ZooKeys 29: 49–71 (2009)
doi: 10.3897/zookeys.29.218
www.pensoftonline.net/zookeys

RESEARCH ARTICLE

A peer-reviewed open-access journal
ZooKeys
Launched to accelerate biodiversity research

A revision of the genus *Zyras (Zyras)* Stephens, 1835 (Coleoptera, Staphylinidae, Aleocharinae). I. Current classification status and the redefinition of the genus

Peter Hlaváč[1], Tomáš Jászay[2]

1 *Na doline 14, SK-040 14 Košice, Slovakia* **2** *Museum of Šariš, Natural History Department, Radničné nám. 13, SK-085 01 Bardejov, Slovakia*

Corresponding author: *Peter Hlaváč* (phlavac@stonline.sk)

Academic editor: *Jan Klimaszewski* | Received 25 October 2009 | Accepted 10 November 2009 | Published 11 December 2009

Citation: Hlaváč P, Jászay T (2009) A revision of the genus *Zyras (Zyras)* Stephens, 1835 (Coleoptera, Staphylinidae, Aleocharinae). I. Current classification status and the redefinition of the genus. Zookeys 29: 49–71. doi: 10.3897/zookeys.29.218

Abstract

The genus *Zyras* is redefined and redescribed based on the study of the type species *Zyras haworthi* (Stephens). Illustrations of all important morphological characters are provided. The status of the genus *Zyras* (s.l.) is discussed. A list of all species attributed to the subgenus *Z.* (*Zyras*), including the species described as *Zyras* (s.str.), is also given.

Keywords

Coleoptera, Staphylinidae, Aleocharinae, Lomechusini, *Zyras*, taxonomy, myrmecophily

Introduction

The Lomechusine genus *Zyras* Stephens, with currently 802 species and 54 subgenera (Hlaváč, Newton and Maruyama, in prep.), is certainly one of the largest and most problematic genera of the subfamily Aleocharinae. All species of the genus are believed to be free predators (synechtrans) of various species of ants. The taxonomic chaos in this genus is manifested by the fact that 122 species were described only as *Zyras* without any affilation to a subgenus. Another 68 species originaly described as *Zyras* were subsequently synonymyzed or transferred to different genera.

Until 2006, seven subgenera already have been raised to generic level, *Myrmoecia* (Mulsant & Rey) by Seevers (1978), *Aulacocephalonia* (Bernhauer) and *Homalodonia* (Bernhauer) by Kistner and Jacobson (1981), *Paramyrmoecia* (Scheerpeltz) by Kistner and Elliot (1985), *Macrogerodonia* (Bernhauer) and *Stichodonia* (Bernhauer) by Pace (1986a, 1999b) and *Trachydonia* (Bernhauer) by Kistner (1997). Maruyama (2006) revised the complex of subgenera *Pella* Stephens, *Lepla* Tottenham, *Pellochromonia* Reitter and *Myrmelia* Mulsant & Rey, in which he synonymyzed all these taxa with *Pella* and *Pella* was treated as a valid genus. Finally, Assing (2009) raised *Peltodonia* (Bernhauer) to the genus level. The genus *Razia* Blackwelder, 1952 (new name for *Allocota* Bernhauer, 1916; not to be confused with *Aloconota* Thomson, 1958) is now placed in the tribe Homalotini and it is a valid subgenus of *Gyrophaena* Mannerheim, 1830 (Newton and Thayer 2003).

As a consequence of these changes, the following 52 subgenera of the genus *Zyras* have remained valid (Hlaváč, Newton and Maruyama, in prep.): *Acanthocnemidonia* Bernhauer, *Acrothoraconia* Bernhauer, *Androdonia* Bernhauer, *Anophthalmodonia* Bernhauer, *Antronia* Bernhauer, *Aplastonia* Bernhauer, *Apostenonia* Bernhauer, *Apterygodonia* Scheerpeltz, *Aulacodonia* Bernhauer, *Botsa* Blackwelder, *Callodonia* Bernhauer, *Cameronodonia* Dvořák, *Camonia* Bernhauer, *Cephalodonia* Bernhauer, *Colpodonia* Bernhauer, *Craspa* Blackwelder, *Crateodonia* Bernhauer, *Ctenodonia* Wasmann, *Dentothalmonia* Last, *Diaulaconia* Bernhauer, *Euryalonia* Bernhauer, *Eurydonia* Bernhauer, *Euryncephalodonia* Scheerpeltz, *Euryndonia* Bernhauer, *Fealina* Bernhauer, *Glossacantha* Gemminger & Harold, *Grammodonia* Bernhauer, *Hylozyras* Iablokoff-Khnzorian, *Isothoracodonia* Bernhauer, *Lastia* Dvořák, *Leptodonia* Bernhauer, *Neotropopella* Scheerpeltz, *Pachydonia* Bernhauer, *Paragrammodonia* Bernhauer, *Parophthalmonia* Bernhauer, *Platydonia* Bernhauer, *Polydonia* Bernhauer, *Pycnodonia* Bernhauer, *Remionia* Blackwelder, *Rhopalodonia* Cameron, *Rocnema* Blackwelder, *Sinozyras* Pace, *Subversoris* Last, *Synthoracodonia* Scheerpeltz, *Taprodonia* Cameron, *Termidonia* Motschulsky, *Termitelia* Cameron, *Termitodonia* Cameron, *Trigonodonia* Bernhauer, *Trigonozyras* Cameron, *Tropidonia* Bernhauer, *Visendor* Last.

The logical question must be "Is it really possible that all these very numerous taxa, distributed worldwide, form a monophyletic group?" This question is not new and it has already been raised twice, first by Seevers (1965: 238) ["*The taxonomic state of the vast Zyras complex is one of great confusion and the proposal of more than 50 subgenera has not helped clarify matters very much*"] and later by Kistner (1972: 148) ["*Also each species alleged to Zyras (s. str.) in the literature will need to be checked before its inclusion in the redefined genus is settled. For example, I have not seen a species from sub-Saharan Africa which really belongs to this genus. It is highly likely that Zyras in the future will be a very small genus*"]. We fully agree with these two opinions, except for the number of species of true *Zyras,* which is anticipated to grow to at least 200 species.

The distribution of the genus seems to be mainly in the holarctic region with only three species in the USA and Canada (Klimaszewski et al. 2005), five species in the western Palaearctic region and a large number of species in eastern Palaearctic, Oriental and perhaps also in the Australian regions. We have not seen, like Kistner (1972),

any true *Zyras* from sub-Saharan Africa or from America south of USA. Of six species of *Zyras* reported by Ashe (Navarrete-Heredia et al. 2002) from Mexico, two species already have been transferred to another genus, *Pella fauveli* (Sharp) and *Myrmoecia tapinomatis* Mann (Klimaszewski et al. 2005). The remaining four species should be checked, but they, highly likely, will not be members of true *Zyras* either.

We are sure that many, if not all, species currently attributed to different subgenera of *Zyras*, have nothing or very little in common with the true *Zyras*. For the subgenera *Diaulaconia* (Hlaváč 2005: 153) and *Glossacantha* (Hlaváč 2005; Maruyama 2006, respectivelly) that has been already discussed, although the new status of both genera has not been officially changed. In our opinion, *Zyras* is a very characteristic and well defined genus, and any further fragmentation should be carefully re-considered.

The majority of subgenera, still attributed to *Zyras*, were very poorly defined mainly by Bernhauer [34 subgenera described in the period of 1928–1936, four were later renamed by Blackwelder (1952) and one is synonym], Cameron [six subgenera, one renamed later by Dvořák (1981)], Scheerpeltz (four subgenera in 1963–1976), Last [4 subgenera, one later renamed by Dvořák (1984)] and Wasmann (3 subgenera, one synonym) (Hlaváč, Newton and Maruyama, in prep.). Unfortunately even the final and most recent papers by Pace (1999a, 1999c) did not bring any light to the *Zyras* taxonomic problem.

Material and methods

The main goal of this article is to redefine the genus *Zyras* based on its type-species, *Zyras haworthi* (Stephens). The material used for this study was taken from some institutions listed below.

Specimens prepared for the morphological study were examined with Leica S8A-PO stereo-microscope and Nikon SMZ – 1B stereo-microscope with diffuse lighting at magnifications up to 105×. Male genitalia and other dissected parts were studied using a Meopta transmitted-light microscope at magnification up to 450×. Genital segments were dissected and treated with lactic acid. All drawings were made using a drawing tube. The dissected and mounted parts were mounted and pinned with the specimen.

Depository abbrevations

The material is deposited in following collections:

CMS Collection of Michael Schülke, Berlin, Germany;
CPH Collection of Peter Hlaváč, Košice, Slovakia;
CVA Collection of Volker Assing, Hannover, Germany;
NMW Naturhistorisches Museum (Harald Schilhammer), Vienna, Austria;
SDEI Senckenberg Deutsches Entomologisches Institut (Lothar Zerche), Germany;
SMB Šarišské Múzeum Bardejov (Tomáš Jászay), Slovakia.

Tribe Lomechusini Fleming, 1821

Genus *Zyras* Stephens, 1835

Zyras Stephens, 1835: 430. Type species: *Zyras haworthi* (Stephens), established by decision of the International Commission on Zoological Nomenclature (ICZN 1961, Opinion 599)

Zyras Stephens: Cameron, 1939: 497 (key to subgenera and species of India, Myanmar and Sri Lanka); Kistner 1972: 143 (redescription); Scheerpeltz 1974: 39 (key to African subgenera); Seevers 1978: 153 (key to Nearctic species); Dvořák 1980 (key to species of Czech and Slovak Republic, including *Pella, Lepla, Pellochromonia, Zyras, Myrmoecia*); Dvořák 1984: 200 (key to Palaearctic species including China); Hastir and Gaspar 2001 (biology); Klimaszewski et al. 2005: 714 (restricted redefinition, key to species of America north of Mexico).

Diagnosis. *Zyras* (*Zyras*) can be distinguished from the other genera of Lomechusini by a combination of the following characters: 1) whole body shiny, unicoloured or often with different colouration for head, pronotum, elytra and abdomen, sometimes covered with long setae; 2) all antennomeres petiolate, antennomere III about as long as pedicel; 3) neck absent; 4) pronotum usually with well-defined median antebasal fovea; 5) abdomen simple, not physogastric, parallel-sided; 6) simplified aedeagus, median lobe with enlarged basal capsule and narrowly conical apical lobe; 7) spermatheca sclerotized, very small with narrowly elongate capsule and with extremely long and highly coiled spermathecal duct.

Description. *Body* (Fig. 1) slender, subparallel-sided. Body length highly variable, ranging from 3–9 mm, whole body always shiny, unicoloured, or often with different colouration for head, pronotum, elytra and abdomen.

Head (Figs 2, 3) slightly wider than long, posterior margin slightly covered by anterior edge of pronotum, neck absent; temples long, round, about as long as diameter of eyes or longer; occipital suture present, not visible dorsally, ventrally reaching hypostoma, hypostoma narrow; surface with erect or appressed setae. Gula long, evenly divergent from anterior to posterior; submentum fused to gula, broadly expanded anteriorly. Eyes large, oval in lateral view, prominent.

Antennae (Fig. 4) with all antennomeres petiolate, antennomere III about as long as II, when bent backwards slightly exceeding base of pronotum.

Labrum (Fig. 5) much wider than long, with shallow median excavation; surface covered with numerous pseudopores and about ten real pores, except on posterior and lateral areas; antero-lateral areas each with 4–6 macrosetae of different length.

Mandibles (Figs 6–9) almost symmetrical, lacking teeth, with 3–4 small setae present dorsally, mesal areas of dorsal and ventral surfaces covered with numerous pseudopores, prostheca with inner margin pubescent.

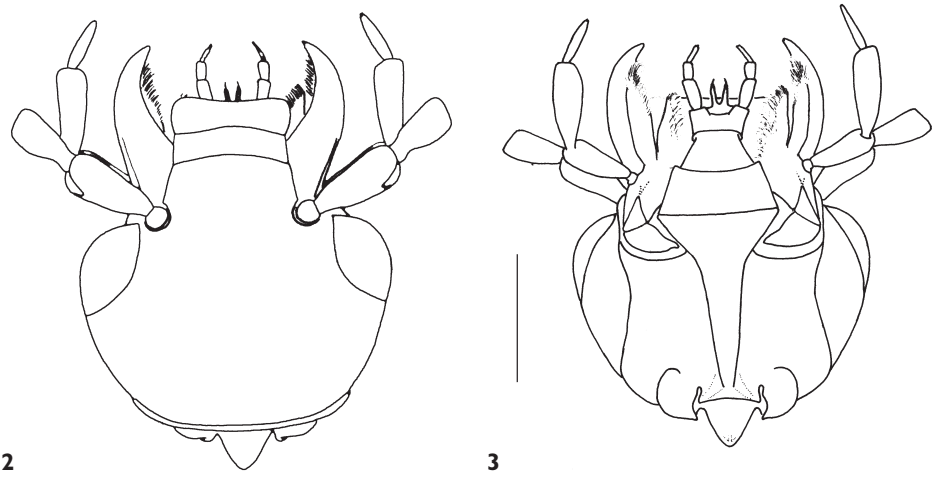
Maxilla (Fig. 10) is generalized in shape like for other Lomechusini, with elongate galea and shortened lacinia, palpomere I minuscule, palpomere II slightly curved and gently shorter that palpomere III, terminal palpomere about three times as short as III, pointed apically.

Figure 1. *Zyras (Zyras) haworthi* (Stephens), dorsal view (approximative length of photograped specimen is 7.1 mm)

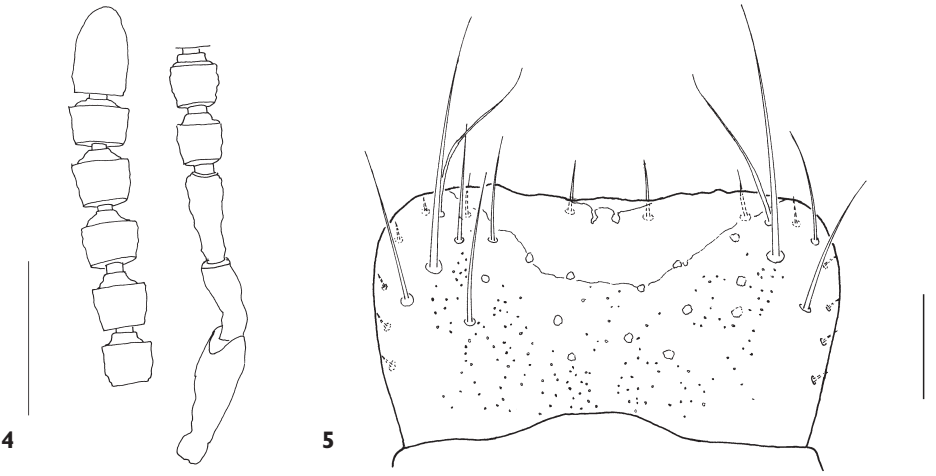
Mentum (Fig. 11) trapeziform, posterior and anterior margins truncate, with setae, surface covered with pseudopores bearing minute setae, and about 6–8 pores with longer setae present on antero-lateral areas.

Labium (Fig. 12) with prementum with two real pores and one setal pore mesolaterally, with about 30–40 pseudopores behind medial setae, apodeme with large, truncate process, lateral lobes of apodeme gently curved, assimetrical, bifurcate apicaly. Ligula bilobed, each lobe long, pointed apically, with fine apical seta. Labial palpus with first segment long, more than twice as long as second and clearly thicker, third segment slightly longer than second and about twice as slender as second.

Pronotum slightly wider than long (Fig. 1), anterior margin straight, posterior margin evenly rounded, posterior corners small but well-defined, smooth or entirely or



Figures 2–3. *Zyras (Zyras) haworthi* (Stephens). **2** head, dorsal aspect **3** head, ventral aspect (scale = 0.5mm)

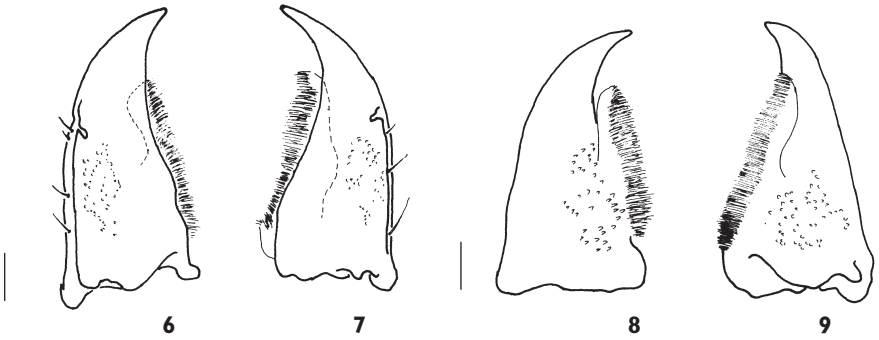


Figures 4–5. *Zyras (Zyras) haworthi* (Stephens). **4** antennae (scale = 0.5mm) **5** labrum, dorsal (scale = 0.1mm)

partially coarsely punctured and sparsely covered with erect long setae, macrosetae on lateral margins present, well-defined, median antebasal fovea usually present (may be missing in some species, for instance *Z. bakerianus*).

Elytra subparallel-sided (Fig. 1) with well-defined sutural groove throughout, combined width of elytra about twice as wide as long on suture, sutural striae well-defined through whole length. Scutellum triangular.

Mesoventrite (Figs 13, 14) much shorter than metaventrite, coarsely and densely punctured, setation only on sides, mesoventral process large, round. Mesocoxal cavities sepa-



Figures 6–9. *Zyras (Zyras) haworthi* (Stephens). **6** left mandible, dorsal aspect (scale = 0.1mm) **7** rigth mandible, dorsal aspect (scale = 0.1mm) **8** rigth mandible, ventral aspect (scale = 0.1mm) **9** left mandible, ventral aspect (scale = 0.1mm)

rated, isthmus wide but short. Metaventrite rectangular, slightly wider than long, shining, irregularly and coarsely punctured, with long erect setae, metaventral process truncate.

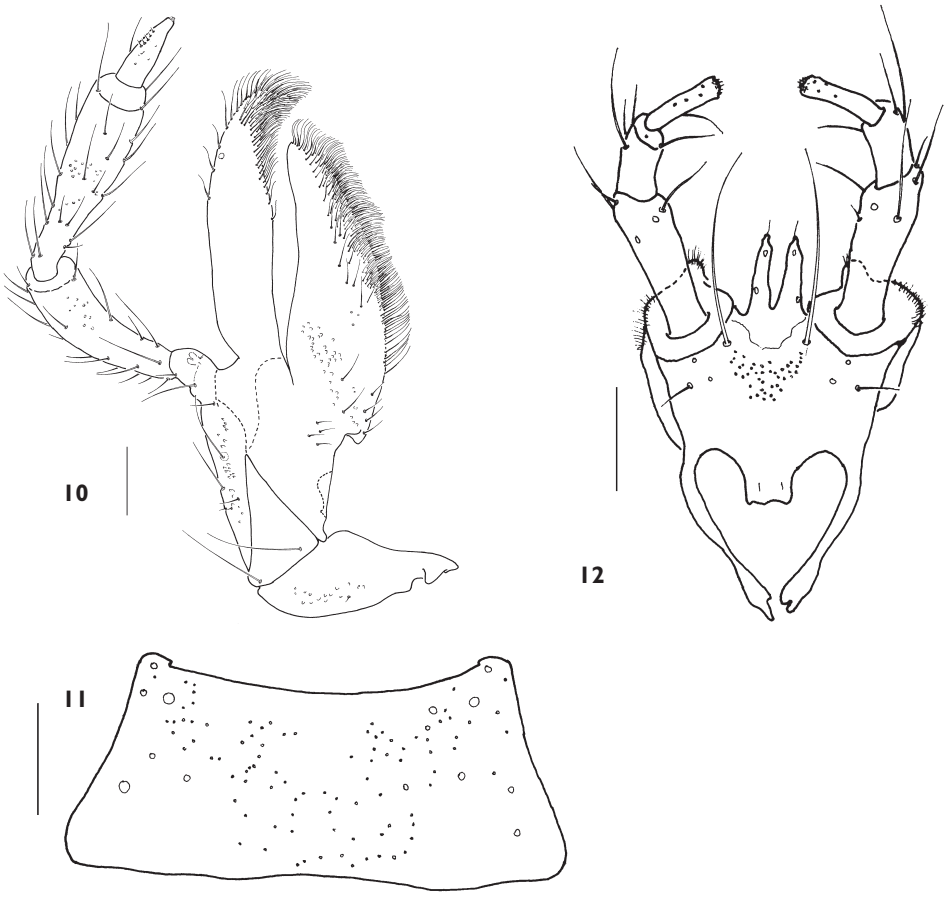
Legs (Kistner, 1972: 145, Fig. 3, B, C, D) with procoxae very long, only slightly shorter than profemur, mesocoxae suboval, metacoxae subtriangular; pro- and mesotrochanter small, metatrochanter slightly larger, rounded at apex; femora flattened, narrowest at base, with punctures and setation; all tibiae straight, very slightly dilated apicad, with dense setation, each apex with two stout setae; tarsal formula 4-5-5, tarsi generalised, metatarsus twice as long as protarsus.

Abdomen simple, not physogastric, parallel-sided, at base with punctures and with long setae on side; paratergites well-developed on tergites III–VII; tergites with posterior margin straight; sternite with surface moderately to densely covered with setae; eighth abdominal segment (Figs 15–18) species characteristic and also bearing sexual characters; tergite VIII (Figs 15, 17) narrowed posteriad, truncate apically, apex crenate or dentate, sternite VIII (Figs 16, 18) narrowed posteriad, at apex rounded in male and truncate in female, apical setae in female longer and thicker than in male. Ninth tergite as in (Figs 19, 20), lateral lobes in male asymmetric, absent in female as in most Aleocharines (Maruyama 2006). Ninth sternite of male as in (Figs 21, 22) elongate, somewhat pointed at base, expanded apicad and truncate at apex, with well-defined sharp corners, oblong in middle, bearing setae which are longer and dense on sides.

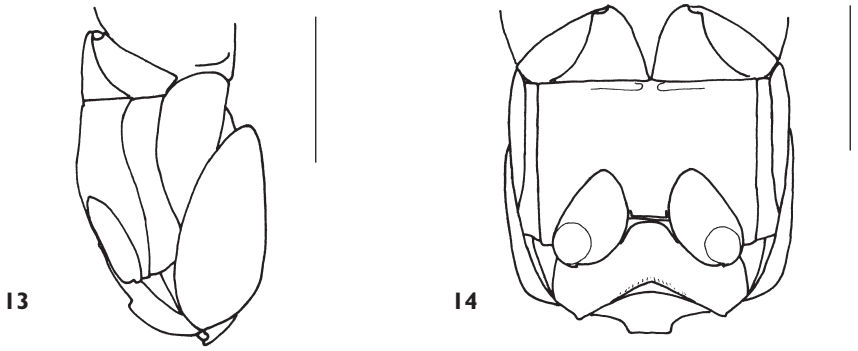
Aedeagus (Figs 23–25) simple, median lobe composed of enlarged basal capsule and narrowly conical apical lobe, copulatory piece weakly-defined or absent. Parameres (Fig. 26) long, clearly longer than apical lobe, composed of condylite, paramerite and velum, apical lobe of paramerite bears four macrosetae, apical lobe elongate, exceeding apex of velum.

Spermatheca (Fig. 26) sclerotized, very small with narrowly elongate capsule, capsule curved and slender apicad, with extremely long spermathecal duct, coiled many times forming a bundle.

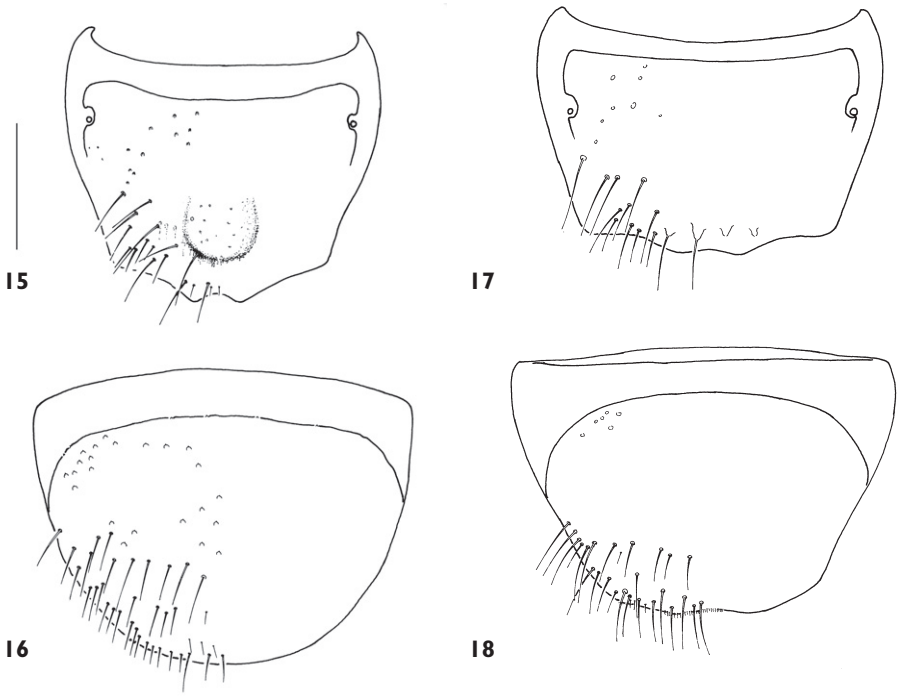
Biology. In general, it is believed that all species of *Zyras* (*Zyras*) are free living predators or synechtrans of different species of ants according to Wasmann's categori-



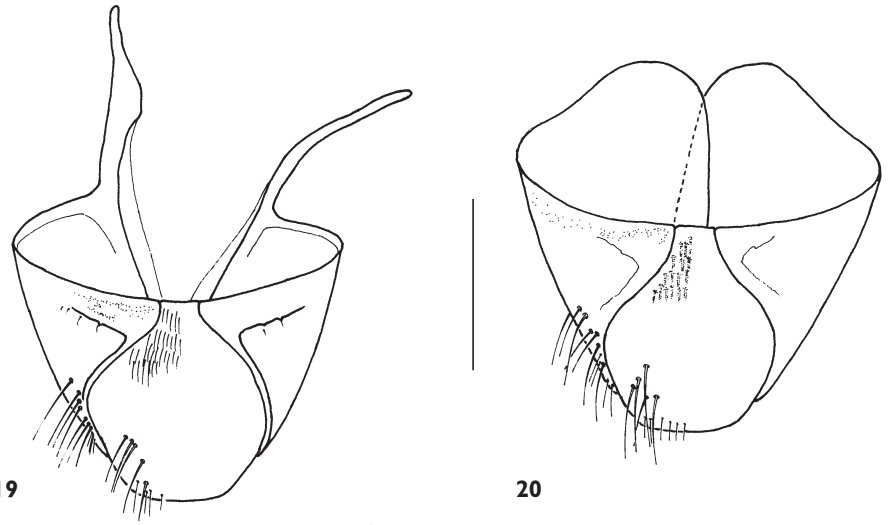
Figures 10–12. *Zyras (Zyras) haworthi* (Stephens). **12** maxilla (scale = 0.1mm) **11** mentum (scale = 0.1mm) **12** labium (scale = 0.1mm)



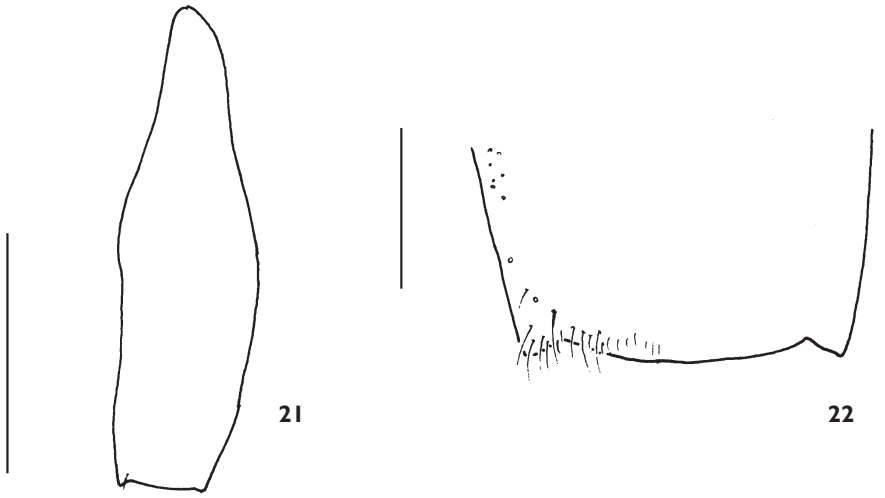
Figures 13–14. *Zyras (Zyras) haworthi* (Stephens). **13** metaventrite and mesoventrite lateral (scale = 1mm) **14** metaventrite and mesoventrite ventral (scale = 1mm)



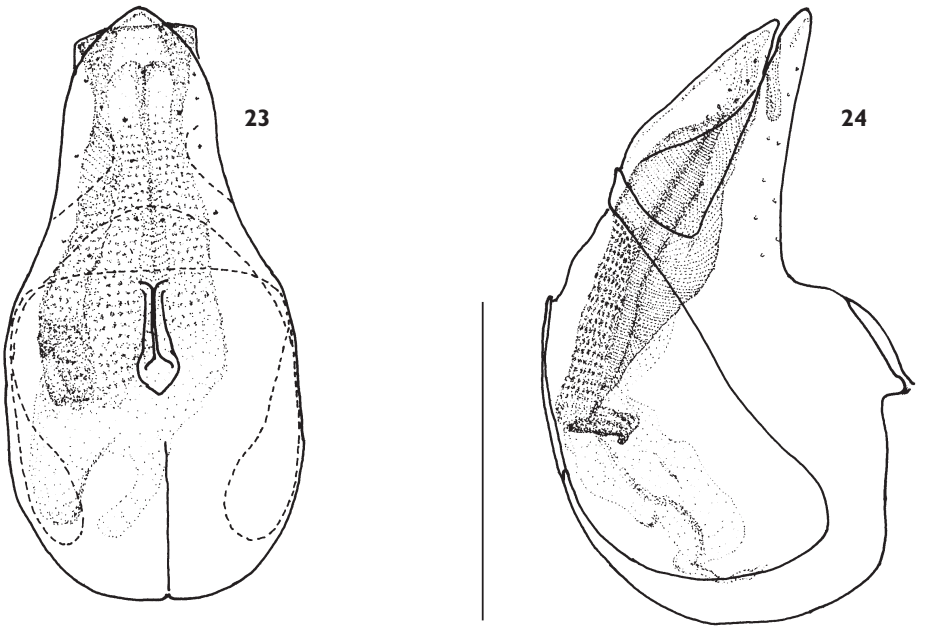
Figures 15–18. *Zyras (Zyras) haworthi* (Stephens). **15** tergite VIII male **16** sternite VIII male **17** tergite VIII female **18** sternite VIII female (scale = 0.5 mm)



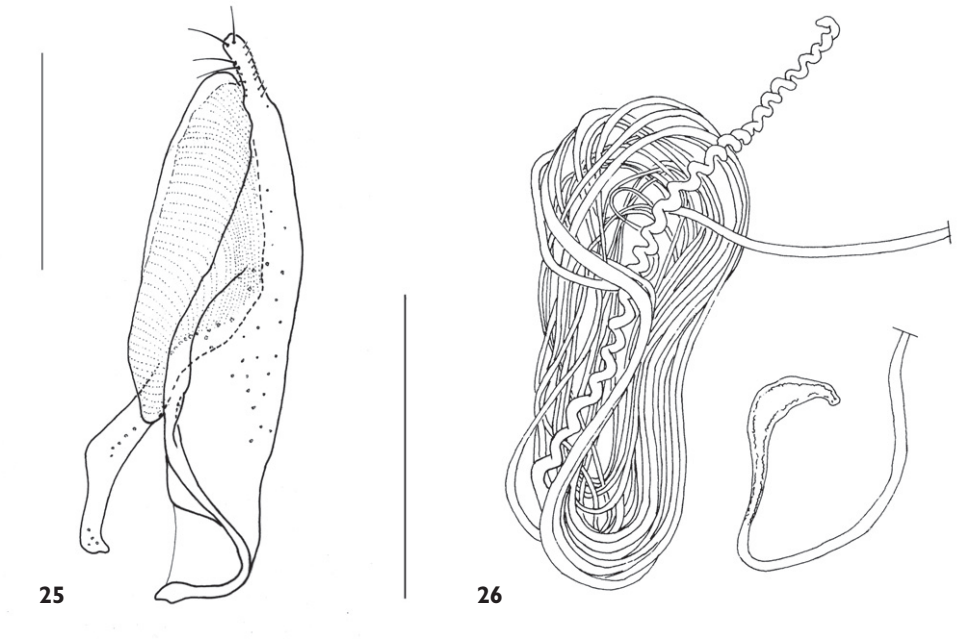
Figures 19–20. *Zyras (Zyras) haworthi* (Stephens). **19** tergites IX and X male (scale = 0.5 mm) **20** tergites IX and X female (scale = 0.5 mm)



Figures 21–22. *Zyras (Zyras) haworthi* (Stephens). **21** sternite IX male (scale = 0.5 mm) **22** apex of sternite IX male (scale = 0.1mm)



Figures 23–24. *Zyras (Zyras) haworthi* (Stephens). **23** aedeagus, ventral aspect **24** aedeagus, lateral aspect (scale = 0.5mm)



Figures 25–26. *Zyras (Zyras) haworthi* (Stephens). **25** paramera (scale = 0.5mm) **26** spermateca (scale = 0.5mm)

zation (Hölldobler and Wilson, 1990). However there is almost no clear evidence for this. Hastir and Gaspar (2001) showed that it is difficult to classify *Zyras haworthi* in any of Wasmann's categories. They have also shown that *Zyras haworthi* is more numerous in localities where *Formica sanguinea* Latreille is also present.

Distribution. Actually worldwide distributed, but most probably restricted to the Palearctic, Nearctic, Oriental and Australian regions (see discussion above, Introduction). However, due to current taxonomic problems of the genus, it is not possible to be more precise.

Zyras (Zyras) haworthi (Stephens)

Figures 1–26

Aleochara haworthi Stephens, 1832: 126. Type locality: Norfolk
Bolitochara elegans Heer, 1839: 350. Type locality: Helvetia
Zyras nigricollis Motschulsky, 1845: 41. Type locality: Tschougoueff, Russie méridionale

Material examined. **Austria:** 1 ♀: Austria, Mistelbach env., Eichenwald, 11.V.2002/M. Schülke (CMS); 1 ♂: Bisamberg near Vienna, 25.VII.10, coll. Künnemann (SDEI); 1 ♀: Steiermark, coll. Stierlin (SDEI); 1 ♂: Styria, Reitter, coll. Künnemann (SDEI). **Azerbaijan:** ♂: Kasp.Meer-Geb., Talysch, 1897, von Heyden (SDEI). **Bosnia and Hercegovina:** 3♂♂: Bjelašnica Plan., Gipfelregion, Bosn., 1902, coll. Leonhard (SDEI); 2♂♂:

Bosnia, 1902, Maklen-Pass, O. Leonhard (SDEI); 1 ♂: Herzegovina, Jablanica, 1901, O. Leonhard (SDEI). **Bulgaria:** 4♂♂, 3♀♀: NO Bulg., Senokos, 20km O Tolbuchin, 4.5.-19.6.1987, leg. Penev, *Querc. roboris* et *pedunculiflorae*, Barberfallen (SDEI); 1 ♀: Bulg., Or. Eminska Planina, Vlas, 10.V.1987, leg. Behne, Heinig, aus Laubschicht gesiebt unter *Quercus* und *Ulmus carpinifolia*, (CVA); 2♀♀: Bulg., Samokov, M. Hilf, 1911, Coll. O. Leonhard (SDEI); 1 ♀: NO Bulg., Srebarna, 20km Wsilistra, 17.6.-11.7.1987, leg. Penev (SDEI); 1 ♀: Bulg., Rila-Geb., 23.VII.1985, Musala, 2500 m, leg. Zerche (SDEI). **Czech Republic:** 3♂♂: Prag, Coll. Kraatz (SDEI); 1♀: Prag, Skalitz[ky], Coll. Weise (SDEI); 1♀: Prag, coll. Stierlin (SDEI); 1♀: Bohemia (SDEI); 1♂, 2♀♀: Prag, (Dieck), coll. von Heyden (SDEI); 2♀♀: Prag, Lokay, coll. von Heyden (SDEI); 1♂: Moravia, Coll. Koltze (SDEI); 3♂♂, 2♀♀: Prag, Coll. Koltze (SDEI); ♂: Slatz, Prag, Stussiner, Coll. Weise (SDEI); 1ex.: Paskau [= Paskov], V-95, coll. Koltze (SDEI). **Croatia:** 3ex.: Oestr [=Oesterreiches] Küstenland, Fužine, 1906, leg. M. Hilf, Coll. O. Leonhard (SDEI). **France:** 1♂: France, Alpes Maritimes, Col de Castillon, Südseite 350 m nördl. Monti, I. Wolf leg., 5.5.1996 (CMS); 1ex.(lacking last segments of abdomen): France, Midi Pyréneés, S/Ax les Thermes, Umg. L´Hospitalet, Ariege, 1300m, 21.VI.1999, leg. I. Wolf (CVA); 1♀: Francia, A. Marittime, Sospel, 1.VI.1999, 500m, leg. F. Angelini (CVA); 1♂: Corsica, 1905, Cervione, Coll. O. Leonhard, 21.7. (SDEI); 1♂, 1♀: Rhone, Cl. Rey, Coll. Leonhard (SDEI). **Germany:** 1♀: D-Niedersachsen, E Schladen, Hedeper, Westerberg, VI.2001, L. Schmidt (CVA); 1♀: D. Niedersachsen, Hildesheim-Ochter-Trillkegut, 10.VII.2001, Sprick (CVA); 1♂, 1♀: D. Sachsen-Anhalt, Stendal, Badingen, 24.VI.1993, Sprick (CVA); 1♂: Erzgebirge, Stollberg, Uhmann, 4.6.24 (SDEI); 1♂: Mark, Umgb., Oderberg, 29.V.27 (SDEI); 1♂: Erlang [=Erlangen], Coll. Kraatz (SDEI). **Italy:** 1♂: Italia, Lazio, Colli Albani, Commune Rocca di Papa, Monte Cava, 600–800m, 9.05.1998, leg. I. Wolf, (CMS); 1♀: Calabria-Orsomarso, Grisolia (CS), 11.IX.1993, 700m, leg. F. Angelini; 1♂, 1♀: Toscana, I. Elba, Cavo (LI), 15.5.1998, 250m, F. Angelini (CVA); 1♂, 1♀: Calabria, Sta. Eufemia, lg. Paganetti, coll. Franklin Műller (SDEI). **Macedonia:** 1♂: Skoplje, Mac., 25.VI.54, leg. F. Schubert (NMW). **Portugal:** 1♀: P-Algarve, 52, W Monchique, 554m, Rubus, 37°18'53N, 8°33'55W, 15.IV.2002, Meybohm (CVA); 1♀: P-Algarve, 46, Monchique, above road to Alferce, 591m, 37°19'20N, 8°31'52W, 10.IV.2002, Meybohm (CVA). **Poland:** 1♂: Liegnitz [=Legnica], Pfeil, coll. von Heyden (SDEI); 1♀: Schwdnitz [Schweidnitz = Świdnica], Letzner (SDEI); 1♀: Gerhardt, Liegnitz [= Legnica], Coll. Rottenberg, (SDEI); 1♂, 1♀: Mühlgast [near Wohlów.], Rottenberg (SDEI). **Romania:** 1♀: NE Romania, Negulesti, 25km SE Piatra Neamt, 500m, 18.vi.1996, P. Hlaváč lgt. (CPH); 1♂: Banat 1909, Herkulesbad, leg. M. Hilf, Coll. O. Leonhard (SDEI); 1♂: Banat 1909, Orsova, leg. M. Hilf, Coll. O. Leonhard, 7.VI. (SDEI). **Serbia:** 1♂: Serbia, Pirot env. Zvonce, banja Prskalo, 520m presev [sifting], above river, 28.IV.2002, lgt. T. Jászay (SMB). **Slovakia:** 1♂: Slovakia (Košice), Herľany env., sifting, 1.v.2004, P. Hlaváč lgt. (CPH); 1♂: Slovakia centr., Bacúch, 6.vii.1990, T. Lackner lgt. (CPH); 1♂: Pieniny-Poľana, zemné pasce [traps], 30.6.1989, leg. Svatoň (SMB); 1♂: Nová Bošáca, St. hora, 6.5.93, Majzlan lgt. (SMB); 1♂: Slovakia centr., Trenčín env., 24.6.99, O. Majzlan lgt. (SMB); 1♂: Parkan [= Štúrovo], Coll. Weise (SDEI). **Sloveni-**

ja: 1♀: Slo Zalog, 3.6.1996, Zg. Kašelj, B. Drovenik leg (CVA). **Spain:** 2♀♀: Spanien, Lugo, Sierra Ancares, 2.8.1984, leg. J. C. Otero (CVA). **Turkey:** 1♂: TR Mersin (33), road to Arslanköy, 5km SE Aladağ, 700m, 36°54'45N 34° 31'44E, leg. 10.5.2004 Brachat & Meybohm (CVA); 1♀: TR.-Mersin [51], road to Arslanköy, 5km SE Aladağ, 700m, 36°54'45N, 34° 31'44E, 10.V.2004, C. Besuchet (CVA); 1♀: TR Antakya 10, 400m, E Yeşilkent, 30.IV.2002, 36°57N, 36°15E, Meybohm & Brachat (CVA); 2♂♂: Ovacik, Tunceli, 1400m, Asm, F. Schubert, 6/76 (NMW).

Description. *Body* (Fig. 1) 5.5–7.0 mm long. Head and pronotum dark reddish-black, elytra reddish-brown, lateral part of apices of elytra with black spot, legs yellowish-brown, antennae yellowish-brown with antennomeres I–III lighter.

Head 1.15 times as wide as long, on sides with long erect golden setae. Antennae (Fig. 4) with scape almost twice as long as pedicel, pedicel slightly longer than antennomere III, antennomeres IV–VII about the same length, IV–VI slightly transverse, antennomeres VII-X rhombic, clearly extended apicad, X shortest, terminal antennomere about as long as antennomere III, almost twice as long as wide at base, round at apex.

Pronotum (Fig. 1) 1.25 times as wide as long and 1.28 times as long as head, irregularly punctured, setose and with about five long black macrosetae on each side.

Mesoventrite (Fig. 14) regularly, coarsely punctured on the whole surface. Metaventrite 1.5 times as wide as long and 3.5 times as long as mesoventrite (measured in mid line), smooth in the middle, coarsely punctured on sides, here also with erect golden setae.

Abdomen two-coloured, densely punctured apex of visible tergites III–V dark reddish-brown, base much lighter and bearing setae, tergites VI–VII dark reddish-brown almost on the whole surface, densely punctured at base and with few but long apical setae, paratergite III–VII well defined covered with setae, paratergites III–V punctured.

Sexual dimorphism: females have different structure of abdominal tergites and sternites VIII, IX and X (Figs 15–21). Tergite VIII with small median tubercle in male, tubercle lacking in female, truncate apex is much narrover in male than in female, median excavation deeper in male than in female; sternite VIII round in male, truncate in female; tergite IX with asymmetric lateral lobes in male, lateral lobes lacking in female.

Host ants. The following ant genera have been reported as hosts of *Zyras* (*Zyras*): *Formica* sp., *Lasius* (*Dendrolasius*) sp., *Liometopum* sp., *Myrmica* sp.

Distribution. Almost whole Europe, Armenia, Azerbaijan, Georgia, Russia, Algeria, Tunisia, Japan

Checklist of species of the subgenus *Zyras* (*Zyras*) (Stephens)

A detailed world catalogue of the tribe Lomechusini is near completion (Hlaváč, Newton and Maruyama, in. prep.). The purpose of this checklist is to provide a listing of all species which were described as, or placed subsequently in the subgenus *Zyras* (*Zyras*), or *Zyras* (s.str.). All species described as *Zyras* without subgeneric affilation are excluded from this list. The list is arranged by zoogeographical regions. This division is a practical solution for the better orientation within the genus.

Nearctic region:

This area includes America north of Mexico, i.e. USA and Canada. All three species listed here are true *Zyras* and were revised recently (Klimaszewski et al. 2005).

1. ***obliquus*** (Casey, 1894: 325) (*Myrmedonia*). Distribution: USA, Canada
   = *pseudohaworthi* Klimaszewski, 2002: 53
2. ***planifer*** (Casey, 1894: 326) (*Myrmedonia*). Distribution: USA
   = *schwarzi* Wasmann, 1894: 207 (*Myrmedonia*)
3. ***rudis*** (LeConte, 1866: 372) (*Myrmedonia*). Distribution: USA

West Palaearctic region:

This area, as defined here, includes the whole of Europe, northern Africa, Arabian peninsula, Caspian region and Siberia to Lake Baikal. All five species recorded here are true *Zyras*.

4. ***collaris*** (Paykull, 1789: 50) (*Staphylinus*). Distribution: Europe, Russia (European), Azerbaijan, Georgia, Algeria
5. ***cultus*** Last, 1960: 14. Distribution: Algeria, Eritrea, Angola
6. ***fulgidus*** (Gravenhorst, 1806: 163) (*Aleochara*). Distribution: Europe, Russia (European), Georgia, Iran, Near East
7. ***haworthi*** (Stephens, 1832: 126) (*Aleochara*). Distribution: Europe, Armenia, Azerbaijan, Georgia, Russia, Algeria, Tunisia, Japan
   = *elegans* (Heer, 1839: 350) (*Bolitochara*)
   = *nigricollis* Motschulsky, 1845: 41
8. ***maculipennis*** Gridelli, 1921: 87 (*Zyras fulgidus* var. *maculipennis*). Distribution: Caucasus, Kazachstan, Uzbekistan

East Palaearctic region:

This area includes Siberia east from Lake Baikal, Nepal, northern India, China, Taiwan, Koreas, Japan and Russia Far East. Currently there are 36 species described from this region and one *nomen nudum*.

9. ***abacus*** Dvořák, 1984: 194. Distribution: Kazakhstan, Kyrgyzstan
10. ***beijingensis*** Pace, 1993: 114. Distribution: China (Beijing)
11. ***britannorum*** Pace, 1992: 140. Distribution: Nepal
12. ***chinkiangensis*** Bernhauer, 1939: 148. Distribution: China (Jiangsu)
13. ***coloratus*** Cameron, 1939: 545 [*Zyras* (*Pella*)]. Distribution: India (Uttar Pradesh)

14. ***condignus*** Last, 1969: 279. Distribution: India (Uttar Pradesh), Nepal, Vietnam
= *distinctus* Cameron, 1939: 540, preoccupied, not *Zyras distinctus* Biering, 1937
15. ***cylindricornis*** Dvořák, 1981: 56. Distribution: Japan, Korea, China (Liaoning)
16. ***exasperatus*** Schubert, 1908: 610. Distribution: India (Himachal Pradesh)
17. ***fratrumkadooriorum*** Pace, 1998: 968. Distribution: China (Hong Kong)
18. ***fugax*** (Sharp, 1888): 289 (*Myrmedonia*). Distribution: Japan, Korea
19. ***gardneri*** Cameron, 1939: 538. Distribution: India (West Bengal)
20. ***hirsutiventris*** (Champion, 1927: 245) (*Myrmedonia*). Distribution: India (Uttar Pradesh), Nepal
21. ***hauserianus*** Bernhauer, 1933b: 46. Distribution: China (Xinjiang)
22. ***hongkongensis*** Pace, 1999a: 684. Distribution: China (Hong Kong)
23. ***championi*** Cameron, 1939: 537. Distribution: India (Himachal Pradesh)
24. ***illecebrosus*** Last, 1982: 81. Distribution: Mongolia
25. ***iridescens*** (Sawada, 1970: 49). (*Bolitochara*) Distribution: Japan
26. ***kraatzi*** Schubert, 1908: 609. Distribution: India (Himachal Pradesh, Uttar Pradesh), Nepal
= *ignicauda* (Champion, 1927: 245) (*Myrmedonia*)
27. ***manjushri*** Pace, 1992b: 142. Distribution: Nepal
28. ***morvani*** Pace, 1986b: 182. Distribution: Nepal
29. ***nigroaeneus*** Cameron, 1939: 543. Distribution: India (Himachal Pradesh)
30. ***notaticornis*** Pace, 1998: 971. Distribution: China (Hong Kong, Zheijang)
31. ***optatus*** (Sharp, 1888: 289) (*Myrmedonia*). Distribution: Japan
32. ***pallipes*** Pace, 1992: 140. Distribution: Nepal
33. ***particornis*** (Sharp, 1888: 290) (*Myrmedonia*). Distribution: Japan, Russia (Far East), Korea, China (Liaoning)
34. ***perforatus*** (Champion, 1921: 178) (*Myrmedonia*). Distribution: India (Sikkim/West Bengal, Uttar Pradesh), Nepal
35. ***pictus*** (Sharp, 1874: 11) (*Ilyobates*). Distribution: Japan, Korea
36. ***pindarae*** (Champion, 1921: 179 (*Myrmedonia*). Distribution: India (Uttar Pradesh), Nepal
37. ***restitutus*** Pace, 1993: 114. Distribution: China (Sichuan)
38. ***ruficauda*** Cameron, 1939: 543. Distribution: India (West Bengal), Nepal
39. ***seminigerrimus*** Bernhauer, 1933a: 54. Distribution: China (Sichuan)
40. ***shaanxiensis*** Pace, 1998: 971. Distribution: China (Shaanxi)
41. ***sibiricus*** Bernhauer, 1914: 68. Distribution: Russia: Siberia, Korea
42. ***song*** Pace, 1993: 112. Distribution: China (Yunnan)
43. ***songanus*** Pace, 1993: 114. Distribution: China (Beijing)
44. ***wei*** Pace, 1993: 114. Distribution: China (Guizhou)

The occurence of all species of *Zyras* (*Zyras*) from Asia is usually restricted to a rather small area, with the exception of *Zyras geminus* Kraatz, which is widely distrbiuted as reported in the literature.

45. ***geminus*** **(**Kraatz, 1859: 27) (*Myrmedonia*). Distribution: Sri Lanka, India, Indonesia (Java, Sumatra), Taiwan , Philippines, Japan (Iriomote Island)
sinorum Rougemont, 2001: 111. Distribution: China (Hong Kong), NOMEN NUDUM

Indochina:

This region includes southern Myanmar, Thailand, Cambodia, Vietnam and continental Malaysia. There are currently 21 species included.

46. ***alboantennatus*** Pace, 1986a: 460. Distribution: Myanmar
47. ***angkoricola*** Pace, 2004: 292. Distribution: Cambodia, Thailand
48. ***bartolozzii*** Pace, 2003: 68. Distribution: Malaysia (Malay peninsula)
49. ***benenensis*** Pace, 2001: 196. Distribution: Vietnam
50. ***birmanus*** Scheerpeltz, 1965: 350. Distribution: Myanmar
51. ***chumphonensis*** Pace, 2004: 292. Distribution: Thailand
52. ***drugmandi*** Pace, 2004: 293. Distribution: Thailand
53. ***ferrugineiventris*** Scheerpeltz, 1965: 349. Distribution: Myanmar
54. ***ferrugineus*** Cameron, 1939: 541. Distribution: Myanmar
55. ***fustigans*** Pace, 2000a: 77. Distribution: Thailand
56. ***glabricollis*** Scheerpeltz, 1965: 358. Distribution: Myanmar
57. ***kambaitiensis*** Scheerpeltz, 1965: 347. Distribution: Myanmar
58. ***malaisei*** Scheerpeltz, 1965: 345. Distribution: Myanmar
59. ***nitens*** Cameron, 1944: 108. Distribution: Malaysia (Malay peninsula)
60. ***pseudobirmanus*** Scheerpeltz, 1965: 351. Distribution: Myanmar
61. ***quasar*** Dvořák, 1996: 6. Distribution: Vietnam
62. ***semiasperatus*** Scheerpeltz, 1965: 353. Distribution: Myanmar
63. ***setosipennis*** Scheerpeltz, 1965: 356. Distribution: Myanmar
64. ***setosivestis*** Scheerpeltz, 1965: 354. Distribution: Myanmar
65. ***thaiorum*** Pace, 1986a: 460. Distribution: Thailand
66. ***variolatus*** Pace, 2003: 68. Distribution: Malaysia (Malay peninsula)

Asian tropical islands:

This region includes all Indonesia excluding Papua, Malaysia (Borneo: Sabah and Sarawak) and Philippines. There are 23 species described.

67. ***adulescens*** **(**Pace, 1987: 212) (*Drusilla*). Distribution: Malaysia (Borneo: Sabah)
68. ***alboterminalis*** Pace, 2008: 150. Distribution: Malaysia (Borneo: Sabah)
69. ***alternans*** (Cameron, 1925: 45) (*Myrmedonia*). Distribution: Indonesia (Sumatra)

70. ***bryanti*** Cameron, 1943b: 141. Distribution: Malaysia (Borneo: Sarawak)
71. ***daiaccorum*** Pace, 2008: 152. Distribution: Malaysia (Borneo: Sabah)
72. ***drescheri*** Cameron, 1939: 17. Distribution: Indonesia (Java)
73. ***elegantulus*** Cameron, 1939: 20. Distribution: Indonesia (Java)
74. ***facundus*** Last, 1969: 279. Distribution: Indonesia (Java)
= *semirufus* (Cameron, 1939: 18), preoccupied, not *Myrmedonia semirufa* Bernhauer, 1902
75. ***flavorufus*** Cameron, 1939: 18. Distribution: Indonesia (Java)
76. ***gratellus*** Cameron, 1939: 20. Distribution: Indonesia (Java)
77. ***kinabaluensis*** Pace, 2008: 148. Distribution: Malaysia (Borneo: Sabah)
78. ***louwerensi*** Cameron, 1939: 19. Distribution: Indonesia (Java)
79. ***matangensis*** Cameron, 1943b: 141. Distribution: Malaysia (Borneo: Sarawak)
80. ***montanus*** (Bernhauer, 1915: 152) (*Astilbus*). Distribution: Malaysia (Borneo: Sarawak)
81. ***mortuorum*** Pace, 1990: 99. Distribution: Philippines (Luzon)
82. ***nigerrimus*** Cameron, 1943b: 142. Distribution: Malaysia (Borneo: Sarawak)
83. ***paederinus*** Pace, 2008: 153. Distribution: Malaysia (Borneo: Sabah)
84. ***pallipyga*** Pace, 2008: 150. Distribution: Malaysia (Borneo: Sabah)
85. ***preangeranus*** Cameron, 1939: 17. Distribution: Indonesia (Java)
86. ***pervariolosus*** Pace, 2008: 150. Distribution: Malaysia (Borneo: Sabah)
87. ***punctipennis*** Cameron, 1939: 18. Distribution: Indonesia (Java)
88. ***quadriterminalis*** Pace, 2008: 149. Distribution: Malaysiad (Borneo: Sabah)
89. ***shiva*** Pace, 1987: 216. Distribution: Indonesia (Lombok, Bali)

Southern India and Sri Lanka:

This region includes India south from Himalayan region and Sri Lanka. There are 9 species included.

90. ***castaneus*** (Motschulsky, 1861: 150) (*Myrmedonia*). Distribution: Sri Lanka
91. ***hastatus*** Fauvel, 1904: 64. Distribution: India (Karnataka)
92. ***hirtus*** (Kraatz, 1859: 25) (*Myrmedonia*). Distribution: Sri Lanka, Taiwan
93. ***indicus*** Cameron, 1944: 108. Distribution: India (Karnataka)
94. ***parageminus*** Pace, 1988: 335. Distribution: Sri Lanka
95. ***rufescens*** Cameron, 1939: 534. Distribution: Sri Lanka
96. ***nilgiriensis*** Cameron, 1939: 537. Distribution: India (Tamil Nadu)
97. ***optimus*** Cameron, 1939: 534. Distribution: India (Tamil Nadu)
98. ***proximus*** Cameron, 1939: 538. (*Zyras* (s.str.), TL: Nilgiri Hills) Distribution: India (Tamil Nadu)

Afrotropical region and temperate South Africa:

This region includes sub-Saharan Africa and the Republic of South Africa. All species attributed today to the true *Zyras* were described by Horace Last (1956, 1960, 1962, 1977, 1980) and Roberto Pace (1996). We suspect that these African species are not true *Zyras* and belong to other subgenera.

99. ***basilewskyi*** Last, 1956: 219. Distribution: Rwanda, Cameroon, Burundi, Ghana, Dem. Rep. Congo
100. ***bonus*** Last, 1977a: 947. Distribution: Dem. Rep. Congo
101. ***bramtonus*** Last, 1962: 222. Distribution: Senegal, Ghana, Dem. Rep. Congo
102. ***conjectus*** Last, 1960: 12. Distribution: Gabon, Spanish Guinea, Angola
103. ***flavipennis*** Last, 1956: 218. Distribution: Burundi, Ghana, Nigeria, Rwanda, Dem. Rep. Congo
104. ***mutarensis*** Pace, 1996: 231. Distribution: Zimbabwe
105. ***nakuruensis*** Pace, 1996: 231. Distribution: Kenya
106. ***nigritus*** Last, 1980: 176. Distribution: Rep. South Africa (Cape, Natal)
107. ***planctos*** Last, 1977b: 81. Distribution: Ghana
108. ***punctus*** Last, 1967: 109. Distribution: Angola, Burkina Faso, Nigeria, Dem. Rep. Congo
= *punctus* var**.** *croceus* Last, 1967: 110
109. ***tambachensis*** Pace, 1996: 228. Distribution: Kenya

Australian region:

Australia plus New Zealand, New Guinea and New Caledonia. There are only three species known from this region.

110. ***biroi*** Last, 1980: 161. Distribution: New Guinea
= *biroi* var. *subflavus* Last, 1980: 161
111. ***hirsutus*** Cameron, 1943a: 353. Distribution: Australia (Victoria)
112. ***papuanus*** Pace, 2000b: 159. Distribution: Papua New Guinea

Neotropical region:

Mexico, Central and South America (including Caribbean islands). There are two species from this vast area known today. We believe that true *Zyras* do not occur in Neotropics and both species probably belong to other genera of Lomechusini.

113. ***distinctus*** Bierig, 1937: 281. Distribution: Cuba
114. ***paecesanus*** Pace, 1997: 36. Distribution: Colombia

References

Assing V (2009) New species and additional records of Lomechusini from the Palaearctic region (Coleoptera: Staphylinidae: Aleocharinae). Stuttgarter Beiträge zur Naturkunde Serie A, Neue Serie 2: 201–226.

Bernhauer M (1914) Neue Staphyliniden der paläarktischen Fauna. Coleopterologische Rundschau 4: 65–68.

Bernhauer M (1915) Neue Staphyliniden der indo-malaiischen Fauna, insbesondere der Sunda-Insel Borneo (9. Beitrag). Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien 65: 134–158.

Bernhauer M (1928 (1926)) Zur Kenntnis der Staphyliniden-Gattung *Zyras* Steph. (17. Beitrag zur Staphylinidenfauna Afrikas). Archiv für Naturgeschichte 92 (A) (7): 19–75.

Bernhauer M (1933a) Neues aus der Staphylinidenfauna China's. Entomologisches Nachrichtenblatt [Troppau] 7: 39–54.

Bernhauer M (1933b) Neuheiten der chinesischen Staphylinidenfauna. Wiener Entomologische Zeitung 50: 25–48.

Bernhauer M (1939 (1938)) Zur Staphylinidenfauna von China und Japan (11. Beitrag). Entomologisches Nachrichtsblatt [Troppau] 12: 145–158.

Bierig A (1937) Algunos nuevos estafilinidos (Col. Staph.) Cubanos. Memorias de la Sociedad Cubana de Historia Natural "Felipe Poey" 11: 273–283.

Blackwelder RE (1952) The generic names of the beetle family Staphylinidae, with an essay on genotypy. Bulletin of the United States National Museum 200: 483.

Cameron M (1939) Coleoptera, Staphylinidae. In: Sewwll RBS (Ed) Fauna of British India, including Ceylon and Burma, Vol. IV, parts I & II. Taylor & Francis, London, 59–61.

Cameron M (1925) Descriptions of new species of oriental Staphylinidae. Annali del Museo Civico di Storia Naturale di Genova 52: 34–49.

Cameron M (1939) Fauna Javanica. The Staphylinidae collected by Mr. F. C. Drescher. Part III. Tijdschrift voor Entomologie 82: 1–29.

Cameron M (1943a) New species of Staphylinidae (Col.) from Australia and New Guinea. Annals and Magazine of Natural History (11) 10: 336–354.

Cameron M (1943b) New species of Staphylinidae (Col.) from Borneo. Entomologist's Monthly Magazine 79: 39–42, 139–143, 183.

Cameron M (1944) Descriptions of new Staphylinidae (Coleoptera). Proceedings of the Royal Entomological Society of London (B) 13: 11–15, 49–52, 104–108.

Champion GC (1921) Some Indian Coleoptera (6). Entomologist's Monthly Magazine 57: 177–184, 201–206.

Champion GC (1927) Some Indian Coleoptera (23). Entomologist's Monthly Magazine 63: 245–250.

Casey TL (1894 (1893)) Coleopterological notices, V. Annals of the New York Academy of Sciences 7: 281–606, pl. 1.

Dvořák M (1980) Československé druhy rodu *Zyras* Stephens (Col. Staphylinidae). Entomologické Problémy 16: 93–98.

Dvořák M (1981) Zwei neue ostasiatische Arten und nomenklatorische Bemerkungen zur Gattung *Zyras* (Coleoptera, Staphylinidae). Acta Entomologica Bohemoslovaca 78: 53–60.

Dvořák M (1984) Zur Kenntnis einiger myrmekophiler Staphylinidae Coleoptera). Acta Entomologica Bohemoslovaca 81: 190–203.

Dvořák M (1996) Einigen neue myrmekophile oder termitophile Arten des Tribus Zyrasini aus Südasien (Coleoptera, Staphylinidae, Aleocharinae). Coleoptera, Schwanfelder Coleopterologische Mitteilungen 23: 1–15.

Fauvel A (1904) Staphylinides de l'Hindoustan et de la Birmanie. Revue d'Entomologie 23: 43–70.

Gravenhorst JLC (1806) Monographia Coleopterorum Micropterorum. H. Dieterich, Gottingae [Göttingen]. 248 pp.

Gridelli E (1921) Beitrag zur Kenntnis der palaearktischen Staphyliniden. Koleopterologische Rundschau 9: 87.

Hastir P, Gaspar Ch (2001) La myrmécophilie chez les Staphylinidae: la cohabitation de *Zyras haworthi* Stephens et de *Formica sanguinea* Latreille. Notes faunistiques de Gembloux, 43: 17–26.

Heer O (1839) Fauna coleopterorum Helvetica. Pars I, fasc. 2. Orelii, Fuesslini et Sociorum, Turici [Zurich], 145–360.

Hlaváč P (2005) Notes on *Zyras* (*Diaulaconia*) *orientalis* Bernhauer (Coleoptera: Staphylinidae: Aleocharinae), with description of a new species from Hong Kong. Klapalekiana, 41(3–4): 151–155.

Hlaváč P, Newton AF, Maruyama M (in prep.) The world catalogue of the tribe Lomechusini (Staphylinidae, Aleocharinae).

Hölldobler B, Wilson EO (1990) The Ants. Springer, Berlin, 732 pp.

Kistner DH (1972) Studies of Japanese myrmecophiles. Part I: The genera *Pella* and *Falagria* (Coleoptera, Staphylinidae). In: Entomological Essays to Commemorate the Retirement of Professor K. Yasumatsu, Hokurynken, Tokio 141–165.

Kistner DH (1997) In: Kistner DH, Weissflog A, Rosciśzewski K, Maschwitz U (1997) New species, new genera, and new records of myrmecophiles associated with army ants (Aenictus sp.) with the description of a new subtribe of Staphylinidae (Coleoptera: Formicidae: Aenictinae). Sociobiology 29(2): 123–221.

Kistner DH, Elliott DE (1985) A revision of the genus *Paramyrmoecia* with the description of a new species (Coleoptera: Staphylinidae). Entomologica Scandinavica 16: 311–320.

Kistner DH, Jacobson HR (1981) A revision of the genera *Creodonia* and *Aulacocephalonia*, with notes on their behavior and relationships (Coleoptera: Staphylinidae). Sociobiology 6 (1): 61–100.

Klimaszewski J (2002) In: Klimaszewski J, Winchester NN. Aleocharine rove beetles (Coleoptera Staphylinidae) of the ancient Sitka spruce forest on Vancouver Island, British Columbia, Canada. Mémoires de la Société Royale Belge d'Entomologie 40: 3–126.

Klimaszewski J, Pelletier G, Maruyama M, Hlaváč P (2005) Canadian species of the *Zyras* group of genera and review of the types from America north of Mexico. Revue Suisse de Zoologie 112(3): 703–733.

Kraatz G (1859) Die Staphylinen-Fauna von Ostindien, insbesondere der Insel Ceylan. Archiv für Naturgeschichte 25 (1): 1–193, pls. 1–3.

Last HR (1956) Coleoptera Staphylinidae: The genus *Zyras* and allies. In: Contributions à l'étude de la faune entomologique du Ruanda-Urundi (Mission P. Basilewsky 1953), LXXXVI. Annales du Musée Royal du Congo Belge, Tervuren (Série 8º: Sciences Zoologiques) 51: 201–220.

Last HR (1960) New species of *Zyras* (Col. Staphylinidae) from Africa. Bulletin de l'Institut Royal des Sciences Naturelles de Belgique 36 (46): 1–16.

Last HR (1962 (1961)) Coleoptera Staphylinidae, genus *Zyras*. In: Le Parc National du Niokolo-Koba (deuxième fascicule). Mémoires de l'Institut Français d'Afrique Noire 62: 219–224.

Last HR (1967) *Zyras* Stephens, and allied genera (Col. Staphylinidae) from Angola. Publicações Culturais da Companhia de Diamantes de Angola 76: 85–117.

Last HR (1969 (1968)) Changes in the nomenclature of the genus *Zyras* Stephens (Col., Staphylinidae). Entomologist's Monthly Magazine 105: 279.

Last HR (1977a) New species of *Zyras* from Africa (Coleoptera Staphylinidae). Revue de Zoologie Africaine 91: 913–954.

Last HR (1977b) The *Zyras* Stephens and related genera from Ghana (Coleoptera, Staphylinidae) II. Folia Entomologica Hungarica (N.S.) 30 (1): 77–83.

Last HR (1980) Notes and changes in nomenclature of the African species of the genus *Zyras* Stephens (Coleoptera Staphylinidae). Revue de Zoologie Africaine 94: 160–182.

Last HR (1982) New species of *Zyras* from Mongolia (Coleoptera: Staphylinidae). Acta Zoologica Academiae Scientiarum Hungaricae 28 (1–2): 81–82.

LeConte JL (1866) Additions to the coleopterous fauna of the United States. No. 1. Proceedings of the Academy of Natural Sciences of Philadelphia 1866: 361–394.

Maruyama M (2006) Revision of the Palearctic species of the myrmecophilous genus *Pella* (Coleoptera, Staphylinidae, Aleocharinae). National Science Museums Monographs No. 32: 1–207.

Motschulsky V (1845) Remarques sur la collection de Coléoptères russes de Victor de Motschoulsky. Bulletin de la Société Impériale des Naturalistes de Moscou 18 (1 & 2): 3–127, pls. 1–3; errata, p. 549

Motschulsky V (1861) Essai d'un catalogue des insectes de l'ile Ceylan. 1-ière livraison. Bulletin de la Société Impériale des Naturalistes de Moscou 34 (Première partie): 95–155, 1 pl.

Navarrete-Heredia JL, Newton AF, Thayer MK, Ashe JS, Chandler DS (2002) Guía ilustrada para los géneros de Staphylinidae (Coleoptera) de México. Illustrated guide to the genera of Staphylinidae (Coleoptera) of Mexico. Universidad de Guadalajara & CONABIO, México. 401 pp.

Newton AF, Thayer MK (2003) Catalog of higher taxa of Staphyliniformia and genera and subgenera of Staphylinoidea [online]. Chicago: Field Museum of Natural History. http://www.fieldmuseum.org/peet_staph/db_1a.html [last updated 14 October 2003].

Pace R (1986a) Aleocharinae del Perù (Coleoptera, Staphylinidae). Redia 69: 417–467.

Pace R (1986b (1985)) Aleocharinae dell'Himalaya raccolte da Guillaume de Rougemont (Coleoptera Staphylinidae). Bollettino del Museo Civico di Storia Naturale di Verona 12: 165–191.

Pace R (1986c (1984)) Aleocharinae della Thailandia e della Birmania riportate da G. de Rougemont (Coleoptera, Staphylinidae). Bollettino del Museo Civico di Storia Naturale di Verona 11: 427–468.

Pace R (1987 (1986)) Aleocharinae dell'Asia sudorientale raccolte da G. de Rougemont (Coleoptera, Staphylinidae). Bollettino del Museo Civico di Storia Naturale di Verona 13: 139–237.

Pace R (1988 (1987)) Aleocharinae dello Sri Lanka raccolte da Marc Tronquet (Coleoptera Staphylinidae). Bollettino del Museo Civico di Storia Naturale di Verona 14: 315–338.

Pace R (1990) Aleocharinae delle Filippine. 82º contributo alla conoscenza delle Aleocharinae. In: Berti N (Ed), Miscellanées sur les Staphylins. Mémoires du Muséum National d'Histoire Naturelle (A: Zoologie) 147: 57–113.

Pace R (1992) Aleocharinae nepalesi del Museo di Ginevra. Parte VI: Myrmedoniini (Coleoptera, Staphylinidae). Revue Suisse de Zoologie 99 (1): 125–145.

Pace R (1993 (1990)) Aleocharinae della Cina (Coleoptera, Staphylinidae). Bollettino del Museo Civico di Storia Naturale di Verona 17: 69–125.

Pace R (1996) Aleocharinae della sottoregione Africana Orientale al Museo di Ginevra (Coleoptera Staphylinidae) Parte III (conclusione). Revue Suisse de Zoologie 103 (1): 195–258.

Pace R (1997) Aleocharinae della Colombia e dell'Ecuador: Parte III (conclusione) (Coleoptera, Staphylinidae). Revue Suisse de Zoologie 104: 17–48.

Pace R (1998) Aleocharinae della Cina: Parte IV (Coleoptera, Staphylinidae). Revue Suisse de Zoologie 105: 911–982.

Pace R (1999a) Aleocharinae di Hong Kong (Coleoptera, Staphylinidae). Revue Suisse de Zoologie 106: 663–689.

Pace R (1999b) Aleocharinae della Namibia raccolte dalla spedizione entomologica "Namibia 1992" del Museo di Storia Naturale di Berlino (Coleoptera Staphylinidae). Memorie della Società Entomologica Italiana 77: 161–212.

Pace R (1999c) Faune de Madagascar, 89. Insectes Coléoptères: Staphylinidae Aleocharinae. Faune de Madagascar, Paris. 261 pp.

Pace R (2000a (1999)). Aleocharinae della Thailandia (Coleoptera, Staphylinidae). Bollettino del Museo Regionale di Scienze Naturali, Torino 17: 39–86.

Pace R (2000b) Aleocharinae di Papua-Nuova Guinea (Coleoptera, Staphylinidae) (156° contributo alla conoscenza delle Aleocharinae). Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Entomologie 70: 109–163.

Pace R (2001) Aleocharinae aus Vietnam in der Sammlung des Naturkundemuseums Erfurt (Coleoptera, Staphylinidae). Veröffentlichungen des Naturkundemuseums Erfurt 20: 193–200.

Pace R (2003) Aleocharinae della Penisola di Malacca (Malaysia) (Coleoptera, Staphylinidae). Bollettino del Museo Regionale di Scienze Naturali, Torino 20 (1): 33–78.

Pace R (2004) Aleocharinae di Thailandia, Cambogia, Laos e Malaysia (Coleoptera, Staphylinidae). Belgian Journal of Entomology 6 (2): 243–302.

Pace R (2008) Generi e specie della tribù Lomechusini del Borneo (Coleoptera, Staphylinidae). Revue Suisse de Zoologie 115 (1): 107–156.

Paykull G (1789) Monographia Staphylinorum Sveciae. J. Edman, Upsaliae [Uppsala]. 8 + 81 pp.

Rougemont GM de (2001) The staphylinid beetles of Hong Kong: Annotated check list, historical review, bionomics and faunistics (44th contribution to the knowledge of Staphylinidae). Memoirs of the Hong Kong Natural History Society 24: 1–146.

Sawada K (1970) Aleocharinae (Staphylinidae, Coleoptera) of the IBP-Station in the Shiga Heights, Central Japan, II. Contributions from the Biological Laboratory, Kyoto University 23 (1): 33–60.

Seevers CH (1965) The systematics, evolution and zoogeography of staphylinid beetles associated with army ants (Coleoptera, Staphylinidae). Fieldiana: Zoology 47: 139–351.

Seevers CH (1978) A generic and tribal revision of the North American Aleocharinae (Coleoptera: Staphylinidae). Fieldiana: Zoology 71: 275 pp.

Scheerpeltz O (1974) Coleoptera aus Nordostafrika, Staphylinidae. Acta Entomologica Fennica 31: 1–49.

Schubert K (1908) Beitrag zur Staphylinidenfauna Ostindiens (West-Himalaya) (Col.). Deutsche Entomologische Zeitschrift 1908: 609–625.

Sharp D (1874) The Staphylinidae of Japan. Transactions of the Entomological Society of London 1874: 1–101.

Sharp D (1888) The Staphylinidae of Japan. Annals and Magazine of Natural History (6) 2: 277–295.

Stephens JF (1832) Illustrations of British entomology, or a synopsis of indigenous insects, containing their generic and specific distinctions, with an account of their metamorphoses, times of appearance, localities, food, and economy, as far as practicable. Mandibulata, Vol. 5. Baldwin & Cradock, London. pp. 1–240, pls. 24–26.

Stephens JF (1835) Illustrations of British entomology, or a synopsis of indigenous insects, containing their generic and specific distinctions, with an account of their metamorphoses, times of appearance, localities, food, and economy, as far as practicable. Mandibulata, Vol. 5. Baldwin & Cradock, London. pp. 369–477.

Wasmann E (1894) Kritisches Verzeichniss der Myrmekophilen und Termitophilen Arthropoden. Mit Angabe der Lebensweise und mit Beschreibung neuer Arten. F. L. Dames, Berlin. xiii + 231 pp.