On *Zyras* sensu strictu in the East Palaearctic and Oriental regions, with a focus on the faunas of the Himalaya, India, Sri Lanka, Thailand, and Sulawesi (Coleoptera: Staphylinidae: Aleocharinae: Lomechusini)

With 277 figures, 10 maps, 2 keys and 1 table

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**Abstract**

The species of the nominal subgenus of the lomechusine genus *Zyras* Stephens, 1835 of the Himalaya, India, Sri Lanka, and Sulawesi are revised. Additional species from other parts of the East Palaearctic and Oriental regions are addressed. In all, 40 species are described and/or illustrated, 14 of them for the first time: *Zyras* (*Zyras*) *ambulans* spec. nov. (Thailand), *Z. (*Zyras*) *brevilobatus* spec. nov. (Thailand), *Z. (*Zyras*) *densihirtus* spec. nov. (Sulawesi Utara), *Z. (*Zyras*) *densissimus* spec. nov. (Sulawesi Utara), *Z. (*Zyras*) *latilobatus* spec. nov. (South India), *Z. (*Zyras*) *longilobatus* spec. nov. (India: Meghalaya), *Z. (*Zyras*) *luteipes* spec. nov. (India: Meghalaya), *Z. (*Zyras*) *morulus* spec. nov. (Nepal: Dhaulagiri, Annapurna), *Z. (*Zyras*) *nigrihirtus* spec. nov. (Sulawesi Utara), *Z. (*Zyras*) *parahirtus* spec. nov. (Borneo), *Z. (*Zyras*) *parvicollis* spec. nov. (Thailand), *Z. (*Zyras*) *russiceps* spec. nov. (Thailand, Malaysia), *Z. (*Zyras*) *titan* spec. nov. (Sulawesi Utara), and *Z. (*Zyras*) *truncatus* spec. nov. (Nepal: Dhaulagiri). As many as 28 synonymies are proposed: *Zyras alternans* (Cameron, 1925) = *Z. optimus* Cameron, 1939, syn. nov.; *Z. bartolozzii* Pace, 2003 = *Z. alboterminialis* Pace, 2008, syn. nov.; *Z. bettotanus* Cameron, 1930 = *Z. drescheri* Cameron, 1939, syn. nov., = *Z. atrapicalis* Assing, 2016, syn. nov.; *Z. brignolii* (Pace, 1986) = *Z. thainiger* Pace, 2012, syn. nov.; *Z. castaneus* (Motschulsky, 1861) = *Z. adulescens* (Pace, 1987), syn. nov., = *Z. britannorum* Pace, 1992, syn. nov., = *Z. fratrumkadoororum* Pace, 1998, syn. nov., = *Z. chumphonensis* Pace, 2004, syn. nov., = *Z. dibrugarhensis* Pace, 2011, syn. nov.; *Z. preangerae* Cameron, 1939 = *Z. louwerensi* Cameron, 1939, syn. nov., = *Z. chinkiangensis* Bernhauer, 1939, syn. nov., = *Z. setosipennis* Scheerpelitz, 1965, syn. nov., = *Z. alboantennatus* Pace, 1986, syn. nov., = *Z. sichuanorum* Pace, 2012, syn. nov.; *Z. geminus* (Kraatz, 1859) = *Z. indicus* Cameron, 1944, syn. nov., = *Z. shiva* Pace, 1992, syn. nov., = *Z. manjushri* Pace, 1992, syn. nov., = *Z. hongkongensis* Pace, 1999, syn. nov., = *Z. benenensis* Pace, 2001, syn. nov., = *Z. parageminus* Pace, 2010, syn. nov., = *Z. neoparageminus* Hlavač, Newton & Maruyama, 2011, syn. nov., = *Z. subgenimus* Pace, 2012, syn. nov.; *Z. articollis* Assing, 2016, syn. nov.; *Z. parageminus* Pace, 1998 = *Z. nameiensis* Pace, 2011, syn. nov.; *Z. pindarae* (Champion, 1921) = *Z. ruficauda* Cameron, 1939, syn. nov.; *Z. proximus* Cameron, 1939 = *Z. drugmandi* Pace, 2004; syn. nov. *Zyras novinversus* nom. nov. is proposed for the preoccupied name Z. *inversus* Pace, 2012, syn. nov. Lectotypes are designated for *Zyras exasperatus* Schubert, 1908, *Z. drescheri* Cameron, 1939, *Z. gratellus* Cameron, 1939, *Myrmedonia perforata* Champion, 1921, and *Hygroptera castanea* Motschulsky, 1861. Remarkable cases of colour polymorphism and of sexual dimorphism are discussed. A key to the *Zyras* sensu strictu species of the Himalaya, India, and Sri Lanka, a key to the species recorded from Thailand, and an updated catalogue of the *Zyras* sensu strictu species of the Palaearctic and Oriental regions are provided. Additional records of numerous named and several unnamed species are reported. The revised distributions of 37 species are mapped. The subgenus is currently represented in the Palaearctic and Oriental regions by a total of 124 described species. The countries with the greatest diversity are China (46 named species), Malaysia (20),...
India (20), Indonesia (18), Thailand (13), and Nepal (12). The subgenus is reported from Sulawesi for the first time (five named and two unnamed species). Based on a revision of type material, eleven species are not included in, or excluded from, *Zyras* sensu strictu, and *Zyras unicolor* Cameron, 1939 is tentatively moved to *Drusilla* Leach, 1819.

**Taxonomic acts**

*Zyras* (*Zyras*) ambulans spec. nov. – urn:lsid:zoobank.org:pub:FD33C1AE-F7D9-4E3A-A053-A2CAA7261CFB
*Z. (Z.) brevilobatus* spec. nov. – urn:lsid:zoobank.org:act:6C8B4EA9-8A7B-40FB-B1C9-938C01CCD509
*Z. (Z.) densihirtus* spec. nov. – urn:lsid:zoobank.org:act:47C7587-9B06-4CD1-821D-60742B4CA3BB
*Z. (Z.) densissimus* spec. nov. – urn:lsid:zoobank.org:act:C82B20D3-1259-4461-B077-00D26B579091
*Z. (Z.) latilobatus* spec. nov. – urn:lsid:zoobank.org:act:AD2822BC-9922-4004-97DE-0E845B6634DF
*Z. (Z.) longilobatus* spec. nov. – urn:lsid:zoobank.org:act:97F2CE3E-586F-438D-BB4C-26238A1A5D76
*Z. (Z.) luteipes* spec. nov. – urn:lsid:zoobank.org:act:EB837A27-74A8-4E5A-BBRC-ABC18704B04D
*Z. (Z.) morulus* spec. nov. – urn:lsid:zoobank.org:act:EB837A27-74A8-4E5A-BBRC-ABC18704B04D
*Z. (Z.) nigripilinus* spec. nov. – urn:lsid:zoobank.org:act:EB837A27-74A8-4E5A-BBRC-ABC18704B04D
*Z. (Z.) parahirtus* spec. nov. – urn:lsid:zoobank.org:act:EB837A27-74A8-4E5A-BBRC-ABC18704B04D
*Z. (Z.) parvicollis* spec. nov. – urn:lsid:zoobank.org:act:EB837A27-74A8-4E5A-BBRC-ABC18704B04D
*Z. (Z.) russiceps* spec. nov. – urn:lsid:zoobank.org:act:EB837A27-74A8-4E5A-BBRC-ABC18704B04D
*Z. (Z.) titian* spec. nov. – urn:lsid:zoobank.org:act:EB837A27-74A8-4E5A-BBRC-ABC18704B04D
*Z. (Z.) truncatus* spec. nov. – urn:lsid:zoobank.org:act:EB837A27-74A8-4E5A-BBRC-ABC18704B04D
*Z. (Z.) novinversus* nom. nov. – urn:lsid:zoobank.org:act:EB837A27-74A8-4E5A-BBRC-ABC18704B04D

**Key words**

Coleoptera, Staphylinidae, Aleocharinae, Lomechusini, East Palaearctic region, Oriental region, taxonomy, new species, new synonyms, replacement name, new combination, lectotype designations, keys to species, catalogue, additional records, distribution maps, polymorphism, sexual dimorphism.

**Zusammenfassung**

Arten der Untergattung *Zyras* Stephens, 1835 sensu strictu der Orientalis und südlichen Ostpaläarktis, insbesondere die der Himalaya-Region, Indiens, Sri Lankas, Thailands und von Sulawesi werden revidiert. Insgesamt 40 Arten werden beschrieben und/oder abgebildet, darunter 14 neue Taxa: *Zyras* (*Zyras*) ambulans spec. nov. (Thailand), *Z. (Z.) brevilobatus* spec. nov. (Thailand), *Z. (Z.) densihirtus* spec. nov. (Sulawesi Utara), *Z. (Z.) densissimus* spec. nov. (Sulawesi Utara), *Z. (Z.) latilobatus* spec. nov. (Südindien), *Z. (Z.) longilobatus* spec. nov. (Indien: Meghalaya), *Z. (Z.) luteipes* spec. nov. (Indien: Meghalaya), *Z. (Z.) morulus* spec. nov. (Nepal: Dhaulagiri, Anna-purna), *Z. (Z.) nigripilinus* spec. nov. (Sulawesi Utara), *Z. (Z.) parahirtus* spec. nov. (Borneo), *Z. (Z.) parvicollis* spec. nov. (Thailand), *Z. (Z.) russiceps* spec. nov. (Thailand), *Z. (Z.) titian* spec. nov. (Sulawesi Utara) und *Z. (Z.) truncatus* spec. nov. (Nepal: Dhaulagiri). Insgesamt 28 Namen werden synonymisiert: *Zyras alternans* (Cameron, 1925) = *Z. optimus* Cameron, 1939, syn. nov.; *Z. bartolozzi* Pace, 2003 = *Z. abbotinalis* Pace, 2008, syn. nov.; *Z. bettotanus* Cameron, 1930 = *Z. drescheri* Cameron, 1939, syn. nov., = *Z. atrapicalis* Assing, 2016, syn. nov.; *Z. brignolii* (Pace, 1986) = *Z. thainiger* Pace, 2012, syn. nov.; *Z. castaneus* (Motschulsky, 1861) = *Z. adulescens* (Pace, 1987), syn. nov., = *Z. britannorum* Pace, 1992, syn. nov., = *Z. fratrumkodoorium* Pace, 1998, syn. nov., = *Z. chumphonensis* Pace, 2004, syn. nov., = *Z. digigrarunensis* Pace, 2011, syn. nov.; *Z. preangera* nus Cameron, 1939 = *Z. louwerensis* Cameron, 1939, syn. nov., = *Z. chinkiangensis* Bernhauer, 1939, syn. nov., = *Z. setosipennis* Scheerpeltz, 1965, syn. nov., = *Z. alboventatus* Pace, 1986, syn. nov., = *Z. sychianorum* Pace, 2012, syn. nov.; *Z. geminus* (Kraatz, 1859) = *Z. indicus* Cameron, 1944, syn. nov., = *Z. shiva* Pace, 1992, syn. nov., = *Z. manjushri* Pace, 1992, syn. nov., = *Z. hongkongensis* Pace, 1999, syn. nov., = *Z. benenensis* Pace, 2001, syn. nov., = *Z. parageminus* Pace, 2010, syn. nov., = *Z. neoparageminus* Hlaváč, Newton & Maruyama, 2011, syn. nov., = *Z. subgeminus* Pace, 2012, syn. nov., = *Z. articollis* Assing, 2016, syn. nov.; *Z. parageminus* Pace, 1998 = *Z. name- riensis* Pace, 2011, syn. nov.; *Z. pindarae* (Champion, 1921) = *Z. ruficauda* Cameron, 1939, syn. nov.; *Z. proximus* Cameron, 1939 = *Z. drugmandi* Pace, 2004, syn. nov. Das primäre Homonym *Zyras inversus* Pace, 2012, syn. nov., wird durch *Z. novinversus* nom. nov. ersetzt. Für *Zyras exasperatus* Schubert, 1908, *Z. drescheri* Cameron, 1939, *Z. gratellus* Cameron, 1939, *Myrmedonia perforata* Champion, 1921 und *Hygroptera castanea* Motschulsky, 1861 werden Lektotypen designiert. Bemerkenswerte Fälle von Farbpolymerismen und Sexualdimorphismen werden diskutiert. Eine Bestimmungstablelle der Arten des Himalaya, Indiens und Sri Lankas, eine Bestimmungs- tabelle der aus Thailand nachgewiesenen Arten sowie ein aktualisierter Katalog der Arten der Ostpaläarktis und der Orientalis werden erstellt. Weitere Nachweise von zahlreichen beschriebenen und mehreren unbeschriebenen
1 Introduction

According to a recent revision of the fauna of China, Taiwan, and Hong Kong (Assing 2016a), the nominal subgenus of *Zyras* Stephens, 1833 included 158 species, 126 of them distributed in the Palearctic and Oriental regions sensu Schülke & Smetana (2015). Three additional species, one from New Guinea (Pace 2015), one from China, and one from Indonesia (Assing 2016b) have been described in the meantime. Aside from the West Palearctic region, the only regions whose *Zyras* sensu strictu faunas have been studied systematically, comprehensively, and recently are China, Taiwan, and Hong Kong (together 50 named species), Vietnam (six species), and Borneo (14 species) (Assing 2015, 2016a; Pace 2008).

The original aim of the present study was a revision of the *Zyras* sensu strictu species of the Himalaya and India. The latest synoptic work on the fauna of this region dates back to Cameron (1939a). However, several of the species recorded from the area had also been reported from elsewhere and an examination of material from other parts of the Oriental region revealed that some species are remarkably widespread. Consequently, previously unrevised species recorded from Thailand, Laos, and adjacent regions had to be included in the study. Moreover, in the course of the present revision, additional material from the Greater Sunda Islands (Sumatra, Java, Borneo, Sulawesi) became available. However, most of the species described from these islands still require a revision of types, so that only part of the material is treated in the present study. The specimens from Sulawesi were of particular interest, since no species of *Zyras* sensu strictu had been recorded from there.

2 Material and methods

The material treated in this study is deposited in the following collections:

| Institution                  | Collections |
|------------------------------|-------------|
| BMNH The Natural History Museum, London | (R. G. Booth) |
| IRSNB Institut Royal des Sciences Naturelles de Belgique, Bruxelles | (Y. Gérard) |
| MCSNV Museo Civico di Storia Naturale, Verona | (L. Latella, via Adriano Zanetti) |
| MHNG Muséum d’Histoire Naturelle, Genève | (G. Cuccodoro) |
| MNB Museum für Naturkunde, Berlin | (J. Frisch, J. Willers) |
| SMTD Staatliches Museum für Tierkunde, Dresden | (O. Jäger) |
| NME Naturkundemuseum Erfurt | (M. Hartmann, assisted by W. Apfel) |
| NMP National Museum of Natural History, Praha | (J. Hájek) |
| SDEI Senckenberg Deutsches Entomologisches Institut | (L. Behne) |
| ZMM Zoological Museum of the Moscow Lomonosov State University | (A. Gusakov) |
| cAss author’s private collection | |
| cHla private collection Peter Hváváč, Prague | |
| cKle private collection Andreas Kleeberg, Berlin | |
| cMar private collection Munetoshi Maruyama, Fukuoka | |
| cRou private collection Guillaume de Rougemont, Oxford | |
| cSme private collection Aleš Smetana, Ottawa | |

The morphological studies were conducted using a Steini SV 11 microscope (Zeiss Germany) and a Jenalab compound microscope (Carl Zeiss Jena). The images were created using a photographing device constructed by Arved Lompe (Nienburg) and CombineZ software, as well as a digital camera (Nikon Coolpix 995). The maps were created using MapCreator 2.0 (primap) software.

Body length was measured from the anterior margin of the labrum to the abdominal apex, the length of the forebody from the anterior margin of the labrum to the posterior margin of the elytra, head length from the anterior margin of the clypeus (without ante-clypeus) to the posterior constriction of the head, elytral length at the suture from the apex of the scutellum to the posterior margin of the elytra, and the length of the aedeagus from the apex of the ventral process to the base of the aedeagal capsule. The “parameral” side (i.e., the side where the sperm duct enters) is referred to as the ventral, the opposite side as the dorsal aspect.
3 Results

3.1 General remarks

The present study yielded 14 species new to science, four from Sulawesi Utara (Indonesia), three from India, two from Nepal, three from Thailand, one from Thailand and Peninsular Malaysia, and one from the Indonesian part of Borneo. Moreover, based on a revision of type material of species that had been assigned to Zyras sensu strictu, some of them doubtfully, or whose affinities with this subgenus had been suggested in the literature, eleven species are not included in, or excluded from, this subgenus. Remarkably, as many as 28 synonymies were discovered. These synonymies almost exclusively refer to widespread species, whose distributions – and, accordingly, whose intraspecific variation – had largely been underestimated. One such widespread species, Z. geminus, now has nine junior synonyms, Z. preangeranus and Z. castaneus have five. In many cases, the descriptions of the junior synonymies are based exclusively on females. Also, a significant number of these names had been made available in articles dealing with miscellaneous Staphylinidae or Aleocharinae, without a study of type material of already described species. Zyras sensu strictu is now represented in the Palearctic and Oriental regions by a total of 124 described species. The subgenus is reported from Sulawesi for the first time (five named and two unnamed species). At present, the countries with the greatest diversity are China (46 named species), Malaysia (20), India (20), Indonesia (18), Thailand (13), and Nepal (12). The type material of some species, however, particularly those described from Java, Sumatra, and Borneo, has not yet been revised and some additional material from these islands has not been examined. Thus, it seems likely that a future study focusing on the Greater Sunda Islands will eventually result in the discovery of both more new species and additional synonymies. A diagnosis of Zyras sensu strictu species often requires the examination of character combinations, mostly including the aedeagus, despite the fact that the median lobe is often of rather uniform shape and that the internal structures are of little use for taxonomic purposes. In some cases, the apical lobe of the paramere provides additional characters. The spermatheca, on the other hand, is completely unsuitable for an identification of species (it lacks any appreciable interspecific variation), which is why it is not illustrated in the descriptions provided in this study. In some species, the male secondary sexual characters are distinctive, especially the shape of tergite VIII (e.g., Z. proximus, Z. novinversus) and sternite VIII (e.g., Z. condigmus, Z. truncatus, Z. nitens). An identification is often complicated by different degrees of intraspecific variation. Some species are of generally constant coloration, size, punctuation, etc., whereas others are subject to enormous variation. This applies to both widespread species and species with more restricted distributions. For instance, in Z. preangeranus, a species whose vast distribution ranges from North Myanmar and China southwards to Sumatra and Borneo, the coloration of various body parts (number of yellowish apical antennomeres, presence/absence and extent of an infuscate spot in the postero-lateral portions of the elytra, anterior segments of the abdomen reddish or more or less extensively darker, and segment VIII yellowish or reddish) are subject to considerable both clinal and non-clinal variation. In Z. pindarac, a species confined to higher altitudes of the Himalaya in North India and Nepal, the abdomen may be completely black, or more or less brownish, or bicoloured with segments VIII-X or VII-X bright-reddish and distinctly contrasting with the black anterior segments. An interesting sexual dimorphism of the elytral punctuation was observed in two species. In Z. pindarae and Z. alternans, the punctuation of the anterior portion of the elytra (near the scutellum) is very dense and somewhat asperate in males, where as it is distinctly less dense, not asperate, and defined in females. The distribution patterns of Zyras sensu strictu species in the southern East Palearctic and Oriental regions range from extremely widespread to more or less locally endemic. Typical examples of the expansive type are Z. geminus and Z. castaneus (present nearly everywhere in the southern East Palearctic and Oriental regions), as well as Z. proximus, Z. preangeranus, and Z. betotanus. These species are typically collected at lower to intermediate elevation and on the wing: with light traps, Malaise traps, and flight interception traps, sometimes in greater numbers. Species with restricted distributions (e.g., Z. morulus, Z. truncatus) are generally collected by sifting and occur at higher elevations (up to > 4000 m). The zoogeography of the vast majority of Zyras sensu strictu species, however, is poorly known, as they have been recorded only on one or few occasions.

3.2 Key to the species of the subgenus Zyras of the Himalaya, India, and Sri Lanka

In total, 25 named and two undescribed species are currently known from the region including the Himalaya (exclusive of China), India, and Sri Lanka. Zyras pindarac, a species of highly variable coloration, keys out at three couplets.
1. Whole body with dense and long and sub-erect to erect pubescence (in dorsal view best visible on the postero-lateral contours of the head, on the lateral margins of the elytra, and on the posterior margins of the sternites) (e.g., Figs 59, 62–64). Body broad and with rather large abdomen (e.g., Figs 95–97). Antennomere XI very short, much shorter than the combined length of antennomeres IX and X, and of broadly conical shape (e.g., Figs 12–13, 21). Apical lobe of paramere very short (e.g., Fig. 184). Zyras hirtus group. .......................................................... 2

   - At least the forebody with distinctly less dense and less conspicuous pubescence. Habitus more slender. Antennomere XI mostly more elongate and not of distinctly conical shape. Apical lobe of paramere usually longer and more slender. .......................................................... 6

2. Forebody black; abdomen blackish-brown to black. .................................................................................................................. 3

   - Pale-coloured or bicoloured species. ........................................................................................................................................ 4

3. Meso- and metafemora distinctly bicoloured, basally yellow and apically infuscate; antennomere XI blackish, not distinctly paler than antennomeres IV–X (Fig. 13). Head and pronotum dark-brown to blackish; elytra reddish with the postero-lateral portions infuscate (Fig. 62). Abdomen bicoloured, with segments II–V reddish and VI–X blackish (Fig. 101). Distribution: South India, Sri Lanka (Map 79). ................................. 5

   - Meso- and metafemora uniform yellowish-black; apices very distinctly darker at most; antennomere XI dark-reddish, somewhat contrasting with the blackish antennomeres IV–X (Fig. 23). Tergites III–V with distinct micropunctation. Median lobe of aedeagus subapically more strongly angled in lateral view and apically less acute (Figs 178–179). Distribution: North India, Nepal (Map 7). .......................................................... 7

   - Meso- and metafemora uniformly dark-yellowish; apices very indistinctly darker at most; antennomere XI dark-reddish, somewhat contrasting with the blackish antennomeres IV–X (Fig. 23). Tergites III–V with distinct micropunctation. Median lobe of aedeagus subapically weakly angled and apically very acute both in lateral and in ventral view (Figs 182–183). Distribution: Northeast India (Map 8). .................................................. luteipes

4. Meso- and metafemora distinctly bicoloured, basally yellowish and apically infuscate. Elytra bicoloured, dark-yellowish with the postero-lateral portion blackish (Fig. 60). Abdomen bicoloured, with segments II–V reddish and VI–X blackish (Fig. 101). Distribution: South India (Map 79). ................................. nilgiriensis

   - Meso- and metafemora uniformly dark-yellowish to reddish; apices very indistinctly darker at most. Coloration of body different. ........................................................................................................................................ 5

5. Antennae distinctly bicoloured, blackish with the apical three antennomeres pale yellowish (Fig. 40). Head and pronotum dark-brown to blackish; elytra reddish with the postero-lateral portions infuscate (Fig. 62). Abdomen bicoloured, reddish with segments V–VIII blackish (Fig. 60). Antenna very long (approximately 3.0 mm) and slender (Fig. 40). Median lobe of aedeagus as in Figs 174–175. Distribution: North India, Nepal (Map 7). ................. hirtus

   - Antennae blackish-brown to blackish, with usually only antennomere XI, rarely X–XI or IX–XI, slightly paler (Fig. 21). Body more or less uniformly reddish to reddish-brown, with abdominal segments VI–VII slightly darker at most (Figs 59, 95). Antenna much shorter (approximately 2.0 mm) and more strongly incrassate (Fig. 21). Median lobe of aedeagus as in Figs 170–171. Distribution: Northeast India (Map 8). .................. gardneri

6. Forebody and abdomen completely blackish. Legs bicoloured with the femora blackish-brown to black and the tibiae yellowish. ........................................................................................................................................ 7

   - Coloration different, at least the abdomen not completely blackish. .......................................................................................... 9

7. Forebody with blueish hue (Fig. 50). Antennae blackish with antennomeres I–II and the base of III yellowish (Fig. 22). Distribution: North India (Map 2). ................................................................. nigroaeneus

   - Forebody without blueish hue. Antennae, including the basal antennomeres, uniformly blackish, or nearly so. ........................................................................................................................................ 8

8. Tibiae blackish, as dark as femora. Ventral process of aedeagus basally broader in ventral view (Figs 263–264). Paramere much longer than median lobe and with rather long and slender apical lobe (Fig. 265). Distribution: Central Nepal (Map 4). ................................................................. morulus

   - Tibiae distinctly paler than femora. Ventral process of aedeagus basally more slender in ventral view (Figs 125–128). Paramere approximately as long as median lobe and short apical lobe (Fig. 129). Distribution: North India, Nepal (Map 2). .................................................. pindarac

9. Abdomen black with the apex (segments VII–X or VIII–X) reddish, strongly contrasting with the anterior segments; forebody black. ........................................................................................................ 10

   - Abdomen of different coloration; forebody usually not uniformly black. ............................................................................. 12
10. Segment VII black or reddish (Figs 82–85). Pronotum with slightly irregular and denser punctuation; elytra with dense and nearly regularly distributed punctuation (Fig. 44). Aedeagus as in Figs 125–129. Distribution: North India, Nepal (Map 2). .................................................................................................................... pindaræ

11. Legs uniformly pale-yellowish. Median lobe of aedeagus as in Figs 117–118. Distribution: North India, Nepal (Map 1). .................................................................................................................... kraatzi

12. Pronotum bright-reddish, strongly contrasting with the blackish head. ................................................................. 13

13. Elytra bicoloured. ............................................................................................................................................................ 14

14. Elytra blackish with the suture and the area near the scutellum extensively yellowish-red (Fig. 54). Antennomeres VIII–X distinctly transverse (Fig. 16). Male sexual characters unknown. Distribution: South India (Map 7). ....................... hastatus

15. Antennae short, 1.3–1.4 mm long, and distinctly incrassate apically; antennomere X at least twice as broad as long (Figs 17–18). Pronotum approximately 1.15 times as broad as long (Figs 55–56). Aedeagus as in Pace (2011: figures 39–40). Small species; length of forebody 2.0–2.2 mm. Distribution: India, Sri Lanka (Map 7). ....................... parageminus

16. Antennae longer and more slender, > 1.7 mm long; antennomere X less than twice as broad as long. Pronotum more slender, or if similarly transverse, pronotum, elytra, tergite II, and anterior impressions of tergites III–V coarsely punctate. Larger species, length of forebody > 2.2 mm. .................................................................................................................... alternans

17. Metafemora bicoloured, yellowish with distinctly infuscate apices. .......................................................................... 18

18. At least profemora, often also mesofemora of uniformly yellowish coloration. Antennomeres IV–VII distinctly oblong (Fig. 9). Eyes approximately as long as distance from posterior margin of eye to posterior constriction of head (Figs 48–49). Pronotum > 1.1 times as broad as long and with straight lateral margins in posterior half (Figs 48–49). Punctuation of pronotum and elytra irregular and moderately coarse (Figs 48–49). Abdominal tergites III–VI with few setiferous punctures at posterior margins (Fig. 94). Male sternite VIII conspicuously acute posteriorly (Fig. 147). Median lobe of aedeagus as in Figs 142–143. Distribution: North India, Nepal (Map 4). ................................................................. condignus

Apices of all femora blackish. Antennomeres VI–VII transverse (Fig. 25). Eyes more than twice as long as distance from posterior margin of eye to posterior constriction of head (Fig. 51). Pronotum < 1.1 times as broad as long and with sinuate lateral margins in posterior half (Fig. 51). Punctuation of pronotum and elytra regular and fine (Fig. 51). Abdominal tergites III–VI with numerous setiferous punctures at posterior margins. Male sternite VIII convex posteriorly (Fig. 149). Median lobe of aedeagus as in Pace (1986: figures 54–55). Distribution: Central Nepal (Map 3). .............................................................................................................. morvani
19. Pronotum with uneven surface and conspicuously irregular punctation more or less grouped in clusters, these clusters at least partly situated in more or less distinct impressions (Fig. 65). Male tergite VIII with four blunt projections posteriorly (Fig. 196). Median lobe of aedeagus as in Figs 191–194. Distribution: Oriental and southern East Palaearctic regions (Map 6).

- Pronotum with smooth surface without impressions (except the usual postero-median impression). Punctuation of pronotal punctation moderately irregularly distributed (Fig. 53). Non-setiferous punctation of the anterior impressions of tergites III–V fine (Fig. 89). Median lobe of aedeagus with moderately slender and acute apex in lateral view (Figs 156–158). Distribution: Northeast India (Map 9). .................................................. \textit{proximus}

20. Male sternite VIII distinctly truncate posteriorly. Ventral process of aedeagus with long, slender, and acute apex in lateral view. Apical lobe of aedeagus long and slender. ................................................................. \textit{truncatus}

- Male sternite VIII convex posteriorly. Ventral process of aedeagus with shorter, less slender, and less acute apex in lateral view. Apical lobe of aedeagus distinctly shorter. ........................................................................................... \textit{longilobatus}

21. Antennae approximately 2.0 mm long and not particularly slender, antennomeres VI–IX transverse (Fig. 24). Pronotum broader, approximately 1.15 times as broad as long, lateral margins straight or weakly convex in posterior half in dorsal view; pronotal punctuation moderately irregularly distributed (Fig. 53). Non-setiferous punctation of the anterior impressions of tergites III–V fine (Fig. 89). Median lobe of aedeagus with moderately slender and acute apex in lateral view (Figs 156–158). Distribution: Northeast India (Map 9). ....... \textit{longilobatus}

- Antennae very long and slender, 2.4–2.6 mm long; antennomeres VI–XI oblong (Fig. 11). Pronotum slender, approximately 1.1 times as broad as long, lateral margins sinuate in posterior half in dorsal view; lateral portions of disc with a cluster of punctures slightly behind middle, otherwise nearly impunctate (Fig. 52). Non-setiferous punctation of anterior impressions of tergites III–V coarse (Fig. 91). Median lobe of aedeagus with conspicuously slender and acute apex in lateral view (Figs 150–151). Distribution: Central Nepal (Map 3). ........................... \textit{truncatus}

22. Anterior impressions of tergites III–V with few fine non-setiferous punctures confined to the middle. Species of rather large size with a rather large, but weakly transverse pronotum (approximately 1.1 times as broad as long). ................................................................................................. \textit{truncatus}

- Anterior impressions of tergite III–V with more numerous non-setiferous punctures everywhere. .......... 23

23. Legs of uniformly pale-brown coloration. Pronotum sparsely and distinctly irregularly punctate; lateral margins not sinuate near posterior angles (Fig. 43). Punctuation of elytra coarse and irregularly distributed, anteriorly dense and somewhat asperate, posteriorly very sparse (Fig. 43). Median lobe of aedeagus as in Figs 121–122. Distribution: Northwest India (Map 1). ..................................................... \textit{esperatus}

- Legs bicoloured, with dark-brown to blackish-brown femora and with paler tibiae and tarsi. Pronotum with nearly regularly distributed punctuation (Fig. 44). Elytra with much finer, much denser, and not distinctly irregularly distributed punctuation, only slightly sparser posteriorly than anteriorly (Fig. 44). Median lobe of aedeagus as in Figs 125–129. Distribution: North India, Nepal (Map 2). ............................................................... \textit{pindarae}

24. Small species; body length 4.3–5.0 mm; length of forebody 1.9–2.1 mm. Antennomere XI conspicuously elongate, approximately as long as the combined length of VIII–X (Fig. 27). Head relatively large in relation to pronotum (ASSING 2016a: figure 97). Aedeagus: ASSING (2016a: figures 272–273). Distribution: Oriental and southern East Palaearctic regions (Map 5).

- Distinctly larger species. Antennomere XI less elongate, shorter than the combined length of VIII–X. .......... 25

25. Anterior third to anterior half of elytra or only humeral portions yellowish, posterior half (including suture) blackish (Fig. 45). Aedeagus as in Figs 132–133. Distribution: North India, Nepal (Map 3). ............... \textit{perforatus}

- Elytra yellowish with the postero-lateral portions more or less triangularly blackish; yellowish coloration extending posteriad along suture to posterior margin, or nearly so (Figs 46–47). ............................................................................... 26

26. Tergites VII–X reddish (Fig. 87). Distribution: North India (Map 1). ................................................. \textit{championi}

- Tergite VII blackish; posterior portion of tergite VIII somewhat infuscate (Fig. 88). Aedeagus as in Figs 136–137. Distribution: Nepal (Map 1). ...................................................... \textit{pallipes
3.3 Key to the species of the subgenus *Zyras* recorded from Thailand

Up to today, 13 named species of *Zyras* sensu strictu have been recorded from Thailand, four of them exclusive. In addition, several unnamed species have been examined, one of them represented by a male without antennae and the remainder represented exclusively by females.

1. Pronotum red. ........................................................................................................................................................................ 2
   - Pronotum dark-brown to black. .................................................................................................................................................. 5

2. Head red, of similar coloration as pronotum (Fig. 61). Elytra with very coarse and dense punctation (Fig. 61). Aedeagus as in Figs 187–188. Distribution: Thailand, Malaysia. ................................................................. russiceps
   - Head blackish. ........................................................................................................................................................................... 3

3. Very large and robust species; length of forebody > 3.5 mm; width of pronotum approximately 1.5 mm. Elytra reddish with the postero-lateral portion more or less distinctly and more or less extensively infuscate. Legs usually uniformly yellowish. Median lobe of aedeagus as in Figs 276–277. Distribution: Oriental and southern East Palaearctic regions (Map 10). ...................................................... preangeranus
   - Smaller and more slender species; length of forebody < 3.5 mm; width of pronotum < 1.2 mm. Elytra blackish, often with slight bluish hue. At least the apices of the femora usually infuscate. .............................................. 4

4. Profemora and the apical halves of the meso- and metafemora blackish-brown to black. Antennae very slender, approximately 2.7 mm long; antennomeres IV–VII distinctly oblong and X very weakly transverse. Elytra with rather coarse punctuation. Distribution: Thailand (Map 8). ................................................................. thaiorum
   - Femora yellowish with the apices usually narrowly infuscate. Antennae much shorter, < 2.3 mm long; antennomeres V–VII not oblong and X distinctly transverse. Elytra with very fine punctuation. Aedeagus: Assing (2016a: figures 274–281). Distribution: Oriental and southern East Palaearctic regions (Map 8). ...................... geminus

5. Legs bicoloured, at least the apices of the meso- and metafemora more or less distinctly infuscate. ......................... 6
   - Legs uniformly pale-yellowish. .................................................................................................................................................... 7

6. Apices of meso- and metafemora narrowly and weakly infuscate. Elytra short and with fine punctuation (Fig. 70); hind wings reduced. Segments II–V of abdomen reddish (Fig. 107). Aedeagus: Figs 212–215. Distribution: South Thailand (Map 10). ................................................................. ambulans
   - Profemora dark-brown; apical halves of meso- and metafemora blackish. Elytra longer and with coarser punctuation (Fig. 66). Most of segments II–V blackish (Fig. 103). Male unknown. Distribution: Thailand, Southwest China (Map 8). ................................................................. brignolii

7. Anterior abdominal tergites of dark coloration (posterior margins of segments may be paler). ................................. 8
   - At least tergites II–V reddish. ...................................................................................................................................................... 10

8. Antennae massive; antennomere XI barely as long as the combined length of IX and X (Assing 2016a: figure 41). Pronotum distinctly transverse, at least 1.2 times as broad as long and approximately 1.3 times as broad as head, rather finely and regularly punctate. Median lobe of aedeagus: Assing (2016a: figures 215–216). Distribution: Thailand, China: Yunnan (Map 8). ................................................................. caloderoides
   - Antennae slender; antennomere XI conspicuously elongate, approximately as long as the combined length of VIII–X (Figs 28–29, 33). Pronotum slender, much less than 1.2 times as broad as long and only slightly broader than head (Figs 65, 69); punctuation coarse and irregularly distributed. ................................................................. proximus

9. Antennae more slender (Figs 28–29). Pronotum with very uneven surface (i.e., with more or less irregular impressions); punctuation conspicuously irregularly distributed (Fig. 65). Male tergite VIII with four blunt projections posteriorly (Fig. 196). Median lobe of aedeagus as in Figs 191–194. Distribution: Oriental and southern East Palaearctic regions (Map 6). ................................................................. parvicollis
   - Antennae less slender (Fig. 33). Pronotum without impressions and with less irregularly distributed punctuation (Fig. 69). Male tergite VIII only with a median pair of less distinct projections posteriorly (Fig. 206). Median lobe of aedeagus as in Figs 208–211. Distribution: Thailand (Map 10). .................................................................
10. Antennomere XI conspicuously elongate, approximately as long as the combined length of VIII–X (Figs 27, 30–31).
   - Antennomere XI less elongate, shorter than the combined length of VIII–X. ................................................. 11

11. Pronotum with uneven surface, more or less irregularly impressed; punctation coarse and irregularly distributed
   (Fig. 67). Anterior impressions of tergites III–V and anterior portion of tergite VI with coarse and dense non-setiferous
   punctation (Fig. 106). Posterior margin of male tergite VIII with four blunt projections (Fig. 201). Median lobe of aedeagus
   as in Figs 198–199. Distribution: Thailand, Laos (Map 5). ................................................................. novinversus
   - Pronotum with smooth surface, without impressions; punctation fine and more or less regularly distributed (Assing
     2016a: figure 97). Anterior impressions of tergites III–V and anterior portion of tergite VI with sparse and very fine
     non-setiferous punctation (Assing 2016a: figure 154). Posterior margin of male tergite VIII with shallow concavity
     in the middle. Median lobe of aedeagus: Assing (2016a: figures 272–273). Distribution: Oriental and southern
     East Palaearctic regions (Map 5). ......................................................... castaneus

12. Pronotum strongly transverse, nearly 1.3 times as broad as long and 1.2 times as broad as head (Fig. 68). Tergite
   VII nearly completely blackish-brown to black (Fig. 102). Median lobe of aedeagus with very short ventral process
   (Figs 203–204). Distribution: Thailand (Map 10). ....................................................................................
   - Pronotum weakly transverse, approximately 1.15 times as broad as long (Assing 2016a: figure 172). Tergite VII
     bicoloured with the anterior third reddish and the posterior two-thirds black (Assing 2016a: figure 174). Median
     lobe of aedeagus: Assing (2016a: figures 231–232). Distribution: Oriental and southern East Palaearctic regions
     (Map 9). ................................................................. bettotanus

3.4 Descriptions and additional records

_Zyras (Zyras) kraatzi_ Schubert, 1908
(Figs 1, 42, 79, 117–120, Map 1)

_Zyras kraatzi_ Schubert, 1908: 609 f.
_Myrmedonia (Zyras) ignicauda_ Champion, 1927: 245 f.

Type material examined: Syntype 9: “Kulu 7 / sg. Zyras, Kraatzi m. type. / Typus / Kraatzi m. / Syntypus Zyras kraatzi
Schubert, 1908, labelled by MNHUB 2016” (MNB).

Additional material examined: Nepal: 1 ex., Annapurna, Bargachap, 2100 m, beaten from vegetation, 22.VIII.1995, leg.
Jäger (SMTD).

Comment: _Zyras kraatzi_ was described based on an unspecified number of syntypes from “Kulu, Himalaya, ca. 2000 m”
(Schubert 1908). The original description of _Z. ignicauda_ is based on an unspecified number of syntypes from “Jaunsar, Chakrata
Division, U.P.” (Champion 1927). _Zyras ignicauda_ was placed in synonymy with _Z. kraatzi_ by Cameron (1939a). Only one
syntype of _Z. kraatzi_, a female, was located in the collections of MNB.

Redescription: Species of moderate size; body length 5.5–6.5 mm; length of forebody 2.5–2.9 mm. Coloration
(Figs 1, 42, 79): body black, except for the bright-reddish abdominal segments VII–X; legs pale-yellowish; antennae
blackish-brown to black, with antennomeres I–II indistinctly paler and XI dark-yellowish to reddish; maxillary
apalpi yellowish to pale-brown, with the apical palpomere yellowish.

Head (Fig. 42) distinctly transverse, broadly impunctate along middle; punctation in lateral dorsal portions rather
fine and sparse. Eyes distinctly longer than postocular region in dorsal view. Antenna (Fig. 1) 2.0–2.1 mm long
and moderately massive; antennomeres IV approximately as long as broad or weakly transverse, VI–X of gradually
increasing width and increasingly transverse, X approximately 1.5 times as broad as long, and XI as long as, or
slightly longer than the combined length of IX and X.

Pronotum (Fig. 42) weakly transverse, 1.08–1.1 times as broad as long and 1.2 times as broad as head, X
approximately 1.5 times as broad as long, and XI as long as, or
slightly longer than the combined length of IX and X. 

Elytra (Fig. 42) approximately 0.8 times as long as pronotum; punctuation coarse, rather dense near anterior
margins and scutellum, rather sparse elsewhere; scutellum with rather coarse and dense punctuation anteriorly,
impunctate in posterior portion. Hind wings present.

Abdomen (Fig. 79) slightly narrower than elytra, with rather shallow anterior impressions on tergites III–V;
antero impressions of tergites III–V each with few fine non-setiferous punctures in the middle, laterally
impunctate or nearly so; tergites III–IV with a lateral setiferous puncture on either side and with four setiferous
punctures at posterior margins; tergite V with a
lateral setiferous puncture on either side and with six setiferous punctures at posterior margin; tergite VI with a narrow transverse band of non-setiferous punctures anteriorly, with a lateral setiferous puncture on either side, and with six setiferous punctures at posterior margin; tergite VII with a narrow transverse band of non-setiferous punctures anteriorly and with two transverse series of 6–8 setiferous punctures posteriorly, posterior margin with palisade fringe; tergite VIII (Fig. 119) with two transverse series of long black setae near posterior margin, posterior margin concavely excised in the middle, on either side of this concavity with a weakly pronounced triangular projection.

**Type material examined**: Lectotype ♂: Zyras senexpunctatus Schubert, 1908, labelled by MNHUB 2016 / Lectotypus [sic] Zyras exasperatus Schubert, 1908, labelled by MNHUB 2016 / Lectotypus ♂ Zyras exasperatus Schubert, det. V. Assing 2016 / Zyras exasperatus Schubert, 1908 / Typus exasperatus m. / Holotypus [sic] Zyras exasperatus Schubert, 1908, labelled by MNHUB 2016 / Lectotypus ♂ Zyras exasperatus Schubert, desig. V. Assing 2016 / Zyras exasperatus Schubert, det. V. Assing 2016 / Zyras exasperatus Schubert, 1908: 610 f.

**Type specimen indicated above was collected by beating vegetation.**

**Comment**: The original description is based on an unspecified number of syntypes from “Kulu, Himalaya, ca. 3000 m” (Schubert 1908). Only one syntype, a slightly teneral male, was located in the collections of the MNH. This specimen is designated as the lectotype.

**Redescription**: Body length 7.0 mm; length of forebody 3.3 mm. Coloration (note that the holotype is teneral; mature specimens are most likely of significantly darker coloration) (Figs 2, 43): head dark-brown; pronotum and elytra brown, with the postero-lateral portions of the elytra slightly and diffusely darker; abdomen: tergites II–VI brown with paler posterior margins and paratergites, tergites VII–X reddish; legs yellowish-brown; antennae dark-brown with antennomere XI reddish-brown; maxillary palpi brown, with the apical palpomere yellowish.

**Elytra (Fig. 43) 0.84 times as long as pronotum; punctuation in lateral dorsal portions moderately fine and moderately sparse. Eyes slightly longer than postocular region in dorsal view. Antenna (Fig. 2) 2.6 mm long and slender; antennomeres IV–V weakly oblong, VI–VII approximately as long as broad, VIII–X weakly transverse, X much less than 1.5 times as broad as long, and XI slightly longer than the combined length of IX and X. Pronotum (Fig. 43) weakly transverse, broadly impunctate along middle; punctuation in lateral dorsal portions moderately fine and moderately sparse. Eyes slightly longer than postocular region in dorsal view. Antenna (Fig. 2) 2.6 mm long and slender; antennomeres IV–V weakly oblong, VI–VII approximately as long as broad, VIII–X weakly transverse, X much less than 1.5 times as broad as long, and XI slightly longer than the combined length of IX and X. Pronotum (Fig. 43) weakly transverse, broadly impunctate along middle; punctuation in lateral dorsal portions moderately fine and moderately sparse. Eyes slightly longer than postocular region in dorsal view. Antenna (Fig. 2) 2.6 mm long and slender; antennomeres IV–V weakly oblong, VI–VII approximately as long as broad, VIII–X weakly transverse, X much less than 1.5 times as broad as long, and XI slightly longer than the combined length of IX and X.

**Abdomen slightly narrower than elytra, with rather shallow anterior impressions on tergites III–V; anterior impressions of tergites III–V each with few scattered fine non-setiferous punctures in the middle, laterally impunctate; tergites III–IV with a lateral setiferous puncture on either side and with four setiferous punctures at posterior margins; tergite VI with a lateral setiferous puncture on either side and with six setiferous punctures at posterior margin; tergite VII with a narrow transverse row of approximately ten non-setiferous punctures confined to the middle of anterior portion (laterally impunctate), with a lateral setiferous puncture on either side, and with six setiferous punctures at posterior margin; tergite VII with a narrow transverse band of non-setiferous punctures anteriorly, with a median pair of setiferous punctures at posterior fourth, and with a transverse series of six setiferous punctures near posterior margin, posterior margin with palisade fringe; tergite VIII (Fig. 123).
with 14 long black setae near posterior margin, posterior margin concavely excised in the middle, on either side of this concavity with a triangular projection.

♂: sternite VIII (Fig. 124) with strongly convex posterior margin; median lobe of aedeagus 0.9 mm long and shaped as in Figs 121–122; paramere nearly as long as median lobe, with rather short and slender apical lobe.

♀: unknown.

Comparative notes: Based on the external and sexual characters, Z. exasperatus is closely related to Z. kraatzi and allied species. It differs from the sympatric Z. kraatzi by larger body size, paler coloration (but note that the lectotype is tenereal), longer and more slender antennae, a less convex pronotum (cross-section) with less sparse punctuation, denser, coarser, and somewhat asperate or granulose punctation of the elytra, even fewer non-setiferous punctures on the abdomen, and by the larger aedeagus with a slightly broader crista apicalis and a ventral process of slightly different shape. The possibility that Z. imigus from Pakistan and Afghanistan is conspecific with Z. exasperatus cannot be ruled out completely. Mature males of Z. exasperatus would be needed to assess intraspecific variation of coloration and other characters.

Distribution: This species is currently known only from the type locality in Himalachal Pradesh, Northwest India (Map 1). The previous record from Uttarakhand (Assing 2016a) is based on a misidentification.

Zyras [Zyras] pindarae (Champion, 1921)  
(Figs 3–5, 44, 82–85, 125–131, Map 2)

Myrmedonia [Zyras] pindarae Champion, 1921: 179.

Zyras [Zyras] ruficauda Cameron, 1939a: 543; syn. n.

Type material examined: Z. pindarae: Holotype ♀: “Pindar V. Almora, U.P., 8–11,000 ft., July 1920 H.G.C. / 3613 / Myrmedonia (Zyras) pindarae Champ. / E.M.M. 1921, det. G.C.C. / 1921-141 / Holotype / Holotype / Myrmedonia (Zyras) pindarae, det. R.G. Booth 2016” (BMNH).

Z. ruficauda: Syntype ♂ [in poor condition: most of head and right elytron missing; dissected prior to present study]: “Holotype [sic] / Ghum dist., Tiger Hill, 8,500–10,000 ft., v–vi.1931, Dr. Cameron / Z. ruficauda Cam. Type / M. Cameron. Bequest. 1955-147 / Zyras ruficauda Cam., det. R. Pace 1989, Holotypus [sic] / Syntypus ♀ Zyras ruficauda Cameron, rev. V. Assing 2016” (BMNH).

Comment: The original description of Z. pindarae is based on a unique specimen of unspecified sex from “Pindar Valley ... in Kumaon” (Champion 1921), that of Z. ruficauda on an unspecified number of syntypes from “Ghum district: Tiger Hill” (Cameron 1939a). Only one syntype of Z. ruficauda was located in the Cameron collection at the BMNH. Since it is a female in poor condition, it is not designated as the lectotype.

An examination of the types and of the additional material listed below revealed that this species appears to occur in four colour morphs (see also the notes on intraspecific variation below), one with a uniformly black abdomen, one with the abdomen more or less extensively brown, one with segments VII–X reddish, and one with only segments VIII–X reddish. They are hypothesized to belong to the same species based on the following arguments. First, other significant external differences were not observed, neither in the punctuation of the forebody and the abdomen, nor in the shape of the antennae, nor in the proportions of the various body parts. Second, the anterior portions of the posterior segments may be partly paler also in specimens with a seemingly uniformly black abdomen (anterior portions visible only when the respective segments are fully visible). Third, no differences were found in the shape of the aedeagus. And finally, the different colour morphs have sympatric distributions and have on several occasions been collected in the same locality. In consequence, there is little doubt that the type material of Z. pindarae and Z. ruficauda is conspecific, so that the latter is placed in synonymy with the former.

Additional material examined: Abdomen completely black: Nepal: 1 ♀, Dhaulagiri, Parbat region, Ghar Khola valley, near Chitre, 2400 m, 24.V.2004, leg. Kleeberg (cKle); 1 ♂, Dhaulagiri, Parbat region, near Chitre, 2400–2600 m, 27.V.2004, leg. Kleeberg (cAss); 1 ♂ [identified by Pace as Z. condignus], S-slope of Dhaulagiri range, above Pathlekhraka, 28°32’N, 83°29’E, 2500–2700 m, 12.V.2009, leg. Schmidt (NME); 1 ♂ [identified by Pace as Z. condignus], S-slope of Dhaulagiri range, N Banduk, 28°28’N, 83°35’E, 2400–2600 m, 8.V.2009, leg. Schmidt (NME); 1 ♀, 2 exs., Annapurna, Sikles range, Dhara Kharka, N’ Sikles, 2150 m, 27.IV.1996, leg. Schmidt (SDEI, cAss); 1 ♂, Annapurna, Sikles range, N Pokhara, Kyojo Kharka, N Sikles, 2600 m, 29.IV.1996, leg. Schmidt (SDEI); 1 ex., Annapurna, Sikles range, N Pokhara, Hogo (=Hugo) Kharka, N’ Sikles, 1850 m, 4.V.1996, leg. Schmidt (cAss); 1 ex., same data, but 28.IV.1996 (SDEI); 1 ♂, 1 ♀, Annapurna, Sikles range, Nyauli Kharka, S Sikles, 2400 m, 21–24.IV.1996, leg. Schmidt (SDEI); 1 ♀ [nanistic], Annapurna, N Pokhara, small river near Sikles, 2200 m, 24.IV.1996, leg. Jäger (SMTD); 1 ♀, Rolwaling, between Simigaon and Nyimare, 2600 m, 17.V.2000, leg. Kleeberg (cKle); 1 ♀, Lalitpur district, Phulchoki, 2650 m, 13.X.1983, leg. Löbl & Smetana (MHNG); 1 ♂, Bagmati province, Malemchi, 2800 m, 14.IV.1981, leg. Löbl & Smetana (MHNG); 1 ♀, Parbat district, Ghoro-pani Pass, N-slope, 2700 m, 6.X.1983, leg. Löbl & Smetana (MHNG).

Abdominal segments VII–X reddish: Nepal: 1 ♂, Bagmati province, Pokhare NE Barahbise, 2800 m, 2.V.1981, leg. Löbl & Smetana (MHNG).

Abdominal segment VII–X reddish: Nepal: 1 ♂, Dhaulagiri, Baglung Lekh, 30 km W Baglung, 2800 m, 21.V.2004.
leg. Kleeberg (cAss); 1 ♂, Annapurna, Marsyangdi valley, valley to Bargachap, 1700–2200 m, 22–23.VIII.1995, leg. Schmidt (SDEI); 1 ♂, Annapurna, Sikles range, Dhara Kharka, N Sikles, 2150 m, 27.IV.1996, leg. Schmidt (SDEI); 1 ♂, Parbat District. Ghoropani Pass, N slope, 2700 m 6.X.1983, leg. Smetana & Löbl (MHNG); 1 ♂ [identified by Pace as Z. condignus], S-slope of Dhaulagiri range, above Pathlekhaarka, 28°32’N, 83°29’E, 2500–2700 m, 12.V.2009, leg. Schmidt (NME); 1 ♂ [identified by Pace as Z. condignus], S-slope of Dhaulagiri range, N Banduk, 28°28’N, 83°35’E, 2400–2600 m, 8.V.2009, leg. Schmidt (NME).

**Abdomen brownish**: Nepal: 1 ♂ [teneral; identified by Pace as Z. perforatus], Bagmati province, Pokhare NE Barabise, 2700 m, 2.V.1981, leg. Löbl & Smetana (MHNG); 1 ♂ [teneral], Dhaulagiri, Parbat region, Chitre, 2500 m, 26.V.2004, leg. Kleeberg (cKle); 1 ♂, Rolwaling Himal, Simigau village, ca. 2600 m, 28.V.2000, leg. Schmidt (cKle); 1 ♂, Kathmandu, Shivapuri National Park, 2200 m, 24.V.2004, leg. Chaudary (cAss).

**Redescription**: Species of variable size; body length 6.5–8.3 mm; length of forebody 3.1–3.8 mm (one nanistic specimen: body length 6.0 mm; length of forebody 2.7 mm). Coloration (Figs 3–5, 44, 82–85): body completely black, or with the abdominal apex (segments VII–X or VIII–X) reddish, or with the abdomen brown with blackish-brown tergites VI–VII and yellowish-brown margins of tergites III–V; legs bicoloured with the femora blackish-brown to black and the tibiae and tarsi yellowish-brown; antennae black, with antennomere XI dark-reddish to dark-brown; maxillary palpi dark-brown to blackish-brown, with the apical palpomere yellowish.

Head (Fig. 44) distinctly transverse, broadly impunctate along middle; punctuation in lateral dorsal portions moderately coarse and moderately dense. Eyes slightly longer than postocular region in dorsal view. Antenna (Figs 3–5) 2.4–2.9 mm long and moderately massive; antennomeres IV and V approximately as long as broad, VI–X weakly transverse, X much less than 1.5 times as broad as long, and XI as long as, or slightly shorter than the combined length of IX and X.

Pronotum (Fig. 44) weakly transverse, 1.05–1.17 times as broad as long and 1.27–1.40 times as broad as head, broadest near anterior angles, distinctly tapering posteriad; lateral margins straight in posterior half (dorsal view); punctuation moderately sparse to moderately dense and slightly irregularly distributed, in antero-lateral portion with sparsely punctate patches on either side; midline rather narrowly impunctate; lateral margins each with four moderately long blackish setae.

Elytra (Fig. 44) 0.75–0.80 times as long as pronotum; punctuation subject to sexual dimorphism, dense and coarse; scutellum with rather coarse and dense punctuation anteriorly, glossy and impunctate in posterior portion. Hind wings fully developed. Metatarsomere I approximately as long as the combined length of II–IV, or nearly so.

Abdomen (Figs 82–85) slightly narrower than elytra, with rather shallow anterior impressions on tergites III–V; anterior impressions of tergites III–V each with few non-setiferous punctures in the middle, laterally impunctate; tergites III–V with a lateral setiferous puncture on either side and with four setiferous punctures at posterior margins; tergite VI with few non-setiferous punctures anteriorly, with a lateral setiferous puncture on either side, and with six setiferous punctures at posterior margin; tergite VII with few non-setiferous punctures anteriorly, and with two transverse series of 4–6 setiferous punctures posteriorly, posterior margin with palisade fringe; tergite VIII (Fig. 130) with two transverse series of long black setae near posterior margin; posterior margin concavely excised in the middle, shape of this excision subject to weak sexual dimorphism.

♂: punctuation of elytra somewhat irregularly distributed, very dense and coarse near scutellum, slightly less dense and less coarse elsewhere; posterior excision of tergite VIII with a pronounced acute process on either side (Fig. 130); sternite VIII (Fig. 131) with convex posterior margin; median lobe of aedeagus 0.95–1.15 mm long and shaped as in Figs 125–128; paramere (Fig. 129) approximately as long as median lobe and with short apical lobe.

♀: punctuation of elytra nearly regularly distributed, slightly less dense and less coarse than in male; posterior excision of tergite VIII with less pronounced process on either side; posterior margin of sternite VIII weakly concave in the middle.

**Intraspecific variation**: *Zyras pindarae* is the first example of a species of *Zyras sensu strictu* with a pronounced colour polymorphism. The abdomen may be of uniformly black coloration, or brown with blackish segments VI–VII, or bicoloured with either segments VII–X or VIII–X reddish (Figs 82–85). The different colour morphs may occur syntopically. The aedeagus of all morphs is identical (Figs 125–128).

**Comparative notes**: Based on the similar punctuation pattern of the forebody and the abdomen, on the similar morphology of the antennae, and on the weakly transverse pronotum, *Z. pindarae* is attributed to the *Z. kraatzi* group. It is distinguished from other species of this group by the colour polymorphism of the abdomen, the sexual dimorphism of the elytra punctuation, only slightly irregularly distributed punctuation of the elytra (practically regular in females), the punctuation pattern of the abdomen, and by the shape of the median lobe of the aedeagus.

**Distribution and natural history**: The known distribution includes North India (Uttar Pradesh, West Bengal) and Nepal (Map 2). For previous records from Nepal see Pace (1992, 2006) and Assing (2016b). Four of the examined specimens from Nepal had been identified by Pace as *Z. condignus* and one as *Z. perforatus*, which casts some doubt on previous records by Pace (1992, 2006).
The altitudes range from 1850 to 2800 m. In one locality, *Z. pindarae* was found together with *Z. truncatus*, in one with *Z. pallipes*, and in several localities together with *Z. perforatus*.

**Zyras (Zyras) morulus** spec. nov.

(Figs 260–265, Map 4)

**Type material**: Holotype ♂: “NEPAL, Dhaulagiri-Himal, Kali Gand. vall., Yak Kharka (upp. Marpha), 41–4600 m, 12./13.VII.1998, leg. Jäger / Holotypus ♂ Zyras morulus sp. n., det. V. Assing 2016” (SMTD). Paratypes: 1 ♂: same data as holotype (cAss); 1 ♂ [slightly teneral] “NEPAL HIMALAYA, SE Annapurna mts., Telbrung Danda / Abies-Rhododendr.-forest, 10.VI.1997, lg. Jäger” (SMTD); 1 ♀: “NEPAL, Myagdi distr., S-slope Ruyachaur Duri, 33–3400 m, 24.VI.1998, Berndt/Schmidt / Ankauf A. Dobbertin, Rostock, 2001, Museum Dresden” (SMTD); 1 ♂: “S Lamjun Himal, E-slope Taunja Danda, 3900 m, 11.8.95 / NEPAL / Myrmedonia Annapurna Mts., leg. Frabrizi, Jäger, Schmidt / DEI Ankauf J. Schmidt 1999” (SDEI).

**Etymology**: The specific epithet (Latin, adjective: black) alludes to the nearly completely black coloration of the whole body.

**Description**: Body length 7.0–8.5 mm; length of forebody 3.3–3.6 mm. Coloration: body completely black, except for the reddish to dark-brown tarsi, the reddish apical maxillary palpomere, and sometimes the dark reddish-brown antennomere XI.

Elytra with punctuation not subject to sexual dimorphism, dense, but near scutellum not extremely dense (similar to the condition in female *Z. pindarae*). Abdominal segment VII on whole surface with sparse non-setiferous micro-punctuation. Other external characters (Figs 260–262) as in *Z. pindarae*.

♂: shapes and chaetotaxy of tergite and sternite VIII as in *Z. pindarae*; median lobe of aedeagus 0.9–1.0 mm long and shaped as in Figs 263–264; paramere (Fig. 265) 1.3 mm long, much longer than median lobe, and with rather long and slender apical lobe.

♀: tergite and sternite VIII as in *Z. pindarae*.

**Comparative notes**: *Zyras morulus* is readily distinguished from the highly similar and evidently closely related *Z. pindarae* particularly by black tibiae, different punctuation of the male elytra and of the abdominal tergite VII, by a basally much broader ventral process of the aedeagus (ventral view), and (both absolutely and relatively) distinctly longer parameres with a longer and more slender apical lobe of the paramere.

**Distribution and natural history**: The type specimens were collected in four localities in the Dhaulagiri and Annapurna ranges (Map 4). The species appears to be confined to high-altitude habitats; the elevations range from approximately 3300 to above 4100 m. One specimen collected in June is slightly teneral.

**Zyras (Zyras) perforatus** (Champion, 1921)

(Figs 6, 45, 86, 132–135, Map 3)

**Myrmedonia (Zyras) perforata** Champion, 1921: 178 f.

**Type material examined**: Lectotype ♂, present designation: “Swal R Basin, Almora U.P., Feb ’19. HGC / 2723 / Myrmedonia (Zyras) perforata Ch. / E.M.M., 1921, det. G.C.C. / 1921-141 / Type H.T. [curator label] / Syntype [curator label] / Lectotype ♂ Myrmedonia perforata Champion, desig. V. Assing 2016 / Zyras perforatus (Champion), det. V. Assing 2016” (BMNH). Paralectotype ♀: same data as holotype (BMNH).

**Comment**: The original description is based on type material from “Swal River Basin [type: ii.1919]” and an unspecified number of specimens from “W. Almora, and Nainital [var.], all in Kumaon” (Champion 1921). The variety from Nainital was subsequently described as *Z. championi* by Cameron (1939a). Pace (1992) reported three specimens of *Z. perforatus* from Nepal. Two of them were examined, but only one of them actually belongs to *Z. perforatus*, the other to *Z. pindarae*.

Two type specimens, a male and a female from Swal River Basin were located in the collections of the BMNH. One of them has a curator label stating “Holotype” attached to it, but neither of them was labelled by Champion himself as such. It is not clear whether Champion’s use of the term “type” refers to an individual specimen or to all the specimens (type as opposed to variety) collected in Swal River Basin. Since Champion did not label a specimen as the type, the latter is assumed to be the case and the male is designated as the lectotype.

**Additional material examined**: Nepal: 1 ♀, Annapurna, Sikles range, S Sikles, above Garlang, 1900–2500 m, 19–20.IV.1996, leg. Schmidt (SDEI); 1 ex., 20 km W Pokhara, Panchase mt., NW slope, 2400 m, 21.V.1997, leg. Jäger (SMTD); 1 ex., Annapurna, NE Pokhara, plateau N Sikles, 2200 m, 27.IV.1996, leg. Schmidt & Jäger (cAss); 1 ♂, 1 ♀, Kathmandu, Shivapuri National Park, 2200 m, 24.V.2004, leg. Chaudary (cKle, cAss); 1 ♀, Kathmandu, Shivapuri Lekh, slope W of Bagmati river, 2000–2300 m, leg. Schmidt (NME); 1 ♀, Bagmati province, Pokhare NE Barahbise, 2700 m, 7.V.1981, leg. Löbl & Smetana (MHNG); 1 ♀, Rolwaling Himal, Simigaon to Dugong Kharka, 2200–2600 m, 13.V.2000, leg. Schmidt (cKle).

**India**: 1 ♀, Arunachal Pradesh, Dirang env., 27°21’N, 92°13’E, 1700–1900 m, 8.–22.V.2006, leg. Pacholátko (BMNH).

**Redescription**: Relatively large species: body length 6.5–7.6 mm; length of forebody 3.2–3.6 mm. Colora-
tion (Figs 6, 45, 86): forebody black, with the humeral portions of the elytra more or less extensively dark-yellowish; abdomen: tergites II blackish-brown, III–IV pale-reddish, V pale-reddish with the middle usually more or less extensively infuscate, VI blackish with the paratergites and the narrow lateral portions reddish, VII blackish, VIII uniformly reddish (type material) or distinctly bicoloured with the anterior half reddish-yellow and the posterior half black (material from Nepal), IX–X reddish-yellow, and sternite VIII of similar coloration as tergite VIII; legs yellow; antennae blackish-brown to blackish, with antennomeres I–II and the basal portion of III reddish-yellow and antennomere XI dark-reddish to brown; maxillary palpi dark-yellowish. Head (Fig. 45) distinctly transverse, median portion extensively impunctate; punctures in lateral portions very sparse and moderately coarse. Eyes slightly longer than postocular region in dorsal view. Antenna (Fig. 6) 2.5–2.7 mm long and slender; antennomeres IV weakly oblong, V–VI weakly oblong or as long as broad, VII approximately as long as broad, VIII–X weakly transverse, X less than 1.5 times as broad as long, and XI approximately as long as the combined length of IX and X. Pronotum (Fig. 45) 1.10–1.15 times as broad as long and 1.25–1.30 times as broad as head, broadest in anterior half; disc with scattered and very irregularly distributed double punctation (i.e., with both coarse and fine punctures); midline broadly impunctate; lateral margins with four long black setae. Elytra (Fig. 45) approximately 0.8 times as long as pronotum; punctuation conspicuously sparse and irregularly distributed, less sparse near scutellum, posterior portion of disc only with scattered punctuation and with large impunctate areas; pubescence pale and depressed. Scutellum with coarse and dense punctuation. Hind wings fully developed. Metatarsomere I approximately as long as the combined length of II–IV, or nearly so. Abdomen (Fig. 86) approximately as broad as elytra, with rather shallow impressions on tergites III–V; anterior impressions of tergites III–V each with a transverse row of not very dense and mostly weakly defined non-setiferous punctures; tergites III–IV with a lateral setiferous puncture on either side and with four setiferous punctures at posterior margin; tergite V with a lateral setiferous puncture on either side and with six setiferous punctures at posterior margin; tergite VI with a transverse row of non-setiferous punctures anteriorly, with a lateral setiferous puncture on either side, and with six setiferous punctures at posterior margin; tergite VII with a narrow transverse band of non-setiferous punctures anteriorly and with two more or less irregular transverse rows of setiferous punctures in posterior half, posterior margin with palisade fringe; tergite VIII (Fig. 134) with setiferous punctures only in posterior portion, posterior margin convex, in the middle concave, and on either side of this concavity obtusely produced.

♂: posterior margin of sternite VIII convex (Fig. 135); median lobe of aedeagus 1.0–1.2 mm long and shaped as in Figs 132–133; paramere approximately 1.1 mm long, apical lobe of moderate length.

Comparative notes: Among the Himalayan representatives of the subgenus Zyras, Z. perforatus is most similar to Z. pallipes, from which it differs particularly by larger size, different coloration of the elytra (yellowish coloration confined to humeral portion) and of the abdomen (lateral portions of tergites V and VI reddish), much sparser punctuation of the pronotum and the elytra, and by a larger aedeagus with a ventral process of different shape (especially in ventral view).

Distribution and natural history: This species has been recorded from several localities in North India and Nepal (Map 3). For additional records see Assing (2016b). The altitudes range from approximately 1800 to 2600 m. In several localities, Z. perforatus was found together with Z. pindarae.
rather fine. Eyes longer than postocular region in dorsal view. Antenna (Fig. 7) 2.3 mm long and rather massive; antennomeres IV–V weakly oblong or as long as broad, VI–X increasingly transverse and of gradually increasing width, X approximately 1.5 times as broad as long, and XI approximately as long as the combined length of IX and X. Pronotum (Fig. 46) approximately 1.15 times as broad as long and approximately 1.3 times as broad as head, broadest in anterior half; punctation rather fine, sparse, and very irregularly distributed, with rather large impunctate areas on either side of midline; midline broadly impunctate.

Elytra (Fig. 46) approximately 0.8 times as long as pronotum; punctuation moderately coarse, defined, and very irregularly distributed, rather dense anteriorly and near scutellum, less dense laterally, and very sparse or absent in postero-median portion. Hind wings fully developed. Metatarsomere I approximately as long as the combined length of II–IV.

Abdomen (Fig. 87) nearly as broad as elytra, with moderately deep anterior impressions on tergites III–V; anterior impressions of tergites III–V each with a transverse row of not very dense and mostly weakly defined non-setiferous punctures; tergites III–IV with a lateral setiferous puncture on either side and with four setiferous punctures at posterior margin; tergite V with a lateral setiferous puncture on either side and with six setiferous punctures at posterior margin; tergite VI with a transverse row of non-setiferous punctures anteriorly, with a lateral setiferous puncture on either side, and with six setiferous punctures at posterior margin; tergite VII with a narrow transverse band of non-setiferous punctures anteriorly and with two transverse rows of setiferous punctures in posterior half, posterior margin with palisade fringe; tergite VIII with setiferous punctures only in posterior portion, posterior margin convex and with indistinct concavity in the middle.

♀: unknown.

Comparative notes: This species is readily distinguished from all other Himalayan representatives of similar size by the conspicuous coloration of the abdomen alone.

Distribution: The known distribution is confined to two localities in Uttar Pradesh, North India (Map 1).

Zyras (Zyras) pallipes Pace, 1992
(Figs 8, 47, 88, 136–139, Map 1)

Zyras (Zyras) pallipes Pace, 1992: 140.

Type material examined: Holotype ♀: "Damp mossy grassy earth in shade of trees & rocks / NEPAL: Bakhri Kharka. 84°7.5'E., 28°23'N. 5,500 ft. 24.vi.1954. K.H. Hyatt / B.M. Nepal Expdt., B.M. 1954-540. / Holo- typus Zyras pallipes m., det. R. Pace 1988 / Holotype / Zyras pallipes sp. n., det. R. Pace 1988" (BMNH).

Comment: The original description is based on a unique male holotype from "Nepal, Bakhri Kharka, 87° 75' E–28° 23' N [sic]" (Pace 1992).

Additional material examined: Nepal: 1 ♂, Rolwaling Himal, Simigaon → Dugon Kharka, 2200–2600 m, 13.V.2000, leg. Schmidt (cKle); 1 ♂, Rolwaling Himal, Simigau vill., 2000 m. 2.VI.2000, leg. Schmidt (cAss); 1 ♀ [teneral], Kathmandu, Kakani, 2070 m, Malaise trap, 1–14.VII.1984 (BMNH).

Redescription: Body length 6.0–7.5 mm; length of fore-body 2.7–3.2 mm. Coloration (Figs 8, 47, 88): head and pronotum black; elytra reddish-yellow with the postero-lateral portions blackish; abdomen bicoloured with tergites III–IV, anterior margin of V, and anterior half of VIII pale-reddish, tergites II, V–VII blackish, and posterior half of VIII brown to black; legs yellowish; antennae blackish-brown to black; maxillary palpi yellowish with palpomere III more or less distinctly infuscate. Head (Fig. 47) distinctly transverse, median portion extensively impunctate; punctures in lateral portions moderately dense and moderately coarse. Eyes longer than postocular region in dorsal view. Antenna (Fig. 8) 2.3–2.5 mm long and rather slender; antennomeres IV–V weakly oblong, VI approximately as long as broad, VII–X of gradually increasing width and increasingly transverse, X less than 1.5 times as broad as long, and XI approximately as long as the combined length of IX–X. Pronotum (Fig. 47) rather weakly transverse, 1.10–1.15 times as broad as long and approximately 1.3 times as broad as head, broadest near anterior angles; punctuation not very coarse, rather sparse, and slightly irregularly distributed, on either side of midline with impunctate patches; midline broadly impunctate; lateral setae broken off in all specimens examined. Elytra (Fig. 47) approximately 0.75 times as long as pronotum; punctuation rather coarse, dense, and defined, denser in anterior (especially near scutellum) than in posterior half, very sparse in postero-sutural portion. Hind wings fully developed. Metatarsomere I approximately as long as the combined length of II–IV.

Abdomen (Fig. 88) narrower than elytra, with deep anterior impressions on tergites III–V; anterior impressions of tergites III–V each with a transverse row of rather coarse non-setiferous punctures; tergites III–IV with a lateral setiferous puncture on either side and with four setiferous punctures at posterior margin; tergite V with a lateral setiferous puncture on either side and with six setiferous punctures at posterior margin; tergite VI with a narrow transverse band of non-setiferous punctures anteriorly and with six setiferous punctures at posterior margin; tergite VII with a narrow transverse band of non-setiferous punctures anteriorly, with a lateral setiferous puncture on either side, and with six setiferous punctures at posterior margin; tergite VIII with sparse setiferous punctures arranged in two more or less irregular transverse rows posteriorly, posterior margin with palisade fringe; tergite IX (Fig. 138) with sparse
setiferous punctation only in posterior portion, posterior margin with a pair of two more or less pronounced projections in the middle.

♂: posterior margin of sternite VIII (Fig. 139) strongly convex, in the middle nearly truncate; median lobe of aedeagus (Figs 136–137) approximately 1.0 mm long; ventral process somewhat constricted basally in ventral view; crista apicalis small; paramere approximately 1.2 mm long and with rather slender apical lobe.

♀: posterior margin of sternite VIII weakly concave in the middle.

Comparative notes: Aside from the coloration, especially that of the abdomen and the antennae, Z. pallipes is characterized particularly by the shape of the aedeagus, above all by the basally constricted ventral process. The possibility that Z. pallipes represents a colour morph of Z. championi cannot be ruled out. However, males from the vicinity of the type locality of Z. championi would be required to clarify this.

Distribution and natural history: The known distribution is confined to Central and East Nepal (Map 1). The altitudes range from 1680 to between 2200 and 2600 m.

Zyras (Zyras) castaneus (Motschulsky, 1861) (Fig. 27, Map 5)

Hygroptera castanea Motschulsky, 1861: 150.
Drusilla adulescens Pace, 1987b: 212; syn. n.
Zyras (Zyras) britannorum Pace, 1992: 140 ff.; syn. n.
Zyras (Zyras) fratrumkadooriorum Pace, 1998: 968; syn. n.
Zyras (Zyras) chumphonensis Pace, 2004: 292; syn. n.
Zyras (Zyras) dibrugarhensis Pace, 2011: 36 ff.; syn. n.

Type material examined: H. castanea: Lectotype ♂, present designation: “[red quadrangular label] / [yellow round label] / Type / Hygroptera castanea Motsch, Ind. or. Ceyl. M. Patans [sic] / Lectotypus ♂ Hygroptera castanea Motschulsky, desig. V. Assing 2016 / Zyras castaneus (Motschulsky), det. V. Assing 2016” (ZMM).

D. adulescens: Paratype ♂: “SABAH, Pangi 29-VIII-82, de Rougemont / Paratypus Drusilla adulescens m., det. R. Pace 1983 / Drusilla adulescens n. sp., det. R. Pace 1983 / Zyras castaneus (Motschulsky), det. V. Assing 2017” (cRou).

Z. britannorum: Holotype ♀: “NEPAL: 4500’, Kathmandu, British Embassy, 20.v.–23.vi.1983. / At light / M.J.D. Bren- dell, 1983-222 / Holotype Zyras britannorum m., det. R. Pace 1988 / Zyras britannorum sp. n., det. R. Pace 1988” (BMNH).

Z. fratrumkadooriorum: see Assing (2016a).

Z. chumphonensis: see Assing (2016b).

Z. dibrugarhensis: Holotype ♂: “INDIA Assam, Dibrug- arth, 3.VI.2006, G. de Rougemont / Flight interception trap / Holotypus Zyras dibrugarhensis [sic] m., det. R. Pace 2010 / Zyras dibrugarhensis [sic] sp. n., det. R. Pace 2010 / Zyras britannorum Pace, det. V. Assing 2016” (cRou). Paratype ♀: same data as holotype (cRou).

Comment: Motschulsky (1861) based the original description of Hygroptera castanea on an unspecified number of syntypes from “la sommité du Mont Patan- nas” (Sri Lanka). Hlaváč et al. (2011) erroneously give Myrmédonia castanea as the original combination. The sole syntype in the Motschulsky collection at the ZMM, a male in fair condition, is designated as the lecto- type. An examination of this specimen revealed that it is conspecific with the type material of Z. britannorum, Z. fratrumkadooriorum, Z. chumphonensis, and Z. dibrugarhensis.

Drusilla adulescens was described based on a male holotype and a male paratype from “Sabah, Pangi” (Pace 1987b). The species was moved to Zyras by Pace (2008). An examination of the paratype revealed that it is conspec-ific with Z. castaneus.

The original description of Z. britannorum is based on a unique female holotype from “Nepal, Kathmandu, British Embassy” (Pace 1992). In the original description of Z. dibrugarhensis, which is based on a male holotype and three female paratypes from “India, Assam, Dibru- garth”, Pace (2011) compares the species with “M. [sic] tianmumontis Pace, 1998 from China”, but not with Z. britannorum or any other geographically close species; moreover, the name tianmumontis is unavailable and Pace never described any Zyras (s. str.) species from Tianmu Shan.

Zyras fratrumkadooriorum Pace, 1998, a species described from Hong Kong, was revised by Assing (2016a) and has a junior synonym, Z. chumphonensis Pace, 2004, which was described from Thailand (Assing 2016b).

An examination of the type specimens of Z. britannorum and Z. dibrugarhensis revealed that not only are they conspecific with each other, but also with Z. fratrumkadooriorum and Z. castaneus. In consequence, Z. adulescens, Z. britannorum, Z. fratrumkadooriorum, Z. chumphonensis, and Z. dibrugarhensis are all placed in synonymy with Z. castaneus.

For a detailed description and illustrations of external and the male sexual characters see Assing (2016a) (as Z. fratrumkadooriorum).

Additional material examined: India: 2 ♀♀, Arunachal Pradesh, 8 km S Jamiri, Sessa env., 27°07–09’N, 92°34’E, 350 m, 26.V.–4.VI.2005, leg. Dembický (BMNH, cAss). Thailand: see paratypes of Z. drugmandi in the section on Z. proximus. Laos: 1 ex., Kham Mouan province, ca 70 km NNE Muang Khammouan, Nakai village, 560 m, V.2002, leg. Strba (cAss). Malaysia: 1 ♀, W. Pahang, Genting Tea Estate, 600 m, Malaise trap by stream, XI.1981 (BMNH); 1 ♀, Pahang district, 30 km NE Raub, Laba Lembik, 3°56’N, 101°38’E, 300 m, 22.IV.–15.V.2002, leg. Jendek & Šauša (cHla); 1 ♀, Sabah, Sandakan, S Lokan, flight interception trap, IX.1996, leg.
**Zyras nigroaeneus** Cameron, 1939

(Figs 22, 50, 81, 140–141, Map 2)

Zyras (Zyras) nigroaeneus Cameron, 1939a: 543 f.

Type material examined: Syntype ♂ [aedeagus missing]: ‘Narkanda 9230’, Simla Hills / Fungus / Dr. Cameron. 14-IX.1921 / Z. nigraeneus [sic] Cam Type / M. Cameron. Bequest. B.M. 1955-147 / Holotype / Syntypus Zyras nigroaeneus Cameron, rev. V. Assing 2016’ (BMNH).

Comment: The original description is based on an unspecified number of syntypes from ‘Simla Hills : Narkanda, alt. 9230 feet’ (Cameron 1939a). Only one syntype, a male without aedeagus, was located in the Cameron collection.

Additional material examined: India: 1 ♂, Uttar Pradesh, Nainital Div., Kumaon, leg. Champion (BMNH).

Redescription: Species of slender habitus. Body length 5.1–6.0 mm; length of forebody 2.7–2.8 mm. Coloration (Figs 22, 50, 81): whole body black, forebody with a faint blueish hue; legs bicoloured: femora blackish-brown, tibiae and tarsi pale-yellowish; antennae blackish-brown with antennomeres I–II and the base of III yellowish; maxillary palpi brown, with the terminal palpomere yellowish. Head (Fig. 50) moderately transverse, median portion extensively impunctate; punctures in lateral portions sparse and coarse. Eyes longer than postocular region in dorsal view. Antenna (Fig. 22) approximately 1.8 mm long and moderately slender; antennomeres IV–V approximately as long as broad, VI–X increasingly transverse and of gradually increasing width, X approximately 1.5 times as broad as long, and XI barely as long as the combined length of IX and X. Pronotum (Fig. 50) approximately 1.1 times as broad as long and approximately 1.25 times as broad as head, not distinctly tapering posteriorly, broadest approximately in the middle; lateral margins weakly convex in dorsal view; punctation coarse, sparse, and very irregularly distributed, with rather large impunctate areas on either side of midline; midline broadly impunctate. Elytra (Fig. 50) 0.86–0.93 times as long as pronotum; punctation moderately coarse, defined, rather sparse, and regularly distributed; interstices on average approximately three times as broad as diameter of punctures. Hind wings fully developed. Metatarsomere 1 shorter than the combined length of II–IV.

Abdomen (Fig. 81) narrower than elytra, gradually tapering from base to apex, with sharp paratergites; anterior impressions on tergites III–V rather shallow; anterior impressions of tergites III–V each with a transverse row of sparse and fine non-setiferous punctures; tergites III–IV with a lateral setiferous puncture on either side and with four setiferous punctures at posterior margin; tergite V with a lateral setiferous puncture on either side and with six setiferous punctures at posterior margin; tergite VI with a transverse row of non-setiferous punctures anteriorly, with a lateral setiferous puncture on either side and with six setiferous punctures at posterior margin; tergite VII with a transverse band of sparse and fine non-setiferous punctures anteriorly and with scattered setiferous punctures in posterior portion, posterior margin with palisade fringe; tergite VIII (Fig. 140) with sparse setiferous punctures only in posterior portion, posterior margin convex and with distinct concavity in the middle.

♂: sternite VIII (Fig. 141) much longer than tergite VIII, posteriorly strongly convex; aedeagus not available. ♀: posterior margin of sternite VIII shallowly concave in the middle.

Comparative notes: Among its geographically close congers, *Z. nigraeneus* is characterized particularly by its slender habitus, the conspicuous coloration of the body and the legs, and by the punctuation pattern of the abdomen.

Distribution and natural history: This species is currently known only from its type locality in Himachal Pradesh and from one locality in Uttar Pradesh, North India (Map 2). The syntype was collected at an altitude of approximately 2800 m.
**Zyras (Zyras) condignus** Last, 1969

(Figs 9, 48–49, 94, 142–147, Map 4)

**Zyras (Zyras) distinctus** Cameron, 1939a: 540 f.; preoccupied. **Zyras (Zyras) condignus** Last, 1969: 279 f.; replacement name.

**Type material examined:** Syntype ♀: “Chakrata Dist. Manijgaon 6500’ / Z. distinctus Cam Type / M. Cameron. Bequest. B.M. 1955-147 / Holotype / Syntypus: 2

Additional material examined: Nepal: 2 ♀ ♀ Bagmati province, Phulchauki near Kathmandu, 1700 m, 10.V. 1981, leg. Lobl (MHNG, cAss); 1 ♀, Nagarjun Forest near Kathmandu, 1650 m, 1.IV.1981, leg. Lobl & Smetana (MHNG); 1♂, Rolwaling Himal, Simigaon, 2000 m, 2.VI. 2000, leg. Kleeberg (cAss); 3♂♂, Khandbari district, Arun river, Num env., 1500–1600 m, 10.IV.1982, leg. Smetana (MHNG, cAss); 1♂ [teneral], Gandaki Province, 10 km NW Pokhara, Yamdi Khola Valley, 1100 m, 3.VI.2002, leg. Schmidt (NME).

**Redescription:** Body length 5.6–7.2 mm; length of forebody 2.7–3.1 mm. Coloration (Figs 9, 48–49, 94): forebody brown; abdomen uniformly blackish-brown, or blackish-brown with the paratergites partly paler, or bicoloured with tergites II–V reddish to dark-reddish, tergites VI–VII dark-brown, and VIII dark-reddish with the middle more or less extensively dark-brown to blackish-brown; legs yellowish with the apices of the meso- and metafemora more or less distinctly and more or less extensively infuscate; antennae brown to dark-brown with antennomeres I–II or I–III more or less distinctly paler and XI reddish; maxillary palpi pale reddish-brown with palpmere IV yellowish.

Head (Figs 48–49) distinctly transverse, median portion extensively impunctate; punctures in lateral portions sparse and moderately coarse. Eyes longer than postocular region in dorsal view. Antenna (Fig. 9) 2.4–2.8 mm long and slender; antennomeres IV–VII oblong, VIII approximately as long as broad, IX–X very weakly transverse, and XI much shorter than the combined length of IX and X.

Pronotum (Figs 48–49) approximately 1.15 times as broad as long and 1.20–1.25 times as broad as head, broadest at anterior angles, weakly tapering posteriad; lateral margins not distinctly sinuate in posterior half in dorsal view; punctuation coarse and very irregularly distributed, on either side of midline with extensive impunctate areas; surface of disc conspicuously uneven, in postero-lateral portion usually with a densely punctate impression of variable size and shape on either side; lateral margins each with four long and erect black setae, one of them inserting near anterior and one near posterior angle, and two in between; pubescence of disc short, depressed, and pale.

Elytra (Figs 48–49) 0.80–0.85 times as long as pronotum; punctuation moderately coarse, very dense, and defined, regularly distributed; whole disc with dense, moderately long, fine, and sub-erect pale pubescence, laterally with long, stout, and erect setae. Hind wings fully developed. Metatarsomere I nearly as long as the combined length of II–IV.

Abdomen (Fig. 94) slightly narrower than elytra, with deep anterior impressions on tergites III–V; anterior impressions of tergites III–V each with a transverse row of rather weakly defined pits; tergite III with a lateral setiferous puncture on either side and with a transverse row of six setiferous punctures bearing long brown setae near posterior margin; tergite IV with a lateral setiferous puncture on either side and with a transverse row of approximately eight setiferous punctures near posterior margin; tergite V with a lateral setiferous puncture on either side and with a transverse row of approximately ten setiferous punctures at posterior margin; tergite VI anteriorly with a transverse row of non-setiferous punctures, with a transverse row of four setiferous punctures in posterior portion, and with numerous setiferous punctures at posterior margin; tergite VII anteriorly with some non-setiferous punctures and posteriorly with irregular setiferous punctuation, posterior margin with palisade fringe; tergite VIII (Fig. 146) with brown long setae only in posterior half, posterior margin convex, in the middle often weakly concave; all sternites with numerous long brown setae posteriory.

♂: sternite VIII (Fig. 147) apically conspicuously acute; median lobe of aedeagus approximately 0.7 mm long and shaped as in Figs 142–143; paramere (Figs 144–145) approximately 0.9 mm long, apical lobe distinctly modified, long, depressed, and apically rounded.

♀: posterior margin of sternite VIII convex, in the middle sometimes weakly concave.

**Comparative notes:** Despite the dense and long pubescence of the abdominal sternites, *Z. condignus* does not belong to the *Z. hirtus* group, as can be inferred particularly from the modified and conspicuously long apical lobe of the paramere. Instead, the morphology of the paramere, the slender habitus, and the similar modifications of the pronotum suggest that it is allied to *Z. proximus* and *Z. novinversus*. The species is readily distinguished from other geographically close consubgener particularly by the modifications of the pronotum, the conspicuous shape of the male sternite VIII, the shape of the median lobe of the aedeagus, and by the modified shape of the apical lobe of the paramere.

**Distribution and natural history:** The confirmed distribution is confined to Uttarakhand, North India and several localities in Nepal. The records reported by Pace (2006) may be doubtful; two examined specimens identi-
fied by him as *Z. condignus* in fact belong to *Z. pindareae*. Records from Vietnam and Taiwan (Hlaváč et al. 2011) are most likely based on misidentifications. They probably refer to *Z. proximus*.

The altitudes range from 1100 to 2000 m. One specimen collected in June is teneral.

**Zyras (Zyras) morvani** Pace, 1986

(Figs 25, 51, 93, 148–149, Map 3)

**Zyras (Zyras) morvani** Pace, 1986c: 182.

**Type material examined:** Holotype ♀: “Takumsibang, 1750 m. IV.73, P. Morvan / Coll. Rougemont / Holotypus Zyras morvani m., det. R. Pace 1983 / Zyras morvani n. sp., det. R. Pace, 1983 / Zyras morvani Pace, det. V. Assing 2016” *(MCSNV).*

**Comment:** The original description is based on a unique male from “Nepal, Takum Sibang” *(Pace 1986c).*

**Additional material examined:** Nepal: 1 ♀, Annapurna, Marsyangdi valley, Syangde env., 1100 m, 30.V.1993, leg. Schmidt (cAss).

**Redescription:** Body length 5.6–6.0 mm; length of fore-body 2.6–2.7 mm. Coloration (Figs 25, 51, 93): head black; pronotum and elytra dark-brown to blackish-brown; abdomen dark-brown to blackish-brown with the anterior portions of the paratergites paler; legs yellow with the apices of all femora blackish; antennae with the basal 3–4 antennomeres dark-brown to blackish-brown and the remainder gradually becoming paler towards apex, apical 3–5 antennomeres dark-yellowish; maxillary palpi brown to dark-brown with palpmere IV yellowish.

Head (Fig. 51) moderately transverse, median portion extensively impunctate; punctures in lateral portions sparse and fine. Eyes large and bulging, more than twice as long as distance from posterior margin of eye to posterior constriction of head in dorsal view. Antenna (Fig. 25) approximately 2.0 mm long and moderately slender; antennomeres IV weakly oblong, V approximately as broad as long, VI–X of gradually increasing width and increasingly transverse, X approximately 1.5 times as broad as long or nearly so, and XI barely as long as the combined length of IX and X.

Pronotum (Fig. 51) weakly transverse, 1.03–1.07 times as broad as long and 1.13–1.15 times as broad as head, broadest in anterior half, distinctly tapering posteriorly; lateral margins distinctly sinuate in posterior half in dorsal view; punctuation fine and slightly irregularly distributed; lateral margins each with five long and erect black setae, anterior margins with an additional long and erect black seta on either side; pubescence of disc rather long, sub-erect, and pale.

Elytra (Fig. 51) 0.78–0.82 times as long as pronotum; punctuation fine, moderately dense, and regularly distributed; whole disc with dense, long, and sub-erect pale pubescence, laterally with long, stout, and erect setae. Hind wings fully developed. Metatarsomere I longer than the combined length of II and III.

Abdomen (Fig. 93) slightly narrower than elytra, with rather deep anterior impressions on tergites III–V; anterior impressions of tergites III–V each with a transverse row of numerous rather weakly defined grooves; tergite III with a lateral setiferous puncture on either side and with numerous fine setiferous punctures at posterior margin; tergites IV and V with a median pair of setiferous punctures, with a lateral setiferous puncture on either side, and with numerous fine setiferous punctures at posterior margin; tergite VI with a transverse row of non-setiferous punctures anteriorly, with a transverse row of rather numerous setiferous punctures at posterior third, and with numerous setiferous punctures at posterior margin; tergite VII with a transverse band of non-setiferous punctures anteriorly and with two transverse rows of setiferous punctures posteriorly, posterior margin with palisade fringe; posterior margin of tergite VIII with a shallow median concavity (Fig. 148).

♂: sternite VIII (Fig. 149) oblong, strongly convex posteriorly; median lobe of aedeagus approximately 0.7 mm long and shaped as figured by Pace (1986c); paramere slightly longer than median lobe, apical lobe not distinctly modified, moderately long and apically acute.

♀: posterior margin of sternite VIII convex, in the middle indistinctly concave.

**Comparative notes:** Though similar in size and habitus to *Z. condignus*, *Z. morvani* differs from this species in numerous characters, such as much shorter and less slender antennae with more transverse antennomeres VI–X, the coloration of the antennae and the legs, much larger eyes, a more slender pronotum with sinuate lateral margins and a smooth surface, finer and practically regular punctuation of the pronotum and the elytra, a different punctuation pattern of the abdomen (particularly the much more numerous setiferous punctures at the posterior margins of the tergites), a completely different shape of the male sternite VIII, and the shapes of the median lobe and the parameres of the aedeagus.

**Distribution and natural history:** The currently known distribution is confined to two localities in the Dhaulagiri and Annapurna ranges, Nepal (Map 3), where the two known specimens were collected at altitudes of 1100 and 1750 m.
**Zyras (Zyras) truncatus** spec. nov. (Figs 11, 52, 91, 150–155, Map 3)

**Type material:** Holotype ♂: “NEPAL Himalaya, Dhawalagiri, 2004, Region Parbat / Chitre, 2500 m, 25.05.2004, leg. A. Kleeberg / Holotypus ♂ **Zyras truncatus** sp. n., det. V. Assing 2016” (cAss). Paratypes: 1 ♂: “NEPAL Himalaya, Dhawalagiri, 2004, Region Parbat / near Chitre, Ghar Kholo valley, ~2400 m, 24.05.2004, leg. A. Kleeberg” (cKle); 1 ♀: “NEPAL Himalaya, Dhawalagiri, 2004, Region Parbat / near Chitre, 2.4–2.600 m [sic], 27.05.2004, leg. A. Kleeberg” (cKle).

**Etymology:** The specific epithet (Latin, adjective) alludes to the apically truncate male sternite VIII.

**Description:** Body length 5.6–6.3 mm; length of fore-body 2.5–2.8 mm. Coloration (Figs 11, 52, 91): head black; pronotum blackish-brown to black; elytra blackish with the humeral portion reddish-yellow and the suture narrowly dark-reddish; abdomen with segments II–V brown, segments VI–VII blackish (except for the partly brown margins), and segments VIII–X dark-brown to blackish-brown; legs dark-yellowish to yellowish-brown; antennae dark-brown with antennomeres I–II and the blackish-brown; legs dark-yellowish to yellowish-brown; antennae dark-brown with antennomeres I–II and the base of III yellowish-brown and the apical 1–2 antennomeres more or less distinctly pale-brown; maxillary palpi dark-yellowish with palpomere IV paler yellowish.

Head (Fig. 52) rather weakly transverse, median portion extensively impunctate; punctures in lateral portions very sparse and moderately coarse. Eyes slightly longer than postocular region in dorsal view. Antenna (Fig. 11) approximately 2.4–2.5 mm long and very slender; antennomeres IV–IX oblong, X approximately as broad as long, and XI approximately as long as the combined length of IX and X, or nearly so. Pronotum (Fig. 52) slender, approximately 1.1 times as broad as long and approximately 1.2 times as broad as head, broadest in anterior half, moderately tapering posteriorly; lateral margins sinuate in posterior half in dorsal view; punctuation rather coarse and very irregularly distributed, arranged in a cluster behind the middle of lateral surface; antero-lateral and postero-lateral portion of lateral surface impunctate or nearly so; midline broadly impunctate; lateral margins each with four long and erect black setae; pubescence of disc pale, thin, rather short, and more or less depressed.

Elytra (Fig. 52) approximately 0.85 times as long as pronotum; punctuation moderately coarse and moderately irregularly distributed, rather dense anteriorly, gradually becoming sparser posteriorly, and sparse to very sparse near posterior margin; disc with moderately long, fine, and depressed pale pubescence. Hind wings fully developed. Metatarsomere I approximately as long as, or slightly shorter than the combined length of II–IV.

Abdomen (Fig. 91) slightly narrower than elytra, with rather deep anterior impressions on tergites III–V; tergite II impunctate; anterior impressions of tergites III–V and anterior portion of tergite VI each with a transverse row of coarse, but weakly delimited pits of non-setiferous punctures; tergite III with a lateral setiferous puncture on either side and with a transverse row of six setiferous punctures near posterior margin; tergites IV–VI with a lateral setiferous puncture on either side and with 8–10 setiferous punctures at or near posterior margins; tergite VII with scattered fine non-setiferous punctures anteriorly and with two irregular transverse series of few setiferous punctures posteriorly, posterior margin with palisade fringe; tergite VIII (Figs 152, 154) with moderately dense dark setae in posterior third, without sexual dimorphism, posterior margin with distinct concavity.

♂: sternite VIII (Fig. 153) nearly as long as broad, much longer than tergite VIII, strongly tapering posteriorly and with distinctly truncate posterior margin; median lobe of aedeagus (Figs 150–151) 0.70–0.75 mm long; ventral process slender, subapically very slender, and apically very acute in lateral view; paramere approximately 0.85 mm long, apical lobe very long and slender.

♀: sternite VIII (Fig. 155) much shorter and more transverse than in male, posterior margin indistinctly concave in the middle.

**Comparative notes:** Based on several derived character conditions, particularly the slender body, long and slender antennae, a conspicuously irregular distribution of the pronotal punctuation, irregularly punctate elytra, the punctuation pattern of the pronotum, a posteriorly strongly tapering male sternite VIII with a distinctly truncate posterior margin, an apically very slender ventral process of the aedeagus, and a conspicuously long apical lobe of the paramere, **Z. truncatus** is undoubtedly very closely related to **Z. glabricollis** Scheerpeltz, 1965 from Northeast Myanmar and related species (**Z. extensus** Assing, 2016 and **Z. rectus** Assing, 2016, both from Northwest Yunnan, China). It is distinguished from all these species by a more slender pronotum with (more) distinctly sinuate lateral margins in posterior half and additionally as follows:

- from **Z. glabricollis** by more extensively blackish elytra and by a longer median lobe of the aedeagus with a less strongly curved ventral process in lateral view;
- from **Z. extensus** by denser punctuation of the more extensively blackish elytra and by a shorter median lobe of the aedeagus with an apically shorter and less slender ventral process of the aedeagus;
- from **Z. rectus** by more slender antennae (**Z. rectus**: antennomere IX not oblong), more densely and less irregularly distributed punctuation of the elytra, a posteriorly distinctly truncate male sternite VIII, and an aedeagus with an apically more slender ventral process (lateral view) and with a less prominent crista apicalis.

For illustrations of **Z. glabricollis**, **Z. extensus**, and **Z. rectus** see Assing (2016a).
**Distribution and natural history:** The specimens were collected in three close localities near Chitre in the Dhaulagiri range, Central Nepal (Map 3), at altitudes between 2400 and approximately 2500 m.

**Zyras (Zyras) longilobatus** spec. nov.

(Figs 24, 53, 89, 156–160, Map 9)

**Type material:** Holotype ♀: “NE INDIA, Meghalaya, Khasi Hills, Mawsynram, 25°18’N, 91°29’E, 800±100 m, P. Pacholátko leg. 5.–9.vi.2006 / BMNH(E) 29006-48” (Holotypus ♀ Zyras longilobatus sp. n., det. V. Assing 2016)” (BMNH). Paratypes: 2 ♀ ♀: same data as holotype (BMNH); 1 ♂: “NE INDIA, Meghalaya, SW of Cherrapunjee, 25°13’–14’N 91°40’E, 900 m, L. Dembický leg., 1–24.v.2005, BMNH 2006-48” (cAss).

**Etymology:** The specific epithet alludes to the conspicuously long apical lobe of the paramere.

**Description:** Body length 5.2–6.7 mm; length of fore-body 2.5–2.9 mm. Coloration (Figs 24, 53, 89: head and pronotum black; elytra dark-yellowish with the postero-lateral portions extensively black; abdomen black with the posterior margins of segments III–VI narrowly paler brown; legs pale-yellowish; antennae blackish with the basal two antennomeres pale-brown; maxillary palpi pale-brown with palpomere IV yellowish. Head (Fig. 53) distinctly transverse, median portion extensively impunctate; punctures in lateral portions sparse and moderately coarse. Eyes distinctly longer than postocular region in dorsal view. Antenna (Fig. 24) approximately 2.0 mm long; antennomeres IV weakly oblong or as long as broad, V approximately as long as broad or weakly transverse, VI–X increasingly transverse, X approximately 1.5 times as broad as long, and XI approximately as long as the combined length of IX and X.

Pronotum (Fig. 53) approximately 1.15 times as broad as long and approximately 1.35 times as broad as head, broadest in anterior half, weakly tapering posteriad; lateral margins straight or weakly convex in posterior two-thirds in dorsal view; punctuation rather coarse and moderately irregularly distributed, on either side of midline with extensive impunctate areas; midline broadly impunctate; lateral margins each with four long and erect black setae. Elytra (Fig. 53) 0.80–0.85 times as long as pronotum; punctuation rather coarse, dense, and defined, nearly regularly distributed, slightly less dense posteriorly than anteriorly; disc with short, fine, and depressed pale pubescence. Hind wings fully developed. Metatarsomere I approximately as long as the combined length of II–IV.

Abdomen (Fig. 89) slightly narrower than elytra, with rather deep anterior impressions on tergites III–V; tergite II with moderately sparse non-setiferous punctuation; anterior impressions of tergites III–IV each with a transverse row of rather weakly defined non-setiferous punctuation; anterior impression of tergite V with a transverse band of somewhat irregular non-setiferous punctuation; tergite III with a lateral setiferous puncture on either side and with four setiferous punctures at posterior margin; tergite IV with a lateral setiferous puncture on either side and with six–eight setiferous punctures near posterior margin; tergite V with a lateral setiferous puncture on either side and with 6–8 setiferous punctures at posterior margin; tergite VI anteriorly with a transverse band of non-setiferous punctures, with a lateral cluster of several setiferous punctures on either side, and with approximately ten setiferous punctures at posterior margin; tergite VII anteriorly with a transverse band of non-setiferous punctures and posteriorly with two transverse rows of setiferous punctures, posterior margin with palisade fringe; tergite VIII with long black setae in posterior third, posterior margin with sexual dimorphism. ♀: posterior margin of tergite VIII (Fig. 159) with a distinct median concavity, on either side of this concavity with a distinct acute process; sternite VIII (Fig. 160) distinctly shorter and less slender antennae, much less rugose, and a less derived morphology of the median lobe of aedeagus approximately 0.7 mm long and shaped as in Figs 156–157; paramere (Fig. 158) approximately 0.8 mm long, apical lobe very long and slender. ♂: posterior margin of tergite VIII with shallow median concavity, but without distinct process on either side of this concavity; posterior margin of sternite VIII distinctly concave in the middle.

**Comparative notes:** The conspicuously long and slender apical lobe of the paramere and the posteriorly strongly tapering male sternite VIII with a truncate posterior margin suggest that Z. longilobatus is somewhat allied to the Z. glabricollis group. It is, however, distinguished from other species of this group by distinctly shorter and less slender antennae, much less irregular punctuation of the pronotum, a relatively larger pronotum, much more regularly distributed punctuation of the elytra, distinctly shorter legs, much finer non-setiferous punctuation of the abdominal tergites III–V, and a less derived morphology of the median lobe of the aedeagus.

**Distribution and natural history:** The specimens were collected in two localities in Meghalaya, Northeast India (Map 9), at altitudes of approximately 800–900 m.
Zyras (Zyras) geminus (Kraatz, 1859)

(Map 6)

Myrmedonia gemina Kraatz, 1859: 27.
Zyras (Zyras) indicus Cameron, 1944: 108; syn. n.
Zyras (Zyras) shiva Pace, 1987b: 216 ff.; syn. n.
Zyras (Zyras) manjushri Pace, 1992: 142.; syn. n.
Zyras (Zyras) hongkongensis Pace, 1999: 684 ff.; syn. n.
Zyras (Zyras) benenensis Pace, 2001: 196 f.; syn. n.
Zyras (Zyras) parageminus Pace, 2010b: 319 ff.; preocc.; syn. n.
Zyras (Zyras) neoparageminus Hlaváč, Newton & Maruyama, 2011; replacement name; syn. n.
Zyras (Zyras) subgeminus Pace, 2012b: 339; replacement name; syn. n.
Zyras (Zyras) articollis Assing, 2016a: 172 ff.; syn. n.

Type material examined: M. gemina: see Assing (2016a).
Z. indicus: Holotype ♀: “974 / Anantapur, Mysore. E.A. Glennie, 17.X.1933 / At Light / Z. indicus Cam. Type / M. Cameron. Bequest. 1955-147. / Holotype / Holotype Zyras indicus Cameron, det. R.G. Booth 2010 / Zyras geminus (Kraatz), det. V. Assing 2016” (BMNH).
Z. shiva: Paratype ♀: “LOMBOK, Sesaut [=Sesaot], 12.IV.1981, Rougemont / Allotopus Zyras shiva det. R. Pace 1983 / Zyras shiva n. sp., det. R. Pace 1983 / Zyras geminus (Kraatz), det. V. Assing 2017” (cRou).
Z. manjushri: see comment below.
Z. hongkongensis: see Assing (2016a).
Z. benenensis: see Assing (2016a).
Z. articollis: see Assing (2016a).

Comment: According to the original description of Z. indicus, which is based on a unique specimen from “Mysore : Anantapur”, this species is distinguished from Z. geminus by a slightly more slender pronotum, shorter and stouter antennae, slight differences in the coloration of the antennae, finer and sparse punctuation of the pronotum, slightly finer and more asperate punctuation of the elytra, and fewer (non-setiferous) punctures on the abdominal tergites VI and VII (Cameron 1944).
An examination of the holotype, however, revealed that, even regarding the characters pointed out by Cameron (1944), it is highly similar to the type material of Z. geminus.
Zyras shiva was described based on a male holotype and a female paratype from “Lombok, Sesaut”, and a female paratype from “Bali, Lake Bratan” (Pace 1987b).
An examination of the paratype from the type locality revealed that it is conspecific with Z. geminus.
According to Pace (1992), the unique female holotype of Z. manjushri from “Nepal, Prov. Bagmati, Tarang Marang” is deposited in MHNG. A thorough search for this specimen in the collections of the MHNG, however, was unsuccessful (Cuccodoro, e-mail 1 June, 2016). Thus, the whereabouts of the holotype are unknown, it may even be lost. An examination of material of Z. geminus from Nepal (see additional material below and Assing (2016b)) revealed that it is in complete agreement with the details indicated in the original description of Z. manjushri, suggesting that the holotype, too, is conspecific with Z. geminus. This conclusion is even further confirmed by the following observation: two clearly conspecific specimens collected in the same locality and on the same date in Chitwan National Park, Nepal, had been identified by Pace: one of them as Z. geminus and the other as Z. manjushri (see additional material below).
The unique male holotype of Z. parageminus Pace, 2010 (a junior primary homonym of Z. parageminus Pace, 1988), which was collected in Sumatra, was not examined. However, the external characters pointed out in the original description as distinguishing Z. parageminus from Z. geminus fall within the range of intraspecific variation of Z. geminus (see below) and the shape of the median lobe of the aedeagus is identical (compare figures 67–68 in Pace (2010b) with figures 274–281 in Assing (2016a)). The synonymy of the two replacement names, Z. neoparageminus Hlaváč, Newton & Maruyama, 2011 and Z. subgeminus Pace, 2012, had already been established earlier (Assing 2015).
A study of the holotype of Z. indicus initiated a revision and comparison of material previously identified as Z. geminus, Z. hongkongensis, and Z. articollis (see Assing 2016a). This revision revealed that external characters believed to be species-specific earlier, such as the relative width of the pronotum, the extent of the non-setiferous punctuation of the abdomen, the punctuation of the elytra, and the coloration of the body appendages, as well as slight differences in the shape of the median lobe of the aedeagus (Assing 2016a: figures 274–281) are connected by intermediate conditions and somewhat variable even in specimens from the same region. Moreover, at least most of the more recent material appears to have been collected at light sources or with Malaise traps, as can be inferred from the labels or from the fact that the wings are fully unfolded, these observations suggesting pronounced flight activity and consequently a vast distribution. Pronounced intraspecific variation is generally observed particularly in widespread species. Based on these observations, it appears significantly more plausible to interpret slight differences of external and sexual characters as intra- rather than as interspecific variation. Hence the synonymies indicated above. Nevertheless, there appears to be a clinal trend for the non-setiferous punctuation of the abdomen to be more extensive and more pronounced in populations from the east than in populations from the west of the range of Z. geminus.
For morphological details and illustrations of external and sexual characters see the (re-)descriptions and figures provided for Z. hongkongensis, Z. articollis, and Z. geminus in Assing (2016a).

Additional material examined: Nepal: 1 ♀, Chitwan National Park, Sauraha, 700 m, at MV light, 3.–6.VI. 1983, leg. Brendell (NHMW); 2 ♀ [one identified by Pace as Z. geminus, the other as Z. manjushri], Chitwan
National Park, Sauraha, 27°35’N, 84°29’E, 180 m, bank of Rapti river, at light, 18.IV.2000, leg. Weigel (NME).

India: 1 ♂, Uttar Pradesh, Almora Div., Kumao, leg. Champion (BMNH); 1 ♂, Assam, Bhalukpong, 27°02’N, 92°35’E, 150 m, 26.V.–3.VI.2006, leg. Dembicky (cAss).

Thailand: 1 ♂, Chiang Mai, Thaton, 20°04’N, 99°22’E, 460 m, riverside, at light, 22.VII.2006, leg. Mendel & Barclay (BMNH); 1 ♂, Betong, Yala district, Gunung Cang dun vill., 25.III.–22.IV.1993, leg. Horak & Strnad (cAss). Vietnam: 6 exs., Hoa Binh, leg. de Cooman (MHNG, cAss). Japan: Ryukyu Islands: 2 exs., Ishigaki-jima, Tonoshiro, light trap, 21.V.1999, leg. Shimada (cAss); 1 ex., Ishigaki-jima, Shiramizu, light trap, 8.V.1993, leg. Hayashi (cAss).

Distribution and natural history: The currently known, vast distribution ranges from Nepal, India, and Sri Lanka across South China, Thailand, Laos, and Vietnam eastwards to South Japan and southeastwards to Indonesia (Sumatra, Java, Lombok, Bali) (Map 6); for previous records see Assing (2016a) (as *Z. hongkongensis*).

The specimens known at present were collected at low altitudes, primarily at light sources.

*Zyras* ([*Zyras*] *hastatus* Fauvel, 1904

(Figs 16, 54, 90, Map 7)

*Zyras hastatus* Fauvel, 1904: 64.

Type material examined: Syntypes: 1 ♂: "Belgaum / *hastata* Fvl. / Coll. I.R.Sc.N.B. / Syntypus *Zyras hastatus* Fauvel, rev. V. Assing 2016" (IRSNB); 1 ♂ [damaged; both antennae missing]: "Cotype / Belgaum / 1266 / *hastata* Fvl. / Syntypus ♂ *Zyras hastatus* Fauvel, rev. V. Assing 2016" (BMNH).

Comment: The original description is based on at least two syntypes ("Sexus differentia latet") from "Belgaum" (Fauvel 1904). One syntype was located in the collections of the IRSNB and another in the collections of the BMNH. Both syntypes are females.

Redescription: Body length 4.1–6.0 mm; length of forebody 2.1–2.8 mm. Coloration (Figs 16, 54, 90): head black; pronotum pale-reddish; elytra reddish-yellow; with the postero-lateral portion extensively blackish (leaving only the scutellum and its vicinity, the anterior margin, and the suture reddish-yellow); abdomen bicoloured with tergites II–V pale-reddish, tergite VI black with the anterior margin and the antero-lateral portions reddish, and tergites VII–VIII black; legs pale-yellowish; antennae dark-brown with antennomeres I–III dark-reddish and the apical half of antennomere XI dark-reddish; maxillary palp reddish with the terminal palpomere yellowish.

Head (Fig. 54) moderately transverse, median portion extensively impunctate; punctures in lateral portions moderately dense and large, but shallow. Eyes moderately large, but weakly convex, much longer than postocular region in dorsal view. Antenna (Fig. 16) 1.75 mm long; antennomeres IV approximately as long as broad, V weakly transverse, VI–X of gradually increasing width and increasingly transverse, X approximately 1.5 times as broad as long, and XI conspicuously elongate, nearly as long as the combined length of VII–X.

Pronotum (Fig. 54) distinctly transverse, approximately 1.2 times as broad as long and 1.3 times as broad as head, broadest anterior to middle; lateral margins smoothly convex (dorsal view); punctuation not very coarse, rather sparse, and somewhat irregularly distributed; midline narrowly impunctate; lateral margins each with four long, black setae, anterior margin with an additional long black seta on either side.

Elytra (Fig. 54) 0.85 times as long as pronotum; punctuation moderately coarse, defined, rather dense, and regularly distributed; interstices on average distinctly broader than diameter of punctures. Hind wings fully developed. Metatarsomere I approximately as long as the combined length of II–IV.

Abdomen (Fig. 90) narrower than elytra, with deep anterior impressions on tergites III–V; anterior impressions of tergites III–V each with a transverse row of non-setiferous punctures; tergite III with a lateral long brown seta on either side, posterior margin with three long brown setae on either side and with a median pair of fine short yellowish setae; tergites IV–V with a median pair of punctures, with a lateral seta on either side, posterior margins with four long brown setae on either side, and with a median pair of minute pale setae; tergite VI anteriorly only with few shallow non-setiferous punctures laterally (without such punctures in the middle), with a median pair of punctures, and with approximately 12 setiferous punctures at posterior margin, otherwise impunctate (except for scattered micropunctures); tergite VII anteriorly with a transverse row (not band!) of sparse non-setiferous punctures, with a transverse row of six setiferous punctures at posterior third, and with additional setiferous punctures at posterior margin; tergite VIII with rather sparse long seta only in posterior portion, posterior margin convex, in the middle with indistinct and small concavity.

♂: unknown.

Comparative notes: Among the species of similar coloration (e.g., *Z. beijingensis* Pace, 1993), *Z. hastatus* is characterized by slender antennae with a conspicuously elongate antennomere XI, a relatively strongly transverse pronotum with smoothly convex lateral margins, and the punctuation pattern of the abdomen (particularly of tergites VI and VII).

Distribution: This species is currently known only from the type locality in South India (Map 7).
**Zyras (Zyras) parageminus** (Pace, 1988)

(Figs 17–18, 55–56, 98, Map 7)

**Zyras (Zyras) parageminus** Pace, 1988: 335.

**Zyras (Zyras) nameriensis** Pace, 2011: 36; syn. n.

**Type material examined:** Z. parageminus: Holotype ♀:
"CEYLON, Habarane, 26.III.83, Rougemont / Holotypus Zyras (s. str.) parageminus m., det. R. Pace 1982 / Zyras (s. str.) parageminus n. sp., det. R. Pace 1982 / Zyras parageminus Pace, det. V. Assing 2016" (MCSNV).

Z. nameriensis: Holotype ♀: "INDIA Assam, Nameri N.P., 27.v.2006, G. de Rougemont / Holotypus Zyras nameriensis mihi, det. R. Pace 2010 / Zyras nameriensis n. sp., det. R. Pace 2010 / Zyras parageminus Pace, det. V. Assing 2016" (cRou).

**Comment:** The original description of **Z. parageminus** is based on a unique female from "Sri Lanka, Habaranaz [sic]" (Pace 1988), and of **Z. nameriensis** on a unique male from "India, Assam, Nameri N.P." (Pace 2011). In the description of the latter, Pace (2011) compares the species with **Z. geminus**, but there is no mention of **Z. parageminus**. A comparative study of the two holotypes, however, reveals that they are highly similar, except that the basal two antennomeres are yellowish-red in the holotype of **Z. parageminus** and dark-brown in that of **Z. nameriensis**, and that antennomeres IV–VI are somewhat more transverse in the holotype of **Z. parageminus** than in that of **Z. nameriensis**. It can be inferred from the general condition of the holotype (partly deformed antennomeres, elytra, legs, and abdominal segments; rather dark coloration of pronotum and anterior abdominal segments) that the coloration and other external characters have changed post-mortem, evidently as a result of improper treatment during original dissection (boiling? chemical?), so that the observed differences are most likely artefacts. In any case, the observed differences are insufficient to support the hypothesis that the two holotypes should represent different species, so that **Z. nameriensis** is placed in synonymy with **Z. parageminus**.

**Redescription:** Rather small species; body length 4.5–4.9 mm; length of forebody 2.0–2.2 mm. Coloration (Figs 17–18, 55–56, 98): head and pronotum black; pronotum bright-reddish; abdomen bicoloured with tergites II–V and the anterior margin of tergite VI reddish and the remainder black; legs pale-yellowish; antennae brown to dark-brown with the basal two antennomeres yellowish-red to dark-brown and antennomere XI pale-brown to brown; maxillary palpi dark-yellowish with the terminal palpomere yellowish.

Head (Figs 55–56) distinctly transverse, median portion extensively impunctate; punctures in lateral portions moderately sparse to moderately dense and fine; pubescence long, pale, and sub-erect. Eyes moderately large, much longer than postocular region in dorsal view. Antenna (Figs 17–18) 1.3–1.4 mm long and distinctly incrassate apically; antennomeres IV weakly to moderately transverse, VI–X of gradually increasing width and increasingly transverse, X at least twice as broad as long, and XI rather short and of conical shape, approximately as long as the combined length of IX and X.

Pronotum (Figs 55–56) distinctly transverse, 1.14–1.15 times as broad as long and 1.25–1.27 times as broad as head, broadest anterior to middle; lateral margins very weakly sinuate in posterior half (dorsal view); punctuation of whole disc including midline rather dense and shallow; lateral and anterior margins with numerous long and erect black setae; disc with moderately long and sub-erect pale pubescence.

Elytra (Figs 55–56) approximately 0.8 times as long as pronotum; punctuation moderately fine, rather dense, and regularly distributed. Hind wings fully developed. Legs not particularly slender and with rather short tarsi; meta- tarsomere I approximately as long as the combined length of II and III.

Abdomen (Fig. 98) narrower than elytra, with deep anterior impressions on tergites III–V; anterior impressions of tergites III–V each with a transverse row of weakly defined small impressions; posterior portions of tergites III–V with rather numerous setiferous punctures bearing long dark and moderately long pale setae on disc and at posterior margins; tergites VI and VII anteriorly with moderately dense non-setiferous punctuation and posteriorly with irregular setiferous punctuation, posterior margin with palisade fringe; tergite VIII with setiferous punctuation only in posterior portion, posterior margin weakly concave to truncate.

♂: median lobe of aedeagus approximately 0.55 mm long and shaped as illustrated in Pace (2011: figures 39–40); paramere approximately as long as median lobe and with moderately short apical lobe.

**Comparative notes:** **Zyras parageminus** differs from other similarly coloured representatives of the subgenus **Zyras** by smaller size, shorter and apically much more incrassate antennae, the absence of an impunctate median band on the pronotum, the punctuation pattern of the abdomen, and by the shape of the median lobe of the aedeagus.

**Distribution:** The known distribution is confined to two localities in Sri Lanka and Northeast India (Assam) (Map 7).

**Zyras (Zyras) latilobatus** spec. nov.
[urn:lsid:zoobank.org:act:AD282BC4-9922-4004-97DE-0E84F5B8634F](urn:lsid:zoobank.org:act:AD282BC4-9922-4004-97DE-0E84F5B8634F)

(Figs 19, 57, 92, 161–165, Map 7)

**Type material:** Holotype ♂: "INDIA: Kerala, Ponmudi hill resort, 30 km NE of Trivandrum, 77°06′E; 8°46′N [sic], 1400 m, 28–39.vi.99 [sic], Kejval & Tryzna lgt. / Holotypus ♂ Zyras latilobatus sp. n., det. V. Assing 2016" (NMP). Paratypes: 2 ♂ 1♀: same data as holotype (NMP, cAss).
Etymology: The specific epithet is a composed adjective and alludes to the broad (latus) ventral process of the aedeagus.

Description: Body length 4.3–5.0 mm; length of forebody 1.9–2.2 mm. Coloration (Figs 19, 57, 92): head black; pronotum pale-reddish; elytra reddish-yellow with the posterolateral portion more or less extensively blackish (sometimes leaving only the scutellum and its vicinity, the anterior margin, and the humeral angles reddish-yellow); abdomen bicoloured with tergites II–V pale-reddish, tergite VI pale-reddish with the middle and the posterior portion extensively blackish, tergite VII black with the anterior margin and the anterolateral portions reddish, segment VIII black, and segments IX–X yellowish; legs yellowish; antennae reddish to brown with the basal and apical antennomeres more or less extensively pale-reddish; maxillary palpi yellowish.

Head (Fig. 57) moderately transverse, median portion extensively impunctate; punctures in lateral portions rather sparse and fine. Eyes large, much larger than postocular region in dorsal view. Antenna (Fig. 19) conspicuously slender, approximately 1.9 mm long; antennomeres IV distinctly oblong, V–VIII decreasingly oblong, IX–X as approximately as long as broad or weakly oblong, and XI elongate, approximately three times as long as broad and as long as the combined length of VIII–X, or nearly so.

Pronotum (Fig. 57) slender, 1.04–1.07 times as broad as long and 1.1 times as broad as head, broadest near anterior angles; lateral margins straight (dorsal view); punctuation not very coarse, rather dense, and regularly distributed, even along midline (i.e., median impunctate band absent). Elytra (Fig. 57) approximately 0.8 times as long as pronotum; punctuation rather fine and dense, and regularly distributed, only slightly less dense posteriorly than anteriorly. Hind wings fully developed. Metatarsomere I approximately as long as the combined length of II–IV.

Abdomen (Fig. 92) slightly narrower than elytra, with moderately deep anterior impressions on tergites III–V; anterior impressions of tergites III–V each with a transverse row of very coarse non-setiferous punctures; tergites III–IV with a lateral setiferous puncture on either side, and with four setiferous punctures at posterior margin; tergite V with a lateral setiferous puncture on either side, and with six setiferous punctures at posterior margin; tergites VI without non-setiferous punctuation anteriorly, with a lateral setiferous puncture on either side, and with six setiferous punctures at posterior margin; tergite VII without non-setiferous punctuation anteriorly, with two transverse series of fine setiferous punctures posteriorly, posterior margin with palisade fringe; tergite VIII (Fig. 164) with setiferous punctures in posterior third, posterior margin smoothly convex, without median concavity.

♂: sternite VIII (Fig. 165) with convex posterior margin; median lobe of aedeagus (Figs 161–162) of compact shape, approximately 0.45 mm long; ventral process of distinctive shape, short, basally broad, apically acute in ventral view, and apically truncate in lateral view; paramere (Fig. 163) slightly shorter than median lobe, with very short and apically truncate apical lobe.

Comparative notes: Zyras latilobatus differs from other species of similar coloration by numerous characters, particularly the conspicuously slender and pale-coloured antennae, a slender pronotum without an impunctate median band, the presence of rather coarse non-setiferous punctuation in the anterior impressions of tergites III–V, but absence of such punctuation in the anterior portions of tergites VI–VII, a smoothly convex posterior margin of tergite VIII (without median concavity), and particularly the distinctive shape of the ventral process of the aedeagus. It is readily distinguished from the similarly coloured Z. hastatus, whose male sexual characters are unknown, by smaller size and especially by much more slender antennae.

Distribution: This species is currently known only from the type locality in Kerala, South India (Map 7).

Zyras (Zyras) alternans (Cameron, 1925)
(Figs 20, 58, 99, 166–169, Map 8)

Myrmedonia (Zyras) alternans Cameron, 1925: 45 f.
Zyras (Zyras) optimus Cameron, 1939a: 534; syn. n.

Type material examined: Z. optimus: Holotype ♀: "Nilgiri Hills / Z. optimus Cam. Type / Zyras optimus Fvl n. sp., Désiré / M. Cameron. Bequest. 1955-147. / Holotype / Holotype Zyras optimus Cameron 1939, det. R.G. Booth 2016 / Zyras alternans (Cameron), det. V. Assing 2016" (BMNH).

Comment: Zyras alternans was described based on an unspecified number of syntypes from “Sumatra, Lago Toba” (Cameron 1925). The type material deposited in the natural history museum in Genoa was revised and illustrated by Pace (2010b), who erroneously inferred from the type label attached to one of the specimens that it was the holotype.

The original description of Z. optimus is based on a unique holotype from “Nilgiri Hills” (Cameron 1939a). This specimen is a female, but the male sexual characters, particularly the distinctive aedeagus, of the additional specimens examined from India and other regions (see below) are identical to those of the “holotype” of Z. alternans as figured by Pace (2010b). Thus, the holotype of Z. optimus is undoubtedly conspecific with the type material of Z. alternans.

Additional material examined: India: 1 ♂, Uttarakhand, left side of Kosi River, 5 km N Rannagar, "N29°432 E79°140” [sic], 7–11.VI.2011, leg. Shavrin (cAss); 1 ♂, Tamil Nadu, Nilgiri Hills, Coonoor, 1700 m,
Assing, V: On *Zyras* sensu strictu in the East Palaearctic and Oriental regions

3.–5.X.1991, leg. Schuh (cAss); 1 ♀, Arunachal Pradesh, 8 km S Jamiri, Sessa env., 27°07′–09′N, 92°34′E, 350 m, 26.V.–4.VI.2005, leg. Dembický (BMNH).

Malaysia:

3.–5.X.1991, leg. Schuh (cAss); 1 ♀, Johor, 15 km N Lombong, Kota Tinggi, 27.–30.VII.1992, leg. Schuh (cAss). Indonesia:

1 ♀, West Java, Bogor, 6°33′S, 106°44′E, 180 m, rice field, flight interception trap, 6.VI.2011, leg. Puspitasari.

8 km S Jamiri, Sessa env., 27°07′–09′N, 92°34′E, 350 m, 3°56′N, 101°38′E, 300 m, 22.IV.–15.V.2002, leg. Jendek.

Indonesia:

250 m, flight interception trap, 20.I.–7.II.2004, leg. Barries & Cate (cAss); 80 m, base camp surrounded by *Acacia* plantation, Pahang district, 30 km NE Raub, Laba Lembik, West Java, Bogor, Kebun Raya Bogor, 1°16′S, 116°21′E, 1°16′S, 116°21′E, 80 m, rice field, flight interception trap, 6.VI.2011, leg. Puspitasari (cMar); 1 ♀, Jawa Barat, Bogor, 16 km S Kuta-cane, 350 m, 18.VIII.1992, leg. Barries & Cate (cAss); 1 ♀, 1 ♀, Borneo, E-Kalimantan, 55 km W Balikpapan, PT Fajar Surya Swadaya [area], 3°56′N, 101°38′E, 300 m, 22.IV.–15.V.2002, leg. Jendek.

**Redescription:**

Body length 6.8–7.0 mm; length of forebody 3.0–3.3 mm. Coloration (Figs 20, 58, 99): head black; pronotum pale-reddish; abdomen reddish, with tergite VI reddish or extensively blackish (except for the anterior margin and the antero-lateral portions) and tergite VII always blackish (except for the anterior margin and the antero-lateral portions); legs pale-yellowish; antennae blackish; maxillary palpi blackish-brown with the terminal palpomere pale-yellowish.

Head (Fig. 58) transverse, 1.22–1.27 times as broad as pale-yellowish. palpi blackish-brown with the terminal palpomere legs pale-yellowish; antennae blackish; maxillary palpi blackish-brown with the terminal palpomere pale-yellowish.

Pronotum (Fig. 58) 1.15–1.18 times as broad as long and 1.28–1.30 times as broad as head, broadest in anterior half, distinctly tapering posteriad; lateral margins straight in posterior half (dorsal view); punctuation coarse, rather sparse, and irregularly distributed; laterally with extensive impunctate patches; midline broadly impunctate; lateral margins and antero-lateral portions with numerous long brown setae.

Elytra (Fig. 58) 0.80–0.87 times as long as pronotum; punctuation coarse and defined, subject to sexual dimorphism; scutellum coarsely and granulously sculptured anteriorly and smooth posteriorly. Hind wings fully developed. Metatarsomere I approximately as long as the combined length of IX and X.

Abdomen (Fig. 99) slightly narrower than elytra, with moderately deep anterior impressions on tergites III–V; tergite II with coarse non-setiferous punctuation; tergites III–IV each with a transverse row or band of coarse non-setiferous punctures in anterior impressions, with a lateral setiferous puncture on either side, and with 4–6 setiferous punctures at posterior margins; tergite V with a transverse row or band of coarse non-setiferous punctures in anterior impression, with or without a median pair of setiferous punctures, with a lateral setiferous puncture on either side, and with 6–8 setiferous punctures at posterior margin; tergite VI with a more or less extensive transverse band of coarse non-setiferous punctures anteriorly, with one or few lateral punctures on either side, and with 6–8 setiferous punctures at posterior margin; tergite VII with a more or less extensive transverse band of numerous non-setiferous punctures anteriorly, with one or two transverse series of setiferous punctures posteriorly; tergite VIII (Fig. 168) with approximately 20 black setae posteriorly, posterior margin more or less distinctly concave in the middle.

♂️: punctation of elytra very dense and asperate near anterior margin and near scutellum; sternite VIII (Fig. 169) with convex posterior margin; median lobe of aedeagus 0.72–0.78 mm long and shaped as in Figs 166–167; ventral process very short and apically hooked in lateral view; paramere 0.83–0.90 mm long, with very short apical lobe.

♀️: punctation of elytra defined and clearly separated, not asperate, only slightly denser anteriorly than posteriorly.

**Intraspecific variation:** The coloration of tergite VI, the punctuation of the elytra, and the non-setiferous punctuation of the abdomen appear to be highly variable in this species. Tergite VI is extensively infuscate in the middle and posteriorly in the holotype and the specimens seen from Arunachal, Malaysia and Indonesia, whereas it is uniformly reddish in the remaining non-type specimens from India.

**Comparative notes:** *Zyras alternans* is distinguished from other sympatric species with a similar colour pattern by its relatively large size, robust body, black antennae, the coarse non-setiferous punctuation of the abdomen, and above all by the distinctive shape of the median lobe of the aedeagus.

**Distribution and natural history:** Records from North and South India, as well as from Malaysia, West Java, Sumatra, and Borneo (Map 8) indicate a vast distribution of *Z. alternans*. The altitudes range from 80 to 1700 m. At least most of the specimens were collected on the wing.

*Zyras* (*Zyras*) *hirtus* (Kraatz, 1859)

(Figs 21, 55, 95, 170–173, Map 7)

*Myrmedonia* *hirta* Kraatz, 1859: 25.

**Comment:** The female holotype from “Ceylon” was revised by Assing (2016a), who reported additional records from Sri Lanka and South India.
Material examined: India: 1 ♀, Madras, 15 km E Coonoor, 800 m, 19.XII.1972, leg. Besuchet, Löbl & Mussard (MHNG).

Redescription: Rather large species: body length 6.4–7.8 mm; length of forebody 2.7–3.5 mm. Coloration (Figs 21, 59, 95): body pale-reddish to reddish-brown, rarely with abdominal segment VI somewhat darker; legs yellowish; antennae brown to blackish, with the basal 1–2 and the apical 1–4 antennomeres yellowish to pale reddish; maxillary palpi dark-yellowish with palpmere IV paler yellowish.

Head (Fig. 59) distinctly transverse, median portion extensively impunctate; punctures in lateral portions moderately sparse and moderately coarse; pubescence long and sub-erect to erect. Eyes much larger than postocular region in dorsal view. Antenna (Fig. 21) 1.8–2.2 mm long and distinctly incarnate; antennomeres IV weakly oblong to weakly transverse, V as long as broad or weakly transverse, VI–X of increasing width and increasingly transverse, 2.0–2.5 times as broad as long, and XI short, shorter than the combined length of IX and X.

Pronotum (Fig. 59) of variable shape, 1.09–1.21 times as broad as long and approximately 1.3 times as broad as head, broadest in anterior half; punctuation rather dense, very shallow, and regularly distributed; midline narrowly to broadly impunctate; pubescence suberect and rather long, pale on disc, brown and longer along lateral margins and in antero-lateral portion.

Elytra (Fig. 59) 0.85–0.90 times as long as pronotum; punctuation rather fine, very dense, and shallow, regularly distributed; whole disc with dense and long sub-erect brown pubescence. Hind wings fully developed. Metatarsomere I approximately as long as, or shorter than the combined length of II–IV.

Abdomen (Fig. 95) approximately as broad as elytra, with rather deep anterior impressions on tergites III–V; anterior impressions of tergites III–V each with a transverse row of moderately coarse non-setiferous punctures; tergites III–V with moderately dense and fine setiferous punctuation on disc and at posterior margins; tergite VI with a transverse row or band of non-setiferous punctures anteriorly and with moderately dense setiferous punctuation on disc and at posterior margin; tergite VII with more or less extensive non-setiferous punctuation anteriorly and with moderately sparse to moderately dense setiferous punctuation not arranged in distinct rows in posterior portion, posterior margin with palisade fringe; tergite VIII with rather dense and long yellowish setae in posterior half, posterior margin shallowly concave in the middle; all sternites with long brown pubescence.

♀: posterior margin of sternite VIII convex, in the middle more or less distinctly truncate; median lobe of aedeagus (Figs 170–173) 0.88–1.0 mm long; ventral process subapically angled and apically very acute in lateral view; paramere 0.75–0.80 mm long and with very short and broad apical lobe.

♀: posterior margin of sternite VIII weakly concave in the middle.

Intraspecific variation: The examined specimens from South India differ from those from Sri Lanka by distinctly darker antennae with less transverse antennomeres V–X, a less transverse pronotum, and slightly larger body size. The median lobe of the aedeagus, however, is of nearly identical shape. Therefore, and in view of the rather few specimens examined so far, these differences are interpreted as intra- rather than interspecific variation.

Comparative notes: *Zyras hirtus* is readily distinguished from other species of the *Z. hihurst* group recorded from India and Sri Lanka by the more or less uniformly reddish coloration of the body, by distinctly transverse preapical antennomeres, by the punctuation pattern of the abdomen (particularly the rather dense setiferous punctuation on all tergites), and by the shape of the median lobe of the aedeagus.

Distribution and natural history: The confirmed distribution is confined to Sri Lanka and South India (Map 7). For additional records see Assing (2016a). The altitudes of the known localities range from 300 to 900 m.

*Zyras (Zyras) gardneri* Cameron, 1939

(Figs 40, 62, 96, 174–177, Map 7)

*Zyras (Zyras) gardneri* Cameron, 1939a: 538.

Type material examined: Holotype ♀: “Darjeeling 6000, Bengal., J.C.M. Gardner. IX.1929. / Z. Gardneri Cam Type / M. Cameron. Bequest. B.M. 1955-147 / Holotype / Holotype Zyras gardneri Cam., 1939, det. R.G. Booth 2016 / Holotypus Zyras gardneri Cameron, rev. V. Assing 2016” (BMNH).

Comment: The original description is based on a unique male holotype from “Darjeeling, alt. 6000 feet” (Cameron 1939a).

Additional material examined: Nepal: 1 ♂, 1 ♀, Tama Koshi valley, Chet Chet, 1300 m, 3.VI.2000, leg. Schmidt (cKle, cAss). India: 1 ♀, Uttarakhand, Uttarkashi district, Naluna Sainj env., 30°45’N, 78°34’E, wet litter, 10.–12.IV.2012, leg. Shavrin (cAss); 1 ♂, 4 ♀, Meghlaya, Khasi Hills, Mawsynram, 25°18’N, 91°29’E, 700–900 m, 5.–9.VI.2006, leg. Pacholátko (BMNH, cAss).

Redescription: Large species: body length 6.7–8.3 mm; length of forebody 3.5–3.9 mm. Coloration (Figs 40, 62, 96): head black; pronotum brown to blackish-brown; elytra reddish to reddish-brown, with the postero-lateral
portions diffusely darker; abdomen more or less distinctly bicoloured; tergites II–IV reddish to dark-brown, V–VII (except for the anterior margin of V) dark-brown to blackish, and VIII brown to dark-brown; legs yellowish; antennae bicoloured, blackish-brown with antennomeres IX–XI yellowish; maxillary palpi dark-brown with palpmere IV yellowish to yellow-brown.

Head (Fig. 62) distinctly transverse, median portion extensively impunctate; punctures in lateral portions moderately sparse and moderately coarse. Eyes much longer than postocular region in dorsal view. Antenna (Fig. 40) 2.7–3.0 mm long and rather slender; antennomeres IV–VI oblong, VII approximately as long as broad, VIII–X weakly transverse, X much less than 1.5 times as broad as long, and XI short, shorter than the combined length of IX and X.

Pronotum (Fig. 62) moderately transverse, approximately 1.15 times as broad as long and approximately 1.3 times as broad as head, broadest in anterior half; punctation rather fine and moderately dense, almost regularly distributed; midline narrowly impunctate; anterior margin and anterior half of lateral margins with numerous long brown setae.

Elytra (Fig. 62) 0.85–0.90 times as long as pronotum; punctation moderately coarse, very dense, and defined, regularly distributed; whole disc with dense and sub-erect brown pubescence. Hind wings fully developed. Metatarsomere I approximately as long as, or shorter than, the combined length of II–IV.

Abdomen (Fig. 96) approximately as broad as elytra, with moderately deep anterior impressions on tergites III–V; anterior impressions of tergites III–V each with a transverse row of moderately coarse non-setiferous punctures; tergites III–V with sparse micropunctuation on disc, with a lateral setiferous puncture on either side, and with several setiferous punctures at posterior margins; tergite VI with extensive non-setiferous punctures in anterior half to anterior three-fourths, with micropunctuation in posterior portion with some lateral setiferous punctures and with several setiferous punctures at posterior margin; tergite VII with more or less extensive non-setiferous punctuation in anterior half and with moderately sparse setiferous punctuation not arranged in distinct rows in posterior half, posterior margin with palisade fringe; tergite VIII (Fig. 176) with rather dense and long brown setae in posterior third, posterior margin shallowly concave in the middle; all sternites with long brown pubescence posteriorly.

♂: posterior margin of sternite VIII strongly convex (Fig. 177); median lobe of aedeagus (Figs 174–175) approximately 1.1 mm long; ventral process somewhat constricted basally in ventral view; crista apicalis small; paramere approximately 1.05 mm long and with very short apical lobe.

♀: posterior margin of sternite VIII weakly concave in the middle.

Comparative notes: As can be inferred from external (dense and long pubescence on the forebody and on the abdominal sternites; broad pronotum; rather large body size), as well as from the male sexual characters (apical lobe of paramere very short), Z. gardneri belongs to the Z. hirtus group. Among the species of this group, it is characterized by the coloration (particularly of the antennae), the punctuation pattern of the abdomen, and by the morphology of the median lobe of the aedeagus.

Distribution and natural history: The known distribution is confined to several localities in Nepal and North India (Map 7). The altitudes range from approximately 800 to 1800 m.

Zyras (Zyras) hirsutiventris (Champion, 1927)
(Figs 13, 63, 97, 178–181, Map 7)

Myrmedonia (Zyras) hirsutiventris Champion, 1927: 245.

Type material examined: Holotype ♀: “3573 / 3573 / 1929. 3a7 / C. Almora Dn. Kumaon, U.P., July ‘20 HGC. / Myrmedonia (Zyras) hirsutiventris Ch. Type / Holotype / Holotype Myrmedonia (Zyras) hirsutiventris Champ., det. R.G. Booth 2016” (BMNH).

Comment: The original description is based on a unique specimen from “Central Almora, Kumaon” (Champion 1927).

Additional material examined: Nepal: 1 ♂, Khandbari district, Arun river, Numb, 1500–1600 m, 1927.

Redescription: Large species: body length 6.5–7.5 mm; length of forebody 2.9–3.3 mm. Coloration (Figs 13, 63, 97): forebody black; abdomen blackish-brown to black; legs dark-yellowish, with the profemora dark-brown and the apical two-fifths or the apical halves of the meso- and metafemora blackish; antennae blackish, with the basal three antennomeres dark-brown; maxillary palpi dark-brown with palpmere IV yellowish.

Head (Fig. 63) distinctly transverse, median portion extensively impunctate; punctures in lateral portions moderately sparse and moderately coarse. Eyes longer than postocular region in dorsal view. Antenna (Fig. 13) 2.1–2.5 mm long and rather slender; antennomeres IV oblong or as long as broad, V–VI approximately as long as broad or weakly transverse, VII–X of increasing width and increasingly transverse, X approximately 1.5 times as broad as long, and XI of distinctly conical shape, short, much shorter than the combined length of IX and X.

Pronotum (Fig. 63) approximately 1.15 times as broad as long and approximately 1.3 times as broad as head, broadest in anterior half; lateral margins distinctly sinuate in

Assing, V: On Zyras sensu strictu in the East Palaearctic and Oriental regions
posterior half in dorsal view; punctuation rather fine and dense, regularly distributed; midline narrowly impunctate; pubescence brown, long, and sub-erect to erect. Elytra (Fig. 63) approximately 0.9 times as long as pronotum; punctuation dense and fine, only slightly less dense posteriorly than anteriorly; whole disc with dense and sub-erect brown pubescence. Hind wings fully developed. Metatarsomere I nearly as long as the combined length of II–IV.

Abdomen (Fig. 97) approximately as broad as elytra, with moderately deep anterior impressions on tergites III–V; anterior impressions of tergites III–V each with a transverse row of shallow and indistinct grooves (not punctuation); tergites III–V each with two transverse rows of rather numerous setiferous punctures posteriorly; tergite VI with extensive non-setiferous punctuation in anterior half, with micropunctuation and with scattered setiferous punctures in posterior half; tergite VII with non-setiferous punctuation in anterior half and with setiferous punctuation not arranged in distinct rows in posterior half, posterior margin with palisade fringe; tergite VIII (Fig. 180) with moderately dense punctuation everywhere, except near anterior margin, posterior margin shallowly concave in the middle; all sternites with long brown pubescence posteriorly.

\( \sigma: \) sternite VIII (Fig. 181) strongly convex posteriorly; median lobe of aedeagus (Figs 178–179) 0.78–0.83 mm long; paramere 0.87 mm long and with short apical lobe.

Comparative notes: Like Z. gardneri, this species belongs to the Z. hirtus group. It is readily distinguished from Z. gardneri by the different coloration of the antennae, the elytra, the abdomen, and the legs, by less slender antennae with distinctly more transverse preapical antennomeres, as well as by the different punctuation pattern of the abdomen. Regarding the shape of the ventral process of the aedeagus, Z. hirsutiventris is similar to Z. flexus Assing, 2016 from Fujian (China), from which it differs by darker coloration of the whole body (including the legs and antennae) and the larger aedeagus (Z. flexus: length of median lobe 0.7 mm) with an apically less strongly angled ventral process (lateral view). For illustrations of Z. flexus see Assing (2016a).

Distribution and natural history: The currently known distribution is confined to three localities in North India (Uttarakhand, Assam) and Nepal (Map 7). The above male from East Nepal was already reported by Pace (1992). The altitudes range from 150 to approximately 1550 m.

\[ \text{Zyras (Zyras) luteipes} \]

Type material: Holotype \( \sigma: \) “NE INDIA Meghalaya, Khasi Hills, Mawsynram, 25°18’N 91°29’E, 800±100 m, P. Pacholátko leg., 5.–9.vi.2006 / BMNH(E), 2006–48 / Holotypus Zyras luteipes sp. n., det. V. Assing 2016” (BMNH).

Etymology: The specific epithet is a noun in apposition composed of the Latin adjective luteus (yellow) and the Latin noun pes (foot). It alludes to the nearly uniformly yellowish legs, one of the characters distinguishing this species from the similar Z. hirsutiventris.

Description: Large species: body length 7.5 mm; length of forebody 3.2 mm. Coloration (Figs 23, 64, 100): forebody black; abdomen blackish-brown; legs dark-yellowish, with the apices only indistinctly and narrowly darker; antennae blackish, with the basal three antennomeres brown and antenomem XI dark-reddish; maxillary palpi blackish-brown with palpomere IV yellowish.

Other external characters (Figs 23, 64, 100) as in Z. hirsutiventris, except as follows: Tergites III–V with distinct and moderately dense micro-punctuation in posterior three-fifths.

\( \sigma: \) sternite VIII as in Fig. 185; sternite VIII (Fig. 186) less strongly convex posteriorly; median lobe of aedeagus (Figs 182–183) 0.85 mm long; ventral process apically more acute both in lateral and in ventral view, and less distinctly angled subapically in lateral view; paramere (Fig. 184) 0.87 mm long and with short apical lobe.

Comparative notes: Zyras luteipes is evidently very closely related to Z. hirsutiventris, from which it is only distinguished by the coloration of the legs and the antennae, the micropunctuation on the abdominal tergites III–V, and by the shape of the ventral process of the aedeagus.

Distribution and natural history: The type locality is situated in Meghalaya (Map 8) at an altitude of approximately 800 m.

\[ \text{Zyras (Zyras) nilgiriensis} \]

Type material examined: Holotype \( \sigma: \) “Nilgiri Hills. A.K. Weld Downing / a 967 / Z. nilgiriensis Cam. Type / M. Cameron. Bequest. B.M. 1955–147. / Holotype / Holotype Zyras nilgiriensis Cam., det. R.G. Booth 2016” (BMNH).

Comment: The original description is based on a unique specimen from “Nilgiri Hills” (CAMERON 1939a).

Redescription: Large species: body length 7.5 mm; length of forebody 3.3 mm. Coloration (Figs 12, 60, 101): head and pronotum blackish; elytra dark-yellowish with the
postero-lateral portions blackish; abdomen bicoloured, with segments II–V reddish and segments VI–VIII blackish; abdomen bicoloured, antennae brown with the basal three antennomeres reddish and antennomere XI dark-reddish; maxillary palpi reddish.

Head (Fig. 60) strongly transverse; punctation fine and rather dense in lateral portions, sparse along middle; pubescence brown, long, and erect. Eyes approximately as long as postocular region in dorsal view. Antenna pubescence brown, long, and erect. Eyes approximately as long as broad, VI–X of increasing width and increasingly transverse, X approximately 1.5 times as broad as long, and XI short, shorter than the combined length of IX and X.

Pronotum (Fig. 60) 1.21 times as broad as long and 1.5 times as broad as long, and XI short, shorter than the combined length of IX and X.

Abdomen (Fig. 101) nearly as broad as elytra, with punctation rather fine and dense, fine, and regularly distributed; whole disc with setiferous punctures at posterior margin; tergite VI with extensive and dense punctation of the abdomen, suggesting that both specimens are conspecific.

Comparative notes: Zyras nilgiriensis, too, belongs to the Z. hirtus group, as can be inferred from the habitus (robust body; pronotum weakly convex in cross-section), the short antennomere XI, long pubescence on the whole body, and the punctuation pattern of the abdomen. Among the species of this group, it is characterized by the coloration, relatively short antennae, and by the punctuation and pubescence of the abdomen.

Distribution: This species is currently known only from the type locality in South India (Map 9).

Zyras (Zyras) tumidicornis ASSING 2016

Material examined: China: 1 ♂, 2 ♀, SW-Sichuan, Sabde, 29°04′N, 101°25′E, 3400 m, 25.VI.2001, leg. Janata (cSme, cAss).

Comment: The known distribution of Z. tumidicornis is confined to the Chinese provinces Sichuan and Yunnan (ASSING 2016a).

Zyras (Zyras) hauserianus BERNHAUER, 1933

Material examined: China: 1 ♀, Heilongjiang, Harbin, 12.VI.1966, leg. Hammond (BMNH).

Comment: The confirmed distribution of this species was confined to the type locality in the border region between China (Xinjiang) and Kazakhstan (ASSING 2016a). The above female is distinguished from the holotype by uniformly reddish tergites III–V, but shares with it the morphology of the reddish antennae (antennomeres IV–X all distinctly transverse) and the conspicuously dense punctuation of the abdomen, suggesting that both specimens are conspecific.

Zyras (Zyras) birmanus SCHEERPETZ, 1965

Material examined: Myanmar: 1 ♂, Kambaiti pass, 2130 m, 9.V.1934, leg. Malaise (BMNH).

Comment: The known distribution includes Northeast Burma and Southwest China (Yunnan) (ASSING 2016a).

Zyras (Zyras) preangeranus CAMERON, 1939

Material examined: Z. louwerensi: Holotype ♀: "G. Pandan, Res Madiden, E. Java / Z. louwerensi Cam. Type / Holotype / M. Cameron, Bequest. B.M. 1955-147 / Zyras preangeranus Cameron, det. V. Assing 2017" (BMNH).
Additional material examined: Thailand: 1 ♀ [teneral], Doi Angkhang, 24.X.2010, leg. Rougemont (cRou). Laos: 12 exs., Phongsaly province, Phongsaly env., 1300–1500 m, V.2004 (cMar, cAss). Malaysia: 35 exs., Selangor, Ulu Gombak Field Studies Centre, 250 m, flight interception trap, III.2004, leg. Maruyama et al. (cMar, cAss); 2 ♂♂, 1 ♀, Pahang, 30 km NE Raub, Laba Lembik, 3°56’S, 101°38’E, 300 m, IV–V.2004 (cMar, cAss); 4 exs., Sabah, Danum valley, B.R.L., flight interception trap, 14–16.II.2007, leg. Rougemont (cRou, cAss). Laos: 14–16.II.2007, leg. Rougemont (cRou, cAss); 3°56’N, 101°38’E, 300 m, IV–V.2002, leg. Jendek & Šauša (cMar); 4 exs., Sabah, Danum valley, B.R.L., flight interception trap, VIII.2001, leg. Brendell & Mendel (BMNH).

Comment: The original description of *Z. louwerensi* is based on a unique type specimen from “E. Java: G. Pandan, Res. Maiden” (CAMERON 1939b) deposited in the Cameron collection at the BMNH. The type material of *Z. chinkiangensis*, *Z. preangeranus*, *Z. setosipennis*, *Z. alboanennatus*, and *Z. sichuanorum* had been examined earlier (ASSING 2016a). Additional material examined from various regions in the southern East Palaearctic and the Oriental regions (ASSING 2015, 2016a; material listed above) has shown that this species is highly variable in coloration and other external characters. Moreover, the median lobe of the aedeagus of the type material of *Z. chinkiangensis*, *Z. preangeranus*, *Z. alboanennatus*, and *Z. sichuanorum* is practically identical (see figures in ASSING 2016a); the unique holotypes of *Z. setosipennis* and *Z. louwerensi* are females. These observations suggest that all these names refer to the same widespread and variable species. According to the covers of the respective issues, the descriptions of both *Z. chinkiangensis* and *Z. preangeranus* were published in May, 1939. An exact date is indicated in neither case, so that 31 May, 1939 must be assumed as the publication date for both descriptions. *Zyras preangeranus* is designated as the senior name, as the corresponding type material is in better condition, rendering *Z. chinkiangensis*, *Z. louwerensi*, *Z. setosipennis*, *Z. alboanennatus*, and *Z. sichuanorum* its junior synonyms. Interestingly, while in nearly all the specimens seen from Peninsular Malaysia, Laos, and Borneo the antennae have the apical four antennomeres pale-yellow, those from Java are more variable in this respect: the antennae have two (twelve specimens), three (two specimens), or four (one specimen) yellowish apical antennomeres. Also, while the legs are usually uniformly yellow, two of the Malaysian specimens and some from Borneo have the apices of the meso- and metatibiae slightly infuscate. The material from Java is of slightly smaller average size and generally darker coloration, often with the middle of the pronotum brownish, the posterolateral portions of the elytra more or less distinctly and more or less extensively infuscate, and the anterior abdominal tergites extensively brown, whereas in the material from Peninsular Malaysia the elytra are uniformly reddish and in that from Laos they are reddish with the extremes of the posterolateral portions slightly darker. Finally, segment VIII of the abdomen is yellow in specimens from Java and Borneo, while it tends to be reddish in material seen from other regions. The aedeagus of a male from Java is illustrated in Figs 276–277.

The vast distribution of *Z. preangeranus* includes South and East China (Sichuan, Yunnan, Jiangsu), Myanmar, Thailand (new record), Laos (new record), Malaysia (new record), Vietnam, and Indonesia (Java, Borneo) (new record) (Map 10).

*Zyras* (Zyras) *russiceps* spec. nov.

(Figs 14, 61, 114, 187–190)

**Type material:** Holotype ♀: “W.THAILAND: 300 m., Thung Yai Wildlife Sanctuary. 15°28’N – 98°48’E. / Tak Province, Umphang District, Song Bae Stream. 18–27.iv.1988. / Evergreen rain forest. M.J.D. Brendell. B.M. 1988-183 / / Holotypus Zyras russiceps sp. n. det. V. Assing 2016” (BMNH). Paratypes: 2 ♀♀: same data as holotype (BMNH, cAss); 1 ♂: “MALAYSIA: Selangor, Ulu Gombak Field Studies Centre (250 m), 2–18.III.2004 (FIT), Maruyama M. et al.” (cMar).

**Etymology:** The specific epithet is a noun in apposition and alludes to the distinctive coloration of the head (russus: red).

**Description:** Rather large species; body length 7.5–8.3 mm; length of forebody 3.3–3.4 mm. Coloration (Figs 14, 61, 114) distinctive: head and pronotum reddish; elytra blackish-brown to black, with only the anterior margin (visible in antero-dorsal view) narrowly reddish; abdomen bicoloured: tergites II–V reddish, VI reddish with the median portion extensively black, and VII–VIII blackish except for the reddish anterolateral portions, segments IX–X brownish; legs pale-yellowish; antennae black with the basal two antennomeres reddish to reddish-brown and the apical 2–4 antennomeres pale-yellow to dark-yellow, more or less sharply contrasting with the black preceding antennomeres; maxillary palpi reddish with the terminal palpomere yellowish.

Head (Fig. 61) distinctly transverse, middle and anterior portion extensively impunctate; punctuation in lateral and posterior dorsal portions sparse and rather coarse. Eyes very large, nearly twice as long as postocular region in dorsal view. Antenna (Fig. 14) 2.5–2.6 mm long; antennomeres IV–V weakly oblong, VI approximately as broad as long, VII–X of gradually increasing width and increasingly transverse, X approximately 1.5 times as broad as long, and XI approximately as long as the combined length of IX and X.
Pronotum (Fig. 61) approximately 1.15 times as broad as long and 1.3 times as broad as head, broadest near anterior angles, distinctly tapering posteriorly; lateral margins straight in posterior two-thirds (dorsal view); punctation coarse and nearly regularly distributed, with or without impunctate patches in antero-lateral portion; impunctate median band narrow or indistinct; lateral margins each with five long black setae, antero-lateral portion of disc with several additional long black setae. Elytra (Fig. 61) approximately 0.8 times as long as pronotum; punctation very coarse and very dense, slightly sparser at posterior margin; interstices much narrower than diameter of punctures (except at posterior margin). Hind wings fully developed. Metatarsomere I elongate, slightly longer than the combined length of II–IV. Abdomen (Fig. 114) approximately as broad as elytra, with moderately deep anterior impressions on tergites III–V; anterior impressions of tergites III–V each with a row of non-setiferous punctures; tergite III with a lateral setiferous puncture on either side, with or without scattered additional setiferous punctures on disc, and with approximately twelve setiferous punctures at posterior margin; tergite IV with a transverse row of approximately eight setiferous punctures across disc and with 14 setiferous punctures at posterior margin; tergite V with a transverse row of approximately ten setiferous punctures across disc and with 12–16 setiferous punctures at posterior margin; tergite VI with a transverse band of numerous non-setiferous punctures anteriorly, with a transverse row of 10–12 setiferous punctures across disc and with 12–14 setiferous punctures at posterior margin; tergite VII with a broad transverse band of numerous non-setiferous punctures in anterior portion, and with two transverse series of setiferous punctures each composed of 10–14 punctures in posterior portion, posterior margin with palisade fringe; tergite VIII (Fig. 189) with numerous long black setae in posterior third, posterior margin convex or obtusely pointed in the middle, without median concavity; sternites III–VIII with numerous long dark setae in posterior portion. \( \delta \): sternite VIII (Fig. 190) with strongly convex posterior margin and with numerous long black setae in posterior half; median lobe of aedeagus (Figs 187–188) 0.98 mm long; ventral process apically acute both in lateral and in ventral view, subapically abruptly bent; paramere as long as median lobe and with conspicuously short apical lobe.

**Comparative notes:** *Zyras russicope* belongs to the *Z. hirtus* group, as can be inferred from the chaetotaxy of the body, the morphology of the median lobe of the aedeagus, and the short apical lobe of the paramere. It is distinguished from other species of this group recorded from Thailand and adjacent regions by the distinctive coloration (particularly of the head) alone. In addition, it is characterized by the conspicuously dense and coarse punctation of the elytra, by the punctation pattern of the abdomen, and by the shape of the median lobe of the aedeagus.

**Distribution and natural history:** The known distribution is confined to the type locality in West Thailand and one locality in Selangor, Peninsular Malaysia. The specimens from Thailand were probably collected on the wing (Malaise trap?) in an evergreen rain forest at an altitude of 300 m, the paratype from Malaysia was taken with a flight interception trap at 250 m, in both cases together with several other species of *Zyras* sensu strictu.

**Type material examined:** *Drusilla brignolii* Pace, 1986b: 487. *Zyras (Zyras) thainiger* Pace, 2012b: 340; syn. n.

**Additional material examined:** China: 1 \( \delta \), Yunnan, Baoshan Pref., mountain range 22 km S Tengchong, 24°49′N, 98°29′E, 1750 m, secondary forest, litter sifted, 2.VI.2007, leg. Schülke (cAss).

**Redescription:** Body length 6.5–7.3 mm; length of forebody 2.9–3.2 mm. Coloration (Figs 15, 66, 103): forebody black; abdomen black, except for the dark-reddish anterior margins, antero-lateral portions, and anterior portions of the paratergites of the abdominal tergites III–VII; legs yellowish with the profemora dark-brown.
and the apical halves of the meso- and metafemora blackish; antennae dark-brown with antennomere XI yellowish; maxillary palpi dark-brown with the terminal palpomere yellowish.

Head (Fig. 66) moderately transverse, middle and anterior portion extensively impunctate; punctuation in lateral and posterior dorsal portions sparse and distinct. Eyes moderately large and bulging, slightly longer than postocular region in dorsal view. Antenna (Fig. 15) 2.4–2.7 mm long; antennomeres IV–VII of gradually decreasing length and decreasingly oblong, IV distinctly, VII weakly oblong, VIII as long as broad, IX–X weakly transverse, and XI approximately as long as the combined length of IX and X.

Pronotum (Fig. 66) weakly transverse, 1.10–1.12 times as broad as long and 1.17–1.24 times as broad as head, broadest anteriorly, distinctly tapering posteriad; lateral margins straight or weakly sinuate in posterior two-thirds (dorsal view); punctuation coarse and irregularly distributed, middle and lateral portion with rather extensive impunctate patches; lateral margins each with four long, black setae, anterior margin with an additional long black seta on either side.

Elytra (Fig. 66) 0.78 times as long as pronotum; punctuation coarse and rather dense, and more or less regularly distributed; interstices on average slightly broader than diameter of punctures. Hind wings fully developed. Metatarsomere I approximately as long as the combined length of II–IV.

Abdomen (Fig. 103) approximately as broad as elytra, with moderately deep anterior impressions on tergites III–V; anterior impressions of tergites III–V without non-setiferous punctures; tergite III with a lateral cluster of some punctures bearing long dark setae on either side and with sparse fine punctures at posterior margin; tergites IV and V with or without a median pair of setiferous punctures, with a lateral setiferous puncture on either side, and with approximately ten distinct punctures at or near posterior margin; tergite VI with a transverse series of non-setiferous punctures at anterior margin, with a transverse row of 2–6 setiferous punctures across the middle, and with approximately ten setiferous punctures at or near posterior margin; tergite VII with a narrow transverse band of non-setiferous punctures anteriorly, setiferous punctuation similar to that of tergite VI; tergite VIII with sparse setiferous punctures in posterior third, posterior margin smoothly convex.

σ: unknown.

Comparative notes: Among other geographically close congeners, Z. brignolii is characterized particularly by the coloration (black body with distinctly bicoloured legs), a slender habitus, an irregularly punctate pronotum, the punctuation pattern of the abdomen, and a smoothly convex posterior margin of the abdominal tergite VIII.

Distribution and natural history: The species is currently known only from two localities in North Thailand (one at approximately 20°10’N, 99°37’E and one in or near Bangkok) and one locality in the west of the Chinese province Yunnan (Map 8). The specimen from Yunnan, which represents the first record from China, was sifted from litter and dead wood in a secondary forest at an altitude of 1750 m.

Zyras [Zyras] nigrapicalis Assing, 2016

Material examined: Myanmar: 1 ♀, Kambaiti pass, 2130 m, 18.V.1934, leg. Malaise (BMNH). Hong Kong: 1 ♂, Lantau, Wag Tong, light trap, 22.27°N, 114.00°E, 22–27.V.2016, leg. Aston (cRou).

Comment: This species was previously known from China (Yunnan, Sichuan) and Taiwan (Assing 2016a). The above specimens represent the first records from Myanmar and Hong Kong.

Zyras [Zyras] proximus Cameron, 1939
(Figs 28–29, 65, 105, 191–197, Map 6)

Zyras (Zyras) proximus Cameron, 1939a:538 f. Zyras (Zyras) drugmandi Pace, 2004: 293 f.; syn. n.

Type material examined: Z. proximus: Holotype ♀: "Nilgiri Hills., A.K. Weld Downing. / a 422 / Z. proximus Cam., det. R.G. Booth 2016" (BMNH).
Z. drugmandi: Holotype ♀: "Coll. I.R.Sc.N.B., Thailand (Loei), Na Haeo (malaise trap), 04–27.VIII.2000, Leg. Constant & Grootaert / Holotypus Zyras drugmandi n. sp., det. R. Pace 2004 / Zyras drugmandi n. sp., det. R. Pace 2004" (IRSNB). Paratypes: 1 ♀: same locality as holotype, "malaise trap, 18–25.III.2001, Leg: P. Grootaert" (IRSNB); 1 ♀ [misidentified; belonging to Z. castaneus]: same locality as holotype, "05–12.V.2001, Leg. Constant & Grootaert / Pitfall Station 5, 2° forest, tall trees; dense ground vegetation, densely covered with litter / not conspecific with holotype, rev. V. Assing 2016" (IRSNB).

Comment: The original description of Z. proximus is based on a unique specimen from "Nilgiri Hills" (Cameron 1939a). The holotype, a female, was located in the Cameron collection at the BMNH.
The original description of Z. drugmandi is based on three females. An examination of these specimens revealed that they are not conspecific, but belong to two species. The holotype and one of the paratypes are conspecific with Z. proximus, whereas the other paratype belongs to Z. castaneus, a species distinguished from Z. proximus by completely different coloration of the abdomen, longer
and more slender antennae with a more elongate antennomere XI, different punctuation of the pronotum, and a different punctuation pattern of the abdomen.

Additional material examined: India: 15 exs., Meghalaya, Khasi Hills, Mawsysnram, 25°18’N, 91°29’E, 700–900 m, 5.–9.VI.2006, leg. Pacholátko (BMNH, cAss); 12 exs., Meghalaya, SW Cherrapunjee, 25°13’–15’N, 91°49’E, 900 m, 5.–24.V.2005, leg. Pacholátko (BMNH, cAss).

China: 1 ♀ [teneral], Guizhou, Fanjing Shan, 27°54’N, 108°42’E, 1050 m, evergreen rain forest, 18.–27.IV.1988, leg. Brendell (BMNH, cAss); 3 exs., Tak province, Umphang district, Song Bae Stream, Thung Yai Wildlife Sanctuary, 15°30’N, 98°48’E, 300 m, edge of Karen clearing, 27.IV.–6.V.1988, leg. Brendell (BMNH, cAss); 3 exs., Tak province, Umphang district, Mae Chan – Mae Klong confluence, Thung Yai Wildlife Sanctuary, 15°30’N, 98°48’E, 300 m, edge of Karen clearing, 27.IV.–6.V.1988, leg. Brendell (BMNH, cAss).

Laos: 2 ♀ ♂, Houa Phan province, Phou Pame Mt., 20°13’N, 104°00’E, 1480–1510 m, 22.IV.–14.V.2008, leg. Kubán (NMP, cAss); 36 exs., Phongsaly province, Phongsaly env., 1300–1500 m, V.2004 (cMar, cAss).

Redescription: Size highly variable: body length 4.5–7.0 mm; length of forebody 1.9–3.0 mm. Coloration (Figs 28–29, 65, 105): head and pronotum blackish-brown; elytra dark-yellowish with the postero-lateral portions more or less extensively dark-brown; abdomen blackish-brown, with the posterior margins of tergites III–V narrowly yellowish-brown; legs pale-yellowish; antennae brown with the basal 2–3 antennomeres pale-reddish; maxillary palpi reddish to dark-brown, with the terminal palpomere yellowish.

Head (Fig. 65) moderately transverse, broadly impunctate along middle, in lateral portions with sparse and moderately coarse punctuation. Eyes large and bulging, much longer than postocular region in dorsal view. Antenna (Figs 28–29) slender, 1.7–2.6 mm long; antennomeres IV–V approximately as long as broad or weakly oblong, VI–VII approximately as long as broad or weakly transverse, VIII–X weakly transverse, X 1.3–1.5 times as broad as long, and XI distinctly elongate, approximately as long as the combined length of VIII–X, or nearly so.

Pronotum (Fig. 65) relatively small (in relation to head), approximately 1.2 times as broad as long and 1.1–1.2 times as broad as head, broadest near anterior angles; lateral margins straight in posterior two-thirds, strongly converging posteriorly; surface very uneven, with impressions of variable size and shape; punctuation distinctive, coarse, very sparse, and very irregularly distributed. Elytra (Fig. 65) 0.8–0.9 times as long as pronotum; punctuation coarse and moderately dense to dense, more or less regularly distributed, somewhat sparser posteriorly than anteriorly. Hind wings fully developed. Metatarsomere I slightly to distinctly shorter than the combined length of II–IV.

Abdomen (Fig. 105) narrower than elytra, with moderately deep anterior impressions on tergites III–V; anterior impressions of tergites III–V each with a row or with a transverse band of shallow to coarse non-setiferous punctures; tergite III with a lateral setiferous puncture on either side and with four setiferous punctures at posterior margin (median pair usually somewhat separated from margin); tergites IV and V with a lateral setiferous puncture on either side and with 4–6 setiferous punctures at posterior margin; tergite VI with a transverse row of sparse non-setiferous punctures at anterior margin, with a lateral setiferous puncture on either side, and with six setiferous punctures at or near posterior margin; tergite VII with scattered and rather fine non-setiferous punctures at anterior margin, with a transverse row of 4–6 setiferous punctures at posterior third, and with usually six setiferous punctures at or near posterior margin, sometimes with a median pair of coarser punctures posteriorly, posterior margin with palisade fringe; tergite VIII with sparse long and black setae in posterior portion, posterior margin sexually dimorphic.

♀: posterior margin of tergite VIII (Fig. 196) with four blunt teeth; sternite VIII (Fig. 197) oblong, posterior margin truncate or convex in the middle; median lobe of aedeagus approximately 0.8–0.9 mm long and shaped as in Figs 191–194; paramere (Fig. 195) significantly longer than median lobe and with elongate apical lobe.

♂: posterior margin of tergite VIII without teeth, simply truncate to indistinctly concave in the middle; posterior margin of sternite VIII broadly and distinctly concave in the middle.

Intraspecific variation: Zyras proximus is subject to enormous intraspecific variation of body size, length of antennae, the number of punctures on the abdomen, the size of the aedeagus, and other characters. While the anterior impressions of tergites IV and V usually only have a single transverse row of non-setiferous punctures in material from Thailand, the non-setiferous punctuation of larger specimens from Northeast India tends to be more extensive.

Comparative notes: As can be inferred from the similar punctuation pattern of the forebody and abdomen, and particularly from the derived shapes of the pronotum (disc with very uneven surface) and of the apical lobe of the paramere (rather long and slender), Z. proximus is closely related to Z. condignus and allied species. Among the species of this group, it is characterized particularly by the elongate antennomere XI, the shapes of the sexually dimorphic tergite and sternite VIII (especially the shape of the male tergite VIII), and by the shape of the aedeagus.

Distribution and natural history: This species has been recorded from South and Northeast India, the Chinese province Guizhou, Thailand, and Laos (Map 6). The teneral female from Guizhou was recorded as Zyras sp. 15 by Assing (2016a). Although this is not explicitly stated on most of the labels, the specimens from Thailand and...
Laos appear to have been collected with flight (Malaise?) traps, as can be inferred from the number of specimens collected in the same locality and from the observation that practically all the specimens have the hind wings fully unfolded. The altitudes range from 300 to approximately 1500 m.

Zyras (Zyras) novinversus nom. nov.

(Figs 30–31, 67, 106, 198–202, Map 5)

Zyras (Zyras) inversus Pace, 2012b: 339; preoccupied.

Type material examined: Holotype ♀: “THAILAND, Doi Angkhang, 24.X.2010, G. de Rougemont / Holotypus Zyras inversus mihi, det. R. Pace, 2011 / Zyras inversus n. sp., det. R. Pace, 2011 / Zyras novinversus nom. n., det. V. Assing 2016” (cRou).

Comment: The original description is based on two females from “Thailand Doi Angkhang” (Pace 2012b). The examined holotype is evidently subject to post-mortem darkening and has the eyes deformed, most likely as a result of the effect of chemicals or other improper treatment during original dissection.

Zyras inversus Pace, 2012 is a primary homonym of Zyras (Glossacantha) inversus Pace, 2001, a species described based on two females from Tamil Nadu in South India (Pace 2001b). The junior primary homonym is here replaced with the nomen novum Zyras novinversus (a combination of novus and inversus). It is, however, with some hesitation that I propose a replacement name. This species is most likely widespread and the possibility that one of the unrevised names described based on material from Java and Sumatra refers to this name cannot be ruled out with certainty.

Additional material examined: Thailand: 7 exs., Tak province, Umphang district, Song Bae Stream, Thung Yai Wildlife Sanctuary, 15°28’N, 98°48’E, 300 m, evergreen rain forest, 18–27.IV.1988, leg. Brendell (BMNH, cAss); 12 exs., Tak province, Umphang district, Mae Chan – Mae Klong confluence, Thung Yai Wildlife Sanctuary, 15°30’N, 98°48’E, 300 m, edge of Karen clearing, 27.IV.–6.V.1988, leg. Brendell (BMNH, cAss). Laos: 15 exs., Phongsaly province, Phongsaly env., 1300–1500 m, V.2004 (cMar, cAss).

Redescription: Body length 4.5–6.6 mm; length of forebody 2.1–2.9 mm. Coloration (Figs 30–31, 67, 106): head and pronotum black; elytra reddish-yellow with the postero-lateral portions blackish, rarely nearly uniformly dark with only the humeral angles indistinctly paler; abdomen with segments II–V reddish (rarely reddish-brown with reddish margins), segment VI reddish or brown with reddish margins, segment VII usually dark-brown to blackish-brown with the anterior portion reddish, rarely completely reddish, segment VIII dark-brown to blackish-brown, segment IX dark-brown, and tergite X reddish; legs pale-yellowish; antennae blackish-brown to black with antennomeres I–II reddish-yellow to brown and the apex of antennomeres XI dark-reddish; maxillary palpi yellowish-brown, with the terminal palpomere yellowish brown.

Head (Fig. 67) moderately transverse, broadly impunctate along middle; punctuation in lateral dorsal portions moderately coarse and sparse. Eyes large, twice as long as postocular region in dorsal view, or nearly so. Antenna (Figs 30–31) 1.9–2.1 mm long; antennomeres IV and V weakly oblong, VI approximately as long as broad, VII approximately as long as broad or weakly transverse, VIII–X of gradually increasing width and increasingly transverse, X approximately 1.5 times as broad as long, and XI elongate, approximately as long as the combined length of VIII–X.

Pronotum (Fig. 67) approximately 1.2 times as broad as long and 1.07–1.15 times as broad as head, broadest near anterior angles, distinctly tapering posteriorly; lateral margins straight or weakly sinuate in posterior two-thirds (dorsal view); punctuation very coarse, very irregularly distributed, arranged in more or less distinct clusters, these clusters often situated in very shallow impressions, middle and lateral portion with extensive impunctate patches; lateral margins each with four long, black setae.

Elytra (Fig. 67) 0.85–0.93 times as long as pronotum; punctuation coarse, defined, moderately dense to dense, and almost regularly distributed, somewhat less dense in posterior portion. Hind wings fully developed. Metatarsomere I shorter than the combined length of II–IV.

Abdomen (Fig. 106) narrower than elytra, with moderately deep anterior impressions on tergites III–V; anterior impressions of tergites III–V with dense and rather coarse non-setiferous punctuation; tergite III with a lateral setiferous puncture on either side and with four setiferous punctures at posterior margin; tergites IV–V with a lateral setiferous puncture on either side (often accompanied by few non-setiferous punctures) and with six setiferous punctures at posterior margin; tergite VI anteriorly with more or less extensive non-setiferous punctuation, with a lateral setiferous puncture on either side (often accompanied by few non-setiferous punctures) and with six setiferous punctures at posterior margin; tergite VII with a transverse band of sparse and rather fine non-setiferous punctures anteriorly, with a transverse series of approximately eight setiferous punctures at posterior fourth, and with scattered setiferous punctures at posterior margin, palisade fringe present; tergite VIII with sparse setiferous punctures in posterior portion, posterior margin with sexual dimorphism.

♂: posterior margin of tergite VIII (Fig. 201) with four weakly pronounced blunt projections; posterior margin of sternite VIII (Fig. 202) weakly convex, nearly truncate in the middle; median lobe of aedeagus approximately 0.75 mm long and shaped as in Figs 198–199; paramere...
Asing, V: On Zyras sensu strictu in the East Palaearctic and Oriental regions

Distribution and natural history: Although currently known only from Thailand and Laos (Map 5), this species is most likely more widespread in the Oriental region, as is suggested by the vast distribution of the similar and closely related Z. proximus, as well as by the fact that at least the examined non-type material was evidently collected on the wing (practically all the specimens have the hind wings fully unfolded). The additional material from Thailand was collected in an evergreen rain forest and at the edge of a clearing at an altitude of 300 m, together with several other species of Zyras sensu strictu, among them numerous Z. proximus. The specimens from Laos were taken at an altitude of 1300–1500 m.

Zyras (Zyras) brevilobatus spec. nov.

Type material: Holotype ♀: “W.THAILAND: 300 m., Thung Yai Wildlife Sanctuary. 15°30’N – 98°48’E. / Tak Province, Umphang District, Mae Chan – Mae Klong confluence. 27.iv.–6.v.1988. / Mixed riverside forest. M.J.D. Brendell. B.M. 1988-183 / Holotypus ♀ Zyras brevilobatus sp. n. det. V. Assing 2016” (BMNH). Paratypes: 2 ♀ ♀ [both without aedeagus!]: same data as holotype (BMNH, cAss).

Etymology: The specific epithet (adjective) alludes to the conspicuously short ventral process of the aedeagus.

Comparative notes: This species is characterized particularly by the conspicuously short ventral process of tergite VIII with convex posterior margin; median lobe of aedeagus (Figs 203–204) 0.8 mm long and with conspicuously short ventral process; paramere (Fig. 205) 0.9 mm long, with moderately long apical lobe.
of the aedeagus. It additionally differs from other species recorded from Thailand by the strongly transverse pronotum, by the coloration of the abdomen in combination with completely dark elytra, and by the punctuation pattern of the abdomen.

**Distribution and natural history:** The type locality is situated in West Thailand (Map 10). The specimens were collected in a mixed forest near a river at an altitude of 300 m, most likely with Malaise or flight interception traps, together with numerous specimens of *Z. proximus* and *Z. novinversus*.

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**Type material**

Holotype †: “W.THAILAND: 300 m., Thung Yai Wildlife Sanctuary. 15°28’N – 98°48’E. / Tak Province, Umphang District, Song Bae Stream. 18–27.iv. 1988. / Evergreen rain forest. M.J.D. Brendell. B.M. 1988-183 / Holotypus † Zyras parvicollis sp. n. det. V. Assing 2016” (BMNH). Paratypes: 3 †: same data as holotype (BMNH, cAss).

**Etymology:** The specific epithet (adjective) alludes to the relatively small and weakly transverse pronotum.

**Description:** Size highly variable: body length 5.8–6.8 mm; length of forebody 2.5–3.0 mm. Coloration (Figs 33, 69, 104): head and pronotum black; elytra dark-yellowish with the postero-lateral portion more or less extensively and rather sharply blackish; abdomen with tergites III–V dark-brown to blackish-brown with the posterior margins and the paratergites more or less extensively dark-reddish, tergite VI blackish-brown to black; legs pale-yellowish; antennae blackish with antennomeres I–II yellowish-brown to brown and the apex of antennomere XI dark-reddish; antennal palpi reddish-brown to dark-brown, with the terminal palpomere yellowish to reddish.

Head (Fig. 69) distinctly transverse, broadly impunctate along middle, in lateral portions with sparse and moderately coarse punctuation. Eyes large and bulging, much longer than postocular region in dorsal view. Antenna (Fig. 33) slender, 2.1–2.3 mm long; antennomeres IV–V weakly oblong, VI approximately as long as broad; VII approximately as long as broad or weakly transverse; VIII–X weakly transverse, X approximately 1.5 times as broad as long, and XI distinctly elongate, approximately as long as the combined length of VIII–X.

Pronotum (Fig. 69) relatively small (in relation to head), approximately 1.2 times as broad as long and 1.10–1.18 times as broad as head, broadest near anterior angles; lateral margins straight or weakly convex in posterior two-thirds (dorsal view), strongly converging posteriorly; surface smooth, without impressions; punctuation coarse, moderately sparse, and moderately irregularly distributed; median line narrowly impunctate or anteriorly with scattered punctures.

Elytra (Fig. 69) 0.88–0.95 times as long as pronotum; punctuation coarse and dense, somewhat sparser in posterior fourth. Hind wings fully developed. Metatarsomere I slightly shorter than the combined length of II–IV.

Abdomen (Fig. 104) slightly narrower than elytra, with moderately deep anterior impressions on tergites III–V; anterior impressions of tergites III–V each with a row or with a transverse band of coarse non-setiferous punctures; tergite III with a lateral setiferous puncture on either side and with four setiferous punctures at posterior margin (median pair somewhat separated from margin); tergites IV and V with a lateral setiferous puncture on either side and with six setiferous punctures at posterior margin; tergite VI with a narrow transverse row of non-setiferous punctures at anterior margin, with a lateral setiferous puncture on either side, and with six setiferous punctures at or near posterior margin; tergite VII with a transverse band of non-setiferous punctures anteriorly, and with two transverse rows of setiferous punctures posteriorly, posterior margin with palpiferous fringe; tergite VIII with sparse long and black setae in posterior portion.

†: posterior margin of tergite VIII (Fig. 206) with a median pair of blunt teeth; sternite VIII (Fig. 207) weakly transverse, posterior margin convex; median lobe of aedeagus 0.80–0.85 mm long and shaped as in Figs 208–211; paramere approximately 0.9 mm long and with moderately long apical lobe.

**Comparative notes:** *Zyras parvicollis* is distinguished from the similarly coloured *Z. proximus* by a pronotum without impressions and with less irregular punctuation, by the presence of only two blunt teeth at the posterior margin of the male tergite VIII, by a transverse male sternite VIII, by the shape of the ventral process of the aedeagus, and by a shorter apical lobe of the paramere. From other sympatric species of similar habitus and punctuation (*Z. novinversus, Z. brevilobatus*), it is readily separated by the different coloration of the abdomen alone.

**Distribution and natural history:** The type locality is situated in West Thailand (Map 10). The specimens were collected in an evergreen rain forest at an altitude of 300 m, most likely with flight (Malaise?) traps, together with *Z. proximus*, *Z. novinversus*, *Z. bettotanus*, and *Z. brevilobatus*.
Zyras †Zyras ambulans †spec. nov.

(Figs 34, 70, 107, 212–215, Map 10)

**Type material:** Holotype ♂: “Thailand, Satun Prov., Thale Ban N.P., 20 km E Satun, 200–400 m, 1.–4.I.1996, leg. Schulz & Vock / Holotypus ♂ Zyras ambulans sp. n., det. V. Assing 2016” (c-Ass).

**Etymology:** The specific epithet is the present participle of the Latin verb ambulare (to walk) and alludes to absence of functional hind wings.

**Description:** Body length 6.2 mm; length of forebody 2.5 mm. Coloration (Figs 34, 70, 107): head blackish-brown; pronotum and elytra dark-brown; abdomen with segments III–V reddish, tergite VI dark-brown with reddish margins, VII and VIII dark-brown with the anterior and posterior margins narrowly paler; legs yellowish with the apices of the meso- and metafemora brown; antennae dark-brown with antennomeres I–II reddish and XI yellow; maxillary palpi dark-yellowish with the terminal palpmere pale-yellowish.

Head (Fig. 70) moderately transverse, middle extensively impunctate; punctuation in lateral dorsal portions sparse and fine. Eyes large and bulging, much longer than postocular region in dorsal view. Antenna (Fig. 34): 2.3 mm long; antennomeres IV–V oblong, VI weakly oblong, VII as long as broad or weakly oblong, VIII–IX very weakly transverse, X less than 1.5 times as broad as long, and XI approximately as long as the combined length of IX and X.

Pronotum (Fig. 70) weakly transverse, approximately 1.1 times as broad as long and 1.2 times as broad as head, broadest anteriorly, distinctly tapering posteriorly; lateral margins straight in posterior two-thirds (dorsal view); punctuation shallow and sparse; midline broadly impunctate; lateral margins anteriorly with two very long, stout, dark setae.

Elytra (Fig. 70) short, approximately 0.7 times as long as pronotum; punctuation moderately dense, moderately coarse, and regularly distributed. Hind wings reduced. Metatarsomere I longer than the combined length of II and III, but shorter than the combined length of II–IV.

Abdomen (Fig. 107) broader than elytra, with moderately deep anterior impressions on tergites III–V; anterior impressions of tergites III–V without non-setiferous punctures; tergites III–VI with a lateral puncture bearing a long black seta on either side and with a transverse row of approximately 10 setiferous punctures at or near posterior margins, at least the lateral punctures of these rows bearing long black setae; tergite VII anteriorly with a cluster of rather sparse shallow non-setiferous punctures and posteriorly with sparse setiferous punctures, posterior margin with narrow palisade fringe; tergite VIII with sparse setiferous punctures only in posterior portion, posterior margin smoothly convex, without median excision or other modifications.

♂: sternite VIII with convex posterior margin; median lobe of aedeagus 0.65 mm long and shaped as in Figs 212–213; paramere (Fig. 214) much longer than median lobe (0.9 mm), with long, flattened, and somewhat club-shaped apical lobe (Fig. 215).

**Comparative notes:** Zyras ambulans is distinguished from all the species previously known from Thailand and Peninsular Malaysia by the reduced hind wings and the morphology of the aedeagus (shape of median lobe; modifications of paramere). It is additionally characterized by the coloration (body, legs, and antennae), a slender pronotum, short elytra, and the punctuation pattern of the abdomen.

**Distribution and natural history:** Thale Ban National Park is situated in the extreme south of Thailand at approximately 6°43’N, 100°10’E, close to the border with Malaysia (Map 10). The holotype was collected at an altitude between 200 and 400 m. Since one of the collectors is a myrmecologist, it may have been found associated with ants.

**Zyras †Zyras nitens** CAMERON, 1944

(Figs 10, 71, 109, 216–221, Map 8)

**Zyras †Zyras nitens** CAMERON, 1944: 108.

**Type material examined:** Holotype ♂: “The Gap, Selangor, F.M.S., Dr. Cameron / Bank of Stream / Debris / Z. nitens Cam. Type / Holotype / Holotypus Zyras nitens Cameron, rev. V. Assing 2016” (BMNH).

**Comment:** The original description is based on a unique specimen from “SELANGOR : The Gap” (CAMERON 1944).

**Additional material examined:** Malaysia: 1 ♀, Selangor, Ulu Gombak Field Studies Centre, 250 m, flight interception trap, III.2004, leg. Maruyama et al. (cMar).

**Redescription:** Body length 5.0–5.8 mm; length of forebody 2.7–2.8 mm. Coloration (Figs 10, 71, 109): head and pronotum dark-brown; elytra brown or dark-reddish with the postero-lateral portions slightly and diffusely darker; abdomen dark-brown, with tergite II, the anterior and antero-lateral portions of tergites III–VI, and most of the paratergites yellowish to yellowish-brown, and with segments IX–X dark-yellowish; legs yellowish with the apices of the meso- and metafemora slightly darker; antennae brown with the basal 2–3 antennomeres pale-reddish and XI pale yellowish to dark-yellowish; maxillary palpi yellowish.

Head (Fig. 71) moderately transverse, median portion extensively impunctate; punctures in lateral portions sparse and fine to moderately coarse. Eyes at least twice as long as distance from posterior margin of eye to poste-
rior constriction of head in dorsal view. Antenna (Fig. 10) 2.4 mm long and slender; antennomeres IV–VIII oblong, IX approximately as long as broad to weakly oblong, X very weakly transverse, and XI slightly shorter than the combined length of IX and X.

Pronotum (Fig. 71) 1.09–1.12 times as broad as long and 1.1–1.2 times as broad as head, broadest in anterior half, weakly tapering posteriad; lateral margins weakly sinuate in posterior half in dorsal view; punctuation coarse and irregularly distributed, on either side of midline with extensive impunctate areas; lateral margins each with four long and erect black setae, one of them inserting near anterior and one near posterior angle, and two in between; anterior margin with an additional long seta on either side; pubescence of disc moderately long, suberect, and pale.

Elytra (Fig. 71) 0.77–0.79 times as long as pronotum; punctuation coarse, moderately dense anteriorly and rather sparse near posterior margins; pubescence suberect, rather long, and pale on disc, dark and stouter at lateral margins. Hind wings present. Metatarsomere I 3.5 times as long as broad; angles apically produced (tened apical lobe of paramere), Z. nitens is closely allied

Distribution and natural history: This species is currently known from two close localities in Selangor, Peninsular Malaysia (Map 8). The holotype was collected from debris on a stream bank, the additional specimen with a flight interception trap at an altitude of 250 m.

Redescription: Body length 4.8–5.3 mm; length of forebody 2.1–2.4 mm. Coloration (Figs 26, 39, 72, 74, 110, 112): head and pronotum reddish to dark-brown; elytra dark-yellowish to reddish with the postero-lateral portions extensively, more or less distinctly, and diffusely darker, or elytra dark-brown with the anterior margin yellowish; abdomen uniformly pale-reddish to blackish-brown with the anterior portions of all tergites yellowish, antennae brown to dark-brown, antennomeres I–II sometimes slightly paler and antennomere XI reddish to dark-brown; maxillary palpi yellowish to dark-brown, with the terminal palpomere pale-yellowish. Head (Figs 72, 74) transverse, approximately 1.25 times as broad as long, broadly impunctate along middle; lateral dorsal portions with scattered fine punctures. Eyes large and bulging, more than twice as long as postocular region in dorsal view. Antenna (Figs 26, 39) 1.55–1.70 mm long; antennomeres IV as long as broad or weakly transverse, V–X of gradually increasing width and increasingly transverse, X 1.5 times to nearly twice as broad as long, and XI conspicuously elongate, as long as, or longer than the combined length of VIII–X.
Pronotum (Figs 72, 74) 1.14–1.15 times as broad as long and 1.10–1.20 times as broad as head, broadest near anterior angles, moderately tapering posteriorly; lateral margins straight or convex in posterior two-thirds (dorsal view); punctation moderately fine to moderately coarse, sparse to moderately dense, and moderately irregularly distributed; laterally with more or less extensive impunctate patches; midline broadly impunctate; lateral margins each with four long brown setae; anterior margin with one long brown seta on either side.

Elytra (Figs 72, 74) approximately 0.85–0.90 times as long as pronotum; punctuation dense, moderately coarse, and more or less regularly distributed; interstices on average as broad as, or slightly broader than diameter of punctures; scutellum with coarse and defined punctuation. Hind wings probably fully developed. Metatarsomere I as long as, or shorter than the combined length of II–IV.

Abdomen (Figs 110, 112) distinctly narrower than elytra, with deep anterior impressions on tergites III–V; tergites III–V each with a transverse row of fine and weakly defined non-setiferous punctures in anterior impressions, with a lateral puncture on either side, and with a variable number of setiferous punctures at posterior margins; tergites IV–VI sometimes with a median pair of setiferous punctures; tergite VI with a transverse row of non-setiferous punctures anteriorly, with a lateral setiferous puncture on either side, and with approximately ten setiferous punctures at posterior margin; tergite VII with a transverse band of non-setiferous punctures anteriorly and with two transverse series of setiferous punctures posteriorly; tergite VIII (Figs 225, 237) with 15 long dark setae posteriorly, posterior margin smoothly convex, truncate, or weakly concave in the middle.

♂: posterior margin of sternite VIII (Figs 226, 238) obtusely angled in the middle; median lobe of aedeagus approximately 0.5 mm long and shaped as in Figs 222–223, 234–235; paramere (Figs 224, 236) relatively small and slender, apical lobe small and with a conspicuously long terminal seta.

♀: posterior margin of sternite VIII weakly convex.

Intraspecific variation: The specimens from Sulawesi are distinguished from those from Peninsular Malaysia and Java by distinctly darker coloration of the forebody and the abdomen, a reddish antennomere XI (distinctly contrasting with the dark antennomeres I-X), and slight differences in the shape of the median lobe of the aedeagus. For comparison see Figs 26, 72, 110, 222–226 versus Figs 39, 74, 112, 234–238. These differences are interpreted as intraspecific variation, also in view of the small number of specimens available.

Comparative notes: This species is readily distinguished from all other consubgenera particularly by the derived morphology and chaetotaxy of the paramere (small apical lobe with conspicuously long apical seta). It is additionally characterized by a conspicuously elongate antennomere XI and by the morphology of the aedeagus.

Distribution and natural history: This species is currently known from two localities in Peninsular Malaysia, one in Java, and one in Sulawesi Utara. The non-type specimens were collected with flight interception and Malaise traps. The altitudes range from 200 to more than 1200 m.

Type material examined: Z. bettotanus CAMERON, 1930

(Map 9)

Zyras (Zyras) bettotanus CAMERON, 1930: 168.
Zyras (Zyras) drescheri CAMERON, 1939b: 17; syn. n.
Zyras (Zyras) atrapicalis ASSING, 2016a: 140 f.; syn. n.

Comment: The original description of Z. bettotanus is based on a unique holotype from “North Borneo; Betto- tan” (CAMERON 1930). HLAVÁČ et al. (2011) list the species as incertae sedis, but PACE (2008) assigned it to Zyras sensu strictu in a key to the Zyras species of Borneo. CAMERON (1939b) described Z. drescheri based on an unspeciﬁed number of syntypes from “Batoerraden: G. Slamat”, “Bandoeng Dagŏ”, and “G. Tangkoeban Prahoec”. Two of the syntypes, a male and a female, were found in the Cameron collection at the BMNH. The male is designated as the lectotype. Zyras atrapicalis was recently described based on material from the Chinese province Yunnan. An examination of the type material of all three names revealed that it is conspecific, so that Z. drescheri and Z. atrapicalis are placed in synonymy with Z. bettotanus. For a detailed description and illustrations see ASSING (2016a).

The coloration of this species is remarkably variable. While the head and pronotum are usually blackish in material from most regions, some specimens from Java have the head and pronotum reddish, or the head reddish and the pronotum brown.

Additional material examined: Thailand: 3 exs., Tak province, Umphang district, Song Bae Stream, Thung Yai Wildlife Sanctuary, 15°28’N, 98°48’E, 300 m, evergreen rain forest, 18–27.IV.1988, leg. Brendell (BMNH); 11 exs., Tak province, Umphang district, Mae Chan – Mae Klong confluence, Thung Yai Wildlife Sanctuary, 15°30’N, 98°48’E, 300 m, evergreen rain forest, 27.IV.–6.V.1988, leg. Brendell (BMNH, cAss); 1 ex., Tak province, Umphang district, Mae Chan – Mae Klong confluence, Thung Yai...
Wildlife Sanctuary, 15°30’N, 98°48’E, 300 m, edge of Karen clearing, 27.IV.–6.V.1988, leg. Brendell (cAss). Malaysia: 1 ♀, Cameron Highlands, 22–30.III.1984, leg. Rougemont (cRou); 7 exs., Selangor, Ulu Gombak Field Studies Centre, 250 m, flight interception trap, III.2004, leg. Maruyama et al. (cMar, cAss); 8 exs., Borneo, Sabah, Sandakan, S Lokan, flight interception trap, III.1997, leg. Chung (BMNH, cAss); 1 ex., same data, but IX.1996 (cAss); 4 exs., Sabah, Sandakan, Sepilok, flight interception trap, X.1996, leg. Chung (BMNH, cAss); 2 exs., Sabah, Danum valley, 250 m, flight interception trap, XI.1997, leg. Martin (BMNH).

**Distribution and natural history:** *Zyras bettotanus* is evidently widespread in the Oriental region (Map 9). It is now known from South China, Thailand, Peninsular Malaysia, Java, and Borneo (Malaysia: Sabah; Indonesia: Kalimantan Tengah; Brunei). At least the majority of the specimens was collected with flight interception and Malaise traps at low altitudes (150–300 m).

*Zyras (Zyras) variolatus* PACE, 2003

(Figs 266–270)

*Zyras (Zyras) variolatus* PACE, 2003: 68 f.

**Material examined:** Malaysia: 1 ♀, Kelantan, Gua Musang, 3.VI.2006, leg. Ciampor (cAss).

**Comment:** When describing *Z. variolatus* based on a unique male from “Malaysia, Pahang, Jerau Water Falls” PACE (2003) compared this species with other *Zyras* species of various subgenera, but not of *Zyras* sensu strictu.

A study of the above male revealed that it is highly similar to *Z. montanus* (see below) and distinguished from that species only by slightly smaller size, slightly more irregular punctuation of the pronotum, slightly shorter elytra with less coarse and less dense punctuation, and a smaller aedeagus (Figs 266–270); for illustrations of the paramere and the male tergite and sternite VIII see Figs 268–270. The specimen differs from the original description by having only antennomere XI (not antennomeres X–XI) yellow. A study of more material, including the holotype, is needed to clarify if the observed differences should be interpreted as intra- or interspecific variation.

*Zyras (Zyras) montanus* (BERNHAUER, 1915)

(Figs 271–275)

*Astilbus montanus* BERNHAUER, 1915: 152 f.

*Zyras (Zyras) montanus* (BERNHAUER, 1915): PACES (2008: 110).

**Material examined:** Borneo: 16 exs., Indonesia, Kalimantan Tengah, Busang–Rekut confluence, 0°03’S, 113°59’E, flight interception trap, VIII.2001, leg. Brendell & Mendel (BMNH, cAss); 1 ex., Brunei, Kuala Belalong FSC, 4°34’N, 115°07’E, 260 m, dipterocarp forest, flight interception trap, 16.VI.1991, leg. Mawdsley (BMNH); 1 ex., Malaysia, Sabah, Sandakan, Sepilok, flight interception trap, X.1996, leg. Chung (BMNH).

**Comment:** *Astilbus montanus* was described from a unique female collected in “Sarawak: Mt. Matang” (BERNHAUER 1915). The holotype was studied and figured by PACE (2008), who moved the species to *Zyras* sensu strictu and attributed the species partly to Bernhauer and partly to Cameron. A study of the examined material revealed that it perfectly matches the original description provided by BERNHAUER (1915). This species is highly distinctive also in external characters such as the coloration (especially of the antennae), the conspicuous punctuation of the head, pronotum, and elytra, and the shape of the postero-median impression of the pronotum. Moreover, as can be inferred also from the observation that the examined material was exclusively collected with flight interception traps, the species is an active flyer. For illustrations of the habitus and the genitalia of this species see PACE (2008) and Figs 271–275, respectively. The figures of the median lobe of the aedeagus provided by PACE (2014) are somewhat misleading and possibly refer to a different species.

*Zyras montanus* is currently known only from Borneo. It seems likely, however, that it is more widespread in the Oriental region. The above material represents the first records from Indonesia and Brunei.

*Zyras (Zyras) bartolozzi* PACE, 2003

*Zyras (Zyras) bartolozzi* PACE, 2003: 68 f.

*Zyras (Zyras) albotalernalis* PACE, 2008: 150; syn. n.

**Material examined:** Borneo: 6 exs., Indonesia, Kalimantan Tengah, Busang–Rekut confluence, 0°03’S, 113°59’E, flight interception trap, VIII.2001, leg. Brendell & Mendel (BMNH, cAss).

**Comment:** *Zyras bartolozzi* was described from a unique male collected in “Malaysia, Pahang, Genting Sempan” (PACE 2003). The original description of *Z. albotaler-
Zyras (Zyras) matangensis Cameron, 1943
(Figs 35, 73, 108, 229–230, 233)

Type material examined: Holotype ♂: “Mt. Matang, W. Sarawak. G.E. Bryant. 19.I.14, 2000 ft / G. 23 / Z. matangensis Cam. Type / Holotype / M. Cameron. Bequest. B.M. 1955–147 / Holotypus Zyras matangensis Cameron, rev. V. Assing 2017” (BMNH).

Comment: The original description is based on a unique holotype from “W. Sarawak: Mt. Matang” (CAMERON 1943).

Additional material examined: Borneo: 1 ♂, Malaysia, Sabah, Sandakan, S Lokan, logged forest, flight interception trap, III.1997, leg. Chung (BMNH); 1 ♀, Malaysia, Sabah, Sandakan, Sepilok, primary forest, flight interception trap, X.1996, leg. Chung (cAss).

Redescription: Body length 5.2–7.5 mm; length of forebody 2.6–3.2 mm. Coloration (Figs 35, 73, 108): forebody reddish to castaneous-brown, elytra of uniform coloration or with the postero-lateral portions slightly paler; legs dark-yellowish; antennae reddish-brown to brown with the basal 2–3 antennomeres reddish and the apex of antennomere XI sometimes slightly paler brown; maxillary palpi reddish with the terminal palpomere yellowish.

Head (Fig. 73) moderately transverse, broadly impunctate along middle; lateral dorsal portions with sparse to moderately dense coarse punctation. Eyes moderately large, as long as, or slightly longer than postocular region in dorsal view. Antenna (Fig. 35) 1.9–2.0 mm long; antennomeres IV approximately as long as broad or weakly transverse, V–X of gradually increasing width and increasingly transverse, X approximately twice as broad as long, and XI short and of conical shape, slightly shorter than the combined length of IX and X.

Pronotum (Fig. 73) weakly transverse, 1.03–1.10 times as broad as long and 1.20–1.25 times as broad as head, broadest in anterior half, distinctly tapering posteriad; lateral margins straight or weakly sinuate in posterior two-thirds (dorsal view); punctuation moderately coarse, moderately dense to dense, and slightly irregularly distributed, laterally with impunctate patches; midline broadly impunctate; lateral and anterior margins with numerous long and erect dark setae.

Elytra (Fig. 73) approximately 0.75–0.80 times as long as pronotum; punctuation fine, moderately sparse to dense; pubescence length, suberect, and pale; lateral margins with numerous stouter, dark and erect setae. Hind wings fully developed. Metatarsomere I slightly to distinctly shorter than the combined length of II–IV.

Abdomen (Fig. 108) broad, nearly as broad as elytra, with moderately deep anterior impressions on tergites III–V; these impressions with or without sparse non-setiferous punctures; tergites III–V with some lateral setiferous punctures on either side, with few scattered non-setiferous punctures on disc, and with 6–8 setiferous punctures at posterior margin, disc without micropunctuation; tergite VI with a transverse band of rather coarse and dense non-setiferous punctures anteriorly, with scattered non-setiferous punctures on disc, and with some setiferous punctures laterally and at posterior margin; tergite VII with a transverse band of rather coarse and dense non-setiferous punctures situated in an anterior transverse impression, with scattered non-setiferous punctures on disc, and with two transverse series of setiferous punctures posteriorly, posterior margin with palisade fringe; tergite VIII with long dark setae in posterior third, posterior margin broadly and weakly concave.

♂: posterior margin of sternite VIII (Fig. 233) with convex posterior margin; median lobe of aedeagus 0.70–0.75 mm long and shaped as in Figs 229–230; paramere 0.75–0.85 mm long and with moderately short apical lobe.

Intraspecific variation: The aedeagus of the non-type male is distinguished from that of the holotype by slightly larger size of the median lobe, a crista apicalis of slightly different shape, and somewhat larger parameres. In the non-type female, the non-setiferous punctuation of tergite VI and VII is much finer and less extensive than in the two males examined. Since no additional evidence was found suggesting that the three specimens represent different species, and in view of the often pronounced variability of Zyras sensu strictu species, the observed differences are attributed to intraspecific variation.

Comparative notes: In general appearance (coloration, size, habitus), Z. matangensis is similar to Z. hirtus, from which it is reliably distinguished only by the completely different shape of the aedeagus. In habitus, coloration, and other external characters, the species is also highly similar...
to Z. flavorufus Cameron, 1939 from Java, from which it differs by darker coloration, a less transverse pronotum with less distinctly sinuate lateral margins, shorter antennae with more transverse antennomeres IV–X, shorter elytra, the punctuation pattern of the abdomen (particularly much coarser and denser non-setiferous punctuation on tergites VI and VII, and by the differently shaped and smaller median lobe of the aedeagus.

**Distribution and natural history:** At present, Z. matangensis is known from three localities in Sarawak and Sabah, Borneo. The additional material was collected with flight interception traps in a primary and a logged forest.

**Zyras** (Zyras) *parahirtus* spec. nov.
(Figs 227–228, 231–232)

**Type material:** Holotype ♂: "INDONESIA: Kalimantan Tengah, Busang–Rekut confl., 0°03’S, 113°59’E / Flight intercept FIT 9, Brendell - Mendel, August 2001 / Barito Ulu 2001′, BMNH(E), 2001-191 / Holotypus ♂ Zyras *parahirtus* sp. n., det. V. Assing 2016” (BMNH).

Paratypes: 2 ♀ ♀: same data as holotype (except “FIT 2” and “FIT 7”, respectively) (BMNH, cAss).

**Etymology:** The specific epithet (adjective) alludes to the external resemblance of this species to Z. hirtus.

**Description:** Body length 6.5–7.5 mm; length of forebody 3.0–3.2 mm. Coloration: forebody dark-reddish to dark-brown, with the elytra at least slightly paler; abdomen dark-reddish, with most of tergite VI somewhat infuscate; legs dark-yellowish; antennae brown to dark-brown with the basal two antennomeres reddish and antennomere XI slightly paler brown; maxillary palpi reddish with the terminal palpomere yellowish.

Other external characters highly similar to those of Z. matangensis, except as follows:

Antenna 2.2–2.3 mm long. Tergites III–V with a transverse row of 4–6 setiferous punctures across middle and with 6–10 setiferous punctures at posterior margins, tergite V additionally with a lateral cluster of setiferous punctures on either side; tergites VI and VII with a transverse band of dense and moderately coarse non-setiferous punctures anteriorly and with sparser non-setiferous punctuation on remainder of surface; posterior margin of tergite VIII (Fig. 232) indistinctly concave in the middle.

♂: posterior margin of sternite VIII broadly convex; median lobe of aedeagus (Figs 227–228) 0.9 mm long and robust; ventral process broadly triangular in ventral view; paramere (Fig. 231) approximately 1.0 mm long and with moderately long apical lobe.

**Comparative notes:** This species is distinguished from the similar and geographically close Z. matangensis only by somewhat larger body size, darker coloration, a slightly different chaetotaxy of the abdomen, and particularly by an aedeagus with a larger median lobe, a ventral process of different shape (especially in lateral view), and a longer apical lobe of the paramere.

**Distribution and natural history:** The type material was collected with flight interception traps in Kalimantan Tengah, Borneo (Indonesia).

### 3.5 Unnamed species

The examined material included females of several evidently undescribed species. Since males are often indispensable for a reliable identification of Zyras sensu strictu species, these species remain unnamed for the time being.

**Zyras** (Zyras) spec. nov. 1

**Material examined:** Nepal: 1 ♀, Annapurna, above Kangsar, 28°41’N, 83°57’E, 4300–4600 m, 11.V.2007, leg. Schmidt (NME).

**Comment:** The above female significantly differs from all other described species recorded from the Himalaya. This, as well as the high altitude at which it was collected, suggests that it belongs to an undescribed species.

**Zyras** (Zyras) spec. nov. 2

**Material examined:** Nepal: 1 ♀, Dhaulagiri Himal, Kali Gandaki valley, Yak Kharka, above Marpha, 4100–4600 m, 12–13.VII.1998, leg. Jäger (SMTD).

**Comment:** The above female is characterized by moderate size (body length 5.3 mm; length of forebody 2.5 mm), dark coloration (body blackish with the posterior margins of the abdominal segments pale-brown; legs with blackish femora and brown tibiae; antennae blackish with antennomere XI dark-reddish), and particularly by fine and sparse punctuation of the pronotum and elytra, a character combination distinguishing it from all other geographically close congeners.

**Zyras** (Zyras) spec. nov. 3

**Material examined:** Thailand: 1 ♂, Satun Prov., Thale Ban N.P., 20 km E Satun, 200–400 m, 1.–4.1.1996, leg. Schulz & Vock (cAss).

**Comment:** The above female probably represents an undescribed species. It was collected in the same locality as Z. ambulans.
**Zyras** (*Zyras*) spec. nov. 4

**Material examined:** Thailand: 1 ♀, Tak province, Umphang district, Song Bae Stream, Thung Yai Wildlife Sanctuary, 15°28’N, 98°48’E, 300 m, evergreen rain forest, 18–27.IV.1988, leg. Brendell (BMNH).

**Comment:** The above female probably represents an undescribed species. It is characterized by small body size (length of forebody 2.0 mm), the coloration (head black; pronotum reddish; elytra dark-yellowish with the postero-lateral portion very weakly and very diffusely infuscate; abdomen pale-reddish with most of tergites VI and VII infuscate; legs yellow; antennae pale-brown with the apical and basal antenomeres yellowish-red), very slender antennae (antenomeres IV–IX oblong), very dense, moderately coarse, and regularly distributed punctation of the pronotum (including midline) and the elytra, and the absence of non-setiferous punctation on tergites VI and VII.

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**Zyras** (*Zyras*) spec. nov. 5

**Material examined:** Borneo: 5 ♂ ♂, Indonesia, Kalimantan Tengah, Busang–Rekut confluence, 0°03’S, 113°59’E, flight interception trap, VIII.2001, leg. Brendell & Mendel (BMNH, cAss).

**Comment:** This probably undescribed species is characterized by rather large size, distinctive coloration (forebody uniformly brown; abdomen blackish with the posterior margins of segments III–VI broadly reddish; legs yellow; antennae blackish with the basalt antenomeres reddish and the apical 3–4 antenomeres yellow), conspicuously coarse and dense punctation of the elytra, and a posteriorly distinctly concave female sternite VIII. In size, habitus, coloration, punctation, and other external characters, this species is similar to *Z. granulipennis* Cameron, 1939 from Java, but distinguished by a more transverse pronotum with numerous long dark setae at the margins and by the punctation of the elytra (more regularly distributed, less dense near the scutellum). At present, it is unclear if these differences should be interpreted as inter- or intraspecific variation.

3.6 The *Zyras* sensu strictu fauna of Sulawesi (Indonesia)

Species of *Zyras* sensu strictu were previously unknown from Sulawesi. The material from this island in the collections of the BMNH is composed of seven species, four of which are described below. *Zyras gratellus* is redescribed in section 3.4. The remaining two species remain undescribed for want of males. All seven species were collected in the same locality, Bogani Nani Wartabone National Park (0°34’N, 123°41’E) in Sulawesi Utara.

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**Zyras** (*Zyras*) *densissimus* spec. nov.

**Type material:** Holotype ♂: "INDONESIA : SULAWESI UTARA, Dumoga-Bone N.P., 24 Februar 1985. / Plot A, ca 200 m, Lowland forest / Flight interception trap 2 / R.Ent.Soc. Lond., Project Wallace, B.M. 1985-10 / 29.21 / Holotypus ♂ *Zyras densissimus* sp. n., det. V. Assing 2016" (BMNH). Paratypes: 1 ♂: same data as holotype (cAss) 1 ♂: same data as holotype, but "May 1985" (BMNH); 1 ♂: same data as holotype, but "April 1985. / Malaise trap / 'Edwards Camp', Lowland forest, 664 m, 26.IV–28.V" (BMNH).

**Etymology:** The specific epithet (adjective) is the superlative of the Latin adjective densus (dense). It alludes to the conspicuously dense and fine punctation of the forebody.

**Description:** Small species; body length 4.0–4.7 mm; length of forebody 1.9–2.1 mm. Coloration (Figs 36, 75, 111): forebody blackish-brown with the anterior and humeral portions, sometimes also the suture, of the elytra more or less extensively reddish-yellow; abdomen dark-brown to blackish-brown with parts or all of tergites II–V and parts of the paratergites reddish to dark-reddish; antennae dark-yellowish with antenomeres IV–VIII more or less distinctly and more or less extensively brown to blackish-brown; maxillary palpi dark-yellowish to pale-brown with the terminal palpomere pale-yellowish.

**Head (Fig. 75)*** distinctly transverse; punctuation very dense and rather fine; along middle without punctation. Eyes large and bulging, more than twice as long as postocular region in dorsal view. Antenna (Fig. 36) very slender, approximately 2.0 mm long; antenomeres IV–V approximately twice as long as broad, V–X of gradually decreasing length and decreasingly oblong, IX weakly oblong, X weakly oblong or as long as broad, and XI as long as the combined length of IX and X.

**Pronotum (Fig. 75)*** weakly transverse, 1.05–1.08 times as broad as long and approximately 1.1 times as broad as head, broadest near anterior angles, moderately tapering posteriad; lateral margins straight in posterior two-thirds (dorsal view); punctuation fine, regular, and conspicuously dense, also along midline; lateral margins without long setae.

**Elytra (Fig. 75)*** approximately 0.85 times as long as pronotum; punctuation similar to that of pronotum; scutellum with very coarse and defined punctuation. Hind wings fully developed. Metatarsomere I approximately as long as the combined length of II–IV.

**Abdomen** (Fig. 111) narrower than elytra, with deep anterior impressions on tergites III–V; tergites III–V each with a transverse row of 6–8 defined, large and deep setiferous punctures in anterior impressions, with a lateral setiferous puncture on either side, but without setiferous punctures at posterior margin; tergite VI with
few fine non-setiferous punctures anteriorly, with a lateral setiferous puncture on either side, without setiferous punctures at posterior margin; tergite VII with scattered fine non-setiferous punctures anteriorly and with two transverse rows of four setiferous punctures posteriorly, each composed of only four punctures, posterior margin with palisade fringe; tergite VIII (Fig. 243) with eight long setae at posterior margin, a few setae postero-laterally, and with fine pubescence in posterior half, posterior margin convex, without median concavity.

♂: sternite VIII (Fig. 244) with fine and rather dense pubescence in posterior half, posterior margin weakly to distinctly convex; median lobe of aedeagus (Figs 239–241) 0.57–0.58 mm long, slender, and of very distinctive morphology; ventral process long and slender, with sinuate lateral margins in ventral view; paramere (Fig. 242) approximately as long as median lobe and with long and slender apical lobe.

♀: posterior margin of sternite VIII weakly concave in the middle.

Comparative notes: This highly distinctive species is readily identified and distinguished from its conspecifics by the characteristic punctuation of the forebody, the punctuation pattern of the abdomen (particularly the absence of setiferous punctures at the posterior margins of tergites III–VI, the large and deep punctures in the anterior impressions of tergites III–V, and the scattered fine non-setiferous punctures in the anterior portions of tergites VI and VII), and by the conspicuous shape of the aedeagus. In addition, it is characterized by small body size, long and slender antennae, the coloration of the antennae, and by the absence of long setae at the pronotal margins.

As can be inferred from the similarly derived punctuation of the forebody and the abdomen, as well as from the similarly slender antennae and habitus, _Z. densissimus_ is closely allied to _Z. bryanti_ CAMERON, 1943 (female holotype examined; male unknown) from Borneo, from which it differs by different coloration (_Z. bryanti_: pronotum pale-reddish; abdominal segments III–V and VIII reddish-yellow), even denser and finer punctuation of the forebody, and a more convex (cross-section) and posteriorly more strongly tapering pronotum (cross-section).

**Distribution and natural history:** The known distribution is confined to Nani Warnabone National Park in Sulawesi Utara, North Sulawesi (Map 10). The type specimens were collected with flight interception and Malaise traps in lowland forest at altitudes of 200–660 m.

_Type material:_ Holotype ♂: “INDONESIA : SULAWESI UTARA, Dumoga-Bone N.P., 26 February 1985. / Plot A, ca 200 m, lowland forest / Flight interception trap 2 / R.Ent.Soc. Lond., Project Wallace, B.M. 1985-10 / 29,16 / Holotypus ♂ _Zyras titan_ sp. n., det. V. Assing 2016” (BMNH). Paratypes: 1 ♂: same data as holotype, but “24 February 1985.” (cAss); 2 ♀: same data as holotype, but “April 1985.” (BMNH).

**Etymology:** The specific epithet (noun in apposition) alludes to the conspicuously large size of this species. Titans in Greek mythology are giants.

**Description:** Very large species; body length 9.5–11.0 mm; length of forebody 4.0–4.3 mm. Coloration (Figs 41, 76, 113): head and pronotum reddish to reddish-brown, pronotum sometimes with paler lateral margins; elytra pale-reddish, occasionally with the lateral margins slightly darker; abdomen with tergites II–VI dark-reddish to brown with the posterior margin broadly pale-reddish, tergites VII–VIII reddish; antennae brown to dark-brown with the basal three antennomeres pale-reddish and the apical 2–3 antennomeres dark-yellowish; maxillary palpi reddish.

Head (Fig. 76) strongly transverse, extensively impunctate along middle; lateral dorsal portions with sparse and coarse punctuation. Eyes large and bulging, more than twice as long as postocular region in dorsal view. Antenna (Fig. 41) 3.1–3.3 mm long; antennomeres IV to dark-brown with the posterior margin broadly pale-reddish, VI approximately as broad as long or weakly transverse, VII–X of gradually increasing width and increasingly transverse, X approximately 1.5 times as broad as long, and XI as long as the combined length of VIII–X, or nearly so.

Pronotum (Fig. 76) rather weakly transverse, 1.07–1.09 times as broad as long and approximately 1.27 times as broad as head, broadest in anterior half; lateral margins straight in posterior two-thirds (dorsal view); punctuation coarse, dense, and somewhat irregularly distributed; laterally with impunctate patches; midline moderately broadly impunctate; lateral margins each with approximately eight stout, long, and erect black setae; anterior and posterior margins, too, with stout, long, and erect black setae; pubescence of disc pale, fine, moderately long, and sub-erect.

Elytra (Fig. 76) approximately 0.8 times as long as pronotum; punctuation dense, near scutellum and anterior portion of suture very dense, asperate, and somewhat granulose. Hind wings fully developed. Metatarsomere I as long as, or longer than the combined length of II–IV.

Abdomen (Fig. 113) narrower than elytra, with deep anterior impressions on tergites III–V; tergites III–V each with a transverse row of coarse non-setiferous punctures in anterior impressions, with a transverse row of usually four setiferous punctures across the middle, and with four to six setiferous punctures at posterior margins; tergite VI with a transverse band of coarse non-setiferous punctures anteriorly, with a transverse row of four setiferous punctures at posterior third, and...
Figs 1–41: Antennae of Zyras spp.: kraatzi (1), exasperatus (2), pindarae (3–5), perforatus (6), championi (7), pallipes (8), condignus (9), nitens (10), truncatus (11), nilgiriensis (12), hirsutiventris (13), russiceps (14), brignolii (15), hastatus (16), parageminus (17–18), latilobatus (19), alternans (20), hirtus (21), nigroaeneus (22), luteipes (23), longilobatus (24), morvani (25), gratellus (Malaysia) (26), castaneus, lectotype (27), proximus (28–29), novinversus (30–31), brevilobatus (32), parvicollis (33), ambulans (34), matangensis (35), densissimus (36), densihirtus (37), nigrihirtus (38), gratellus (Sulawesi) (39), gardneri (40), titan (41). Scale bar: 1.0 mm.
Figs 42–54: Forebody of *Zyras* spp.: *kraatzi* (42), *exasperatus* (43), *pindarae* (44), *perforatus* (45), *championi* (46), *pallipes* (47), *condignus*, holotype (48), *condignus*, Nepal (49), *nigroaeneus* (50), *morvani* (51), *truncatus* (52), *longilobatus* (53), *hastatus* (54).

Scale bar: 1.0 mm.
with six setiferous punctures at posterior margin; tergite VII with a transverse band of coarse non-setiferous punctures anteriorly and with two transverse rows of setiferous punctures posteriorly, posterior margin with palisade fringe; tergite VIII (Fig. 248) with approximately 20 long black setae posteriorly, posterior margin truncate or weakly concave in the middle.

♂: sternite VIII (Fig. 249) with numerous long black setae in posterior half, posterior margin convex; median lobe of aedeagus (Figs 245–246) approximately 1.2 mm long and of robust shape; ventral process basally with a pair of pronounced carinae; paramere (Fig. 247) as long as median lobe and with very small apical lobe with long setae.

Comparative notes: This species is characterized by its conspicuously large size, coarse punctuation, its coloration, the punctuation pattern of the pronotum, and by the male sexual characters. It is distinguished from the similarly large Z. preangera- nomerus (by the coloration (Z. preangera- nomerus: antennomeres I–VII blackish; head much slimmer than the pronotum; abdominal segments II–V reddish), much coarser punctuation of the forebody, less slender antennomeres IV–X, a completely different punctuation pattern of the abdomen, and by a more robust aedeagus with a ventral process of completely different shape. For illustrations of Z. preangera- nomerus see Assing (2016a) and Figs 276–277.

Distribution and natural history: The type locality is identical to that of Z. densissimus. The type specimens were collected with flight interception traps in lowland forest at an altitude of 200 m.

**Zyras (Zyras) densihirtus** spec. nov.

(Figs 37, 77, 115, 250–254, Map 10)

**Type material:** Holotype ♂: "INDONESIA : SULAWESI UTARA, Dumoga-Bone N.P, November 1985. / Plot B, ca 300 m, lowland forest / Malaise trap 2 / R.Ent.Soc. Lond., Project Wallace, B.M. 1985-10 / 29.123 / Holotypus ♂ Zyras densihirtus sp. n., det. V. Assing 2016" (BMNH). Paratype ♂: same data as holotype, but "May 1985. / Plot C, ca 400 m, Lowland forest / Flight interception trap" (cAss).

**Etymology:** The specific epithet (adjective) is composed of the Latin adjectives densus (dense) and hirtus (pubescent). It alludes to the dense punctuation of the elytra and the hypothesized close relationship to Z. hirtus.

**Description:** Body length 7.3–7.5 mm; length of forebody 3.1–3.3 mm. Coloration (Figs 37, 77, 115): forebody black; abdomen blackish with the posterior margins of the segments and the paratergites partly paler brown; legs pale-yellowish with the profemora slightly darker and the apices of the meso- and metafemora narrowly infuscate; antennae black with the apical two antennomeres pale-yellow; maxillary palpi brown to dark-brown, with the terminal palpomere paler.

Head (Fig. 77) moderately transverse, extensively impunctate along middle; lateral dorsal portions with rather dense and coarse punctuation. Eyes large and bulging, much longer than postocular region in dorsal view. Antenna (Fig. 37) approximately 2.2 mm long; antennomeres IV weakly oblong, V approximately as long as broad, VI–X of gradually increasing width and increasingly transverse, X more than 1.5 times as broad as long, and XI of conical shape, shorter than the combined length of VIII–X, or nearly so.

Pronotum (Fig. 77) weakly transverse, 1.03–1.05 times as broad as long and approximately 1.3 times as broad as head, broadest near anterior angles; lateral margins straight in posterior two-thirds (dorsal view); punctuation coarse, dense, and regularly or slightly irregularly distributed, laterally with or without impunctate patch on either side; midline with or without narrowly impunctate band; lateral margins each with four long and erect black setae; anterior margin with one long and erect black seta on either side.

Elytra (Fig. 77) approximately 0.8 times as long as pronotum; punctuation rather coarse and very dense, denser anteriorly than posteriorly. Hind wings fully developed. Legs very slender; metatarsomere I as long as the combined length of II–IV, or nearly so.

Abdomen (Fig. 115) narrower than elytra, with deep anterior impressions on tergites III–V; tergites III–V each with a transverse row of non-setiferous punctures in anterior impressions, those of tergite V dense, those of tergite IV less dense, and those of tergite III sparse; tergites III–V with a transverse row of four setiferous setae across middle and with 6–8 (tergites III–IV) or 8 setiferous setae (tergite V) at posterior margins; tergite VI with a transverse band of non-setiferous punctures anteriorly, with a transverse row of setiferous punctures across middle, and with approximately ten setiferous punctures at posterior margin; tergite VII with a broad transverse band of coarse non-setiferous punctures anteriorly and with two transverse rows of setiferous punctures posteriorly, posterior margin with palisade fringe; tergite VIII (Fig. 253) with numerous long and erect black setae in posterior third, posterior margin distinctly convex.

♂: sternite VIII (Fig. 254) with numerous long black setae in posterior half, posterior margin strongly convex; median lobe of aedeagus (Figs 250–251) 0.8–0.9 mm long; ventral process subapically abruptly angled; paramere (Fig. 252) as long as median lobe and with very small and flattened apical lobe with long setae.

Comparative notes: As can be inferred from the conical shape of antennomere XI, the shape of the ventral process of the aedeagus, and particularly by the short and flattened apical lobe of the paramere, Z. densihirtus is related
to *Z. hirtus* and allied species. Among the species of this group, it is characterized particularly by the coloration, the dense and coarse punctuation of the elytra, the punctuation pattern of the abdomen, the rather sparse long setation of the forebody, and by the shape of the median lobe of the aedeagus.

**Distribution and natural history:** The type locality is identical to that of *Z. densissimus* and *Z. titan* (Map 10).

The specimens were collected with a Malaise trap and a flight interception trap in lowland forest at altitudes of approximately 300 and 400 m.

**Zyras (Zyras) nigrihirtus** spec. nov.

(Figs 38, 78, 116, 255–259, Map 10)

**Type material:** Holotype ♂ [elytra missing]: “INDONESIA: SULAWESI UTARA, Dumoga-Bone N.P., Feb–April 1985. / Plot C, ca 400 m, Lowland forest / Pit fall trap / R.Ent.Soc. Lond., Project Wallace, B.M. 1985-10 / 29.123 / Holotypus ♂ *Zyras nigrihirtus* sp. n., det. V. Assing 2016” (BMNH).

**Etymology:** The specific epithet (adjective) is composed of the Latin adjectives nigri (black) and hirtus (pubescent). It alludes to the black coloration of the body and the hypothesized close relationship to *Z. hirtus*.

**Description:** Body length 6.8 mm. Coloration (Figs 38, 78, 116): body black (note that the elytra of the holotype are missing); legs pale-yellowish; antennae with antennomeres I–II pale-brown, III–VII blackish-brown, and VIII–XI gradually becoming paler, XI yellowish-brown; maxillary palpi blackish-brown, with the terminal palpomere yellow. Head (Fig. 78) moderately transverse, extensively impunctate along middle; lateral dorsal portions with moderately dense and coarse punctuation. Eyes large and bulging, much longer than postocellar region in dorsal view. Antenna (Fig. 38) 1.9 mm long; antennomeres IV approximately as long as broad, VI–X of gradually increasing width and increasingly transverse, X approximately twice as broad as long, and XI of conical shape, approximately as long as the combined length of VIII–X. Pronotum (Fig. 78) rather weakly transverse, 1.08 times as broad as long and 1.3 times as broad as head, broadest in anterior half; lateral margins straight in posterior two-thirds (dorsal view); punctuation coarse, dense, and nearly regularly distributed; midline very narrowly impunctate; lateral margins each with seven long and erect black setae; anterior and posterior margins each with one long and erect black seta on either side. Hind wings fully developed. Legs very slender; metatarsomere I as long as the combined length of II–IV. Abdomen (Fig. 116) with moderately deep anterior impressions on tergites III–V; anterior impression of tergite III with a transverse row of sparse, anterior impressions of tergites IV–V with a transverse row of denser non-setiferous punctures; discs of tergites III–V with fine non-setiferous punctuation on whole surface and with interspersed setiferous punctures; tergites VI–VII with an anterior transverse band of dense non-setiferous punctures, on remainder of disc with less dense non-setiferous punctures everywhere and with interspersed setiferous punctures; posterior margin of tergite VII with palisade fringe. 

♂: tergite VIII (Fig. 258) with numerous long and erect black setae in posterior third, posterior margin convex, without median concavity; sternite VIII (Fig. 259) with numerous long black setae in posterior half, posterior margin strongly convex; median lobe of aedeagus (Figs 255–256) 0.9 mm long; ventral process of sub-triangular shape and apically acute in ventral view, at base with median carina (lateral view); paramere (Fig. 257) as long as median lobe and with very small and flattened apical lobe.

**Comparative notes:** As can be inferred from the subconical shape of antennomere XI, the shape of the ventral process of the aedeagus, and particularly from the short and flattened apical lobe of the paramere, *Z. nigrihirtus* belongs to the *Z. hirtus* group. Among the species of this group, it is characterized particularly by the coloration, the dense and coarse punctuation of the pronotum, the conspicuous punctuation pattern of the abdomen, the rather sparse long setation of the forebody, and by the shape of the median lobe of the aedeagus.

**Distribution and natural history:** The type locality (Map 10) is identical to that of *Z. densissimus*, *Z. titan*, and *Z. densihirtus*. The holotype was collected with a pitfall trap in lowland forest at an altitude of approximately 400 m.

**Unnamed species**

*Zyras (Zyras)* spec. nov. 1

**Material examined:** Indonesia: 1 ♀, Sulawesi Utara, Dumoga-Bone N.P., 490 m, lowland forest, leaf litter, IX.1985 (BMNH).

**Comment:** This probably undescribed species belongs to the *Z. hirtus* group and is characterized by dense and rather coarse punctuation of the forebody and by dark-brown antennae with the apical three antennomeres pale-yellowish (body length: 5.8 mm; length of forebody 2.7 mm).

*Zyras (Zyras)* spec. nov. 2

**Material examined:** Indonesia: 1 ♀, Sulawesi Utara, Dumoga-Bone N.P., banks of Tumpha river, 200–300 m, lowland forest, leaf litter, II.1985 (BMNH).
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Figs 55–67: Forebody of *Zyras* spp.: *parageminus* (55–56; 55: holotype; 56: holotype of *Z. nameriensis*), *latilobatus* (57), *alternans* (58), *hirtus* (59), *nilgiriensis* (60), *russiceps* (61), *gardneri* (62), *hirsutiventris* (63), *luteipes* (64), *proximus*, holotype (65), *brignolii*, holotype of *Z. thainiger* (66), *novinversus* (67). Scale bar: 1.0 mm.
Figs 68–81: Forebody (68–77), head and pronotum (78), and abdomen (79–81) of *Zyras* spp: *brevilobatus* (68), *parvicollis* (69), *ambulans* (70), *nitens*, holotype (71), *gratellus* (Malaysia) (72), *matangensis* (73), *gratellus* (Sulawesi) (74), *densissimus* (75), *titan* (76), *denshirtus* (77), *nigrihirtus* (78), *kraatzi* (79), *asperatus* (80), *nigroaeneus* (81). Scale bar: 1.0 mm.
Comment: This clearly undescribed species is somewhat similar to *Z. nigrihirtus* especially in the coloration of the antennae), but smaller (body length 5.3 mm; length of forebody 2.5 mm) and characterized by extremely dense punctation of the pronotum (without impunctate median band) and the elytra.

3.7 Species not included in, or excluded from, the subgenus *Zyras*

*Zyras* (*Termidonia*) *rufithorax* CAMERON, 1930

*Zyras* *rufithorax* CAMERON, 1930: 158 f.

**Type material examined:** Syntype δ: “Syntype / Catchment Area, 8–10th-April, 1928 / Malay Peninsula, Kedah, Nr. Jitra, / *Zyras rufithorax* Cam. Type / M. Cameron. Bequest., B.M. 1955-147. / *Zyras rufithorax* Cam., det. R. Pace 1984, Lectotype” (BMNH).

Additional material examined: China: 1 ex., Yunnan, Xishuangbanna, 23 km NW Jinghong, Na Ban env., 22°09'N, 100°40'E, 730 m, Malaise trap, 28.VI.2008, leg. Xishuangbanna, 23 km NW Jinghong, Na Ban env., 22°09'N, 100°40'E, 730 m, Malaise trap, 28.VI.2008, leg. Weigel (NME).

**Comment:** The original description is based on a unspecified number of type specimens from “Dehra Dun” (Cameron 1939a). Two syntypes, both of them females, were found in the Cameron collection at the BMNH. While Cameron (1939a) tentatively assigned the species to *Pella Stephens, 1835*, Hlaváč et al. (2011) list it as *Zyras* s. str. An examination of the type specimens revealed that they significantly differ in so many respects (habitus, morphology of antennae, punctuation pattern, absence of non-setiferous punctuation, short legs, etc.) from *Zyras* s. str. that they are treated as incertae sedis here.

*Zyras* (*Termidonia*) *distinguendus* CAMERON, 1950

*Zyras* (*Rynchodonia*) *distinguendus* CAMERON, 1950: 127.

**Type material examined:** Holotype δ (?; not dissected): “Holotype / Wood (rotten) / Raub, Pahang, F.M.S., Dr. Cameron / Z. *distinguendus* Cam. Type / M. Cameron. Bequest., B.M. 1955-147.” (BMNH).

**Comment:** The original description is based on specimen (“Type in my collection”) from “Raub” (Cameron 1950). An examination of this specimen confirmed that it does not belong to *Zyras* sensu strictu.

*Zyras* (*Cameronodonia*) *carinipennis* CAMERON, 1950

*Zyras* (*Thoracodonia*) *carinipennis* CAMERON, 1950: 128.

**Type material examined:** Holotype δ (?; not dissected): “Holotype / Malay Peninsula: Selangor, F.M.S., Kuala Lumpur, Jan. 12th, 1930, H.M. Pendlebury. / Z. (*Thoraco-
Abdomen approximately as broad as elytra, not distinctly tapering posteriad, segments III–VII of subequal width; non-setiferous punctation absent; tergites III–V with very shallow anterior impressions, very sparsely and finely punctate in anterior half and less finely and less sparsely punctate in posterior half; tergites VI–VII sparsely and very finely punctate anteriorly and less finely punctate and more densely punctate in posterior portion; tergite VIII with more distinct and denser punctuation than tergites III–VII; posterior margin of tergite VII with palisade fringe.

\( \sigma \) : unknown.

**Comparative notes:** In body shape, Z. coloratus is somewhat similar to Z. angkoricola (see below), from which Z. coloratus is readily distinguished by much coarser and denser punctation of the forebody alone.

**Distribution:** This species is currently known only from its type locality in Himachal Pradesh, North India.

Zyras (incertae sedis) rufescens Cameron, 1939

Zyras (Zyras) rufescens Cameron, 1939a: 534.

**Type material examined:** Holotype \( \varphi \) : "Ceylon / Ceylon / Z. rufescens Cam. Type / Sharp Coll., 1905-313 / Holotype Zyras rufescens Cam., det. R.G. Booth 2016" (BMNH).

**Comment:** The original description is based on a unique specimen from "Ceylon" (Cameron 1939a). This species differs in numerous respects from all the revised representatives of the subgenus Zyras, i.e., the shape of the head (somewhat resembling that of the genus Orphnebius Motschulsky, 1858), the practically impunctate dorsal surface of the head, the shape of the pronotum (strongly transverse and of transversely quadrangular shape), the presence of conspicuously long setae on the antennae, very finely and sparsely punctate elytra, the complete absence of non-setiferous punctation on the abdomen, the presence of twelve setiferous punctures on the posterior margin of tergite VI (only few setiferous punctures present at the posterior margins of the other tergites), the absence of distinct anterior impressions on tergites III–V, the presence of numerous long black setae in the posterior two-thirds of sternite VIII, the shape and internal structures of the median lobe of the aedeagus (somewhat resembling those of Orphnebius), and by the completely different morphology of the paramere. In consequence, Z. rufescens is excluded from the subgenus Zyras and treated as Zyras incertae sedis. Based on the illustrations provided by Pace (2011), it seems possible that this species is congeneric with Oriyadota orissaensis Pace, 2011.

**Distribution:** The known distribution is confined to Sri Lanka.
Figs 82–99: Abdomen of *Zyras* spp.: *pindarae* (82–85), *perforatus* (86), *championi* (87), *pallipes* (88), *longilobatus* (89), *hastatus* (90), *truncatus* (91), *latilobatus* (92), *morvani* (93), *condignus* (94), *hirtus* (95), *gardneri* (96), *hirsutiventris* (97), *parageminus* (98), *alternans* (99). Scale bar: 1.0 mm.
Figs 100–116: Abdomen of *Zyras* spp.: *luteipes* (100), *nilgiriensis* (101), *brevilobatus* (102), *brignolii* (103), *parvicollis* (104), *proximus*, holotype (105), *novinversus* (106), *ambulans* (107), *matangensis* (108), *nitens* (109), *gratellus* (Malaysia) (110), *densissimus* (111), *gratellus* (Sulawesi) (112), *titan* (113), *russiceps* (114), *densihirtus* (115), *nigrhirtus* (116). Scale bar: 1.0 mm.
Figs 117–133: *Zyras kraatzi* (117–120), *Z. exasperatus* (121–124), *Z. pindarae* (125–131), and *Z. perforatus* (132–133): median lobe of aedeagus in lateral and in ventral view (117–118, 121–122, 125–128, 132–133); male tergite VIII (119, 123, 130); male sternite VIII (120, 124, 131); paramere (129). Scale bars: 0.5 mm.
Figs 134–155: Zyras perforatus (134–135), Z. pallipes (136–139), Z. nigroaeneus, holotype (140–141), Z. condignus (142–147), Z. morvani, holotype (148–149), and Z. truncatus (150–155): male tergite VIII (134, 138, 140, 146, 148, 152); male sternite VIII (135, 139, 141, 147, 149, 153); median lobe of aedeagus in lateral and in ventral view (136–137, 142–143, 150–151); paramere (144–145); female tergite VIII (154); female sternite VIII (155). Scale bars: 0.5 mm.
Figs 156–173: *Zyras longilobatus* (156–160), *Z. latilobatus* (161–165), *Z. alternans* (166–169), and *Z. hirtus* (170–173; 170–171: Sri Lanka; 172–173: South India): median lobe of aedeagus in lateral and in ventral view (156–157, 161–162, 166–167, 170–173); paramere (158, 163); male tergite VIII (159, 164, 168); male sternite VIII (160, 165, 169). Scale bars: 0.5 mm.
Figs 174–190: *Zyras gardneri* (174–177), *Z. hirsutiventris* (178–181), *Z. luteipes* (182–186), and *Z. russiceps* (187–190): median lobe of aedeagus in lateral and in ventral view (174–175, 178–179, 182–183, 187–188); male tergite VIII (176, 180, 185, 189); male sternite VIII (177, 181, 186, 190); paramere (184). Scale bars: 0.5 mm.
Figs 191–207: Zyras proximus (191–197; 191–192: Thailand; 193–197: India), Z. novinversus (198–202), Z. brevilobatus (203–205), and Z. parvicollis (206–207): median lobe of aedeagus in lateral and in ventral view (191–194, 198–199, 203–204); paramere (195, 200, 205); male tergite VIII (196, 201, 206); male sternite VIII (197, 202, 207). Scale bars: 0.5 mm.
Figs 208–226: *Zyras parvicollis* (208–211), *Z. ambulans* (212–215), *Z. nitens*, holotype (216–221), and *Z. gratellus* (Malaysia) (222–226): median lobe of aedeagus in lateral and in ventral view (208–213, 216–217, 222–223); paramere (214, 218, 224); male tergite VIII (219, 225); male sternite VIII (220, 226); apical lobe of paramere (215); postero–median portion of male sternite VIII (221). Scale bars: 208–214, 216–220, 222–226: 0.5 mm; 215, 221: 0.1 mm.
Figs 227–244: *Zyras parahirtus* (227–228, 231–232), *Z. matangensis* (229–230, 233), *Z. gratellus* (Sulawesi) (234–238), and *Z. densissimus* (239–244): median lobe of aedeagus in lateral and in ventral view (227–230, 234–235, 239–241); paramere (231, 236, 242); male tergite VIII (232, 237, 243); male sternite VIII (233, 238, 244). Scale bars: 227–233, 237–238, 243–244: 0.5 mm; 234–236, 239–242: 0.2 mm.
Figs 245–259: *Zyras titan* (245–249), *Z. densihirtus* (250–254), and *Z. nigrihirtus* (255–259): median lobe of aedeagus in lateral and in ventral view (245–246, 250–251, 255–256); paramere (247, 252, 257); male tergite VIII (248, 253, 258); male sternite VIII (249, 254, 259). Scale bars: 0.5 mm.
Figs 260–277: *Zyras mordus* (260–265), *Z. variolatus* (266–270), *Z. montanus* (271–275), and *Z. preangeranus* from Java (276–277): forebody (260); antenna (261); abdomen (262); median lobe of aedeagus in lateral and in ventral view (263–264, 266–267, 271–272, 276–277); paramere (265, 268, 273); male tergite VIII (269, 274); male sternite VIII (270, 275). Scale bars: 260–262: 1.0 mm; 263–277: 0.5 mm.
Map 1: Revised distributions of *Zyras kraatzi* (black and white circles; white circle: type locality), *Z. exasperatus* (white circle), *Z. iniquus* (triangles), *Z. pallipes* (diamonds), and *Z. championi* (white stars) in the Himalaya.

Map 2: Revised distributions of *Zyras pindarae* (black circles) and *Z. nigroaeneus* (white circles) in the Himalaya.

Map 3: Revised distributions of *Zyras perforatus* (black circles), *Z. morvani* (white circles), and *Z. truncatus* (white star) in the Himalaya.
Map 4: Revised distributions of *Zyras condignus* (black circles) and *Z. morulus* (white circles) in the Himalaya.

Map 5: Revised distributions of *Zyras castaneus* (black circles) and *Z. novinversus* (white circles) in the southern East Palaearctic and Oriental regions.
Map 6: Revised distributions of *Zyras geminus* (black circles) and *Z. proximus* (white circles) in the southern East Palaearctic and Oriental regions.

*Zyras* (incertae sedis) *trapeziceps* Dvořák, 1996

Comment: The teneral holotype of *Z. trapeziceps* was studied and illustrated by Assing (2015), who tentatively attributed the species to the subgenus *Zyras*. However, after examination of numerous additional species of *Zyras* sensu strictu, it is regarded as *Zyras* incertae sedis owing to significant differences distinguishing it from the representatives of the nominal subgenus, in particular conspicuously elongate maxillae (including the palpi), a conspicuously trapeziform head, a weakly convex pronotum (cross-section), microreticulate elytra with very fine and dense punctation, and a densely punctate abdomen without non-setiferous punctation.

*Zyras* (incertae sedis) *gibbus* Pace, 1910

Comment: This species was revised, redescribed, and illustrated by Assing (2016a, b). It is closely allied to *Z. trapeziceps* and consequently excluded from *Zyras* sensu strictu, too.

*Zyras* (? *ferrugineus* Cameron, 1939

Type material examined: Holotype ♀ [in poor condition; right elytron missing]: “Holotype / 64521 / Doberty / Birmah, RubyMes” / Fry Coll. 1905.100. / Z. ferrugineus Cam. Type / Holotype Zyras ferrugineus Cam., det. R.G. Booth 2016” (BMNH).

Comment: The original description is based on a unique male from “Burma : Ruby Mines” (Cameron 1939a). Cameron’s original subgeneric assignment was adopted also by Hlaváč et al. (2011). An examination of the
holotype, however, revealed that the specimen certainly does not belong to *Zyras* sensu strictu. In fact, based on external characters (antennal morphology, conspicuously slender maxillary palpi, punctation of the abdomen), the generic assignment is doubtful, too.

*Drusilla? unicolor* (Cameron, 1950), comb. nov: *Zyras unicolor* Cameron, 1950: 126.

**Type material examined:** Holotype ♂ [teneral; in poor condition]: “Holotype / Malaya, Kuala Lumpur, January 1931., H.M. Pendlebury / A. unicolor Cam. Type / M. Cameron. Bequest, B.M. 1955-147.” (BMNH).

**Comment:** In the original description, which is based on a unique male from “Kuala Lumpur”, Cameron (1950) stated that this was a “somewhat anomalous species” somewhat resembling “*Astilbus*” (now a junior synonym of *Drusilla*), but with “the neck much broader”. As can be inferred from his identification label attached to the holotype, he had originally planned to assign the species to *Astilbus*, but eventually decided to describe it in *Zyras*. The external characters suggest that the holotype belongs to *Drusilla* rather than to *Zyras*. Since the specimen is teneral and in generally poor condition, it was not dissected. Mature specimens are presumably of significantly darker coloration.

**4 Revised and updated catalogue of the species of *Zyras* sensu strictu of the Palaearctic and Oriental regions**

A15 = Assing (2015); A16a = Assing (2016a); A16b = Assing (2016b); App = Assing (present paper); B14 = Bernhauer (1914); B15 = Bernhauer (1915); B33a = Bernhauer (1933a); B33b = Bernhauer (1933b); B39 = Bernhauer (1939); C25 = Cameron (1925); C30 = Cameron (1930); C39a = Cameron (1939a); C39b = Cameron (1939b); C43 = Cameron (1943); C44 = Cameron (1944); Ch21 = Champion (1921); Ch27 = Champion (1927); D81 = Dvořák (1981); D84 = Dvořák (1984); D96 = Dvořák (1996);
Map 8: Revised distributions of *Zyras alternans* (black circles), *Z. luteipes* (star), *Z. brignolii* (white circles), and *Z. nitens* (white triangles) in the southern East Palaearctic and Oriental regions.

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References are not indicated for the species distributed in the West Palaearctic region and Japan. Articles containing useful descriptions and illustrations, as well as new taxonomic acts and/or distribution maps are underlined.
Map 9: Revised distributions of Zyras bettotanus (black circles), Z. nilgiriensis (star), and Z. longilobatus (white circles) in the southern East Palaearctic and Oriental regions.

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Map 10: Revised distributions of *Zyras preangeranus* (black circles), *Z. brevilobatus* (white star), *Z. parvicollis* (white star), *Z. ambulans* (white circle), *Z. densissimus* (black star), *Z. titan* (black star), *Z. densihirtus* (black star), and *Z. nigrihirtus* (black star) in the southern East Palaearctic and Oriental regions.

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| Species                  | Distribution                                                                 | References |
|--------------------------|------------------------------------------------------------------------------|------------|
| abacus Dvořák, 1984      | Kazakhstan, Kyrgyzstan                                                       | D84        |
| alternans (CAMERON, 1925)| India; Malaysia: Malay Peninsula; Indonesia: Java, Sumatra, Borneo           | A16a, App, C25, C39a, P10b |
| ambulans sp. n.           | Thailand                                                                     | App        |
| athetoides Assing, 2016  | China: Sichuan                                                               | A16a       |
| atronitens Assing, 2016  | China: Tibet                                                                  | A16a       |
| bangmaicus Assing, 2016  | China: Yunnan                                                                 | A16a       |
| bartozzi Pace, 2003      | Malaysia: Pahang, Sabah (Borneo)                                             | App, P03, P08 |
| beijingensis Pace, 1993  | China: Beijing, Gansu, Shaanxi, Zhejiang                                     | A16a, P93  |
| bartotanus CAMERON, 1930 | China: Yunnan; Thailand; Peninsular Malaysia; Indonesia: Java; Borneo (Malaysia, Indonesia, Brunei) | A16a, App, C30, C39b, P08 |
| bicoloricollis Assing, 2016 | China: Yunnan                                                                 | A16a       |
| birmanus Scheerpeltz, 1965| Myanmar; China: Yunnan                                                      | A16a, App, S65 |
| bisinuatus Assing, 2016  | China: Yunnan                                                                 | A16a       |
| brevilobatus sp. n.       | Thailand                                                                     | App        |
| brignolii (PACE, 1986)   | Thailand; China: Yunnan                                                     | A16a, App, P86b, P12b |
| bryanti CAMERON, 1943    | Malaysia: Borneo: Sarawak                                                   | C43, P08   |
| caloderoides Assing, 2016| China: Yunnan; Thailand                                                     | A16a, A16b |
| castaneus (Motschulsky, 1861)| Nepal; India; Sri Lanka; Thailand; Laos; China: Yunnan; Hong Kong; Malaysia: Pahang, Sabah (Borneo); Brunei; Indonesia: Java, Borneo | A16a, A16b, App, M61, P87b, P92, P98, P04, P08, P11 |
| collaris (PAYKULL, 1789) | southern West Palaearctic                                                     |           |
| condignus Last, 1969     | North India: Uttar Pradesh                                                  | A16a, App, C39a, L69, P06, P13 |
| cylindricornis Dvořák, 1981| Japan; Korea                                                                | D81        |
| dabanicus Assing, 2016   | China: Qinghai                                                               | A16a       |
| daiaccessor Pace, 2008   | Malaysia: Borneo: Sabah                                                     | P08        |
| densihirtus sp. n.       | Indonesia: Sulawesi Utara                                                   | App        |
| densissimus sp. n.       | Indonesia: Sulawesi Utara                                                   | App        |
| discolor Assing, 2016    | China: Fujian                                                                | A16a       |
| elegantulus CAMERON, 1939| Indonesia: Java                                                              | C39b       |
| Species                  | Distribution                                                                 | References |
|--------------------------|------------------------------------------------------------------------------|------------|
| exspoliatus Assing, 2016 | China: Guangxi                                                               | A16a       |
| exasperatus Schubert, 1908| North India: Himachal Pradesh                                                | App, St08  |
| extensus Assing, 2016    | China: Yunnan                                                                | A16a       |
| facundus Last, 1969      | Indonesia: Java                                                              | C39b       |
| = semirufus Cameron, 1939|                                                                               |            |
| fansipanicus Assing, 2015| Vietnam                                                                      | A15        |
| firmicornis Assing, 2016 | China: Fujian                                                                | A16a       |
| flavorus Cameron, 1939   | Indonesia: Java                                                              | C39b       |
| flexus Assing, 2016      | China: Fujian                                                                | A16a       |
| formosanus Assing, 2016  | Taiwan                                                                       | A16a       |
| fugax (Sharp, 1888)     | Japan, Korea                                                                  |            |
| fulgidus (Gravenhorst, 1806) | southern West Palaearctic                                              |            |
| funestus (Dvořák, 1996) |                                                                               |            |
| gardneri Cameron, 1939  | Nepal; North India                                                            | A15, D96   |
| geminus (Kraatz, 1859)   | India; Nepal; Sri Lanka; China: Guangxi, Yunnan; Taiwan; Hong Kong; South Japan; Thailand; Laos; Vietnam; Indonesia | A15, A16a, A16b, App, C44, HNM11, K59, P87b, P92, P99, P01a, P05, P06, P10b, P12b |
| = indicus Cameron, 1944, syn. n. |                                                                               |            |
| = shiva Pace, 1987, syn. n. |                                                                               |            |
| = manjashri Pace, 1992, syn. n. |                                                                               |            |
| = hongkongensis Pace, 1999, syn. n. |                                                                               |            |
| = benenensis Pace, 2001, syn. n. |                                                                               |            |
| = parageminus Pace, 2010, syn. n. |                                                                               |            |
| = neoparageminus Hlaváč et al., 2011, syn. n. |                                                                               |            |
| = subgeminus Pace, 2012, syn. n. |                                                                               |            |
| = articollis Assing, 2016, syn. n. |                                                                               |            |
| gilvipalpis Assing, 2016 | China: Yunnan                                                                | A16a       |
| glabricollis Scheerpeltz, 1965 | Myanmar                                                                     | A16a, S65  |
| granapicalis Assing, 2016 | China: Sichuan                                                               | A16a       |
| granulipennis Cameron, 1930 | Malaysia: Borneo: Sabah                                                      | C30, P08   |
| gratellus Cameron, 1939  | Malaysia; Indonesia: Java, Sulawesi                                          | App, C39b  |
| hastatus Fauvel, 1904    | South India                                                                  | App, F04   |
| hauserianus Bernhauer, 1933 | China: Heilongjiang, Xinjiang?, Kazakhstan?                                   | A16a, App, B33a |
| haworthi (Stephens, 1832) = elegans (Heer, 1839) = nigricollis Motschulsky, 1845 | southern West Palaearctic |            |
| hebes Assing, 2016       | Taiwan                                                                       | A16a       |
| hirsutiventris (Champion, 1927) | Nepal; North India                                                          | App, Ch27  |
| hirtus (Kraatz, 1859)    | Sri Lanka; South India                                                       | A16a, App, K59 |
| illecebrosus Last, 1982  | Mongolia                                                                     | A16a, A16b, L82 |
| inexcisus Assing, 2016   | China: Gansu, Qinghai; Russia: Far East, East Siberia                       | A16a       |
| iniquus Assing, 2016     | Pakistan; Afghanistan                                                       | A16a       |
| iridescens (Sawada, 1970) | Japan                                                                        |            |
| Species                          | Distribution                                      | References       |
|--------------------------------|--------------------------------------------------|------------------|
| *kambaitiensis* SCHERPRTZ, 1965 | Myanmar; China: Yunnan                           | A16a, S65        |
| = *ferrugineiventris* SCHERPRTZ, 1965 |                                                 |                  |
| = *semiasperatus* SCHERPRTZ, 1965 |                                                 |                  |
| *kinabaluensis* PACE, 2008      | Malaysia: Borneo: Sabah                          | P08              |
| *kraatzi* SCHUBERT, 1908        | North India; Nepal                               | A16a, App, C39a, Ch27, P87a, St08 |
| = *ignicauda* (CHAMPION, 1927)  |                                                 |                  |
| *lattilobatus* sp. n.           | South India                                      | App              |
| *lativentris* ASSING, 2016      | China: Yunnan                                    | A16a             |
| *lateipes* sp. n.               | North India: Meghalaya                           | App              |
| *maculicollis* ASSING, 2016     | China: Hubei, Jiangxi, Sichuan                   | A16a, A16b       |
| *maculipennis* GRIDELLI, 1921   | Caucasus region; Middle Asia                     |                  |
| *malaisei* SCHERPRTZ, 1965      | Myanmar; Vietnam                                 | A15, A16a, S65   |
| *matangensis* CAMERON, 1943     | Malaysia: Borneo: Sarawak, Sabah                 | App, C43, P08    |
| *modiglianii* (CAMERON, 1925)   | Indonesia: Sumatra                               | C25, P10b        |
| *montanus* (BERNHAUER, 1915)    | Borneo: Sarawak, Sabah (Malaysia); Kalimantan Tengah (Indonesia); Brunei | App, B15, P08, P14 |
| *mortuorum* PACE, 1990          | Philippines                                      | P09              |
| *morulus* sp. n.                | Nepal: Dhaulagiri, Annapurna                     | App              |
| *morvani* PACE, 1986            | Nepal                                            | P86c, App        |
| *nigerrimus* CAMERON, 1943      | Malaysia: Borneo: Sarawak                        | C43, P08         |
| *nigrapicalis* ASSING, 2016     | Myanmar; China: Yunnan, Sichuan; Taiwan; Hong Kong | A16a, App         |
| *nigricornis* ASSING, 2016      | China: Hubei, Gansu, Shaanxi, Sichuan, Qinghai | A16a             |
| *nigrihirtus* sp. n.            | Indonesia: Sulawesi Utara                       | App              |
| *nigroaeneus* CAMERON, 1939     | North India                                      | App, C39a        |
| *nigrnitens* ASSING, 2016       | China: Yunnan                                    | A16a             |
| *nilgeriensis* CAMERON, 1939    | South India                                      | App, C39a        |
| *nites* CAMERON, 1944           | Malaysia: Selangor                               | App, C44         |
| *notaticornis* PACE, 1998       | China: Guangxi, Zhejiang; Hong Kong              | A16a, P98        |
| *novinversus* nom. n.           | Thailand; Laos                                   | App, P12b        |
| = *inversus* PACE, 2012         |                                                 |                  |
| *optatus* (Sharp, 1888)         | Japan                                            |                  |
| *paederinus* PACE, 2008         | Malaysia: Borneo: Sabah                          | P08              |
| *pallipes* PACE, 1992           | Nepal                                            | App, P92         |
| *pallipyga* PACE, 2008          | Malaysia: Borneo: Sabah                          | P08              |
| *parageminus* PACE, 1998        | India: Assam; Sri Lanka                          | App, P88, P11    |
| = *nameriensis* PACE, 2011, syn. n. |                                                 |                  |
| *parahirtus* sp. n.             | Borneo (Indonesia)                               | App              |
| *particornis* (SHARP, 1888)     | Japan; Korea; Russian Far East                   | App              |
| *parvicollis* sp. n.            | Thailand                                         | A16b, App, Ch21  |
| *perforatus* (CHAMPION, 1921)   | Nepal; North India                               |                  |
| Species | Distribution | References |
|---------|--------------|------------|
| *pervariolosus* Pace, 2008 | Malaysia: Borneo: Sabah | P08 |
| *pictus* (Sharp, 1874) | Japan; Korea | |
| *pindarar* (Champion, 1921) = *ruficauda* Cameron, 1939, syn. n. | Nepal; India: Uttar Pradesh, West Bengal | A16b, App, C39a, Ch21, P92, P06 |
| *porrectus* Assing, 2016 | China: Sichuan | A16b |
| *preangeranus* Cameron, 1939 = *lowerensis* Cameron, 1939, syn. n. = *chinkiangensis* Bernhauer, 1939, syn. n. = *setosipennis* Scheerpeltz, 1965, syn. n. = *alboantennatus* Pace, 1986, syn. n. = *sichuanorum* Pace, 2012, syn. n. | Myanmar; China: Sichuan, Yunnan, Jiangsu; Thailand; Laos; Vietnam; Malaysia: Selangor, Pahang, Sabah, Sarawak (Borneo); Indonesia: Java, Borneo | A15, A16a, App, B39, P86a, C39b, P12a, P12b, S65 |
| *proximus* Cameron, 1939 = *drugmandi* Pace, 2004, syn. n. | India; China: Guizhou; Thailand; Laos | App, C39a, P04 |
| *pulcher* Assing, 2016 | China: Gansu, Sichuan | A16a |
| *punctipennis* Cameron, 1939 | Indonesia: Java | C39b |
| *quadriterminalis* Pace, 2008 | Malaysia: Borneo: Sabah | P08, P14 |
| *quasar* Dvořák, 1996 | Vietnam | A15, A16b, D96 |
| *rectus* Assing, 2016 | China: Yunnan | A16a |
| *rufapicalis* Assing, 2016 | Taiwan | A16a |
| *rufoterminalis* Assing, 2016 | China: Hubei, Sichuan | A16a |
| *russiceps* sp. n. | Thailand; Malaysia: Selangor | App |
| *schuelkei* Assing, 2016 | China: Fujian, Sichuan, Guangxi | A16a, A16b |
| *seminingerrimus* Bernhauer, 1933 | China: Sichuan | A16a |
| *setosivestis* Scheerpeltz, 1965 | Myanmar | A16a, S65 |
| *shaanxiensis* Pace, 1998 | China: Gansu, Hubei, Shaanxi, Sichuan, Yunnan? | A16a, A16b, P98 |
| *sibiricus* Bernhauer, 1914 | Russian Far East; Japan; China: Beijing | A16a, B14 |
| *song* Pace, 1993 | China: Yunnan | A16a, P93 |
| *songanus* Pace, 1993 | China: Beijing | A16a, P93 |
| *subobsolus* Assing, 2016 | China: Sichuan | A16a |
| *tenebricosus* Assing, 2016 | China: Sichuan, Tibet | A16a |
| *tenuicornis* Assing, 2016 | Taiwan | A16a |
| *thaiorum* Pace, 1986 | Thailand | A16a, P86a |
| *titan* sp. n. | Indonesia: Sulawesi Utara | App |
| *truncatus* sp. n. | Nepal: Dhaulagiri | App |
| *tumidicornis* Assing, 2016 | China: Sichuan, Yunnan | A16a, App |
| *variolatus* Pace, 2003 | Malaysia: Pahang, Kelantan | App, P03 |
| *volans* Assing, 2016 | Taiwan | A16a |
| *wunderlei* Assing, 2016 | Indonesia: Bali | A16b |
| *wei* Pace, 1993 = *qingchengensis* Pace, 2012 | China: Fujian, Guizhou, Sichuan, Zhejiang | A16a |
| *yongshengensis* Pace, 2012 | China: Yunnan | A16a |