Sphaeritidae, Synteliidae in Handbook of Zoology Ed. 2

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13.1 Sphaeritidae Shuckard, 1839

Distribution. The family includes a single genus, *Sphaerites* Duftschmid, confined to temperate forested or alpine areas of the northern hemisphere. The six known species include two rather widely distributed species: *Sphaerites glabratus* (Fabricius), widespread across northern Great Britain, northern Europe, and east to Mongolia, eastern Russia, Japan and China (Jilin); and *S. politus* Mannerheim from western North America (southeastern Alaska to northern California, east to Alberta, Idaho and western Montana) and possibly (doubtfully according to Löbl 1996) eastern Russia and Japan (Kryzhanovsky 1989; Löbl 1996; Newton 2000). The remaining four species are known from only a few localities in central China: *S. dimidiatus* Jureček, from Gansu, Shaanxi, and Sichuan provinces; S. *involatilis* Gusakov from Sichuan*; S. nitidus* Löbl from Gansu and Sichuan provinces; and *S. opacus* Löbl & Háva from Shaanxi province (Löbl 1996; Löbl & Háva 2002; Gusakov 2004; Háva 2014).

Biology and Ecology. These usually rare beetles are generally associated with decaying organic matter such as dung, carrion, fungi, fermenting fruit, and sap of dying or dead trees and stumps, but their ecology is poorly known and the full life cycle has not been observed in detail (Newton 2000). *Sphaerites glabratus* has been associated especially with northern conifer forests, sometimes at high altitudes; adults are attracted to sap flows on birch stumps, and have been observed to feed on the sap and mate there; females laid eggs in nearby sap-impregnated soil, and larvae developed quickly with the next generation of adults emerging within a month (Nikitsky 1976). In North America, *S. politus* can be locally common at carrion (Keen 1895), but has been found also in bear dung and in or near compost (Hatch 1961), and in unbaited pitfall and flight traps in old-growth conifer forests (M. Ivie pers. comm.); in Japan, this species (but possibly misidentified, see Löbl 1996) has been collected in pitfall traps in *Pinus* forests at 1800–1980 m elevation (Ôhara 1994). The four Chinese species have all been found at high elevations (2800–3600 m) in the mountains, in one case (*S. dimidiatus*) in scree in an alpine meadow (Löbl & Háva 2002).

Larval feeding was not reported by Nikitsky (1976), and his report of adults feeding on sap requires confirmation. The mouthparts of larvae as well as adults are similar to those of histerids known to be predaceous on soft prey such as Diptera larvae, and it seems likely that both stages of *Sphaerites* are also mainly or strictly predaceous on similar prey. Like histerids, *Sphaerites* adults feign death when disturbed (P. Kovarik pers. comm.).

Fig. 13.1: *Sphaerites dimidiatus* Jureček. Scale line = 2.0 mm. Photo © Peter W. Kovarik.

Morphology, Adults (Fig. 13.1). Length about 4.5–7 mm; body broadly oval, convex; color black (elytra partly red in two Chinese species), moderately shining with slight blue-green metallic reflection; vestiture generally absent except on appendages.

Head less than half as wide as pronotum, deflexed but not retractile, without differentiated neck, surface punctate; eyes large, oval. Epistomal suture present, broadly curved or more or less angulate and with short medial stem (i.e. Y-shaped). Antenna short, weakly geniculate, inserted under slight frontal ridge between eye and mandibular base, antenna in repose bent under head; of 11 antennomeres, scape long and moderately curved; antennomeres 2–8 small, each with or without a few large setae, 8 flattened and appressed against 9; 9–11 together forming a large densely setose club, the antennomeres distinct but immoveably associated, antennomere 11 with a pair of internal vesicles. Labrum short, strongly transverse with straight anterior edge and rounded anterior angles, with two adjacent very long setae near each side; underside and epipharynx with dense setae or microtrichia. Mandibles elongate, strongly projecting, with contiguous molar areas at base, each mandible with a large medially curved acute apex, 1–2 strong subapical teeth, and a setose prostheca that is more than 2/3 as long as the mandible. Maxilla with densely setose galea and lacinia, the latter at apex with a pair of strong non-articulated medially curved teeth, the palpus of four palpomeres, the first very small, the remaining segments stout, the apical palpomere longest, cylindrical or slightly depressed. Labium with densely setose hypopharynx and bilobed ligula; palpigers small, lightly sclerotized, separate; palp of three palpomeres, the apical palpomere longest and stoutest; mentum sexually dimorphic: trapezoidal, flat and well sclerotized in female, transversely oval, slightly concave and translucent in male. Gular sutures complete, well separated throughout. Tentorium: see Stickney (1923).

Prothorax freely movable, not tightly co-adapted to rest of thorax. Pronotum transverse, broadly emarginate anteriorly, sides evenly convex and broader posteriorly, base sinuate, sides strongly and anterior border weakly margined, surface punctate especially laterally; hypomeron broad, explanate, with long acute postcoxal process that does not close the procoxal cavities; notosternal suture complete; prosternum short, with small fingerlike intercoxal process that fits into groove in coxae but does not separate the apices of the coxae. Scutellum moderately large, subtriangular; mesoventrite short, with elevated intercoxal plate; mesanepisternal and mesepimeral sutures complete. Elytra convex, long but abruptly truncate, exposing only pygidium (abdominal tergum VII); striae represented by nine unimpressed rows of punctures which become more or less irregular or obsolescent near base and apex; epipleural fold present, complete. Metathoracic wings present, with large anal lobe and relatively complete venation including distinct radial cell and large RP-MP1+2 loop (former "M-Cu" loop); see Kukalová-Peck & Lawrence (1993: fig. 41) for details and modern venational terminology, but note that MP1+2 is mislabeled MA1+2 there. Metaventrite long, metanepisternal and metepimeral sutures complete; metendosternite with long basal stalk and pairs of long furcal and short anterior arms. Legs with pro- and mesotrochantins exposed; anterior coxae transverse, contiguous, prominent; middle coxae small, globular, well separated by elevated plate of mesoventrite plus flat metasternal process; hind coxae transverse, subcontiguous; trochanters small; femora swollen; tibiae relatively robust with small spines along outer edge but without teeth; tarsi all 5-segmented, tarsomeres slender with a few setae on each; apical tarsomere bearing a pair of large claws and a bisetose empodium between them.

Abdomen at base ventrally not tightly co-adapted to thorax, with five visible lightly punctate sterna (III–VII) and one visible densely punctate tergum (VII); segment VIII and genital segments completely invaginated and lightly sclerotized, sexually dimorphic; spiracles of segments I–VI functional, VII–VIII atrophied; terga increasingly well sclerotized from III–VII; terga IV–V and dorsal edges of sterna II–III with dense patches of microtrichia, tergum VI with apical palisade fringe. Male tergum VIII divided, IX–X entire, sternum VIII with long curved posteriorly directed lateral lobes, sternum IX present. Aedeagus small, subcylindrical; phallobase (basal piece) short, forming a nearly complete but asymmetrical ring; parameres long, nearly completely fused to one another and largely enclosing the slender median lobe. Female terga VIII–IX divided, X entire and situated between halves of IX, sternum VIII divided; ovipositor consisting of paired valvifers and heavily sclerotized coxites, the latter each with a scoop-like outer surface and a small stylus on inner side; spermatheca simple, bulbous. [General reviews and illustrations of adult morphology of *Sphaerites* can be found in Kryzhanovsky & Reichardt (1976) and especially Ôhara (1994), with further details in Hansen (1997; ovipositor), Stickney (1923; head capsule), Williams (1938; mouthparts), Forbes (1926; wing folding pattern), Kukalová-Peck & Lawrence (1993; wing venation with modern terminology), and Crowson (1974; internal anatomy)].

Morphology, Larvae. Body elongate, slightly flattened, surfaces very lightly to moderately pigmented and sclerotized, generally smooth, with sparse vestiture.

Head prognathous, protracted, strongly transverse, without distinct neck; epicranial sutures (dorsal ecdysial lines) separate, without basal stem; stemmata apparently absent. Antenna less than half as long as head width, of three segments, pair of sensoria of second segment conical and situated on outer apex, lateral to insertion of apical segment. Labrum fused to head capsule to form a nasale bearing a single median tooth. Mandibles more or less symmetrical, each with a prominent curved acute apex, a single acute tooth medially, and an abruptly enlarged base that bears a penicillus or tuft of setae. Maxillary groove absent. Cardines distinct, transverse, separated by mentum; stipes elongate, without apical lobes; palp 4-segmented, basal segment with an articulated digitiform appendage on inner side. Labium consisting of prementum, membranous mentum, and a submentum that is fully integrated in the ventral wall of the head capsule; ligula absent; palps 2-segmented, separated by less than the width of one of them. Gula present, elongate.

Thoracic terga and sterna each of four or more sclerotized plates. Legs short, of five segments including tarsungulus.

Abdomen 10-segmented, largely membranous, tergal and sternal areas of segments I–VIII each with a transverse row of asperities and 22 or nine small sclerites, respectively. Tergum IX much longer than preceding terga, of eight small sclerites, and bearing pair of long, 4-segmented urogomphi at apex. Spiracles biforous, present ventrolaterally before mesothorax and dorsolaterally on abdominal segments I–VIII. [Larvae are known only from the description of first-instar larvae of *S. glabratus* reared by Nikitsky (1976), repeated in part by Newton (1991) and Hansen (1997). A very different larva attributed to this species by Crowson (1974) was misidentified according to Nikitsky (1976)]

Eggs. Large, white [Nikitsky 1976]

Pupae. Unknown.

Phylogeny and Taxonomy. *Sphaerites* was first placed in its own family by Shuckard (1839), and maintained as such by Thomson (1862) and others, although many 19th century authors included the genus in the old broad concept of Silphidae (e.g. Horn 1880). Ganglbauer (1899) among others placed the family with clavicorn beetles such as Trogossitidae (as Ostomidae) and Nitidulidae, but Lewis (1882), Sharp & Muir (1912), and Forbes (1926), based on general structure, male genitalia and wing venation and folding patterns, respectively, recognized a close relationship of *Sphaerites* to *Syntelia* Westwood and the family Histeridae; Lewis and Forbes even placed *Sphaerites* and *Syntelia* together in a family Synteliidae. The discovery of larvae (Nikitsky 1976) confirmed a close relationship of the family to Synteliidae and Histeridae. These three families are now invariably placed together in the polyphagan series Staphyliniformia, either in their own superfamily, Histeroidea (e.g. Crowson 1974), or in a monophyletic "histerid group" of families within Hydrophiloidea as a sistergroup to Hydrophilidae *sensu lato* (e.g. Lawrence & Newton 1982). Recent phylogenetic analyses using adult, larval and molecular data have invariably supported the monophyly of these three families together as a group, and the monophyly of Histeridae within this group, but differ in whether Sphaeritidae (Ôhara 1994; Hansen 1997; Beutel 1999; Ślipiński & Mazur 1999; Caterino & Vogler 2002), Synteliidae (Beutel & Leschen 2005; Caterino *et al.* 2005; Hunt *et al.* 2007; Bocak *et al.* 2014; McKenna *et al.* 2015) or Histeridae (Lawrence *et al.* 2011) is the sister taxon to the other two families. These studies and additional ones (e.g. Korte *et al.* 2002) have also often but not always supported or been consistent with the hypothesis that these three families together are the sistergroup to Hydrophilidae *sensu lato* (or Hydrophiloidea *sensu stricto*), although Beutel's (1999) analysis of larval head structure and most of Bernhard *et al.*'s (2009) analyses based on molecular as well as morphological data found these "histerid group" families actually nested within Hydrophiloidea *sensu stricto*, while some of the other studies cited above do not support the close relationship of these groups. Further discussion and details about the phylogenetic relationships of Sphaeritidae may be found in the chapter on Histeridae (**1–13.3**) as well as the studies cited above. Synapomorphies for the family are difficult to identify because of its basal position, but the sexually dimorphic mentum and asymmetrical basal piece of the aedeagus are likely to be two such characteristics. Phylogenetic relationships among the species of *Sphaerites* are at present unclear and in need of study.

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13.2 Synteliidae Lewis, 1882

Distribution. This family includes the single genus *Syntelia* Westwood with a widely disjunct distribution pattern in the mountains of eastern Asia (five species, India and Burma to China, Japan and eastern Russia) and Central America (two described and two undescribed species in Mexico and Guatemala) (Zhou & Yu 2003; pers. obs.). The Asian species are *S. davidis* Fairmaire, *S. mazuri* Zhou, and *S. sinica* Zhou, all from Sichuan province, China; *S. indica* Westwood, from northern India and Burma; and S. *histeroides* Lewis, from Japan and eastern Russia (Siberia). The American species include *S. mexicana* Westwood and *S. westwoodi* Sallé from east central Mexico (state of Veracruz for the former, Oaxaca and Puebla for the latter) and two undescribed species from southern Mexico (Chiapas) and Guatemala.

Biology and Ecology. Most *Syntelia* species are found at moderate to high elevations (1500–3900 m) of mountains in subtropical or tropical zones. The best-known and northernmost species, *S. histeroides*, also occurs at lower elevations, where adults and larvae have been found under the moist bark of decaying logs of various trees including *Phellodendron sachalinensis* (especially with decaying blackened phloem), and in summer at sap flows of young *Quercus* spp. and *Ulmus* sp. (Lewis 1882; Mamaev 1974; Ôhara 1994). Larvae, and presumably adults, of this species are predators on larvae of other insects living under bark; larvae also pupate in chambers under bark, but unlike the histerid *Hololepta amurensis* Reitter found in the same habitat the *Syntelia* larvae do not construct a pupal cocoon (Mamaev 1974). At least some other *Syntelia* species appear also to be associated with decaying logs in forested areas, notably *S. mexicana* and the undescribed Central American species, which were found under bark of *Pinus* logs or under the logs near timberline (Sallé 1873 & C. Marshall pers. comm., respectively). However, the largest and most convex species of the genus, *S. westwoodi*, occurs in high desert areas of the south-central Mexican plateau at 1700–3000 m, where adults have been found several times in the moist fermenting interior of large decaying columnar cacti, feeding on larvae of Diptera (A. Newton pers. obs.).

Morphology, Adults (Fig. 13.2). Length about 10–35 mm; body elongate, robust, more or less parallel-sided, convex; color black, moderately shining to dull, with or without slight blue-green metallic reflection; vestiture generally absent except on appendages.

Head more than 2/3 as wide as pronotum, porrect or slightly deflexed and not retractile, without differentiated neck, surface usually sparsely punctate; eyes large, oval. Epistomal suture absent or vaguely indicated laterally. Antenna short, weakly geniculate, inserted under slight frontal ridge between eye and mandibular base, antenna in repose bent under head, scape and pedicel fitting into distinct groove; of 11 antennomeres; scape long and moderately curved; antennomeres 2–7 small, 8 much wider but short and appressed against 9, 2–8 with at most a few large setae; 9–11 together forming a large densely setose club, the antennomeres distinct but closely associated, antennomere 11 with a pair of internal vesicles. Labrum very short and nearly vertical, immovably attached to front of head capsule but delimited by indistinct, broadly curved or more or less angulate, fine groove posteriorly; underside and epipharynx with dense setae or microtrichia. Mandibles very elongate, strongly projecting, with small contiguous molar areas at base, each mandible with a large medially curved acute apex and 3–4 teeth along long mesial blade-like edge, and a setose prostheca that is more than half as long as the mandible. Maxilla with densely setose galea and lacinia, latter without apical teeth; palpus of four palpomeres, first very small, remaining segments elongate, apical palpomere longest, cylindrical or slightly depressed. Labium with densely setose hypopharynx and bilobed ligula; palpigers large, well sclerotized and separate; palp of three palpomeres, apical one longest; mentum strongly transverse, trapezoidal but slighly emarginate anteriorly, not sexually dimorphic. Gular sutures complete, well separated throughout.

Fig. 13.2: *Syntelia westwoodi* Sallé. Adult, lateral view. Scale line = 2.5 mm. Photo © Peter W. Kovarik.

Prothorax freely movable, not tightly co-adapted to rest of thorax. Pronotum transverse, more or less trapezoidal and widest in anterior third, anteriorly slightly emarginate and with fringe of setae; sides and posterior border strongly margined, surface variably but usually sparsely punctate; hypomeron broad, with long acute postcoxal process that inserts into the intercoxal projection of the prosternum to completely and externally close the procoxal cavities; notosternal suture complete. Prosternum well developed, with short presternum delimited by a vague groove, angularly produced at middle and with fringe of long setae; prosternum posteriorly with large intercoxal process that fits into deep groove in coxae and narrowly separates apices of coxae. Scutellum (exposed portion) moderately large and subtriangular to small, fingerlike; mesoventrite large, more or less flat, with blunt intercoxal process that distinctly separates the mesocoxae; mesanepisternal and mesepimeral sutures complete. Elytra long, flat dorsally and curved ventrad in lateral third to vertical orientation, apically truncate, exposing only pygidium (abdominal tergum VII); striae represented by 3–10 variably impressed, often irregular grooves or rows of punctures; epipleural fold present, complete, adjacent to external edge for most of length. Metathoracic wings present, with large anal lobe and relatively complete venation including distinct radial cell and narrow RP-MP1+2 loop (former “M-Cu” loop); see Kukalová-Peck & Lawrence (1993: fig. 42) for details and modern venational terminology. Metaventrite long, metanepisternal and metepimeral sutures complete, more or less distinct discrimen present; metendosternite with long basal stalk and pairs of long furcal and short anterior arms. Legs with pro- and mesotrochantins concealed; anterior coxae transverse, slightly separated, prominent; middle coxae small, globular, well separated by flat and blunt processes of meso- and metaventrites; hind coxae transverse, subcontiguous;

trochanters small; femora robust; tibiae robust, more or less flattened, with several large teeth bearing articulated spines along outer edge in addition to smaller spines and setae; tarsi all 5-segmented, tarsomeres slender with a few setae on each; apical tarsomere bearing a pair of large claws and a bisetose empodium between them.

Abdomen at base ventrally tightly co-adapted to thorax, with five visible lightly punctate sterna (III–VII) and one visible more densely punctate tergum (VII); sternite III with carina-delimited cavity for reception of metacoxae and acute intercoxal process, sternite II barely visible as minute sclerite between coxae; segment VIII and genital segments completely invaginated and lightly sclerotized, sexually dimorphic; spiracles of segments I–VI functional, VII–VIII atrophied; all terga I–VII well sclerotized, VII more than others; terga IV–VI and dorsal edges of sterna II–V with dense patches of microtrichia, tergum VI also with apical palisade fringe; terga without grooves for reception of elytral processes (as found near midline of at least tergum IV in Histeridae). Male terga VIII–X entire, IX apically emarginate for reception of X and produced anteroventrally into long slender lobes that are connate to one another at their anterior apices; sternum VIII deeply emarginate with densely setose lateral lobes, sternum IX present as elongate lightly sclerotized strip between anteroventral lobes of tergum IX. Aedeagus small, subcylindrical; phallobase (basal piece) short, U-shaped, symmetrical, forming a nearly complete ring; parameres long, nearly completely fused to one another and largely enclosing the slender median lobe. Female tergum VIII entire, IX divided longitudinally, X entire and situated between halves of IX, sternum VIII entire; ovipositor very long, consisting of paired valvifers and heavily sclerotized coxites, the latter each with a scoop-like outer surface and a small stylus on inner side; slender sclerotized rod of uncertain homology present ventrally between valvifers; spermatheca small, complex (Ôhara 1994: Fig. 40 G). [General reviews and illustrations of adult morphology of *Syntelia* can be found in Kryzhanovsky & Reichardt (1976) and especially Ôhara (1994), with further details in Forbes (1926; wing folding pattern) and Kukalová-Peck & Lawrence (1993; wing venation with modern terminology)]

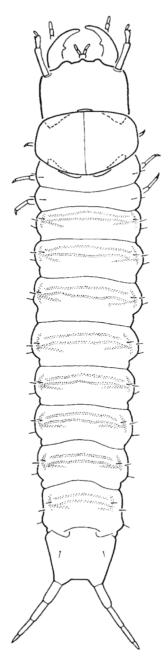

Fig. 13.3: *Syntelia histeroides* Lewis. Mature larva, dorsal view, length 16 mm (after Newton 1991, Fig. 34.306 a).

Morphology, Larvae (Fig. 13.3). Body elongate, parallel-sided, straight, moderately flattened; body surfaces very lightly pigmented and sclerotized, smooth, with sparse vestiture of simple or slightly truncate setae.

Head prognathous, protracted, well sclerotized and pigmented, without distinct neck. Dorsal ecdysial lines absent (instar 2) or with short stem and V-shaped frontal arms that end before antennal foramen (instar 1); endocarinae absent. Pigmented stemmata absent. Antenna 3-segmented, about half as long as head width, two sensoria of preapical segment conical, posterior to apical segment. Antennal insertion separated from mandibular insertion by narrow strip of membrane only. Labrum completely fused to head capsule to form nasale with rounded median projection. Mandibles symmetrical, narrow and falcate, apex with single tooth, mesal surface of base with penicillus or brush of hairs, mola absent. Cardo absent; stipes elongate; maxilla without apical lobes; maxillary palp 4-segmented, first segment with articulated digitiform appendage. Labium consisting of prementum; mentum (at sides) and submentum completely fused with ventral wall of head capsule; ligula absent; labial palps 2-segmented, separated by about width of first palpal segment. Venter of head about as long and well sclerotized as dorsum; gular sutures absent, but indistinct medial ecdysial line present (presumed ecdysial line by comparison with Histeridae). Occipital foramen not divided by tentorial bridge, which is indistinct or absent.

Thoracic terga without asperities; pronotum with large sclerotized plate, meso- and metanotum not well sclerotized. Legs short, 5-segmented including bisetose tarsungulus.

Abdomen 10-segmented, more than twice as long as thorax. Terga and sterna largely membranous, with two transverse rows of asperities on most segments.

Abdominal tergum I with pair of small teeth (egg bursters) in instar 1 only; tergum IX with pair of long 4-segmented urogomphi; segment X distinct but scarcely or not visible from above; anal region oriented posteroventrally, anal hooks absent. [Immature stages are known only for *S. histeroides*, whose larvae have been described by Mamaev (1974), Hayashi (1986) and Newton (1991), and nicely photographed by Zaitsev (2010). Evidently only two instars are present, as in Histeridae]

Eggs. Unknown.

Pupae. Exarate, apparently with functional abdominal spiracles on segments I or II to VI (Mamaev 1974).

Phylogeny and Taxonomy. Westwood (1864) originally placed his new genus *Syntelia* in what is now the cleroid family Trogossitidae, but Lewis (1882) established a new family Synteliidae for the genera *Syntelia* and *Sphaerites* and pointed out the close affinities of this new group to Histeridae. *Sphaerites* has been placed in its own family by most subsequent authors (see chapter on Sphaeritidae by Newton, this volume [**1–13.1**]), leaving Synteliidae monogeneric, but in all subsequent studies these three families have remained closely associated in their own group, Histeroidea, or placed together with Hydrophilidae *sensu lato* in an expanded concept of Hydrophiloidea (**1–12**). Synteliidae has been well supported as either the sistergroup to Histeridae or the sistergroup to (Histeridae + Sphaeritidae) in all recent phylogenetic studies, which are based on larval, adult and molecular data, with the exception of the morphological study of Lawrence *et al.* (2011) which placed it as sistergroup to Sphaeritidae. For more detailed discussion of these studies and their results see the chapters on Histeridae (Kovarik & Caterino, **1–13.3**) and Sphaeritidae (Newton, **1–13.1**) as well as Hansen (1997), Ślipiński & Mazur (1999), Beutel (1999) and Caterino & Vogler (2002). Possible adult synapomorphies of Synteliidae (some of these independently derived within certain Histeridae) include the loss of the epistomal suture, fusion of the labrum to the front of the head, and the externally closed procoxal cavities.

The nine known species of *Syntelia* fall into three distinct species groups:

(1) *S. mexicana* group (*S. mexicana* plus two new species from Mexico and Guatemala): mandibles usually with at least four distinct teeth along mesial edge; elytron with ten more or less complete punctate striae; prosternum with prominent median tubercle or bifid tubercle before coxae, not or indistinctly carinate before this; body dorsum between punctures smooth, shining.

(2) *S. indica* group (all five Asian species): mandibles usually with three distinct teeth along mesial edge; elytron with no more than five more or less complete punctate striae, some of them deeply impressed; prosternum more or less distinctly carinate along midline, without discrete tubercle before coxae; body dorsum between punctures smooth, shining.

(3) *S. westwoodi* group (*S. westwoodi* only): mandibles usually with three distinct teeth along mesial edge; elytron with only three more or less complete, finely impressed striae; prosternum with vague median tubercle before coxae and distinctly carinate along midline before that; body dorsum between punctures finely microsculpured, dull.

Phylogenetic relationships among these groups and the included species remain to be studied, although the more complete elytral striation of the *S. mexicana* group is probably plesiomorphic compared to the reduced striation in the other groups, and the extremely reduced elytral striation and unusual habitat association of *S. westwoodi* suggest these are uniquely derived conditions within the genus.

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13.3 Histeridae Gyllenhal, 1808

Distribution. Histerid beetles are found in all zoogeographic regions, and many taxa have a wide distribution. While the species of some genera such as *Margarinotus* Marseul, *Dendrophilus* Leach, and *Onthophilus* Leach are essentially confined to temperate regions, the greatest diversity occurs in tropical areas. The following list of taxa and their distribution is based primarily on Mazur (2011) and has been updated from then to 2014. Family-group names follow Bouchard *et al.* (2011). [Tishechkin 2003; Lackner 2009 b, 2011, 2012, 2013, 2014 a; Gomy 2010–2011, 2012, 2014; Gomy *et al.* 2011; Gomy & Vienna 2012; Tishechkin & Cárdenas 2012; Tishechkin & Lackner 2012; Dégallier *et al.* 2012; Caterino *et al.* 2012 a, b, 2014; Gomy & Warner 2013; Moura & Almeida 2013; Caterino & Tishechkin 2013 a, b, 2014, 2015; Vienna 2013; Vienna & Ratto 2013; Lackner & Gomy 2014; Lackner & Ratto 2014; Lackner & Tishechkin 2014].

Niponiinae: Palearctic and Oriental regions

Niponius Lewis, (21 spp.), Eastern Palearctic and Oriental regions.

Abraeinae: all regions

Abraeini: all regions

Abraeus Leach, 10 spp., central and western Palearctic with a single western Nearctic species, two New Zealand species, and one species inhabiting Guadeloupe; *Chaetabraeus* Portevin, 44 spp., mainly Afrotropical, Palearctic, and Oriental with 1 Nearctic and 2 Neotropical species; *Spelaeabraeus* Moro, 4 spp., Italy.

Acritini: all regions

Abaeletes Cooman, 2 spp., Vietnam, West Bengal, Nepal; *Acritodes* Cooman, 10 spp., Afrotropical and Oriental; *Acritus* J. L. LeConte, 118 spp., all regions; *Aeletes* Horn, 87 spp., all regions; *Aeletodes* Gomy, 1 sp., New Guinea; *Anophtaeletes* Olexa, 1 sp., Georgia; *Arizonacritus* Gomy & Warner, 1 sp., USA (Arizona, New Mexico), Mexico; *Iberacritus* Yélamos, 2 spp., Spain; *Halacritus* Schmidt, 24 spp., all regions; *Mascarenium* Gomy, 2 spp., Reunion; *Spelaeacritus* Jeannel, 1 sp., Turkey; *Therondus* Gomy, 2 spp., Zaire, Tanzania.

Acritomorphini: Oriental and Australasian regions

Acritomorphus Wenzel, 3 spp., Japan, Philippines, Australia.

Plegaderini: Afrotropical, Holarctic, and Neotropical Regions

Eubrachium Wollaston, 5 spp., southwestern Palearctic, Morocco, Canary Islands; *Phloeolister* Bickhardt, 5 spp., South Africa, Zimbabwe; *Plegaderus* Erichson, 28 spp., mainly Holarctic, with several species inhabiting the northern Neotropics.

Teretriini: all regions

Pleuroleptus G. Müller, 1 sp., southwestern Palearctic; *Teretriosoma* Horn, 9 spp., Neotropical and Nearctic; *Teretrius* Erichson, 76 spp., all regions; *Trypolister* Bickhardt, 1 sp., Brazil, French Guiana; *Xiphonotus* Lacordaire, 2 spp., South Africa, Madagascar.

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