

47. HETEROCERIDAE MacLeay 1825

by Kerry Katovich

Family common name: The variegated mud-loving beetles

Family synonyms: *Acanthapoda* Latreille 1829, *Heterocérites* Castelnau 1840, *Heterocerida* Heer 1841, *Heteroceri* Redtenbacher 1849, *Heterocérides* Lacordaire 1854, *Heterocerini* Schiødte 1866, *Spinipedes* Mulsant and Rey 1872, *Heterocériens* Lameere 1900

Heteroceridae are a widespread and morphologically uniform family. They are easily recognized by the large mandibles, well developed comb of flattened spines on the dorsal margin of the prothoracic and mesothoracic tibiae, and the first visible ventrite with paired, arching stridulatory files. Adult and larval heterocerids are associated with riparian or moist sand and mud habitats.

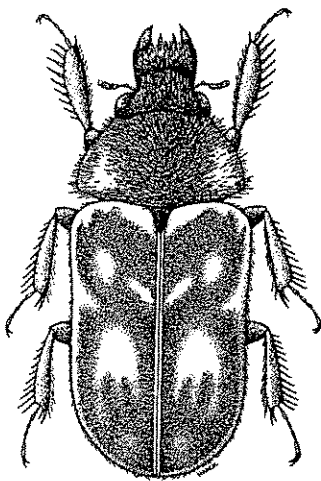


FIGURE 1.47 *Lanternarius brunneus* (Melsheimer) (from Clark and Ratcliffe 1989, used with permission)

Description: (adapted in part from Crowson 1955, Arnett 1971, Pacheco 1964, Lawrence *et al.* 1999) Body elongate, slightly flattened to moderately convex, minute to medium-sized (1-8 mm long). Dorsal surface with distinct hairs or setae. Color variable, light-brown or blackish; elytral disk often variegated, occasionally unicolorous; variegations (when present) usually with undulating yellowish or whitish bands or spots.

Head not or slightly deflexed, visible or partially so from above. Eyes well developed, not or slightly protuberant, finely faceted and lacking

interfacetal setae. Antennae short, when fully extended, not reaching middle of prothorax; antennae with 9-11 antennomeres; first antennomere less than three times the length of 2nd antennomere; antennomeres 6-7 compact, serrate (Augyliini, Heterocerini, Tropicini) or clubbed (Micilini and Elythomerini). Labrum visible, free, membranous or separated by suture line; apex of labrum subtruncate, convex, narrowly rounded or acute, occasionally abruptly produced into an elongate process. Frontoclypeal suture impressed, straight, weakly curved or angulate. Mandibles moderate to well developed; some genera with hypermandibulate males; mandibular apex gradually, moderately or strongly curved mesally, unidentate, bidentate, bilobed, truncate, or rounded; incisor edge of mandible with single, double, or multiple teeth present; mandible with well-developed mola; prostheca well-developed or reduced, if present, bearing a row of tooth-like prolongations, and divided by a notch medially. Maxilla with distinct galea and lacinia; maxillary palpi with apical palpomere cylindrical to fusiform. Ligula deeply emarginate or bilobed. Labial palpi slender, 3-segmented. Maxillary and labial lengths correlated with mandibular length.

Pronotum slightly wider than long, widest medially; lateral sides moderately to strongly curved, weakly or not explanate. Base of prothorax equal to or slightly narrower than base of elytra. Lateral pronotal carinae absent or incomplete; carinae, if present, not raised. Prosternum broadly lobed anteriorly, forming a "chin-piece". Prosternal process gradually expanded, or narrowed then expanded; process strongly elevated and curved dorsally behind coxae, slightly to extensively covering mesosternum, overall forming an elevated keel, separating the mesothoracic coxae. Procoxae slightly projecting below prosternum. Procoxal cavities strongly transverse, broadly open behind externally and internally; protrochantin partially exposed. Scutellum well-developed, triangular. Mesosternum narrow, not divided by a longitudinal suture. Mesocoxal cavities circular to transverse, open laterally, not closed by metepisterna, moderately to widely separated. Mesocoxae not projecting. Metacoxal cavities transverse, contiguous, or narrowly separated. Metacoxae not projecting.

Legs fossorial, with mesothoracic and metathoracic femora similar in size, somewhat swollen. Prothoracic and mesothoracic tibiae enlarged and armed with a row of well developed spines; metathoracic tibiae similar, spines less developed. Tarsal formula 4-4-4; tarsomeres filiform, ventrally with long, sparse hairs; pretarsus with long, slender claws.

Elytra entire, convex, posteriorly rounded; surface irregularly punctate, not punctate, or punctures and striae indistinct. Metathoracic wings well developed. Folding pattern dryopoid-like (*sensu* Crowson 1955). Radial cell of hind wing highly reduced or absent. Medial area of hind wing with three or fewer free veins; oblongum cell absent; wedge cell and anal lobe absent. Posterior edge of wing without fringe of long hairs.

Abdomen with five visible ventrites; sutures complete, occasionally indistinct medially; first visible ventrite with stridulatory file present, arching from antero-lateral corner toward meson; ninth abdominal sternum of the male invaginated, usually well sclerotized; modified into two elongate arms, with the anterior ends approximated, forming a single, anterior arm; ninth abdominal sternum with three distinct forms: U-shaped (Micilini), inverted Y-shaped (Tropicini), and inverted V-shaped (Elythomerinae, Augyliini and Heterocerini); ninth abdominal sternum of females not visible.

Male genitalia (terminology following Pacheco 1964) divided into two pieces (appearing single in Tropicini): the tegmen (phallobase and parameres) and the aedeagus (dorsal plate, anteriorly produced median strut and an internal sac). The phallobase may be divided into a basal piece (formed by two fused or separated, transverse, sclerotized bands) and median plate; the lateral portion of the median plate is designated as the lateral arms of the phallobase. Parameres present or absent, if present, membranous, arising from the basal piece of the phallobase. Internal sac generally well sclerotized dorsally. Female genitalia completely membranous, lacking visible coxites and styli.

Larval body elongate, campedeiform, subcylindrical, widest in thoracic region, tapering posteriorly; 2-10 mm long; dorsal body surface darkly pigmented, smooth; vestiture of short and long hairs. Head prognathous, broad, and protracted. Five stigmata on each side. Antennae very short, 3-segmented, with large, bulbous sensorium on 2nd segment longer than reduced 3rd segment. Labrum large and free. Frontoclypeal suture present. Mandibles symmetrical, somewhat flattened, bidentate. Ventral mouthparts retracted. Legs well developed, 5-segmented; tarsungulus with single seta. Abdominal tergum 9 simple, without urogomphi. Operculum absent. Abdominal segment 10 well-developed, its sternum forming a conical pygopod; tergum of 10th segment reduced; anal region posteriorly or posteroventrally oriented. Spiracles cribiform, appearing annular-uniformous.

Habits and habitats. Natural history information is available for relatively few species, however, Heteroceridae appear to be homogeneous in adult and larval habitats. In general, adults are most commonly associated with riparian habitats, although they are strong flyers and can be found some distance from water. Adults feed in shallow, horizontal tunnels excavated in mud or moist organic sand. Adult stomach contents suggest this family feeds on algae, plankton, and organic material (Silvey 1935). Kaufmann and Stansly (1979) described four distinct tunnel types in *Neoheterocerus pallidus* (Say): feeding galleries, pupal cells, egg chambers, and hibernacula. The tunnels of several individuals may intersect, hence these beetles are often gregarious as adults and larvae. Claycomb (1919) noted that several species may coexist in a given habitat, and their tunnel systems may intersect. Tunnel construction has been documented in detail (Kaufmann and Stansly 1979, Clark and Ratcliffe 1989). Mating apparently occurs within the tunnel system.

Eggs are small, oblong, whitish to pale yellow, turning opaque as they mature. They are deposited together in large numbers, averaging 40-60 eggs within an egg chamber. The concentration of eggs is believed to be related to egg guarding behavior, as demonstrated in female *Lapsus tristis* (Mannerheim) (Folkerts 1989). When confronted by an intruder within the egg chamber, *L. tristis* raised its body, opened and closed its mandibles, and waved its antennae. This defense is likely directed against *Ellipser gurneyi* Gunther (Orthoptera: Tridactylidae), which often lives in close association and frequently use the same tunnel systems. Females apparently produce two broods; in *N. pallidus* a third brood is reabsorbed in the egg stage to provide a fat reserve for the winter months or adverse weather conditions. Adults may

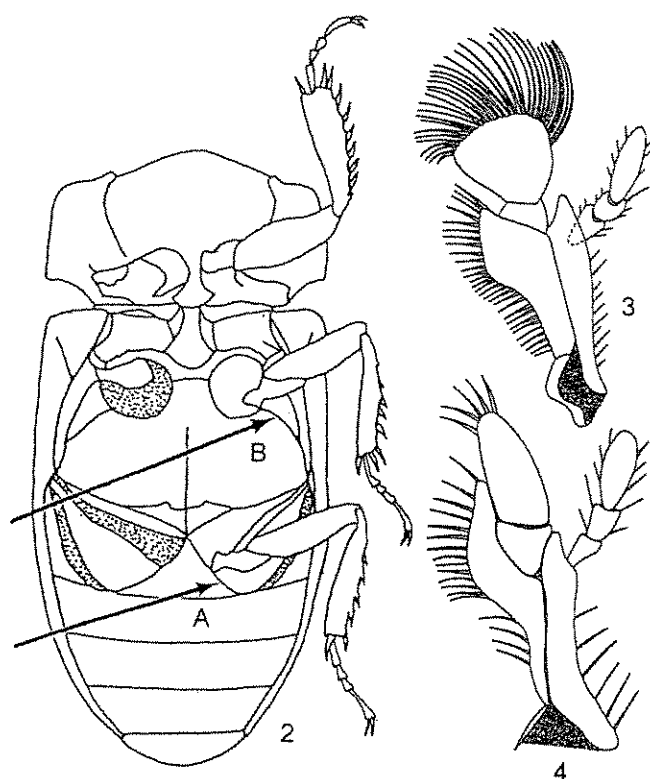
pass these periods in hibernacula. Diapause in northern latitudes usually occurs from October to April. The egg stage lasts approximately 3 days.

Larvae radiate out from the parental tunnel systems, forming their own tunnel systems or using existing tunnels. Larval food is similar to that of the adult. The larval stage is approximately seven days, with approximately four instars. Pupation ranges from three to six days.

The ecology of Heteroceridae is apparently closely tied to the rapidly changing riparian habitat. Frequent fluctuations in water level may cause heavy mortality in eggs, pupae, and larvae; adults are not usually affected (Kaufmann and Stansly 1979). For this reason, population levels may fluctuate dramatically in a given region. This may explain why heterocerids have fairly rapid egg to adult development, a long adult life stage, and overlapping generations. The presence of a breeding generation at any given time may enable survival of local populations.

Status of the classification. Lameere (1900) placed Heteroceridae in his Cantharidiformia. Kolbe (1901) placed Heteroceridae under the superfamily Dascilloidea in the suborder Heterophaga. Ganglbauer (1904) placed Heteroceridae under the series Diversicornia. Based on wing folding and venation, Forbes (1926) placed the family under the superfamily Dryopoidea in the series Dryopiformia. Böving and Craighead (1931) associated the family with Dascilloidea based on larval characters. Jeannel and Paulian (1944) placed the family under the division Cucujoidea, section Cucujaria. Based on adult and larval characters, Crowson (1955) placed Heteroceridae with the superfamily Dryopoidea in the series Dascilliformia. This position was supported by Sanderson (1953), who indicated that larval and adult Heteroceridae show a close relationship to the families Dryopidae, Limnichidae, and Elmidae. Later, Crowson (1981) suppressed Dascilliformia, placing Heteroceridae under Dryopoidea in the series Elateriformia. Currently, Lawrence and Newton (1995) placed Heteroceridae under the superfamily Byrrhoidea in the series Elateriformia; they further elevated Pacheco's (1964) Elythomerini and Heterocerini to subfamily status.

LeConte addressed Heteroceridae in the first true treatment of this family for North America north of Mexico in a series of works (1863-1866), discussing 15 species and describing three new species. Horn (1890) revised *Heterocerus* for "Boreal America" providing useful descriptions and illustrations of 11 species. Zaitzev (1910) provided the most recent catalogue of world Heteroceridae, listing three genera with 133 species, 37 of which were recorded from the New World. Leng (1920), Leng and Mutchler (1927, 1933) and Blackwelder (1939) catalogued the Heteroceridae of North America north of Mexico, listing 16 species under the genus *Heterocerus*. Blackwelder (1944-1957) catalogued the Heteroceridae of Mexico, Central America, the West Indies, and South America, listing 13 species under the genus *Heterocerus*. Pacheco (1964) monographed the New World Heteroceridae, dividing the family into five tribes and 20 genera. Hatch (1965) provided keys to ten species of *Heterocerus* in the Northwest. Downie and Arnett (1996) provided keys to *Augyles*, *Heterocerus*, and *Tropicus* species of northeastern North America.



FIGURES 2.47-4.47. 2. Generalized Heteroceridae, ventral view; A. post-metacoxal line, B. post-mesocoxal line; 3. *Centuriatus auroniscus* (Kiesenwetter), maxilla, dorsal view; 4. *Explorator canadensis* (Fall), maxilla, dorsal view.

Pacheco (1978) provided the most recent catalogue of Heteroceridae north of Mexico.

Charpentier (1967) noted that breaking up *Heterocerus* into numerous genera based on genitalic characters (*sensu* Pacheco 1964) was unnecessary. Miller (1988) stated that in Pacheco's genera, a high degree of variation exists in the male genitalia. Consequently, Miller retained *Heterocerus* (Pacheco's *Lapsus*, *Lanternarius*, *Dampfius*, *Neoheterocerus*, *Peditatus*, and *Efflagitatus*), *Augyles* (Pacheco's *Centuriatus*, *Microaugyles*, and *Explorator*), and *Tropicus* for North America, north of Mexico.

Currently there is no consensus on the tribal or generic level classification of the family. Recent work by several authors has shown some disparity in classification, some recognizing Pacheco's classification (Kaufmann and Stansly 1979, Folkerts 1989), others retaining a more traditional classification (Hatch 1965, Downie and Arnett 1996). Pacheco's (1964) review of the Nearctic, Caribbean, and South American faunas remains the only work of its kind and scope. Heteroceridae has been reviewed for the Notogean and Ethiopian regions (Charpentier 1965, 1967). However, no formal phylogenetic revision for the world has been conducted. Lacking any competing classification schemes based on a complete analysis of New World taxa, Pacheco's work is followed in this chapter. Further work at the generic and tribal level is clearly needed to resolve this issue.

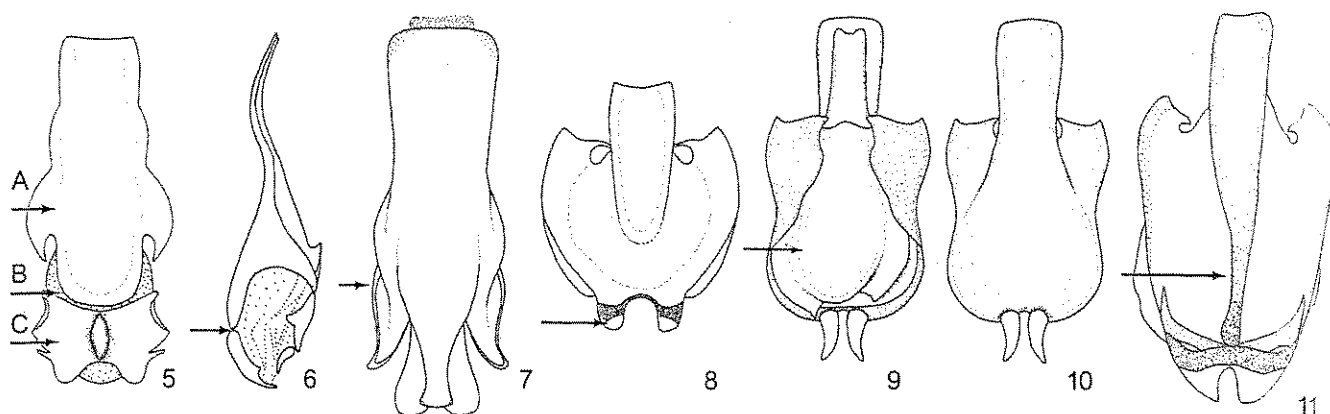
The fossil record of Heteroceridae is rather limited. Ponomarenko (1985) described a new genus, *Heterocerites*, from the lower cretaceous of Mongolia. Clark and Ratcliffe (1989) discussed the potential significance of trace fossils i.e., tunneling in paleoecological work.

Distribution. Heteroceridae are found in all major zoogeographic regions, and consists of approximately 21 genera (20 extant) (Pacheco 1964) and 300 species. Elythomerini (monotypic: *Elythomerus* Waterhouse) are restricted to Australia. Micilini (monotypic: *Micilus*) are Palearctic. Heterocerini and Augyliini are distributed worldwide (absent from the Hawaiian Islands). Tropicini occur in North and South America. Three tribes (10 genera and 34 species) are discussed for North America north of Mexico below. Distributional information for genera is provided in the generic treatment below.

KEYS TO THE NORTH AMERICAN GENERA (After Pacheco 1964)

In this key to genera of North America, only males can be identified beyond *Neoheterocerus*.

1. Post-metacoxal lines present (Fig. 2A) (Augyliini) 3
— Post-metacoxal lines absent 2
- 2(1). Antennae 11-segmented; usually medium to large in size (Heterocerini) 5
— Antennae 9-segmented; small in size, uniform in color, often with a whitish elytral margin (Tropicini) *Tropicus*
- 3(1). Antennae 10-segmented *Microaugyles*
— Antennae 11-segmented 4
- 4(3). Galea broad, flattened, appearing as a golden brush of stout setae (Fig. 3) *Centuriatus*
— Galea not as above, galea with 5 well developed, white setae (Fig. 4) *Explorator*
- 5(2). Post-mesocoxal lines absent *Neoheterocerus*
— Post-mesocoxal lines present (Fig. 2B) 6
- 6(5). Male genitalia without membranous parameres; median plate (Fig. 5A) and basal piece of phallobase (Fig. 5C) separated by a sulcate line (Fig. 5B, 6) *Peditatus*
— Male genitalia with membranous parameres present; median plate and basal piece or pieces of phallobase clearly differentiated or continuous, not separated by a sulcate line 7
- 7(6). Male genitalia with median plate and basal piece of phallobase continuous (Fig. 7), basal piece often produced posteriorly; parameres relatively large and flexible; lateral lobes of phallobase arising from a central point, distally flexed inward *Dampfius*
— Male genitalia without the above combination of characters 8



FIGURES 5.47-11.47. *Peditatus schwarzi* (Horn), male genitalia, ventral view; A. median plate of phallobase, B. transverse sulcate line, C. basal piece of phallobase; 6. *P. schwarzi*, arrow highlights sulcate line of male genitalia, lateral view; 7. *Dampfius collaris* (Kiesenwetter), male genitalia, arrow highlights lateral lobe of phallobase, ventral view; 8. *Lapsus tristis* (Mannerheim), arrow highlights male parameres, ventral view; 9. *Efflagitatus selanderi* Pacheco, male genitalia, arrow highlights dorsal plate of aedeagus, dorsal view; 10. *E. selanderi*, male genitalia, ventral view; 11. *Lanternarius brunneus* (Melsheimer), male genitalia, arrow highlights tapering medial plate of phallobase, ventral view.

- 8(7). Male genitalia with basal piece of phallobase about one half the width of phallobase; parameres rounded and relatively small (Fig. 8) *Lapsus*
 — Male genitalia not as above 9
- 9(8). Male genitalia with parameres usually very small (Fig. 9, 10); dorsal plate of aedeagus usually elongate, distorted, and composed of several differentiated areas which vary in the degree of sclerotization *Efflagitatus*
 — Male genitalia with parameres about as broad as long; median plate of phallobase usually tapering posteriorly (Fig. 11) *Lanternarius*

CLASSIFICATION OF THE GENERA OF AMERICA NORTH OF MEXICO

Number of species, relevant keys, and distributional information are provided for North America north of Mexico. Traditional generic classification is noted where appropriate. Additional information pertinent to each genus is provided. Distributional information for the species should not be considered complete, and is only reflective of previous, limited works on this family.

Heteroceridae MacLeay 1825

Heterocerinae MacLeay 1825

Augyliini Pacheco 1964

Augyliini are distinguished by the following characters: post-mesocoxal and post-metacoxal lines present (Fig. 2A, 2B); antennae 10-11 segmented. Five genera are currently placed under this tribe by Pacheco (1964). Three genera occur north of Mexico (see below); the genera *Taenheterocerus* (Kiesenwetter) and *Augyles* Schiødte are Palearctic and European, respectively. *Augyles* is considered present in North America under the traditional classification scheme *sensu* Miller (1988).

Explorator Pacheco 1964

Monotypic, *E. canadensis* (Fall), known from Alaska to southern Canada. A second species may be present in this genus. *Explorator* is distinguished from other Augyliini by the epipleural line well marked, and galea with five erect, white setae (Fig. 4).

Augyles Schiødte 1866, in part, *sensu* Miller 1988

Centuriatus Pacheco 1964

Two species: *C. aurimicans* (Kiesenwetter), southern Canada south to Texas; *C. compactus* (Fall), southern Canada south to the north-central United States. Key to species in Pacheco 1964. *Centuriatus* is distinguished from other Augyliini by the squamiform hairs on its dorsal surface, epipleural line well marked, compact body, and galea flat, short, and tufted with wrinkled, golden setae (Fig. 3).

Augyles Schiødte 1866, in part, *sensu* Miller 1988

Microaugyles Pacheco 1964

Two species: *M. moleculus* (Fall), southern Canada to central United States; *M. mundulus* (Fall), western United States. Key to species in Pacheco 1964. *Microaugyles* is distinguished from other Augyliini by its unusually small size, poorly sclerotized male genitalia, prostheca small, with 12-17 setae, galea finger-like, with 4-6 long, curved, different sized setae, antennae 10-segmented, and post-metacoxal lines curving gently.

Augyles Schiødte 1866, in part, *sensu* Miller 1988

Heterocerini Pacheco 1964

Heterocerini are distinguished by the following characters: antennae 11-segmented, and post-metacoxal lines absent. Eleven genera are currently placed under this tribe (Pacheco 1964). Six genera are present north of Mexico (see below), with five Neotropical genera: *Culmus* (Mexico), *Olmedous* (Mexico), *Gradus* (Chile), *Eius* (southern Brazil to northeastern Argentina), and *Filiolus* (Cuba). Three species of Heterocerini remain *incertae sedis* (Pacheco 1978).

Lanternarius Pacheco 1964

Approximately six species, widespread across Canada and the United States. Key to species in Pacheco 1964. *Lanternarius* is distinguished by the usually black and shining male genitalia, lobate, usually triangular parameres, basal piece and lateral arms of phallobase heavily sclerotized (Fig. 11), three zig-zag bands on each elytron (these bands forming spots, occasionally vague on older specimens), galea finger-like, with few erect setae, and with oblique pronotal borders.

Heterocerus Fabricius 1792, in part, *sensu* Miller 1988

Neoheterocerus Pacheco 1964

Approximately 13 species, North America to Central Mexico, eleven species north of Mexico, widespread across the United States and Canada. Key to species in Pacheco 1964. *Neoheterocerus* is distinguished from other Heterocerini by the absence of the post-mesocoxal line, the medium to large body size, elytra with zig-zag banding, galea finger-like, with few erect white setae, labrum of hypermandibulate males abruptly produced into an elongate process, and epipleural line absent. Members of this genus will fall into Miller's *Heterocerus* "gnatho group". The natural history of *N. pallidus* was discussed by Kaufmann and Stansly (1979).

Heterocerus Fabricius 1792, in part, *sensu* Miller 1988

Efflagitatus Pacheco 1964

Eight species, primarily South American; one species, *E. selanderi* Pacheco, from Florida. Key to species in Pacheco 1964 and 1969 (modification of 1964 key). *Efflagitatus* is distinguished by small, lobular, usually approximate parameres, aedeagus usually elongate and distorted in appearance (Figs. 9, 10), galea usually short, with a row or tuft of golden colored setae.

Heterocerus Fabricius 1792, in part, *sensu* Miller 1988

Dampfius Pacheco 1964

Approximately six species, widespread, Canada to Texas. Key to species in Pacheco 1964. *Dampfius* is distinguished by the basal piece of the phallobase produced at the posterior end (Fig. 7), and prostheca small, with 15-30 setae. Species of *Dampfius* are morphologically similar and separated by male genitalic characters. Miller (1988) synonymized this genus with *Heterocerus*. The synonymy was based on the non-acceptance of Pacheco's generic designation. All of the members of *Dampfius* fall into Miller's *Heterocerus* "undatus group" (key to species Miller, 1988). The biology of *D. collaris* (Kiesenwetter) was discussed by Folkerts (1989).

Heterocerus Fabricius 1792, in part, *sensu* Miller 1988

Peditatus Pacheco 1964

Three species, two north of Mexico. *Peditatus schwarzi* (Horn), occurs from the north-central United States to the east coast, south to Texas. *Peditatus texanus* Pacheco 1964, is found in Texas. Key to species in Pacheco 1964. *Peditatus* is distinguished by the tegmen divided ventrally into two sclerotized parts by a sulcus (Fig. 5, 6), galea finger-like, with 4-7 short setae, post-mesocoxal

lines strongly marked, and border anterior to stridulatory ridge absent.

Heterocerus Fabricius 1792, in part, *sensu* Miller 1988

Lapsus Pacheco 1964

Monotypic: *Lapsus tristis* (Mannerheim). This species is widespread across Canada and Alaska south to Florida and California. *Lapsus* is distinguished by the triangular tegmen, small, rounded parameres, and rounded, concave dorsal plate of the aedeagus (Fig. 8). Miller (personal communication) stated that *Lapsus* is synonymous with the European *Heterocerus fenestratus* Thunberg. Members of this genus fall into Miller's *Heterocerus* "mollinus group". Natural history information for *L. tristis* and *H. fenestratus* is unknown.

Heterocerus Fabricius 1792, in part, *sensu* Miller 1988

Tropicini Pacheco 1964

Tropicini are distinguished by the following characters: antennae 9-segmented, post-mesocoxal and post-metacoxal lines absent, color pattern simple, mandibles of males usually with dorsal ridge developed into a wide laminar process, and epipleural line absent. This tribe is represented by a single genus *Tropicus* Pacheco 1964. Twenty-seven species are distributed from North to South America.

Tropicus Pacheco 1964.

Twenty-seven primarily Neotropical species. Two species occur North of Mexico: *T. pusillus* (Say), northern United States to Panama, and *T. minutus* (Fall), Texas. No complete key to species is available. Pacheco (1964) provided a key to 11 species. Numerous species have subsequently been added or synonymized. Bameul (1995) provided the most recent species list for the world. *Tropicus* is distinguished by characters given in the tribal diagnosis.

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