllethris dorsalis* (Olivier, 1808): G, male median lobe, ventral; H, female genitalia; I, same, pair in copula, en-face view toward male, apical sclerite visible inside bursa, arrow indicates spine of male apical sclerite penetrating female; J, same as G, close-up of apical sclerite. Scale bars: 0.5 mm.

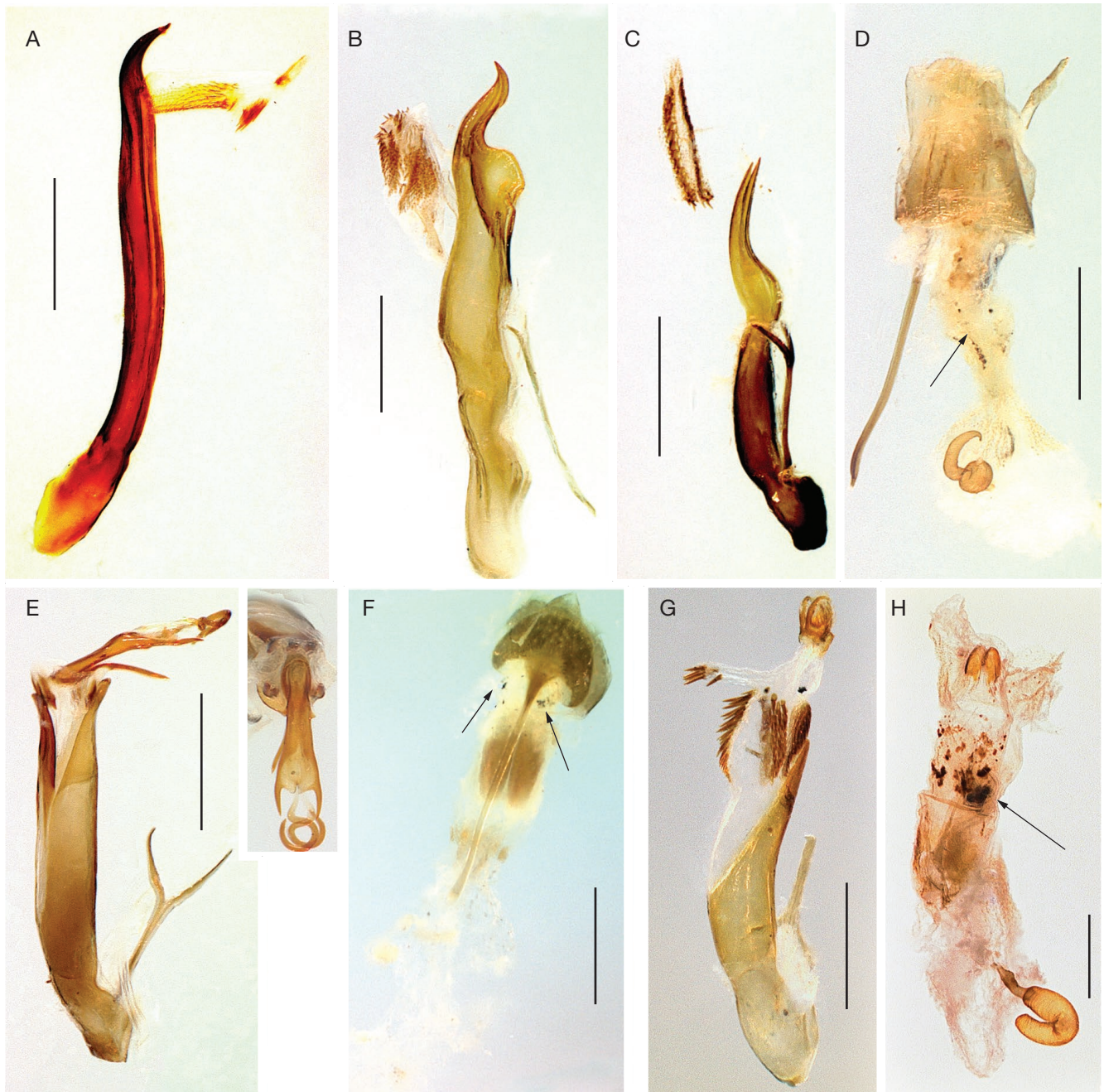


FIG. 10. — Genitalia of Luperina: Scelidites: **A**, *Scelida nigricornis* (Jacoby, 1888), male median lobe with endophallus everted, left side; **B**, *Scelida flaviceps* (Horn, 1893), male median lobe with endophallus partially extruded, right side; **C**, *Scelolyperus lecontei* (Crotch, 1873): **C**, male median lobe with endophallus everted, right side; **D**, female genitalia, **arrow** indicates puncture scars; **E**, *Synetocephalus bivittatus* (LeConte, 1859): **E**, male median lobe with endophallus everted. **Inset**: same, en-face view of endophallus, right side; **F**, same, female genitalia, **arrows** indicate possible scars; **G**, *Pteleon brevicornis* (Jacoby, 1887): **G**, male median lobe with endophallus everted, right side; **H**, female genitalia, **arrow** indicates area of puncture scars. Scale bars: 0.5 mm.

endophallus within. Their description of the appearance of spiculae seen within the median lobe missed several features that are evident in the everted preparation (a third pair of strong basal spiculae and strong ventral comb-like spiculae). Also, their assessment that *Paleosepharia* endophalli are “simpler” than other in genera was not borne out by this study.

Specimens of the New World monoleptine *Eusatrodora* Schaeffer, 1906 species were examined. The male endophallus

(Fig. 13K) differed from other monoleptines in this study by having a pair of sclerotized basal plates in addition to spiculae and cornuti. Two females (Fig. 13L) had evidence of mating (spermatophore material in the bursae), but no scars were found on bursal or vaginal membranes.

A male and a female of *Candezea semiviolacea* (Fauvel, 1862) from New Caledonia were examined. The endophallus could not be everted intact from the very narrow and elongate me-

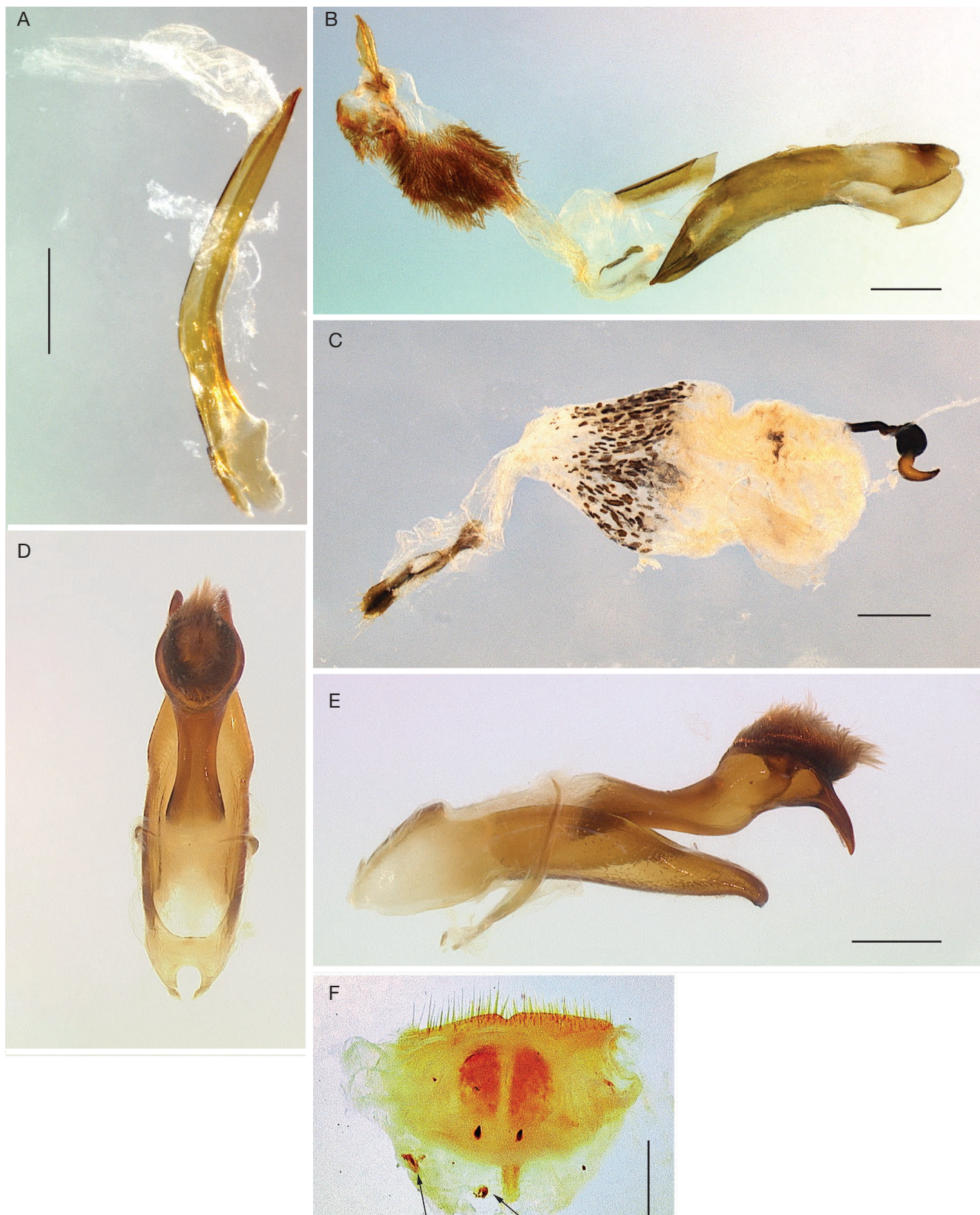


FIG. 11. — Genitalia of Luperina: Phyllobroticites (A) and Exosomites (B-F): **A**, *Phyllobrotica costipennis* Horn, 1893, male median lobe with endophallus everted, right side; **B, C**, *Cneorane femoralis* Jacoby, 1888: **B**, male median lobe with endophallus everted, left side; **C**, female genitalia, **arrow** indicates abraded bursal tissue; **D-F**, *Coeligetes borneensis* Mohamedsaid, 1994: **D**, male median lobe with endophallus everted, dorsal; **E**, right side; **F**, female genitalia, **arrows** indicate puncture scars. Scale bars: 0.5 mm.

dian lobes, but it bore leaf-like apical sclerites and longitudinal lines of medium-length spiculae. The female, however, showed no bursal scars, although there was a spermatophore within.

SURVEY OF FEMALE STRUCTURES

Development of sclerotized structures in the female bursae were also found to be widely distributed in the galerucine genera in this survey, and appeared to be at least somewhat correlated with modifications of the male endophalli. The majority of taxa studied had no modifications in the either the bursa or the vagina; see the female of *Amphelasma decoratum* (Fig. 9B). Most of the Galerucini genera studied had unsclerotized bursae, although in *Monoxia angularis*, the female vagina had longitudinal fields of spinelets (Fig. 2B).

In the Metacyclini, several types of modified bursal membranes were found. The *Hecataeus* female had two lateral areas covered with short denticles (Fig. 4E), whereas in species of *Malacorhinus* (Fig. 4G) and *Exora* the lateral areas had a series of sclerotized bars covered with small bumps. A different arrangement was found in the female of *Masurius* sp., in which the vagina had several large plate-like sclerites (Fig. 4B). *Byblitea jansonii* appeared to have a weakly sclerotized central area of the bursa, which appeared to contain abrasions (Fig. 3F).

In the Luperini examined, the female genital armature ranged from nonexistent (e.g. in the copulating pair of *Amphelasma*, Fig. 9A, B) to heavily sclerotized sets of jaw-like structures (e.g. in *Monoleptites*).

In the Scelidites, the female of *Synetocephalus bivittatus* had a dense field of denticles on its inside surface (Fig. 10F), whereas females of other genera studied had no modifications. In Exosomites, the female of *Cneorane femoralis* had entire posterior part of the bursa lined with shard-like sclerites (Fig. 11C).

Galerucines belonging to the section *Monoleptites* have males with the most elaborate (and dangerous-looking) endophallic modifications (Figs 12A, D, F; 13A, C, E, F, H, I, K), matched by females with the most heavily sclerotized bursal teeth and plates (Figs 12B, C, E; 13B, D, G, J, L). In addition to the studied taxa, females in many other species and genera of *Monoleptites* described from Africa and Southeast Asia also have either one or two pairs of toothed, sclerotized processes within the bursa (e.g. Wagner & Scherz 2002; Wagner 2007, 2020).

DISCUSSION

An overview of the examined galerucines (Table 1) shows that deployable sclerotized endophallic structures are common, and widespread throughout this tribe. However, this study covered only 9% of the total galerucine genera (Nie *et al.* 2017). There are many genera and generic complexes yet to be explored before we have an adequate picture of endophallic development in the Galerucini. Even the fragmentary observations of this study permit some hypotheses to be advanced on generic relationships. One example is the status of the genera *Xanthogaleruca* (Fig. 2G) and *Pyrrhalta* (Matsumura *et al.* 2017). *Xanthogaleruca* has variously been considered a valid

genus, a subgenus, or even a synonym of *Pyrrhalta* (Nie *et al.* 2013; Matsumura *et al.* 2017; see Lee & Bezděk [2021] for a review of recent taxonomy). Both *X. luteola* and *P. maculicollis* have sclerotized ribbons with a row of large, fang-like teeth, a character that is not found in other *Pyrrhalta*. This character supports the opinion that *P. maculicollis* should be transferred to *Xanthogaleruca* under the name *Xanthogaleruca maculicollis* (Motschulsky, 1853) n. comb.

A second example concerns the New World genus *Metrioidea* and its relationship to *Monolepta*. For many years the correct placement of these species was problematical, due to the lack of stable external characters in the two genera (Viswajothi & Clark 2022), and also because the type species of *Metrioidea* is endemic to the Fiji islands. Recently, Beenen (2008, 2013) found that the Fijian *Metrioidea* is congeneric with a cluster of species from New Caledonia and Australia, and these can be clearly distinguished from *Monolepta* based on the structure of the male median lobe. In *Metrioidea* the median lobe is notched or divided at the apex, and has separated dorsal and ventral lobes with the retracted endophallus between them. In the type species of *Monolepta* the median lobe is elongate, tubular, and unnotched at the apex, and the endophallus is entirely retracted into the median lobe (Wagner 2007). The New World *Metrioidea* in this study has a *Monolepta*-type median lobe, and thus should be transferred to *Monolepta*, as proposed for *Monolepta blakeae* n. comb. Thirteen other species listed in *Metrioidea*, mostly from the North American Southwest (Wilcox 1983), should probably be referred to *Monolepta*, at least until further study. In the Old World, particularly the African fauna, study of the genitalia has led to the erection of many new genera (see Wagner [2007] for a summary). In the *Metrioidea* and *Monolepta* species in this study, some have *Monolepta*-style median lobes (Figs 12D; 13A, C, E, I), whereas others do not (Figs 12F; 13F).

An important limitation in this study is that endophallic structures were studied and photographed after everting them in the relatively ample space of a laboratory watch glass. How these structures deploy *in vivo* during copulatory activities could be quite different. During copulation the male endophallus is expanded inside a female bursa, which may considerably constrain the movements and physical relationships between the endophallic sclerites. For example, the extended endophallus of *Agetocera similis* (Fig. 7A) exceeds the dimensions found inside the female bursa (Fig. 7B). There is a similar size mismatch between the large endophallus and the unusually shallow bursa in *Coeligetes borneensis* (Fig. 11D-F), and in the Metacyclini (Figs 3D-J; 4A-C) the various endophallic structures must pass along a narrow vagina and then expand inside a rather small bursa in the species depicted. Almost certainly the orientation of the male sclerites *in copula* would be quite different from what is seen in the photographs in this study, in which the endophalli have been everted in open space. The major contribution of the present study is thus to document the forms of the sclerites and the membranes that connect them, not their positions inside the female during copulation. Only in a subset of species can male positions during copulation be deduced.

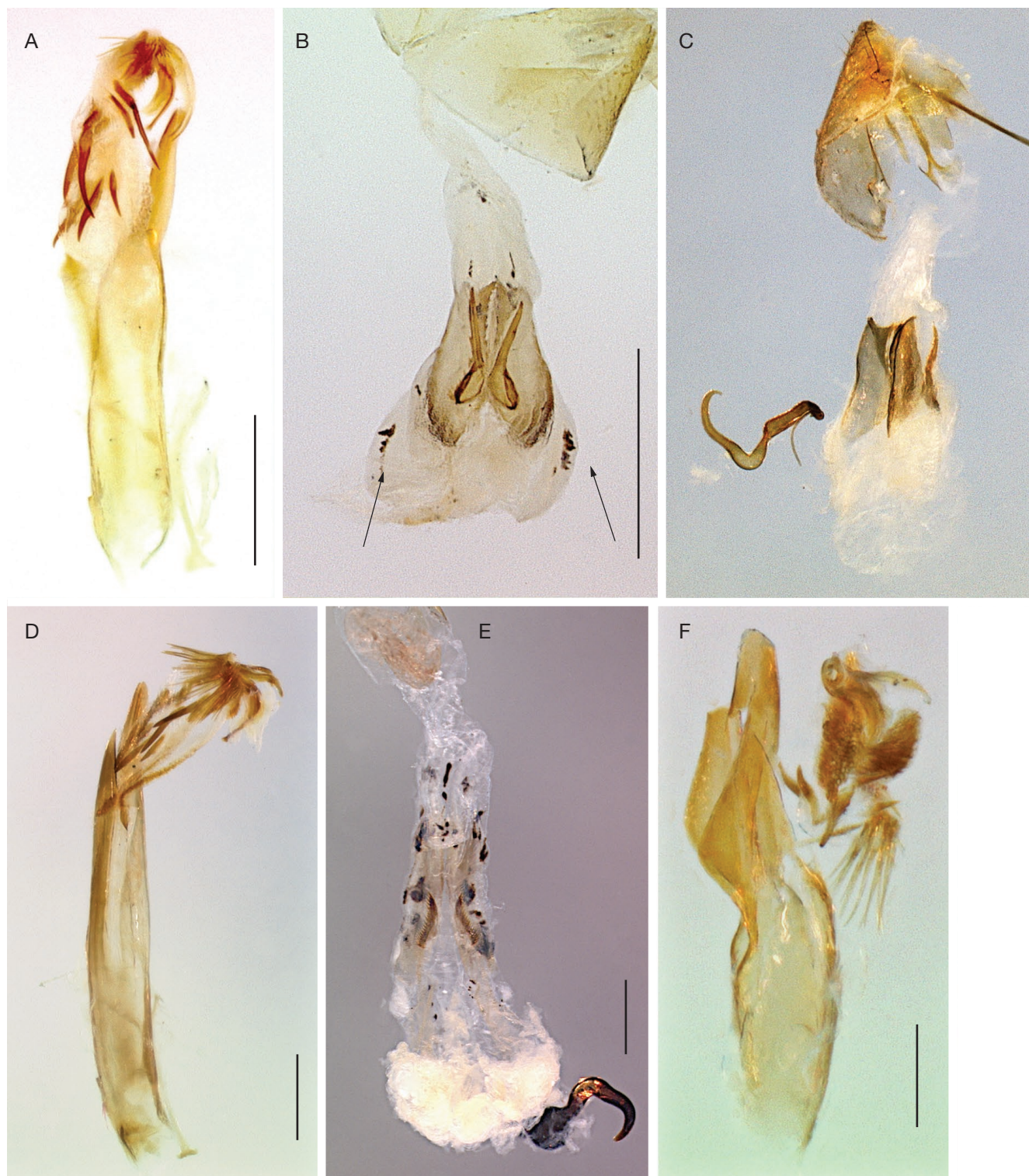


FIG. 12. — Genitalia of Luperina: New World Monoleptites: **A–C**, *Metrioidea blakeae* (Wilcox, 1965) n. comb.: **A**, male median lobe with endophallus everted, right side; **B**, female genitalia, **arrows** indicate puncture scars; **C**, female genitalia with spermatophore and lacking bursal damage; **D, E**, *Monolepta irazuensis* (Jacoby, 1888): **D**, male median lobe with endophallus everted, right side; **E**, female genitalia, puncture scars visible in central portion; **F**, *Monolepta* sp. Ecuador, male median lobe with endophallus partially extruded, left side. Scale bars: 0.5 mm.

Three distinct classes of male sclerites were found in this study: sharpened cornuti and spiculae appear to have the mechanical ability to puncture the bursa (Figs 2G; 3D, E, G, H, J; 4H; 5B; 6A, C–E, G; 7A; 8A–C, E, G, H; 9C, E, J; 10A–C,

E, G; 11B, D; 12A, D, F; 13A, C, E, F, H, I, K); these modifications occur principally in sections of the Luperini, as well as in some Galerucini. The second class consists of movable bars or hook sclerites, which occur in some Hylaspini and



FIG. 13. — Genitalia of Luperina: New and Old World Monoleptites: **A, B**, *Monolepta* sp. Honduras: **A**, male median lobe with endophallus partially extruded, right side; **B**, female genitalia, **arrow** indicates puncture scars; **C, D**, *Monolepta* sp. Nigeria: **C**, male median lobe tip with endophallus everted, left side; **D**, female genitalia, **arrows** indicate puncture scars; **E**, *Monolepta* sp. Sumatra, male median lobe with endophallus everted, right side; **F, G**, *Monolepta laosensis* Kimoto, 1989: **F**, male median lobe with endophallus extruded, right side; **G**, female genitalia; **H**, *Palaeosepharia truncata* Laboissière, 1936, male, apex of median lobe with endophallus everted, left side; **I, J**, *Monolepta* sp. Vietnam: **I**, male median lobe with endophallus everted, left side; **J**, female genitalia, **arrows** indicate puncture scars; **K, L**, *Eusattodera* sp.: **K**, male median lobe with endophallus extruded, right side; **L**, female genitalia. Scale bars: 0.5 mm.

Metacyclini, and to a lesser extent in the Galerucina (Figs 3A, B, D, G; 4C, D, F; 5A). These are less likely to puncture the bursa but would presumably make ejecting a male more difficult for the female (e.g. by kicking [Crudgington & Siva-Jothy 2000]). Finally, some males have very small spinelets or knobs that suggest a stimulatory function, and thus a role for cryptic female choice (Eberhard 1996) in galerucine mating behavior. Genera in Diabroticites appear to be exceptionally diverse in endophallic sclerite development: from no sclerites in *Amphelasma* and *Zischkaiia* to combinations of spines and “sticky pads” (as in *Trirhabda bacharidis*) in numerous species of *Diabrotica* (Derunkov *et al.* 2013), to combinations of spines and (presumably) stimulatory structures as in *Gynandrobrotica* and *Paranapiacaba*.

While the prevalence of sharp endophallic structures in males, and of corresponding scarring in females, implies traumatic mating in many Galerucini, several observations indicated that female damage is not an inevitable result of mating with a well-armed male. *Xanthogaleruca luteola* (Fig. 2H, I) and *Metrioidea blakeae* n. comb. (Fig. 12B, C) had females showing damage, as well as females in each dissected series without scars. Both dissected *Eusattodera* females were apparently undamaged, even though one (Fig. 13L) had clear evidence of spermatophore material in her bursa, indicating that she had previously mated. In *Cneorane femoralis* (Fig. 11C) several females were examined and all showed some signs of bursal scarring, but not to the extent one would predict from the dense field of cornuti on the male endophallus (Fig. 11B). The two pairs of *Phyllecthris dorsalis*, dissected *in copula*, showed further variation of effect of the large spine within the female bursa. In one pair (Fig. 9I) this spine clearly penetrated the female, whereas in the other pair the spine remained within the bursa and no evidence of damage was present.

In the last two decades there has been considerable interest in post-copulatory mating behavior in arthropods, especially in cases in which traumatic mating has been suggested, or confirmed. The case of *Callosobruchus* (Crudgington & Siva-Jothy 2000) is of special interest because of its similarities to *Monolepta elongata*, in which male endophallic spines also penetrate the female bursa. Both cases would appear to be clear-cut examples of male antagonistic behavior. Mating in *Callosobruchus* has been extensively investigated (Crudgington & Siva-Jothy 2000; Edvardsson & Tregenza 2005; Eady *et al.* 2007; Hotzy *et al.* 2012). Evidence that the antagonistic aspects of their mating confers evolutionary benefits to the male is somewhat equivocal. In an experiment in which mated females of *Callosobruchus* had their bursae artificially damaged, Morrow *et al.* (2003) found no behavioral differences (e.g. delay in remating, number of eggs laid) that would be advantageous to a male doing the injuring. Edvardsson & Tregenza (2005) and Wilson & Tompkins (2014) found that while the spines on the male endophallus in *Callosobruchus* do indeed harm the female, this damage does not appear to confer any measurable benefits to male reproductive success (Hotzy & Arnqvist 2009). On the other hand, Edvardsson & Canal (2006) found that female fecundity in *Callosobruchus* increases the longer the mating lasts, whereas Rönn & Hotzy

(2012) found that males with longer spines do not have longer copulations. Several hypotheses have been put forward as explanations for traumatic aspects of *Callosobruchus* mating: reproductive conflict; possible production of male fluids to increase female fecundity; female resistance to extended copulation by kicking to dislodge the male; and stimulation as an alternative to, or modification of, reproductive conflict. A version of this hypothesis, sometimes called the pleiotropic harm hypothesis, holds that the male modifications in *Callosobruchus* are to prevent premature separation during copulation (by female kicking or otherwise), and any damage to females is collateral and conveys, in itself, no special benefits to the male (Morrow *et al.* 2003; Rönn & Hotzy 2012; Wilson & Tompkins 2014). Cordero & Eberhard (2003) and Eberhard (2015) have argued that cryptic female choice can confer evolutionary benefits for members of both sexes, even in cases of traumatic mating. Tallamy *et al.* (2002) found that female choice in *Diabrotica undecimpunctata* determines success of male mating. However, they failed to note what function, if any, the endophallic sclerites might have. While mating studies in Bruchinae have included five species of *Callosobruchus* (Rönn *et al.* 2007; Van Haren *et al.* 2017), this subfamily also displays a wide range of generic diversity of endophallic structures, from the minimally armed *Acanthoscelides* (Schmitt *et al.* 2023) through *Callosobruchus*, to species of *Sennius* Bridwell, 1946 with dense fields of cornuti on their endophalli (Viana & Ribeiro-Costa 2013).

These hypotheses are not necessarily mutually exclusive. Cryptic female choice predicts a relatively high diversity of structural modifications in both sexes (Eberhard 2015), and this is supported in this study by males with a wide variety of cornuti and spines, as well as blunt, sclerotized moveable bars. Additionally, some males such as *Gynandrobrotica* (Fig. 9C), *Paranapiacaba* (Fig. 8G), and *Phyllecthris* (Fig. 9G, J) had finely knobbed or toothed sclerotized structures in addition to sharp spines. This suggests a function for possible internal stimulation of the female. In some of the Monoleptites there is a regionalization of endophallic sclerites (Fig. 13F, H, I, K), with large hooked spiculae restricted to the basal area, and shorter and finer cornuti in the apical half of the endophallus. During the probable sequence of copulation, the long hooked spines would enter the female first and hook into the vaginal region to serve as anchors (*sensu* Rönn & Hotzy 2012), whereas more apical short spiculae would evert well inside the bursa, where they may have stimulatory rather than anchoring functions.

This study also revealed the presence of a variety of sclerotized structures in the internal female genitalia (Figs 2B; 4B, G; 7B; 8D; 10F; 11F; 12B, C, E; 13D, G, J, L) with an apparent trend toward heavier and more elaborate structures coincident with heavier and more potentially damaging endophallic structures in the males, notably in the Monoleptites. In *Callosobruchus maculatus* and at least some other Bruchinae, the females have small spines in the bursa (Kingsolver 1971; Cayetano & Bonduriansky 2015), although the role of these spines was not studied. Schmitt *et al.* (2023) proposed that similar spines in *Acanthoscelides* may help maintain the

spermatophore in position. In the *Galerucini* studied here, female bursal sclerites were less frequently encountered than sclerites in the male, and in most taxa, too few species were examined to determine what trends were present. However, virtually all published illustrations of genitalia in recent taxonomic studies of the Section *Monoleptites* show pairs of toothed sclerites found within female genitalia (Hasenkamp & Wagner 2000; Wagner & Scherz 2002; Wagner 2007, 2020; Lee 2009, 2020; Lei *et al.* 2021).

The biodiversity of the *Galerucini* resides not only in gene trees and external morphology, but also in its diversity of internal copulatory structures in both sexes, which in males run the gamut from modest “sticky pads” in *Trirhabda* or *Caraguata* to “medieval arms lockers” in so many of the *Monoleptites*. Nearly as diverse are structures in the bursa of some females, on the functions of which we can only speculate so far. Up to now, the study of possible traumatic mating in beetles has been confined to a tiny handful of model species. The information in this study shows the wealth of possibilities waiting to be investigated in the *Galerucini*.

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REFERENCES

- AISENBERG A., BARRANTES G. & EBERHARD W. G. 2015. — Post-copulatory sexual selection in two tropical orb-weaving *Leucauge* spiders, in PERETTI A. V. & AISENBERG A. (eds), *Cryptic Female Choice in Arthropods*. Springer International Publishing, Cham, Switzerland: 79-108. https://doi.org/10.1007/978-3-319-17894-3_4
- BEENEN R. 2008. — Contribution to the knowledge of *Galerucinae* of New Caledonia (Coleoptera: Chrysomelidae). *Genus* 19 (1): 65-87.
- BEENEN R. 2013. — Contribution to the knowledge of *Galerucinae* of New Caledonia 2 (Coleoptera: Chrysomelidae). *Genus* 24 (1): 65-108.
- BEZDĚK J. 2016. — Revision of the genus *Coeligetes* from Malaysia and Indonesia, and description of *Coeligetoides* gen. nov. (Coleoptera: Chrysomelidae: Galerucinae). *Zootaxa* 4085 (4): 504-524. <https://doi.org/10.11646/zootaxa.4085.4.3>
- BEZDĚK J. 2017. — Contribution to the knowledge of *Luperogala* with metallic elytra (Coleoptera: Chrysomelidae: Galerucinae). *Entomologische Blätter und Coleoptera* 113: 037-046.
- BEZDĚK J. 2021. — Redefinition of *Liroetis*, with descriptions of two new species and an annotated list of species (Coleoptera: Chrysomelidae: Galerucinae). *Acta Entomologica Musei Nationalis Pragae* 61 (2): 529-614. <https://doi.org/10.37520/aemnp.2021.030>
- BEZDĚK J. & LEE C.-F. 2014. — Revision of *Charaea* (Coleoptera: Chrysomelidae: Galerucinae) from Taiwan. *Zootaxa* 3861 (1): 001-039. <https://doi.org/10.11646/zootaxa.3861.1.1>
- CAYETANO L. & BONDURIANSKY R. 2015. — Condition dependence of male and female genital structures in the seed beetle *Callosobruchus maculatus* (Coleoptera: Bruchidae). *Journal of Evolutionary Biology* 28: 1364-1372. <https://doi.org/10.1111/jeb.12659>
- CORDERO C. 2005. — The evolutionary origin of signa in female Lepidoptera: natural and sexual selection hypotheses. *Journal of Theoretical Biology* 232: 443-449. <https://doi.org/10.1016/j.jtbi.2004.08.031>
- CORDERO C. 2010. — On the function of cornuti, sclerotized structures of the endophallus of Lepidoptera. *Genetica* 138: 27-35. <https://doi.org/10.1007/s10709-009-9363-1>
- CORDERO C. & BAIXERAS J. 2015. — Sexual selection within the female genitalia in Lepidoptera, in PERETTI A. V. & AISENBERG A. (eds), *Cryptic Female Choice in Arthropods*. Springer International Publishing, Cham, Switzerland: 325-350. https://doi.org/10.1007/978-3-319-17894-3_12
- CORDERO C. & EBERHARD W. G. 2003. — Female choice of sexually antagonistic male adaptations: a critical review of some current research. *Journal of Evolutionary Biology* 16: 1-6. <https://doi.org/10.1046/j.1420-9101.2003.00506.x>
- CRUDGINGTON H. S. & SIVA-JOTHY M. T. 2000. — Genital damage, kicking and early death. *Nature* 407: 855-856. <https://doi.org/10.1038/35038154>
- DERUNKOV A., KONSTANTINOV A. S., TISHECHKIN A., HARTJE L. & REDFORD A. J. 2013. — *Diabrotica* ID: identification of *Diabrotica* species (Coleoptera: Chrysomelidae) from North and Central America. USDA APHIS PPQ Center for Plant Health Science and Technology, USDA Agricultural Research Service, University of Maryland, and Louisiana State University. <https://idtools.org/id/beetles/diabrotica/> [accessed 1 April 2024].
- EADY P. E., HAMILTON L. & LYONS R. E. 2007. — Copulation, genital damage and early death in *Callosobruchus maculatus*. *Proceedings of the Royal Society B* 274: 247-252. <https://doi.org/10.1098/rspb.2006.3710>
- EBERHARD W. G. 1996. — *Female Control: Sexual Selection by Cryptic Female Choice*. Princeton University Press, Princeton, 501 + xiv p. <https://doi.org/10.1515/9780691207209>
- EBERHARD W. G. 2015. — Cryptic female choice and other types of post-copulatory sexual selection, in PERETTI A. V. & AISENBERG A. (eds), *Cryptic Female Choice in Arthropods*. Springer International Publishing, Cham, Switzerland: 1-26. https://doi.org/10.1007/978-3-319-17894-3_1
- EBERHARD W. G. 2023. — The functional morphology of species-specific male structures and lack of female coevolution in *Lytta* (*Adicolytta*) *eucera* (Chevrolat, 1834) (Coleoptera: Meloidae). *Ethology, Ecology & Evolution* 35 (5): 584-616. <https://doi.org/10.1080/03949370.2022.2152106>
- EDVARDSSON M. & CANAL D. 2006. — The effects of copulation duration in the bruchid beetle *Callosobruchus maculatus*. *Behavioral Ecology* 17 (3): 430-434. <https://doi.org/10.1093/beheco/arj045>
- EDVARDSSON M. & TREGENZA T. 2005. — Why do male *Callosobruchus maculatus* harm their mates? *Behavioral Ecology* 16 (4): 788-793. <https://doi.org/10.1093/beheco/ari055>
- EPLER J. H. 2010. — *The Water Beetles of Florida – An Identification Manual for the Families Chrysomelidae, Curculionidae, Dryopidae, Dytiscidae, Elmidae, Gyrinidae, Haliplidae, Helophoridae, Hydraenidae, Hydrochidae, Hydrophilidae, Noteridae, Psephenidae, Ptilo-*

- dactylidae and Scirtidae*. Florida Department of Environmental Protection, Tallahassee, 399 + iv p.
- FENG C., YANG X.-K., LIU Y. & LI Z.-Q. 2023. — Revision of *Aplosynx* Chevrolat, 1836 (Coleoptera, Chrysomelidae, Galerucinae) from China, with descriptions of three new species. *ZooKeys* 1154: 159–222. <https://doi.org/10.3897/zookeys.1154.98336>
- FINCKE O. M. 1997. — Conflict resolution in the Odonata: implications for understanding female mating patterns and female choice. *Biological Journal of the Linnean Society* 60: 201–220. <https://doi.org/10.1111/j.1095-8312.1997.tb01492.x>
- FLOWERS R. W. 1999. — Internal structure and phylogenetic importance of male genitalia in the Eumolpinae, in COX M. L. (ed.), *Advances in Chrysomelidae Biology 1*. Backhuys, Leiden: 71–93.
- FLOWERS R. W. & EBERHARD W. G. 2006. — Fitting together: copulatory linking in some Neotropical Chrysomeloidea. *Revista de Biología Tropical* 54 (3): 829–842. <https://doi.org/10.15517/rbt.v54i3.12798>
- HASENKAMP R. & WAGNER T. 2000. — Revision of *Afromaculepta* gen. n., a monophyletic group of Afrotropical galerucine leaf beetles (Coleoptera: Chrysomelidae). *Insect Systematics & Evolution* 31 (1): 3–26. <https://doi.org/10.1163/187631200X00282>
- HOSKEN D. J. & PRICE T. A. R. 2009. — Genital evolution: the traumas of sex. *Current Biology* 19 (13): R519–R521. <https://doi.org/10.1016/j.cub.2009.05.020>
- HOTZY C. & ARNQVIST G. 2009. — Sperm competition favors harmful males in seed beetles. *Current Biology* 19 (5): 404–407. <https://doi.org/10.1016/j.cub.2009.01.045>
- HOTZY C., POLAK M., RÖNN J. L. & ARNQVIST G. 2012. — Phenotypic engineering unveils the function of genital morphology. *Current Biology* 22 (23): 2258–2261. <https://doi.org/10.1016/j.cub.2012.10.009>
- JACOBY M. 1888–1892. — Phytophaga Supplement, in GODMAN F. D. & SALVIN O. (eds), *Biologia Centrali-Americana*. Coleoptera. Volume 6, Part 1. Published for the editors by R. H. Porter, London, 374 p.
- KAMIMURA Y. 2010. — Copulation anatomy of *Drosophila melanogaster* (Diptera: Drosophilidae): wound-making organs and their possible roles. *Zoomorphology* 129 (3): 163–174. <https://doi.org/10.1007/s00435-010-0109-5>
- KAMIMURA Y. 2015. — What is indirect cryptic female choice? Theoretical considerations and an example from a promiscuous earwig, in PERETTI A. V. & AISENBERG A. (eds), *Cryptic Female Choice in Arthropods*. Springer International Publishing, Cham, Switzerland: 255–283. https://doi.org/10.1007/978-3-319-17894-3_10
- KIMOTO S. 1989. — Chrysomelidae (Coleoptera) of Thailand, Cambodia, Laos and Vietnam. IV. Galerucinae. *Esakia* 27: 1–241. <https://doi.org/10.5109/2511>
- KINGSOLVER J. M. 1971. — Description of a new seed beetle from Australia (Coleoptera: Bruchidae). *Journal of the Australian Entomological Society* 10 (3): 179–182. <https://doi.org/10.1111/j.1440-6055.1971.tb00029.x>
- LANGE R., REINHARDT K., MICHIELS N. K. & ANTHES N. 2013. — Functions, diversity, and evolution of traumatic mating. *Biological Reviews* 88 (3): 585–601. <https://doi.org/10.1111/brv.12018>
- LEE C.-F. 2009. — A taxonomic revision of *Monolepta pallidula* species group in Taiwan (Coleoptera: Chrysomelidae: Galerucinae). *Zootaxa* 2170 (1): 15–27. <https://doi.org/10.11646/zootaxa.2170.1.2>
- LEE C.-F. 2016. — Review of the genus *Siemsenius* Weise, 1922 (Coleoptera: Chrysomelidae: Galerucinae) from Taiwan, with descriptions of five new species. *Zootaxa* 4158 (3): 367–384. <https://doi.org/10.11646/zootaxa.4158.3.4>
- LEE C.-F. 2018. — The genus *Paleosepharia* Laboissière, 1936 in Taiwan: review and nomenclatural changes (Coleoptera, Chrysomelidae, Galerucinae). *ZooKeys* 744: 19–41. <https://doi.org/10.3897/zookeys.744.22970>
- LEE C.-F. 2020. — Revision of Taiwanese species of *Atrachya* Chevrolat, 1836 (Coleoptera, Chrysomelidae, Galerucinae): descriptions of three new genera, two new species, and designations of three new synonyms. *ZooKeys* 940: 117–159. <https://doi.org/10.3897/zookeys.940.51800>
- LEE C.-F. & BEENEN R. 2017. — Revision of the Palaearctic and Oriental species of the genus *Oides* Weber, 1801 (Coleoptera: Chrysomelidae: Galerucinae). *Zootaxa* 4346 (1): 001–125. <https://doi.org/10.11646/zootaxa.4346.1.1>
- LEE C.-F. & BEZDĚK J. 2021. — Revision of the genera *Xanthogaleruca* Laboissière, 1932 and *Pyrrhalta* Joannis, 1865 (Coleoptera, Chrysomelidae, Galerucinae) of Taiwan, with type designation of *Galerucella lineatipes* Takei. *ZooKeys* 1039: 1–108. <https://doi.org/10.3897/zookeys.1039.64740>
- LEE C.-F., BEZDĚK J. & STAINES C. L. 2010. — A review of the genus *Agetocera* (Coleoptera: Chrysomelidae: Galerucinae) in Taiwan – are there only two species? *Zootaxa* 2441 (1): 1–19. <https://doi.org/10.11646/zootaxa.2441.1.1>
- LEI Q.-L., XU S.-Y., YANG X.-K. & NIE R.-E. 2021. — Five new species of the leaf-beetle genus *Monolepta* Chevrolat (Coleoptera, Chrysomelidae, Galerucinae) from China. *ZooKeys* 1056: 35–57. <https://doi.org/10.3897/zookeys.1056.65335>
- MATSUMURA Y., SUENAGA H., KAMIMURA Y. & GORB S. N. 2017. — Traumatic mating by hand saw-like spines on the internal sac in *Pyrrhalta maculicollis* (Coleoptera, Chrysomelidae, Galerucinae), in CHABOO C. S. & SCHMITT M. (eds), *Research on Chrysomelidae 7*. *ZooKeys* 720: 77–89. <https://doi.org/10.3897/zookeys.720.13015>
- MOHAMEDSAID M. S. 1994. — Two new species of *Coeligetes* Jacoby from Malaysia (Coleoptera, Chrysomelidae, Galerucinae). *Psyche* 101: 85–92. <https://doi.org/10.1155/1994/80931>
- MORROW E. H., ARNQVIST G. & PITNICK S. 2003. — Adaptation versus pleiotropy: why do males harm their mates? *Behavioral Ecology* 14 (6): 802–806. <https://doi.org/10.1093/beheco/arg073>
- NIE R.-E., ZHOU D.-K., XUE H.-J. & YANG X.-K. 2013. — Notes on black elytron species of *Pyrrhalta* Joannis and the description of a new species from China (Coleoptera, Chrysomelidae, Galerucinae). *ZooKeys* 289: 41–56. <https://doi.org/10.3897/zookeys.289.4266>
- NIE R.-E., BEZDĚK J. & YANG X.-K. 2017. — How many genera and species of *Galerucinae* s. str. do we know? Updated statistics (Coleoptera, Chrysomelidae). *ZooKeys* 720: 91–102. <https://doi.org/10.3897/zookeys.720.13517>
- OKUZAKI Y., TAKAMI Y., TSUCHIYA Y. & SOTA T. 2012. — Mating behavior and the function of the male genital spine in the ground beetle *Carabus clathratus*. *Zoological Science* 29 (7): 428–432. <https://doi.org/10.2108/zsj.29.428>
- REINHARDT K., ANTHES N. & LANGE R. 2015. — Copulatory wounding and traumatic insemination. *Cold Spring Harbor Perspectives in Biology* 7 (5): 1–25. <https://doi.org/10.1101/cshperspect.a017582>
- ŘEZAČ M. 2009. — The spider *Harpactea sadistica*: co-evolution of traumatic insemination and complex female genital morphology in spiders. *Proceedings of the Royal Society B* 276: 2697–2701. <https://doi.org/10.1098/rspb.2009.0104>
- RIZKI A., HAZMI I. R., WAGNER T. H. & IDRIS A. B. 2016. — Redescription of *Paleosepharia truncata* Laboissière, 1936, type species of the genus *Paleosepharia* Laboissière, 1936 (Coleoptera: Chrysomelidae: Galerucinae). *The Coleopterists Bulletin* 70 (2): 395–398. <https://doi.org/10.1649/0010-065X-70.2.395>
- RODRÍGUEZ J. M. S. & MERMUDEZ J. R. M. 2016. — New records and distributional notes for the Neotropical genus *Isotes* Weise, 1922 (Insecta, Coleoptera, Chrysomelidae, Galerucinae). *Check List* 12 (1): 1848. <https://doi.org/10.15560/12.1.1848>
- RODRÍGUEZ V., WINDSOR D. M. & EBERHARD W. G. 2004. — Tortoise beetle genitalia and demonstrations of a sexually selected advantage for flagellum length in *Chelymophra alternans* (Chrysomelidae, Cassidini, Stolinae), in JOLIVET P.,

- SANTIAGO-BLAY J. A. & SCHMITT M. (eds), *New Developments in the Biology of Chrysomelidae*. SPB Academic Publishers, The Hague: 739-748. https://doi.org/10.1163/9789004475335_063
- RÖNN J., KATVALA M. & ARNQVIST G. 2007. — Coevolution between harmful male genitalia and female resistance in seed beetles. *Proceedings of the National Academy of Sciences of the United States of America* 104 (26): 10921-10925. <https://doi.org/10.1073/pnas.0701170104>
- RÖNN J. L. & HOTZY C. 2012. — Do longer genital spines in male seed beetles function as better anchors during mating? *Animal Behaviour* 83 (1): 75-79. <https://doi.org/10.1016/j.anbehav.2011.10.007>
- SÁNCHEZ V., HERNÁNDEZ-BAÑOS B. E. & CORDERO C. 2011. — The evolution of a female genital trait widely distributed in the Lepidoptera: comparative evidence for an effect of sexual coevolution. *PLOS One* 6 (8): 1-7. <https://doi.org/10.1371/journal.pone.0022642>
- SCHMITT M., NEUMANN A. & LIN S.-W. 2023. — Anatomy of male and female genitalia of *Acanthoscelides obtectus* (Say, 1831) (Coleoptera, Chrysomelidae, Bruchinae) in interaction, in CHABOO C. S. & SCHMITT M. (eds), *Research on Chrysomelidae 9. ZooKeys* 1177: 75-85. <https://doi.org/10.3897/zookeys.1177.101621>
- SEENO T. N. & WILCOX J. A. 1982. — Leaf beetle genera (Coleoptera: Chrysomelidae). *Entomography* 1 (1): 1-221.
- SHUTE S. L. 1983. — Key to the genera of galerucine beetles of New Guinea, with a review of *Sastra* and related new taxa (Chrysomelidae). *Bulletin of the British Museum (Natural History), Entomology Series* 46 (3): 205-266.
- SOTA T. & KUBOTA K. 1998. — Genital lock-and-key as a selective agent against hybridization. *Evolution* 52 (5): 1507-1513. <https://doi.org/10.2307/2411321>
- TALLAMY D. W., POWELL B. E. & MCCLAFFERTY J. A. 2002. — Male traits under cryptic female choice in the spotted cucumber beetle (Coleoptera: Chrysomelidae). *Behavioral Ecology* 13 (4): 511-518. <https://doi.org/10.1093/beheco/13.4.511>
- TRACY J. L. & ROBBINS T. O. 2009. — Taxonomic revision and biogeography of the Tamarix-feeding *Diorhabda elongata* (Brullé, 1832) species group (Coleoptera: Chrysomelidae: Galerucinae: Galerucini) and analysis of their potential in biological control of Tamarisk. *Zootaxa* 2101 (1): 1-152. <https://doi.org/10.11646/zootaxa.2101.1.1>
- VAN HAREN M. M., RÖNN J. L., SCHILTHUIZEN M. & ARNQVIST G. 2017. — Postmating sexual selection and the enigmatic jawed genitalia of *Callosobruchus subinnotatus*. *Biology Open* 6: 1008-1012. <https://doi.org/10.1242/bio.025684>
- VIANA J. H. & RIBEIRO-COSTA C. S. 2013. — Review of the largest species group of the New World seed beetle genus *Sennius* Bridwell (Coleoptera: Chrysomelidae), with host plant associations. *Zootaxa* 3736 (5): 501-535. <https://doi.org/10.11646/zootaxa.3736.5.5>
- VISWAJYOTHI K. & CLARK S. M. 2022. — New World genera of Galerucinae Latreille, 1802 (tribes Galerucini Latreille, 1802, Metacyclini Chapuis, 1875, and Luperini Gistel, 1848): an annotated list and identification key (Coleoptera: Chrysomelidae). *European Journal of Taxonomy* 842: 1-102. <https://doi.org/10.5852/ejt.2022.842.1945>
- WAGNER T. 2007. — *Monolepta* Chevrolat, 1837, the most speciose galerucine taxon: redescription of the type species *Monolepta bioculata* (Fabricius, 1781) and key to related genera from (Chrysomelidae, Coleoptera). *Journal of Natural History* 41 (1): 81-100. <https://doi.org/10.1080/00222930601127384>
- WAGNER T. 2020. — Revision of *Monolepta* Chevrolat, 1836 species from North-East Africa (Coleoptera: Chrysomelidae: Galerucinae). *Bonn zoological Bulletin* 69 (2): 225-247. <https://doi.org/10.20363/BZB-2020.69.2.225>
- WAGNER T. & SCHERZ X. 2002. — *Afrocandezea* gen. nov. from tropical Africa (Coleoptera: Chrysomelidae Galerucinae). *Entomologische Zeitschrift* 112: 357-362.
- WILCOX J. A. 1965. — A Synopsis of the North American Galerucinae (Coleoptera: Chrysomelidae). *New York State Museum and Science Service Bulletin* No. 400, 226 p, 17 pls.
- WILCOX J. A. 1983. — *Checklist of the Beetles of North and Central America and the West Indies*. Vol. 8: *The Leaf Beetles and the Bean Weevils*. Family 129. Chrysomelidae. E. J. Brill, New York, 166 p.
- WILSON C. J. & TOMPKINS J. L. 2014. — Countering counteradaptations: males hijack control of female kicking behavior. *Behavioral Ecology* 25 (3): 470-476. <https://doi.org/10.1093/beheco/aru022>
- YANG X., GE S., NIE R., RUAN Y. & LI W. 2015. — *Chinese Leaf Beetles*. Science Press, Beijing, 584 + x p.

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