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DOKTORI (PH.D.) ÉRTEKEZÉS

**INVESTIGATIONS ON THE TAXONOMY AND SYSTEMATICS OF BIG-EYED BUGS (HETEROPTERA:
LYGAEOIDEA: GEOCORIDAE)**

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(HETEROPTERA: LYGAEOIDEA: GEOCORIDAE)

Értekezés doktori (PhD) fokozat elnyerése érdekében

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1. Abstracts

1.1. Abstract

The aim of the recent study was the investigation of the systematic problems of the subfamily Geocorinae (Hemiptera: Heteroptera: Lygaeoidea: Geocoridae). This peculiar taxon needs thorough revisions at both species and generic levels as it was suggested by earlier studies. In course of the present work a combination of morphological knowledge and supplementary molecular sequence data was attempted in order to resolve systematic problems, e.g. the applicability of tribe and subspecies as taxonomic ranks in this family. The study resulted the partial revision of the second largest genus of the subfamily, *Germalus* Stål, 1862 including the description of five new species; the description of two new genus: one distributed in the Indomalayan Region and one from New Caledonia; and the evaluation of the applicability of the subspecies concept in the subfamily. Furthermore, preliminary evidences were acquired on the presence of coherent species-groups in *Geocoris* and the adequacy of tribal classification of Geocorinae. Along with this preliminary reviews and revisions of discussed taxa and are provided.

1.2. Kivonat

Jelen dolgozat célja a Geocorinae alcsalád rendszertani problémáinak vizsgálata volt. Ez a különleges taxon mind faji, mind pedig genusz szinten átfogó revízióra szorul, ahogy azt korábbi tanulmányok is megállapították. A munka során a morfológiai ismeretek és molekuláris szekvenciaadat-elemzés ötvözésével kísérlet történt olyan rendszertani problémák megoldására, mint a tribusz és alfaj rendszertani kategóriák alkalmazhatósága a családban. A vizsgálatok eredményei alapján megtörtént az alcsalád második legnagyobb genuszának (*Germalus* Stål, 1862) részleges revíziója, beleértve öt tudomány számára eddig ismeretlen faj leírását; leírásra került két új genusz: egy az Indomaláj térségből és egy Új-Kaledóniából; az alfaji kategória ezen alcsaládban történő alkalmazhatóságának újraértékelése. Továbbá előzetes bizonyítékok merültek fel a *Geocoris* genuszban feltételezett, koherens fajcsoportokat és az alcsalád tribusz-beosztása helyességét illetően. Ezekkel együtt megtörtént a tárgyalt taxonok előzetes áttekintése és revíziója.

1.3. Auszug

Das Ziel von dieser Forschung war die Prüfung der taxonomischen Probleme von Unterfamilie Geocorinae. Eine umfassende Revision von diesem einzigartigen Taxon ist

notwendig auf beide Art- und Genusebene als es war schon von früheren Forschern empfiehlt. Während der Arbeit morphologische Kenntnis und molekulare Sequenzdaten waren kombiniert zu lösen solchen Problemen wie die Anwendung von taxonomischen Kategorien in der Familie wie Tribus oder Unterart. Auf dem Grunde der Ergebnisse erfolgt eine partielle Revision der zweitgrößten Gattung, *Germalus*; auch Beschreibung von zwei neuen Gattungen aus der Indomalayen Region; Aufwertung von der Anwendung von Unterart als Kategorie in dieser Unterfamilie. Weiterhin, vorläufige Daten waren erworben am kohärent Art-Gruppen von *Geocoris* und Tribus-Zuordnung in der Unterfamilie. Zusammen mit diesen ist eine vorläufige Umschau und Revision von aufgethandelten Taxa auch gemacht.

2. Introduction and review of literature

2.1. Introduction

Big-eyed bugs (Geocoridae: Geocorinae) are peculiar representatives of the superfamily Lygaeoidea (sensu HENRY 1997) in terms of both appearance and feeding habits. These insects are readily recognised by their big, kidney shaped eyes, mostly ovoid habitus, and curved sutures between abdominal tergites. The family consists of nearly 30 genera comprising a sum of circa 290 known species divided into 5 subfamilies of which the nominotypical subfamily, Geocorinae is the most species rich and most widely distributed (HENRY 2009, RENGIFO-CORREA ET AL. 2013, BRAILOVSKY 2016, KÓBOR 2019). Representatives of the subfamily are distributed in almost all biomes with warm and temperate climate or even in extreme biotopes like high mountains or deserts. Unlikely to other lygaeoid bugs which are seed- or sap-feeding, geocorids mostly known to be predaceous (SLATER 1977, SWEET 2000, CASSIS & GROSS 2002). The food range of the species with well-studied autecology includes aphids and thrips, making them useful organisms in terms of biological pest management (KUMAR & ANANTHAKRISHNAN 1985, BUGG ET AL. 1991, BRAMAN ET AL. 2003). However, extensive applied ecological studies require a firm systematical basis which allows reliable identification.

The characteristic appearance of Geocorinae led to serious confusions and errors in terms of the taxonomy and systematics of the taxon. Early descriptions and diagnoses were based on superficial study of easy-to-observe characters, mostly colouration. The erroneous conclusions were later broadly accepted and resulted a nominotypical taxon which is to be considered as “an ill-defined group of species belonging to perhaps several distinct genera” (MALIPATIL 1994) along with a relatively high ratio of mono- and oligotypic genera (e.g. MALIPATIL & BLACKET 2013, KÓBOR 2019a, b). Most of the studies on the representatives of the subfamily in the last decades restricted to description of new species, proposal of synonymies or studies on faunas of particular regions. The regions considered to be thoroughly studied at infrageneric level are the western part of the Palearctic biogeographic realm (PÉRICART 1999), China (ZHENG & ZOU 1981, GAO 2010), Australia (MALIPATIL 1994, CASSIS & GROSS 2002, MALIPATIL & BLACKETT 2013), the eastern part of the United States (READIO & SWEET 1982) and Mexico (BRAILOVSKY 2016). However, several biodiversity hotspots like Madagascar or New Caledonia have remained virtually unstudied since the 1920's until present day.

In course of the present study, based on the available literature on the biosystematics of Geocorinae and examination of material of various collections and recent field collectings, the following topics were investigated:

- 1) an evaluation and investigation of diagnostic and systematic characters at various levels within the subfamily;
- 2) a revision of the applicability of tribe, subspecies categories in the subfamily;
- 3) an evaluation of suspected species-groups along with a revision of the integrity of *Geocoris* Fallén, 1814;
- 4) a taxonomic revision of taxa included in Geocorinae.

The study was carried out with the application of an integrated approach, combining the data retrieved from a morphological study of exoskeletal and genital structures and an analysis of molecular sequence data using cladistic methods.

2.2. A brief overview of the natural history of Lygaeoidea

Lygaeoidea is the second largest superfamily in the infraorder Pentatomomorpha and is to be considered one of the most diverse groups of Heteroptera with more than 4515 species of 770 valid genera divided into 16 families, distributed worldwide (HENRY 2009, author's unpublished data). The status of the superfamily and the included taxa were a subject of debate for decades (e.g. ŠTYS 1967, HENRY & FROESCHNER 1988 or SCHAEFER 1993). Based on the results of an extensive morphological phylogenetic study on the infraorder Pentatomomorpha HENRY (1997) fixed the status of the superfamily Lygaeoidea and revised its family level classification. The results of his study and the resulting classification of Lygaeoidea was accepted by most of the recent authors. Most recent investigation based on molecular sequence data (LI ET AL. 2005) suggest that Lygaeoidea might be paraphyletic, however, this hypothesis needs further support to invalidate the apparently strong morphological basis of the currently accepted classification. A recent and up to date catalogue on the superfamily was published online by HENRY & DELLAPÉ (2020) based on the works of SLATER (1964a, b) and SLATER & O'DONNELL (1995), incorporating all subsequent changes published up to the present day.

In spite of their diversity, representatives of Lygaeoidea can be generally easily delimited from other heteropteran insects by the reduced, simple venation of the hemelytral membrane, mostly lacking closed cells, and the incrassate fore femora (this character is missing in some of the distal taxa) as concluded by HENRY (1997). This study mainly relied on literature data on the morphological characteristics of Lygaeoidea, thus the superfamily's morphology can be considered well-known. Even earlier, comprehensive works provided thorough general descriptions, e.g. FLOR (1860), HORVÁTH (1875). Notable examples on in-depth analysis of separate character complexes are also to be found in the literature, e.g. wing structure (TILLYARD 1926, LAMEERE 1940, SLATER & HURLBUTT 1957), abdominal trichobothria (TULLGREN 1918, BUTLER 1923, GAO ET AL. 2017), or genitalia (VERHOEFF 1893, SINGH-PRUTHI 1925, CHINA 1933, ASHLOCK 1957, SCUDDER 1959).

SLATER (1977) recognised 7 major types of wing modification ranging from the complete absence of fore and hind wings (aptery) to entirely developed wings (macroptery).

Three major habitats typically colonized by lygaeoids were recognized by Slater (1975, 1977) and SLATER & BARANOWSKI (1990). All life stages of geophilic species live on the ground in litter and mostly feed on seeds (except Geocorinae); members of this group are likely to develop flightlessness and types of wing modification. The term laminiphilic is used to describe

lygaeoids (e.g. Blissidae) which live between the stem and leaf sheaths of grasses. These insects also show various forms of wing modifications but staphylinoidy and coleoptery are missing in the group. Arboreal lygaeoids spend most of their life cycle above the ground on dicotyledonous vegetation. Members of this group is always fully winged; and most of the lygaeoids belong here.

Most of the lygaeoid bugs are known as seed-feeders, but there are some sap-feeding taxa as well. The most unusual feeding habits in the superfamily are predation (Geocoridae) (e.g. TAMAKI & WEEKS 1972) and hematophagy (Cleradini) (TORRES ET AL. 2000).

Comprehensive reviews on ecology, life history and human importance of the representatives of the superfamily were published by KIRKALDY (1907), BARBER (1923), SCHUH & SLATER (1995) and SWEET (2000a), citing all important works on the topics. More recently an extensive overview on the evolutionary ecology of family Lygaeidae was published by BURDFIELD-STEEL & SHUKER (2014).

2.3. An overview on big-eyed bugs (Heteroptera: Lygaeoidea: Geocoridae)

2.3.1. Morphology

The taxa included in the family Geocoridae are unusual representatives of Lygaeoidea in terms of morphology. These bugs are readily recognised by combination of following characters: body mostly oval, elongate; head broad with eyes kidney-shaped, stylate; posterior edge of eyes often exceeding or encompassing the anterior margins of pronotum; median third of sutures between abdominal tergites 4/5 and 5/6 curved posteriad medially; abdominal spiracles II-IV dorsal (HENRY 1997).

Despite the common attributes shared by the representatives of the subfamily a high degree of morphological heterogeneity and specialization can be observed within the contained taxa. Ant-mimetics is to be considered as relatively common phenomenon as it is present by geocorid bugs of various regions and biomes of the world e.g. *Bledionotus systellonotoides* Reuter, 1878 (Middle-East, semideserts), *Stenogeocoris horvathi* Montandon, 1913 (Argentina, grasslands), *Cattarus* Stål, 1858 (Central- and South-America, rainforests). Another characteristic group is genus *Epipolops* Herrich-Schaffer, 1850 which can be characterized with strongly stylate eyes and projections of pronotum. The genus *Geocoris* itself shows considerable variety too. Examples on diversity of Geocoridae are shown in Figure 1.

2.3.2. Classification and diversity

The big-eyed bugs (Geocoridae) is a moderately species rich but morphologically rather heterogeneous family of Lygaeoidea (Hemiptera: Heteroptera) distributed in all biogeographic realms of warm and temperate climate. For a long time, the group was recognized as a subfamily within a broadly defined Lygaeidae but it was raised to family rank by HENRY (1997). It currently consists of 5 subfamilies and comprises about 28 valid genera with 288 known species (HENRY 2009, MALIPATIL 2012, RENGIFO-CORREA ET AL. 2013).

Subfamily	Author, year	Number of included genera/species	Distribution
Australocorinae	Malipatil, 2012	1/ 3	Australian
Bledionotinae	Reuter, 1878	1/ 1	Iranian (desert)
Henestarinae	Douglas & Scott, 1865	3/ 14	Palearctic, Neotropic
Geocorinae	Baerensprung, 1860	17/ ~220	sub-cosmopolitan
Pamphantinae	Barber & Bruner, 1933	12/ 49	Neotropic, Australian, Indomalayan

Table 1.: Subfamilies of Geocoridae

The nominotypical subfamily, Geocorinae is by far the largest of the five subfamilies, including more than 220 described species of 16 genera (BRAILOVSKY 2016) with almost worldwide distribution. Australocorinae is a recently established subfamily endemic to Australia (MALIPATIL 2012) consisting of a single genus including 3 species. Representatives of the subfamily Henestarinae are known from the Palearctic Region except for the problematic genus *Coriantipus* Bergroth, 1912 (HENRY ET AL. 2015). The subfamily Bledionotinae consists of a monotypic genus, its single species is myrmecomorphic, distributed in the Middle East from Syria to Tajikistan (SLATER 1964). The morphologically heterogeneous Pamphantinae was reduced to be tribe of Bledionotinae (SCUDDER 1963), but later was resurrected from the synonymy (HENRY 1997). SLATER (1999) classified the included taxa into three tribes: Cattarini, Epipolopini and Pamphantini. Representatives of Pamphantinae was thought to be distributed in the Neotropics apart from *Austropamphantus woodwardi* Slater, 1981, an

Australian species, but recently a new tribe, Indopamphantini, was described to the subfamily including two monotypic genera from the Indomalayan biogeographic realm (MALIPATIL 2017, MALIPATIL & SCUDDER 2018). *Epipolops* Herrich-Schaffer, 1850, the largest genus of the subfamily was subject of the first phylogenetic study published on the family Geocoridae (RENGIFO-CORREA ET AL. 2013). Currently this subfamily comprises altogether 48 species in 12 genera and four tribes (DELLAPÉ & HENRY 2019).

2.3.3. Distribution

Representatives of the family Geocoridae are distributed in almost every biomes of the World with warm and moderate climate (BRAILOVSKY 2016). The species-richness of the family reaches its maximum in the tropics e.g. the Australasian, the Indomalayan and the Neotropical regions.

The Australasian region is one of the most extensively studied and is outstandingly rich in endemic monotypic genera (MALIPATIL 1994, CASSIS & GROSS 2002, MALIPATIL 2012, MALIPATIL & BLACKETT 2013).

In the Neotropics three of the five subfamilies of Geocoridae are present: Geocorinae, Henestarinae and Pamphantinae. However, the status of *Coriantipus inopinatus* is questionable. The region is well-studied, multiple revisionary works were published recently e.g. BARANOWSKI & SLATER (2005), DELLAPÉ (2014), DELLAPÉ ET AL. (2015), HENRY ET AL. (2015), BRAILOVSKY (2016).

The Palearctic realm is inhabited by representatives of Geocorinae, Henestarinae and Bledionotinae. The Western parts of the region was reviewed thoroughly in the large-scale monographic work of PÉRICART (1999) on Euro-Mediterranean Lygaeoidea. KERZHNER (1979) revised the Mongolian fauna of genus *Geocoris* which is a fundamental work in terms of the North-Eastern part of the Palearctic region. The fauna of China is also well-reviewed by the studies of ZHENG & ZOU (1981) and GAO (2010).

In terms of the Nearctic realm the study of READIO & SWEET (1982) is to be mentioned as fundamental publication with valuable taxonomic suggestions on genus *Geocoris* generally.

2.3.4. Ecology

Representatives of the family are mostly geophilic, but some of them are thought to be arboreal according to SLATER (1977) and SLATER & BARANOWSKI (1990). Geophilous species live on

the ground, in the litter layer. These species are often brachypterous and flightless while arboreal species live on plants, having fully developed wings and are ready to fly.

Unlike to most lygaeoid bugs which are obligatory seed- or sap-feeding, Geocoridae are mostly highlighted for their predatory feeding. However, it must be noted that geocorids are rather omnivorous than obligatory predators. In the absence of prey, they can survive on plant parts with preference on seeds and pollen. Prey spectrum of the taxa with well-studied ecology mostly consists of aphids, moth larvae and thrips thus some of the geocorid bugs are to be considered as potentially beneficial organisms in terms of biocontrol and integrated pest management (KUMAR & ANANTHAKRISHNAN 1985, SWEET 2000b).

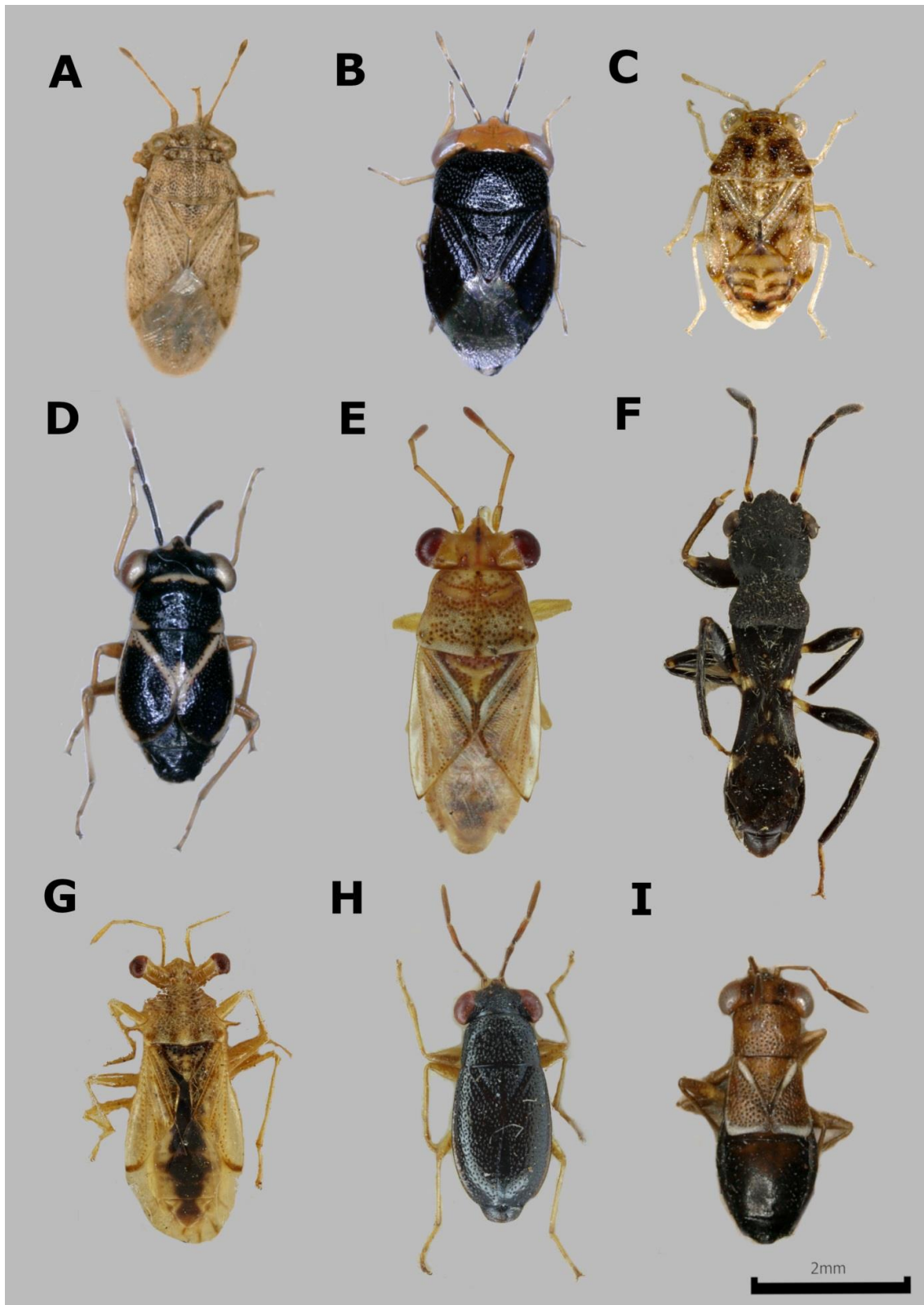


Figure 1. **Examples on diversity of Geocoridae** – A. *Engistus exanguis confurcatus* Horváth, 1911; lectotype, HNHM. B. *Piocoris erythrocephalus erythrocephalus* (Lepeletier and Serville, 1825); HNHM. C. *Nannogermalus marmoratus* (Kóbor, unpublished); paratype, NHMW. D. *Geocoris grylloides* (Linnaeus, 1761); HNHM. E. *Germalus greeni* Distant, 1910; holotype, BMNH. F. *Cattarus formicarius* (Distant, 1893); holotype, BMNH. G. *Epipolops oculuscancri* (Distant, 1893); lectotype, BMNH. H. *Geocoroides polytretus* Distant, 1918, holotype, BMNH. I. *Stenogeocoris horvathi* Montandon, 1913; holotype, HNHM.

2.4. An overview of subfamily Geocorinae Baerensprung, 1860

2.4.1. Morphology

Representatives of Geocorinae can be generally characterized by the combination of the following characters: head pentagonal, eyes moderately or slightly stylate; pronotum mostly trapezoidal, sometimes widened; scutellum triangular with variably developed medial trifurcate carina; hemelytron mostly macropterous or submacropterous, wing polymorphism occur group-specifically; sutures of abdominal tergites IV–VI curved; abdominal spiracles II–IV dorsal and V–VII ventral.

Though the subfamily is a peculiar taxon of Lygaeoidea the delimitation of groups within the subfamily is unclear and the diagnostic characters need to be revised. There are multiple characters suggested which were later overlooked or omitted:

Furrows of vertex were proposed as diagnostic characters by READIO & SWEET (1982). The taxonomic significance of proportion of labiomeres was argued by LINNAVUORI (1972) and later by READIO & SWEET (1982). Morphology of hind wing venation (Fig. 6A) was extensively studied in Lygaeoidea by SLATER & HURLBUTT (1957) and gave examples on Geocorinae, but the character was not studied extensively within the representatives of the subfamily. BERGROTH (1916) suggested on the implication of metathoracic scent efferent apparatus (MTSEA) as diagnostic character, but the character remained virtually unstudied. However, its importance was proved recently in other heteropteran families, e.g. KMENT & VILIMOVÁ (2010). In situ position of male paramere as diagnostic character was proposed by the key of BRAILOVSKY (2016).

2.4.2. Classification and diversity

Geocorinae, the nominotypical subfamily of Geocoridae, is the largest among the five subfamilies of the family comprising about 220 known species of 16 valid genera (BRAILOVSKY 2016). The taxon was first proposed in BAERENSPRUNG's (1860) systematic work on European Heteroptera. The first researcher who extensively studied the taxon was the Swedish hemipterist STÅL (1862a, b, 1866, 1872, 1874) publishing four comprehensive works on the representatives of the subfamily, providing description and keys along. During the second half of the 19th century European representatives of the taxon were extensively studied e.g. by HORVÁTH (1875), PUTON (1879), ACLOQUE (1897). WALKER (1872) catalogued the specimens deposited in the collection of Natural History Museum, London. DISTANT (1893, 1904) provided a strong basis for the research of the Central America and the Indian subcontinent. One of the most

prolific researchers of the subfamily in the first decades of the 20th century was MONTANDON (1907, 1908, 1913a, b, c) – a French hemipterist living in Romania – who described and revised multiple species and genera worldwide and built a notable collection which is now deposited in the Hungarian Natural History Museum (Budapest, Hungary), Kimball Natural History Museum (San Francisco, USA) and Grigore Antipa Museum (Bucharest, Romania).

MONTANDON (1913a) proposed to classify the geocorine genera into two tribes, Geocorini and Germalini. He concluded that Germalini can be defined by the complete ocular sulcus, subequilateral scutellum, and parallel-sided clavus with completely developed claval commissure. Contrastingly, taxa contained in Geocorini show different levels on reduction of ocular sulcus, have elongate scutellum and margins of clavus converging apically, with claval commissure reduced. After purchasing Montandon's collection PARSHLEY (1921) developed this concept based on the work of MONTANDON (1913a) and the collection material, however, the entire hypothesis was never published in detail. This idea never spread widely: the most recent mention of Germalini is found in BARBER'S (1958) study on Micronesian fauna, and this name was omitted by all subsequent authors. The Lygaeidae world catalogue (SLATER 1964) uses tribe Geocorini to separate Psammini which was later upgraded to subfamily (SLATER & SWEET 1965) and recently placed in Piesmatidae (HENRY 1997) from the rest of the subfamily. The tribal classification is presently unused. However, overlooked evidence strongly supports it. SLATER & HURLBUTT (1957) in course of the study of hind wing venation in Lygaeidae concluded that based on the reduction of hamus and presence of intervannals two lineages can be recognised in Geocoridae: the geocorine line has reduced hamus and missing intervannals, and a henestarine line (including *Germalus*) with hamus complete and present intervannals, fused basally. These conclusions were not implied in later studies and the concept of tribal classification of Geocorinae remained virtually forgotten. However, there are multiple examples on such division of subfamilies in Lygaeoidea e.g. Rhyparochomidae (SWEET 1975) or the geocorid Pamphantinae (HENRY 2013).

The largest geocorine genus is the nominotypical *Geocoris* Fallén, 1814, comprising about the two-third of the known species of the subfamily. The genus is currently divided into three subgenera: *Geocoris* Fallén, 1814, *Piocoris* Stål, 1872 and *Eilatatus* Linnavuori, 1972. The status of *Piocoris* was a subject of debate until LINNAVUORI (1972) fixed it as subgenus of *Geocoris*, concluding that the diagnostic characters of the taxon do not merit the usual requirements of generic rank. *Piocoris* was separated from *Geocoris* sensu stricto based on proportion of II and III labial segments (in *Piocoris* segment II is longer than segment III) and the oblique apex of

scutellum. READIO & SWEET (1982) doubted Linnavuori's action exemplifying the case of *Isthmocoris* McAtee, 1914 which was separated with the same certain diagnostic character (proportion of labial segments) from *Geocoris* as *Piocoris*. *Eilatus* was diagnosed with the obliquely truncate apex of antennal segment I, and segment II being armed with small spines. Besides the subgenera, coherent species groups within *Geocoris* were recognized by different authors e.g. READIO AND SWEET (1982) or PÉRICART (1999). MALIPATIL (1994) in course of revising the species of the genus distributed in Australia concluded that *Geocoris* is “an ill-defined group of species belonging to several taxa possibly rank equal to existing genera”, referring to READIO & SWEET (1982).

Germalus Stål, 1862 is the second largest genus of the subfamily with 35 species. The taxon is distributed from the Afrotropical to the Oceanian biogeographic realms. The study of the genus virtually stopped after the 1950's (BARBER 1958) but gained a new momentum in 2010's with the works of MALIPATIL & BLACKETT (2013) and KÓBOR & KONDOROSY (2016, 2017). The status of several species is still uncertain e. g. members of New Caledonian fauna, and there are regions like New Guinea which are virtually unstudied since the first decades of the 20th century. MONTANDON (1913a) established a new genus, *Neogermalus* Montandon, 1913 based on the head shape. Type species of the genus was *Ophthalmicus membranaeus* Montrouzier, 1861 by monotypy. BERGROTH (1916) claimed that the specimen Montandon “re-described” was not conspecific with Montrouzier's taxon and found that the diagnostic characters were unsuitable for generic level definition, thus he synonymized *Neogermalus* with *Germalus*. In the same study, *Ophthalmocoris* (?) *dissidens* Montandon, 1907 was moved to the newly established genus *Nesogermalus* Bergroth, 1916 and was designated as its type species; the new genus was based on the shape of metathoracic scent efferent apparatus (MTSEA) and antenniferous tubercle.

Ninyas Distant, 1882 is morphologically highly similar to representatives of *Germalus*, yet it is distributed in the Caribbean region. The genus can be considered as well-known due to the revisionary works of BARANOWSKI & SLATER (2005) and BRAILOVSKY (2013, 2016). A few of the smaller genera of the subfamily were recently revised or described, e.g. *Isthmocoris* McAtee, 1914 (READIO & SWEET 1982), *Stylogeocoris* Montandon, 1913 (MALIPATIL 1994) or *Ausogeocoris* Malipatil, 2013, but most of the other taxa need revision.

2.4.3 Distribution

Representatives of the subfamily are to be found in almost all biomes of warm and temperate climate. Some species inhabits extreme places like high mountains or deserts. However, tropical regions are richest in species: the number of taxa descend as we move further from Equator, though there are few species – especially in the Palaearctic Region – which nearly reach the Arctic circle (author's unpublished data). One of the most diverse and species rich biogeographical realms is the Australasian Region, with several endemic, mono- or oligotypic taxa as concluded by MALIPATIL (1994), MALIPATIL & BLACKETT (2013) and KÓBOR (2019a, b).

2.4.4. Ecology

In terms of autecology and lifecycle, members of the genus *Geocoris* along with other Palaearctic taxa included in PÉRICART'S (1999) comprehensive work on Euro-Mediterranean representatives of the subfamily are to be considered as well-known.

The most extensively studied species in this regard is the Nearctic *Geocoris punctipes* (Say, 1831) (e.g. COHEN 1985, BUGG ET AL. 1991, TORRES & RUBERSON 2006). Furthermore, research on the lifecycle, feeding habits and rearing of the Nearctic *Geocoris bullatus* (Say, 1831), *Geocoris pallens* Stål, 1854 (TAMAKI & WEEKS 1972) and *Geocoris uliginosus* (Say, 1831) (BRAMAN ET AL. 2003), the Oriental *Geocoris ochropterus* (Fieber, 1844) (KUMAR & ANANTHAKRISHNAN 1985), *Geocoris varius* (Uhler, 1860) or *Geocoris proteus* Distant, 1883 (SAITO ET AL. 2005) and the Australian *Geocoris lubra* Kirkaldy, 1907 (MANSFIELD ET AL. 2007) were conducted. Predatory behaviour in genus *Germalus* was recorded by USINGER (1936).

3. Materials and methods

3.1. Material studied

Specimens studied and processed in the course of this study are mostly originated from the collections of following museums:

BMNH – The Natural History Museum, London, United Kingdom

BPBM – Bernice P. Bishop Museum, Honolulu, Hawaii

HNHM – Hungarian Natural History Museum, Budapest, Hungary

KNHM – Kimball Natural History Museum, San Francisco, USA

MZMB – Moravian Museum, Brno, Czech Republic

MNHN – Museum National d’Histoire Naturelle, Paris, France

NHMB – Naturhistorisches Museum, Basel, Switzerland

NHMW – Naturhistorisches Museum, Vienna, Austria

NHRS – Swedish Museum of Natural History, Stockholm, Sweden

PCTR – the Personal collection of Thibault Ramage, France

PCZJ – the Personal collection of Zdenek Jindra, Prague, Czech Republic

RBINS – Royal Belgian Institute of Natural Sciences, Brussels, Belgium

RMCA – Royal Museum of Central Africa, Tervueren, Belgium

SEMC – University of Kansas Biodiversity Institute (Snow Entomological Collections), Lawrence, USA

USIL – University of Silezia, Katowice, Poland

ZMHB – Natural History Museum, Berlin, Germany

Specimens subject of molecular studies were collected in 2014-2018 by Előd Kondorosy (University of Pannonia, Keszthely, Hungary), Barna Páll-Gergely (Institute of Plant Protection, Centre for Agricultural Research, Hungarian Academy of Sciences, Budapest, Hungary), Dávid Rédei (Nankai University, Tianjin, China), Marcos Roca-Cusachs (Department of Evolutionary Biology, Ecology and Environmental Sciences, Faculty of Biology, University of Barcelona, Spain), specimens are summarized in the following table:

Genus	species	Localities	Notes
<i>Geocoris</i> Fallén, 1814	<i>collaris</i> Puton 1878	Iberian Peninsula, Canary Islands (Spain)	
	<i>erythrocephalus</i> Lepeletier & Serville, 1825	France, Hungary, Italy, Iberian Peninsula (Spain)	2 specimens collected in the same locality (Hungary)
	<i>lineola</i> (Rambur, 1839)	Iberian Peninsula (Spain)	2 specimens collected in the same locality
	<i>pubescens</i> (Jakovlev, 1871)	Iberian Peninsula (Spain)	
	<i>varius</i> (Uhler, 1860)	Yunnan (China)	
	<i>ochropterus</i> (Fieber, 1844)	Yunnan (China)	
<i>Germalus</i> Stål, 1862	<i>greeni</i> Distant, 1910	Yunnan (China)	
	<i>sobrinus</i> (Stål, 1859)	Yunnan (China)	

Table 2. List of specimens subject of DNA extraction

Label data processing

Label data cited verbatim; lines on labels separated with “/”, content of labels separated with “//”. Specimens marked with “†” were subject of DNA extraction. Handwritings on labels of specimens originated from museum collections were identified with the help of HORN’s (1926) work on entomological collections.

Life Science Identifier (LSID) of species – if applicable – was acquired from Lygaeoidea SpeciesFile (LSF) (DELLAPÉ & HENRY 2019). Literature data not listed in LSF-database is cited respectively.

Label data was recorded in comma delimited text (.csv) format using Microsoft Excel Standard 2010 software. GPS coordinates belonging to collection sites (if not available) were acquired from Google Maps in decimal format. Data deficient records (e.g. locality too generally defined) were excluded from database. File was processed with QGIS 2.18.7 software; maps were generated with the implying GlobCover v2.3 raster (ARINO ET AL. 2010) and WWF terrestrial ecosystems shape (OLSON ET AL. 2001) layers for projection.

3.2. Morphological study

Taxonomy. Examination of exoskeletal and genital structures was performed using Leica Mz 9 5 stereoscopic and Keyence VHX 5000 digital microscopes. Photo documentation was done by

the author using Keyence VHX 5000 digital microscope. Photos of *Apennocoris pilosulus* Montandon, 1907 syntype was taken by Scott Bundy (New Mexico State University).

Genitalia were examined after removal of the whole abdomen and soaking it overnight in lactic acid solution at room temperature. When soaking in lactic acid, structures remain more flexible than by KOH maceration according to the author's experience. This method also prevents "overmacerating" of structures (BLAHNIK ET AL. 2007), thus additional dye staining is not necessary before further dissection, observation or photographic documentation.

Measurements were made using an ocular micrometer and were performed on scaled photos with the use of the ImageJ software. Values are given in millimetres; values for primary types (holotype or lectotype) are indicated by bold letters, range of paratypes and other materials are given in parentheses. Missing appendages or non-measurable characters are marked with "n/a".

General morphological terminology used in this article was adapted from TSAI ET AL. (2011) and MALIPATIL & BLACKETT (2013). Terminology for external structures of the metathoracic scent efferent apparatus (MTSEA) was adapted from KMENT & VILÍMOVÁ (2010). Terminology for wing morphology was adapted from SLATER & HURLBUTT (1957) and SLATER (1975, 1977).

Morphology was reviewed and revised based on the works of MONTANDON (1913a), BERGROTH (1916), ASHLOCK (1957), SLATER & HURLBUTT (1957), BARBER (1958), READIO & SWEET (1982), MALIPATIL (1994), HENRY (1997), PÉRICART (1999), MALIPATIL & BLACKETT (2013) and BRAILOVSKY (2016).

Tribal and generic level keys were partly adapted from MALIPATIL (1994), PÉRICART (1999) and MALIPATIL & BLACKETT (2013).

Due to page constraints, short diagnoses are provided in the "Taxonomy" subchapter. Detailed descriptions, label data and measurements can be found in the cited articles of the author.

Cladistic analysis. Besides the type species of genera considered as valid (SLATER 1964, SLATER & O'DONNELL 1995, HENRY & DELLAPÉ 2019), representatives of species groups suggested by READIO & SWEET (1982) and PÉRICART (1999) were included in the analysis.

Characters analysed were derived by the critical review of literature data acquired in course of the revision of morphology as specified above. Definitions of characters are found in Appendix 1. A character matrix of 31 characters was generated using the software Mesquite 3.6 (MADISSON & MADISSON 2018); 26 characters were coded as binary and 5 as multistate

(Appendix 2). Character polarization followed the outgroup method of NIXON & CARPENTER (1993).

Parsimony analysis was performed with TNT 1.1 software (GOLOBOFF ET AL. 2008) using Traditional Search method with default settings under equal weights. All characters were treated non-additive. Support values were estimated with Majority- Rule Consensus of resulted trees.

3.3. Molecular sequence data analysis

For the purpose of DNA extraction, entire abdomens of previously identified individuals were dissected. Genital capsules were removed and preserved for further morphological study; voucher specimens were deposited in the Hemiptera Collection of HNHM. DNA extraction was performed with use of Sigma-Aldrich “REDEExtract-N-Amp™ Seed PCR Kit” according to manufacturer’s protocol. The amplification was done with the C1-J-1718 and C1-N-2191 primers (LOXDALE & LUSHAI 1998) in 100 µl total volume. This primer is fitted for the barcode region of COI but was designed for arthropods. The temperature profile of reaction was the following: initial denaturation for 4 minutes at 95 °C; 35 cycles of 30 seconds at 95 °C, 1 minute at 50 °C, 2 minutes at 72 °C; final extension for 10 minutes at 72 °C. PCR-product was purified with Roche “High Pure PCR Product Purification Kit” according to manufacturer’s protocol. Purified product was imaged on 1% agarose gel dyed with EtBr. Sequencing was done at BayGen Genomic Unit of Biological Research Centre, Hungarian Academy of Sciences (Szeged, Hungary).

Additional sequences were acquired from NCBI GenBank with the use of BLAST tool (see table for accession number).

Species	Codes in trees	NCBI Accession Number
<i>Geocoris (Geocoris) ater</i> (Fabricius, 1787)	GeoateGer1	KM022926
<i>Geocoris (Geocoris) discopterus</i> Stål, 1874	GeodicCnd1	
<i>Geocoris (Geocoris) dispar</i> (Waga, 1839)	GeodisGer1	KM022291
<i>Geocoris (Piocoris) erythrocephalus</i> (Lepelletier & Serville, 1825)	PioeryFra1	KJ541560
<i>Geocoris (Geocoris) grylloides</i> (Linnaeus, 1761)	GeogryGer1	KM021943
	GeogryGer2	KM021986

<i>Geocoris (Geocoris) howardi</i> Montandon, 1908	GeohowCnd1	HQ105696
	GeochowCnd2	HQ105697
<i>Geocoris (Geocoris) limbatus</i> (Stål, 1874)	GeolimCnd1	KR041225
<i>Geocoris (Geocoris) pallens</i> Stål, 1854	GeopalCnd1	
<i>Geocoris (Geocoris) uliginosus</i> (Say, 1831)	GeouliCnd1	
<i>Germalus sp. 1.</i>	GersppFrP1	AY252930
	GersppFrP2	AY253137
<i>Germalus sp. 2.</i>	GersppFrP3	KX053267

Table 3. List of additional sequences acquired from NCBI GenBank

Sequences were aligned using the ClustalW software. The final dataset comprised 29 sequences with length of 398bp, representing 15 species of 3 genera. Length of sequences were cropped to the shortest sequence. Maximum Likelihood analysis was performed with use of MEGA X (KUMAR ET AL. 2018) and RAxML 8.0.0. (STAMATAKIS 2014) software. TAMURA-NEI (1993) substitution model with a discrete Gamma distribution was chosen based on the Akaike information criterion (AIC) scores of MEGA X software's model estimation tool. Bootstrap value (FELSENSTEIN 1985) was set to 1000 replicates in each case. KIMURA (1980) 2-parameters distance estimation was run pairwise using MEGA 7; results were processed and interpreted with the use of Microsoft Excel Professional Plus 2010 software.

4. Results and Discussion

4.1. A review of morphological characteristics of Geocorinae

Head (Fig. 2) – Generally pentagonal, eyes moderately or slightly stylate. Moderately stylate eyes which sometimes erect or prorect are characteristic mostly in *Germalus* and allies (Fig. 2A). In *Geocoris* and closely related genera eyes at most slightly stylate (Fig. 2B-C); occasionally vertex broadened, head nearly lunate (e.g. *Piocoris*, *Geocoris ochropterus* and closer relatives) (Fig. 2C). Ocular sulcus complete (*Germalus* and allied genera) or reduced (*Geocoris* and relatives). Surface of vertex rugose or smooth, rarely punctate (*Ausogeocoris*, *Unicageocoris*); if rugose then frequently with fine decumbent pubescence. Vertex frequently with transversal furrows anterior to ocelli (Fig. 2B) or longitudinal median furrow on vertex of various length (Fig. 2C). Clypeus of characteristic shape in certain groups (Figs. 2A–C). Jugal sutures of clypeus usually present, occasionally reduced (*Geocoris* and some closely related genera). Antenniferous tubercle usually unarmed, occasionally armed with tooth-like process (New Caledonian taxa, e.g. *Nesogermalus*). Antennomeres usually simple, in *Eilatus* armed with spine-like bristles. Labial trough open or partly closed, U- or V-shaped (*Germalus*, *Stylogeocoris* and related genera) or closed or at most slightly open, Y-shaped (*Geocoris* and allies), with a suture of variable length probably representing remnant of margin of trough. Labiomeres of variable length, length of labiomere I apparently not independent from development of labial trough; taxonomic significance of labiomere proportions is not fully explored but in certain cases it might be used for defining generic level taxa.

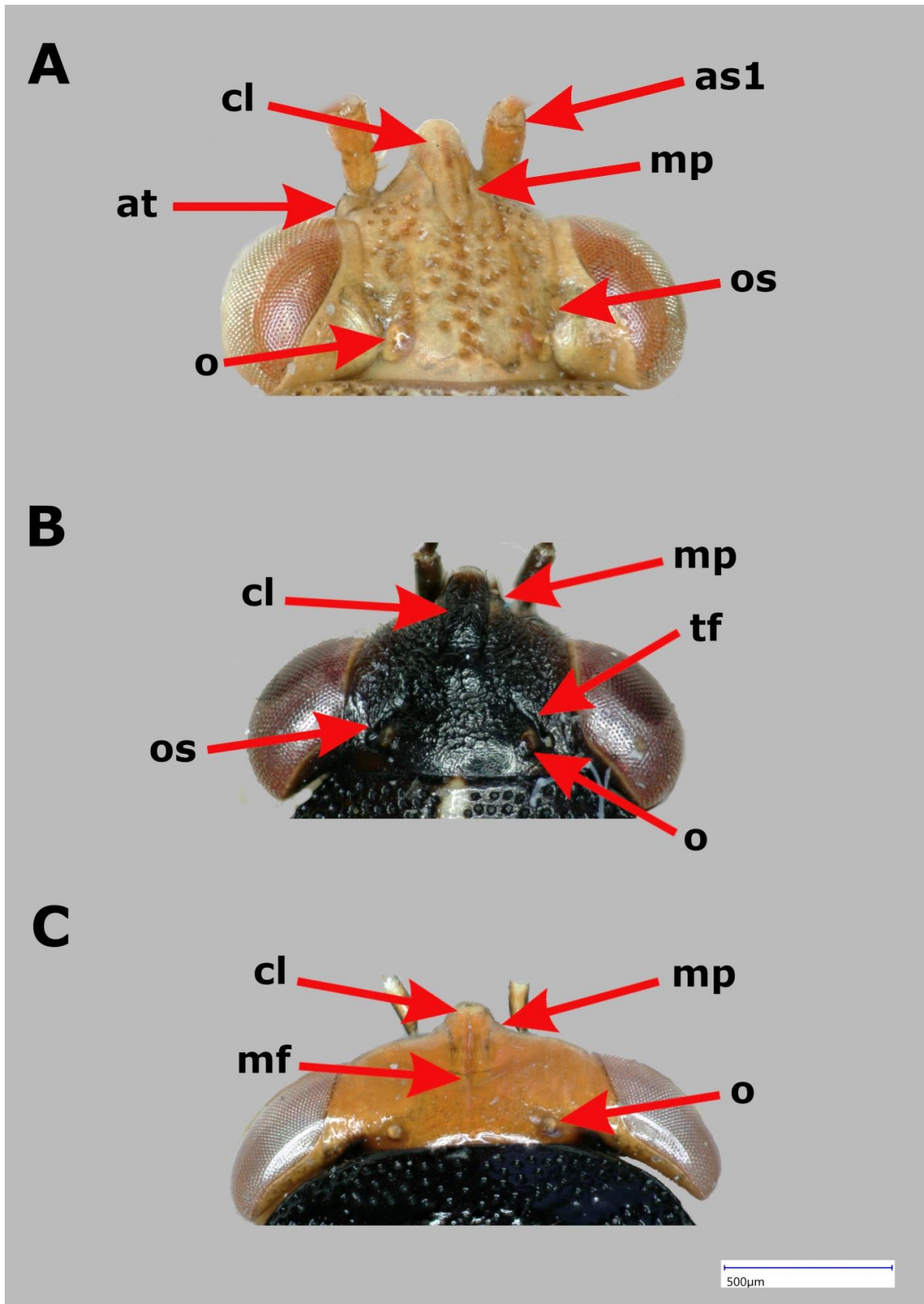


Figure 2. **Characters of head and cephalic appendages in Geocorinae (I)** – A. Head in dorsal view of *Ausogeocoris westraliensis* Malipatil, 2013; Head in dorsal view of *Geocoris ater* spp. Fabricius 1787; Head in dorsal view of *Picooris erythrocephalus* spp. (lettering: at – antenniferous tubercle, as1 – antennal segment 1, cl – clypeus, mp – mandibular plates, o – ocellus, oc – ocular sulcus)

Thorax and thoracic appendages (Figs. 1, 4–6) – Pronotum from semi-circular to rectangular but most commonly trapezoidal with slight impressions on lateral margins (Fig. 1). Surface variably punctate, sometimes with silvery pubescence, thoracic callosities, anterior and posterior margins and humeral angles with variously extensive impunctate areas. Integument glabrous or finely, inconspicuously pilose, occasionally with dense silvery pubescence (e.g. *Geocoris pubescens*) or erect setae dorsally (*Apennocoris*). Pronotal callosities variously developed (Figs. 4A and B), a few species with median longitudinal carinae; both characters of diagnostic value at species level.

Scutellum triangular, either subequilateral (*Germalus* and allied genera) or elongate (*Geocoris* and closer relatives); apex mostly sharply pointed, sometimes rounded (*Piocoris* and some Indomalayan *Geocoris* species) (Figs. 4C–E); with a variously developed median trifurcate carina, characteristically reduced in *Geocoris* and allies (Figs. 4C–E); integument densely punctate except carina.

Fore wing: clavus usually clearly distinguishable, with subparallel margins and well developed, conspicuous claval commissure (*Germalus* and allies) or with margins gradually converging apically and claval commissure reduced (*Geocoris* and allies); in short-winged morphs sometimes indistinguishably fused with corium (see later by wing polymorphism). Punctuation of corium highly variable, from punctures arranged along corial veins to evenly punctate (Figs. 5A–E); in New Caledonian geocorines and in *Ninyas* arranged in a characteristic S-shape (figure 5D).

Wing polymorphism mostly found in *Geocoris* and closely allied genera. In case of some Nearctic and Palaearctic *Geocoris* species, e.g. *Geocoris ater* Fabricius, 1787 or *Geocoris bullatus* (Say, 1831), macropterous and brachypterous individuals can be observed within the same population. Coleoptery can usually be found in species distributed in highland regions, e.g. *Geocoris chinai* Kiritshenko, 1931 (Tibet), *Geocoroides polytretus* Distant, 1918 (Nilgiri Mts., southern India) (Fig. 1H) or *Pseudogeocoris fallaciosus* Montandon, 1913 (Tanzania). The most uncommon modification, staphylionidy, can be observed in *Stenogeocoris horvathi* Montandon, 1913 (Fig. 1I). In *Germalus* and allies, wings are always fully developed. In regard of metathoracic wing venation two separate lineages are recognisable: the “germaline-line” where hamus and basally fused intervannals are present (Fig. 6B) and a “geocorine-line” where hamus underwent different levels of reduction and intervannals are missing (Fig. 6C).

Metathoracic scent efferent apparatus (MTSEA) either with oval or irregular-shaped ostiole, opening narrowing gradually into vestibular scar, with elongate peritreme, peritremal surface of various size and shape (can reach up to 2/3 of metapleurite), evaporative area covering most of the metapleurite, frequently extending to posterior half of mesopleurite (Fig. 6A) (“germaline-line”); or ostiole more or less round, closing sharply, resulting in a longer vestibular scar, peritreme bulging, peritremal surface missing, evaporative area restricted mostly to the immediate surroundings of the peritreme (“geocorine-line”). The punctuation of evaporative area, length and shape of peritremal surface and exact shape of ostiole have diagnostic value at species level in the “germaline-line”, whilst the extent and shape of evaporative area, shape of peritreme and ostiole and the arrangement of vestibular scar can be considered as species-level discriminatory characters in the “geocorine-line”. Metapleurite undivided or divided into two lobes by a furrow above the metacoxa (in *Germalus* and allies).

Legs usually without peculiarities. Femora unarmed; tibiae with longer pubescence, in some genera (e.g. *Umbrageocoris*) with spine-like, erect setae which is possibly a sign of adaption to predatory behaviour and serves to catch and grab prey.

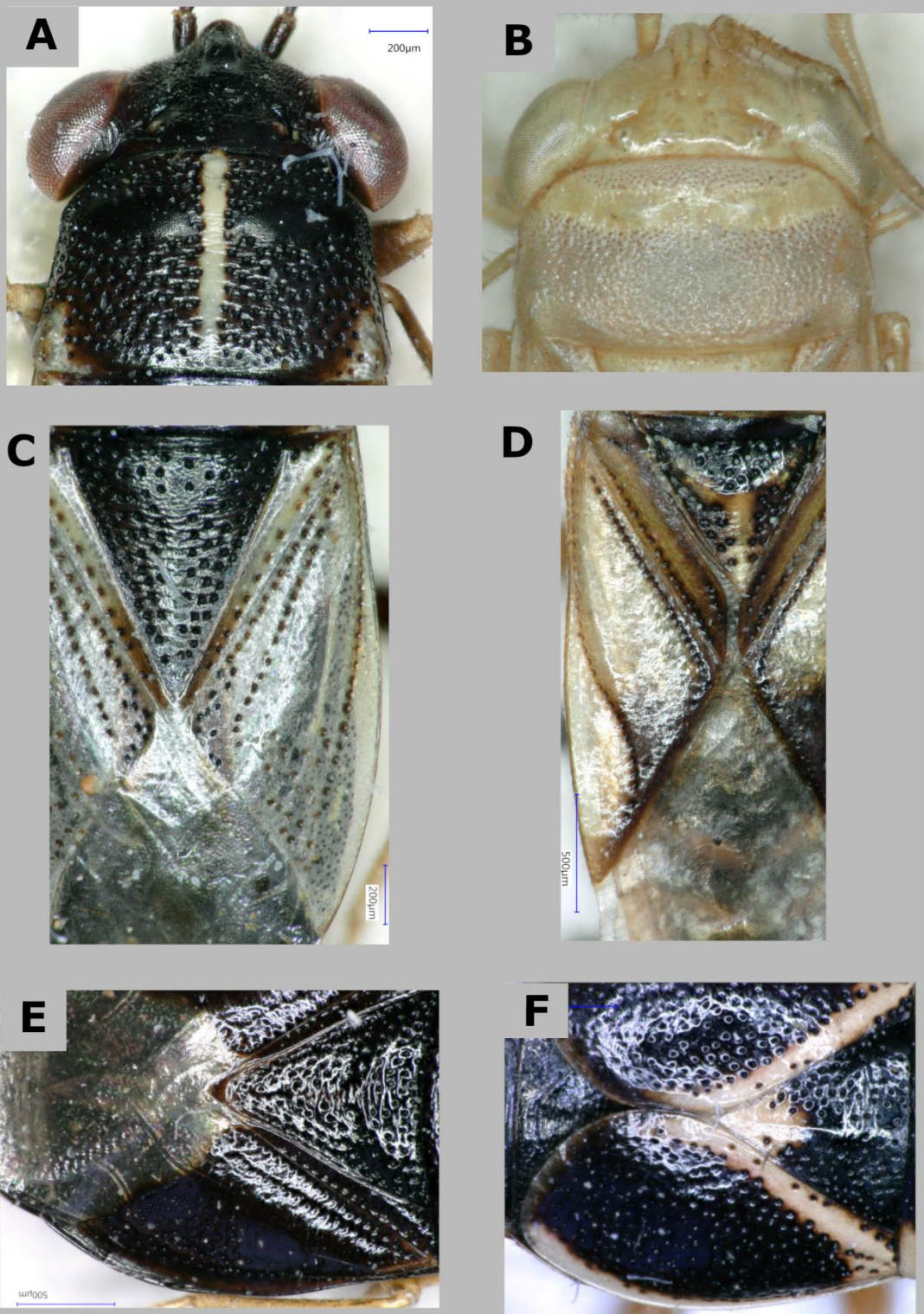


Figure 3. Thoracic dorsum of Geocorinae: Pronotum – *Geocoris ater* (A), *Eilatus chloroticus* (B); scutellum and hemelytron – *Geocoris ater* (C), *Neogermalus membranaeus* (D), *Picochris erythrocephalus* (E); hemelytron – *Geocoris grylloides* (F).

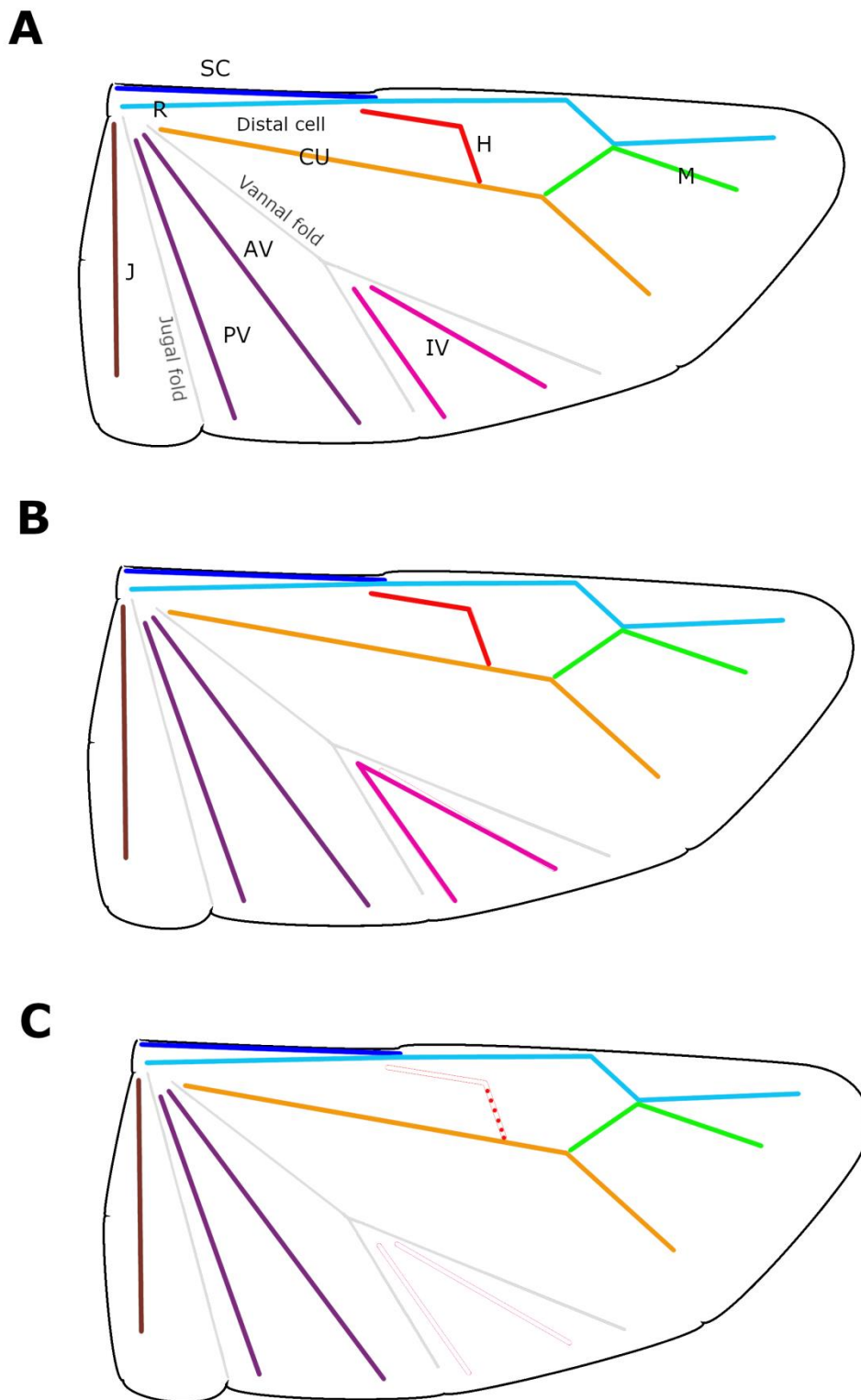


Figure 4. **Metathoracic wing in Geocorinae (diagrammatic)**: A. Lygaeoidea, generalized, B. Germalini, C. Geocorini. (Lettering of veins: AV – Anterior vannal; CU – Cubitus; H – hamus; IV – intervannals; J – Jugal; M – Media; PV – Posterior vannal; R – Radius; SC – Subcosta)

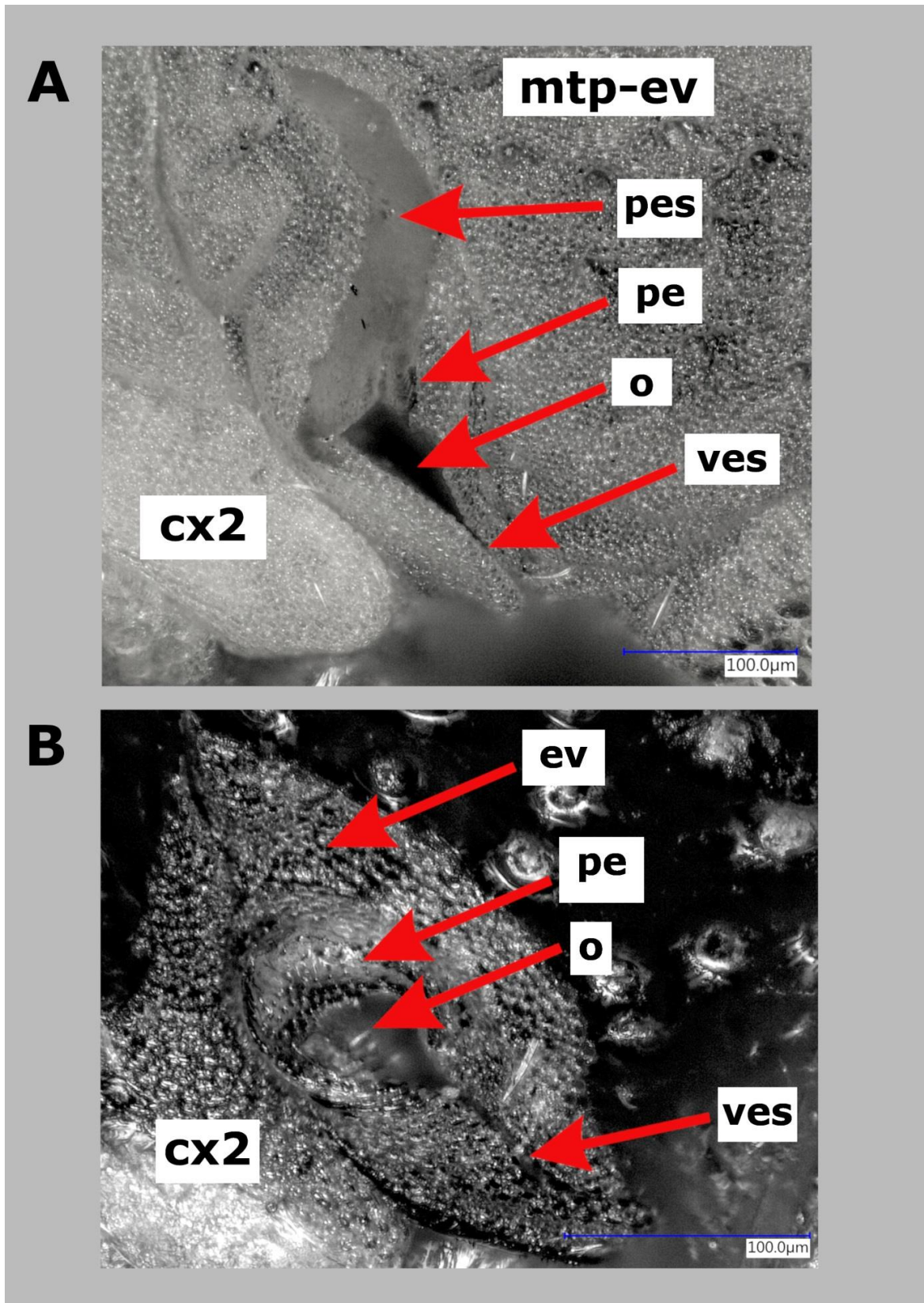


Figure 5. Metathoracic scent efferent apparatus in Geocorinae: A. *Germalus costalis* Van Duzee, 1932 (Geocorinae: Germalini), holotype, BPBM; B. *Umbrageocoris maai maai* Kóbor, 2019 (Geocorinae: Geocorini), holotype, BPBM. (Lettering: cx2 – mesocoxa; ev – evaporative area; mtp-ev – metapleurite with evaporative area; o – ostiole; pe – preitreme; pes – peritremal surface; ves – vestibular scar)

Abdomen – Sutures of abdominal tergites 4/5 and 5/6 curved posteriad medially as in other taxa of the family Geocoridae. Abdominal dorsum is smooth in most of the genera included, but rugose (*Umbrageocoris*) or punctate (*Stylogeocoris*) surfaces occur as well. Abdominal venter often with fine, decumbent pubescence; stronger, erect setae may occur near genital capsule, most frequently in *Germalus*, but occasionally in other taxa of the subfamily.

Female genitalia. Length of ovipositor shows considerable interspecific variations in some of the genera; in *Germalus* – similarly to *Henestaris* – reaches up to abdominal connexiva IV (Fig. 7C), whilst in *Geocoris* it is shorter, not exceeding segment VII (Fig. 7D). Spermatheca similar in most of the cases, only spermathecal duct bears considerable, generic level differences, as it can be bent, looped or coiled (Figs. 7E–F.).

Male genitalia. Pygophore has two main characters which can be applied at generic level: shape of posterior opening; shape of lateral processes. Shape of opening is more variable even on generic level, but shape of processes can be divided into a blunt “germaline type” and a sharply pointed “geocorine type”. Relative position of male parameres in pygophore was found to be overlapping in *Geocoris* and allies and crossing each other, forming an X shape in taxa related to *Germalus*.

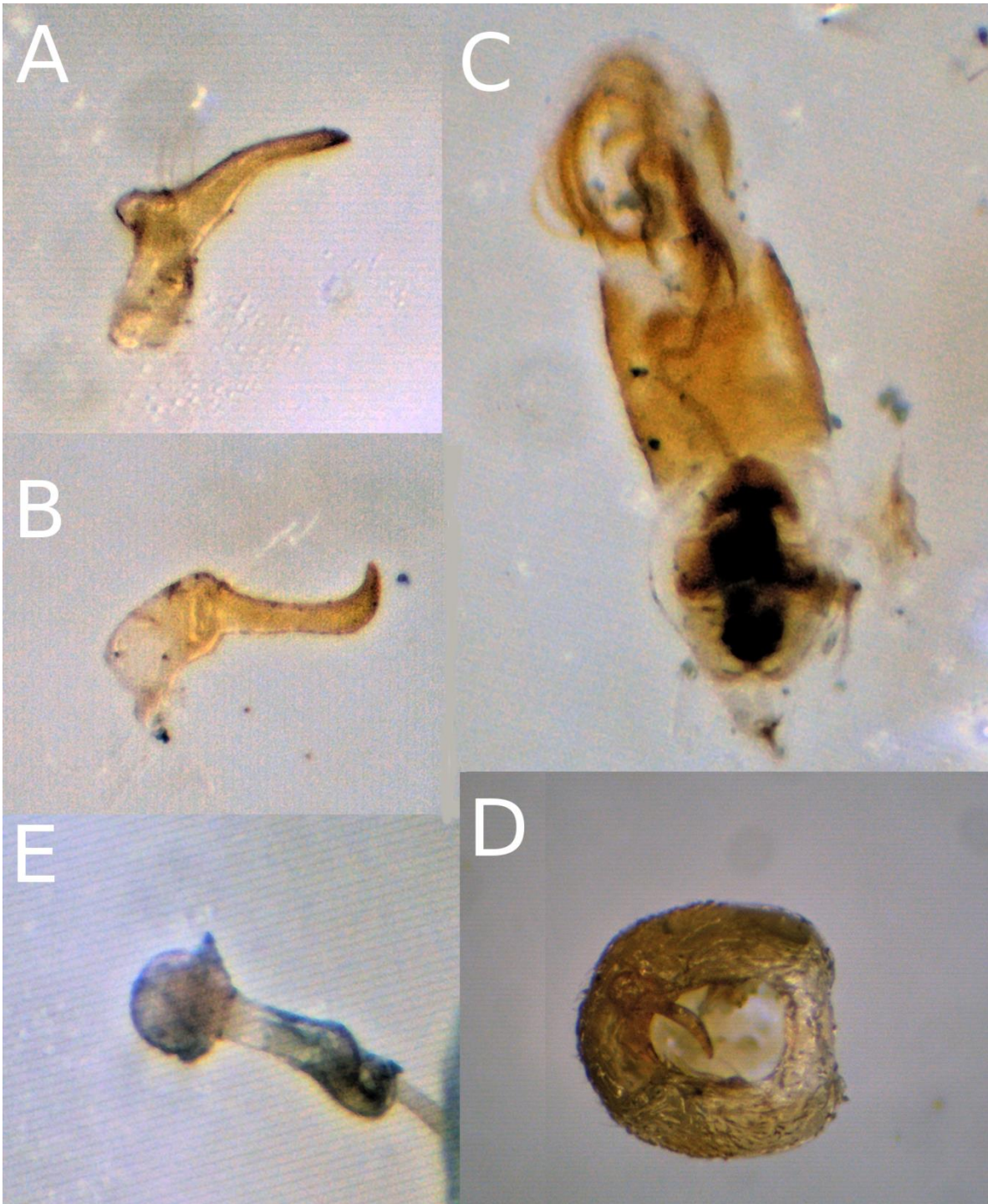


Figure 6. **Genital structures in Geocorinae I.** – *Germalus banari* Kóbor & Kondorosy, 2016: A. male paramere in dorsolateral view, B. male paramere in anterolateral view, C. male aedeagus, D. male pygophore in posterior view, E. female spermatheca.

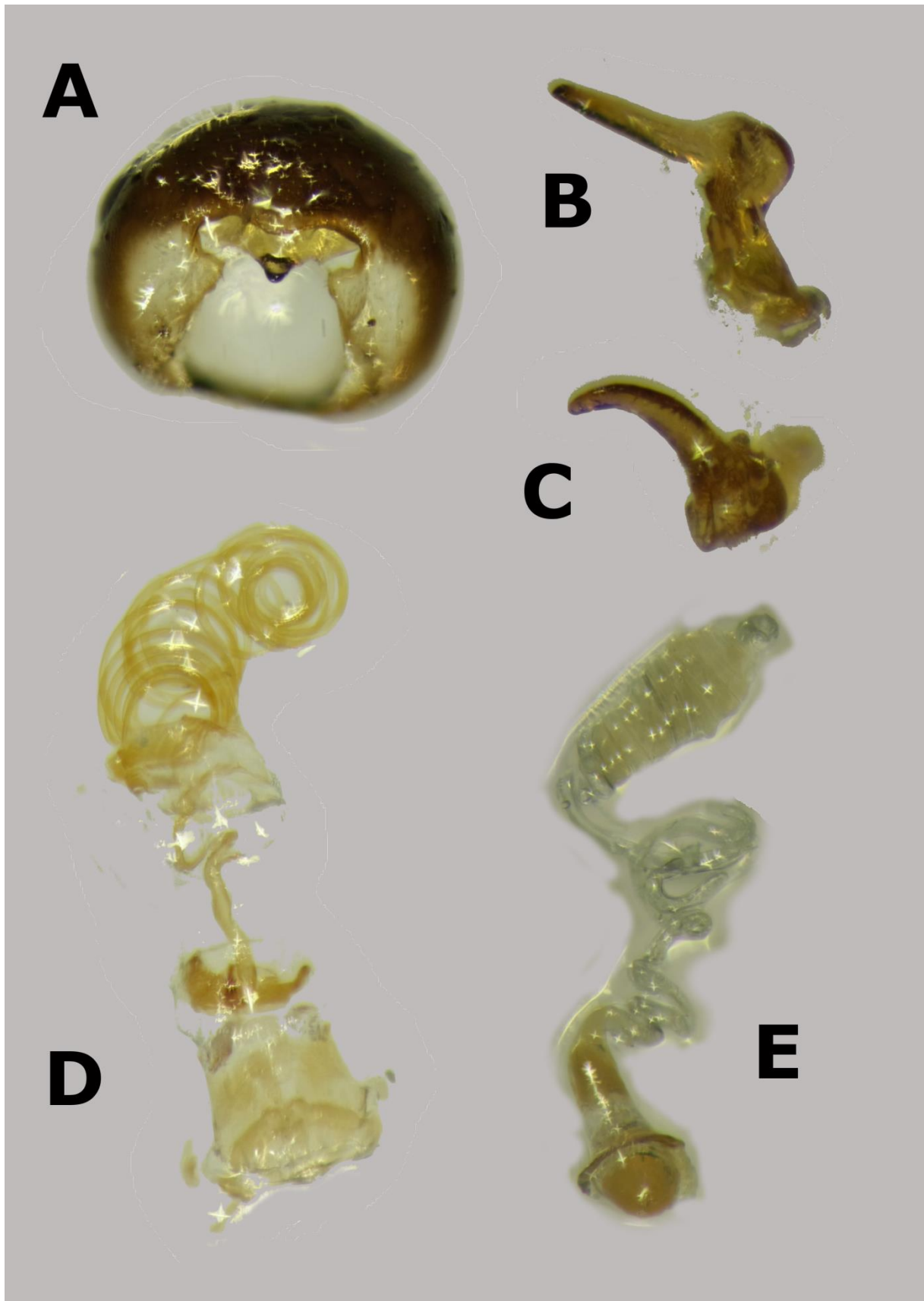


Figure 7. **Genital structures in Geocorinae II.** – *Geocoris margaretarum* Kóbor, 2018: A. male pygophore in posterior view, B: male paramere in dorsolateral view, C. male paramere in posterolateral view, D. male aedeagus, E. female spermatheca.

4.2. Contributions to the classification of Geocorinae

4.2.1. The applicability of the subspecies concept

The concept of subspecies was a source of controversy among researchers of systematic zoology since its existence. MAYR (1942) defined subspecies as genetically distinct, geographically separate populations of a species which have potential to freely interbreed at zones of contact. WILSON & BROWN (1953) considered this category as “superfluous” and “ineffective” and suggested merely recognizing geographical races even if there were morphological differences between them. In contrast, INGER (1961) and MAYR (1982) encouraged the recognition of subspecies when a geographic variant could be clearly distinguished from other conspecific but allopatric individuals based on morphological characters. The above examples represent the main competing concepts for recognition of subspecies. It should be noted that different authors used very different model organisms ranging from birds to ants and butterflies (but never Heteroptera), and it is unclear whether a given concept can universally be applied to all kind of organisms.

As consequence of Article 45.6.4. of the International Code of Zoological Nomenclature (ICZN 1999) several taxa in the subfamily Geocorinae, which were originally proposed as of infra-specific rank (usually “varieties”), were upgraded to subspecies level without any argument or specific taxonomic action. In the course of an integrated taxonomic study on the Palearctic representatives of Geocorinae, the status of the varieties of *Geocoris erythrocephalus* (Fig. 1B) described by HORVÁTH (1895, 1907) were revisited.

The morphological study revealed that no significant differences can be observed in major, distinctive character between the three “varieties” of *G. erythrocephalus*. Colouration patterns, however, showed remarkable differences in relation of geographic distribution: the diagnostic characters of the variety “*marginellus*” (Fig. 8B) could be observed in 97.06% of specimens originated from the Iberian Peninsula. Besides of the single available syntype in HNHM, only one individual corresponding to the variety “*litoreus*” could be examined, originating from a location remote from the type locality (Fig. 8A). Transitional forms (“nr. *litoreus*” and “nr. *marginellus*”; nr. = “near”), partly showing characteristics of the varieties, were found occasionally and isolated, thus they are judged to merely represent more than phenotypical expression of intrasubspecific genetic variance.

The results of Maximum Likelihood of COI sequences performed with MEGA 7 software showed that sequences of *G. erythrocephalus* form a well-defined subclade (Fig. 9C) among other *Geocoris* sequences. Within this subclade two lineages can be delimited: one comprising specimens originating from the Iberian Peninsula (Esp1, Esp2), and one containing all other European specimens (Italy, France and Hungary). Kimura 2-parameters distance estimation resulted an average 3.125% distance between *G. erythrocephalus* specimens from the Iberian Peninsula and other European localities. When attempting barcoding gap detection on the whole dataset these distance values took place between the peaks of infra-, intersubspecific and interspecific blocks (Fig. 8D). Interspecific distance was lowest at 5.657% in case of sibling species (e.g. *G. ater* – *G. lineola*). The same results show that the average infrasubspecific variability of COI sequences is 0.8% among the Geocorinae represented in this study. This corresponds with the findings of PARK ET AL. (2011) who detected a maximum infraspecific variance of 1.39% in Geocorinae (this study did not deal with subspecific categories). Outlying values were the resulted by specimens of *Geocoris collaris* with distance value of 4.966%. These specimens were collected in two locations which are clearly isolated from each other (the Canary Islands and the Iberian Peninsula) and possibly represent two of the four subspecies of the taxa recognised as valid. These results suggest that the Iberian populations of *G. erythrocephalus* form a very closely related, separate or diverging lineage from other Euro-Mediterranean populations (Fig. 8E).

The results of our study on the taxonomic status of the subspecies of *G. erythrocephalus* concluded that two of the three described infrasubspecific taxa (HORVÁTH 1895, 1907) should be recognised as valid subspecies, and one of them is indeed merely a phenotypical manifestation of infrasubspecific genetic variance. Furthermore, the subspecies concept was found to be applicable for the Geocorinae preferably with the following criteria: 1) the subspecies' population(s) should be a clearly delimited part of the species' area defined by geographical barriers which minimize the possibility of interbreeding with population of typical form or other variants; 2) mean genetic distance should significantly exceed maximum infrasubspecific distance, in case genus *Geocoris* (and possibly in Geocorinae) this means 3-4% K2P distance value when analysing cytochrome-oxidase subunit I divergence; 3) this distance should correlate with clearly definable morphological or at least colour characters which can be observed in at least 95% of the individuals [as proposed by O'NEILL (1982)].

When describing a subspecies, it is suggested to use a trinomen referring to the distribution of the subspecies (e.g. "*Geocoris (Geocoris) ater slovenica*"), indicating that the subspecies

occurs only in a part of the species' range which can be clearly delimited. If one prefers to name the subspecies referring to one of its main characteristics, e.g. *G. erythrocephalus marginellus* (which means "marginated"), then it is advised to indicate the distribution in quotation marks right after the trinomen, e.g. *Geocoris (Piocoris) erythrocephalus marginellus* (Horváth, 1907) "Iberian race", following the proposal of WILSON & BROWN (1953). In the latter case the specification of the distribution is not considered to be part of the scientific name and should be used only as reference in studies.

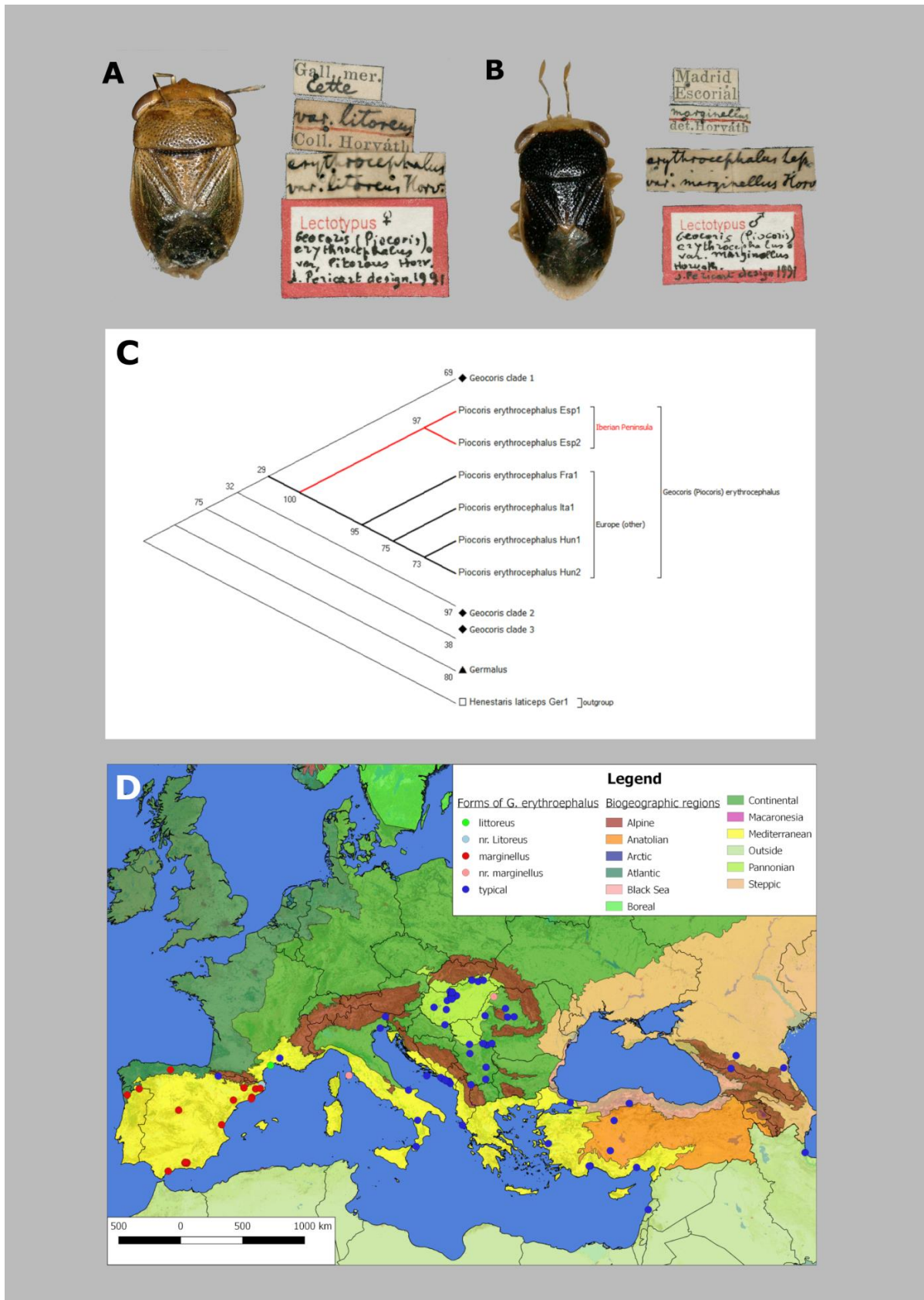


Figure 8. The applicability of subspecies concept in Geocorinae – A. dorsal habitus and labels of lectotype of *Piocoris erythrocephalus litoreus* (HNHM), B. dorsal habitus and labels of lectotype of *Piocoris erythrocephalus marginellus* (HNHM), C. consensus tree of phylogenetic reconstruction of COI sequences (MEGA9), D. distribution of *Piocoris erythrocephalus* subspecies in the Euro-Mediterranean region.

4.2.2. Species groups within *Geocoris* based on molecular evidence (preliminary results)

The nominotypical genus, *Geocoris*, with its three subgenera and 137 described species, is the largest genus of subfamily Geocorinae. One of the subgenera, *Piocoris* Stål, 1872, was originally described as a separate genus within the subfamily. Its status was debated until LINNAVUORI (1972) fixed it as subgenus of *Geocoris* along with the description of the third subgenus, *Eilatus* Linnavuori, 1972. The downgrading of the taxon was justified with ineligible discriminatory characters (ratio of labial segments II and III, rounded apex of scutellum). This decision was later disputed by READIO & SWEET (1982) but no change in LINNAVUORI'S (1972) classification was explicitly proposed. Their study exemplified the case of *Isthmocoris* MacAtee, 1914: this genus is separated from *Geocoris* on the basis of the proportion of labial segments II and III, similarly to the former definition of *Piocoris*. The heterogeneity and ill-defined nature of the genus was suggested by multiple studies, e.g. READIO & SWEET (1982), MALIPATIL (1994), or PÉRICART (1999). These conclusions and arguments suggest that the monophyly of the genus should be revised along with the redefinition of generic and subgeneric level characters. My recent study attempted to provide a baseline for the group-level revision of *Geocoris* combining morphological knowledge and results of molecular sequence data analysis.

The consensus tree of 1000 pseudoreplicates acquired by phylogenetic reconstruction of COI sequences (Fig. 10) resulted three main clades within the samples belonging to subfamily Geocorinae. Clade A contains species belonging to genus *Germalus*, clade B contains species belonging to *Piocoris* which is currently subgenus of *Geocoris*, and clade C consists of *Geocoris* species. Within clade C the species groups identified and suggested by Péricart (1999) are to be recognized (marked with asterix). Besides these groups species distributed in the Nearctic biogeographic region formed a coherent subclade and two further lineages are to be recognized: the first contains Mediterranean taxa *Geocoris collaris* and *G. pubescens*, the other *Geocoris ochropterus* and *G. varius* which are distributed in the Eastern Palaearctic (costal region of China, Korean Peninsula and Japan) and Indomalayan Regions.

Kimura 2-parameters distance estimation resulted an overall mean distance value of 18.5%. To estimate mean distance values between different groups two grouping methods were applied: 1) currently accepted taxa only; 2) species-groups and lineages rank equal to existing genera.

- 1) In case if only currently accepted genera and subgenera are applied for grouping, mean within-group distance values were 14% in *Geocoris* and 12% in *Germalus*. *Piocoris* had 2% mean distance, but the group contained sequences belonging to a single species (*P. erythrocephalus*) originated from different locations. In case of other sequences belonging to same taxa this value was between 0–1%. The difference can be explained with the subspecies of *P. erythrocephalus* as discussed in the previous chapter.

Between-group distances were showing values as follows: *Geocoris*–*Piocoris* 20.4%; *Geocoris*–*Germalus* 22.5%; *Geocoris*–*Henestaris* (outgroup) 27.8%; *Piocoris*–*Germalus* 23.5%; *Piocoris*–*Henestaris* 26.4%; *Germalus*–*Henestaris* 25.1%.

- 2) Applying the suggested groups and recognised lineages as rank-equal categories resulted an average within-group distance of 9%. Values in case of groups of *Geocoris* ranged between 2–6% except in *Geocoris ochropterus*-group which was of suspiciously outlying value (30%), thus it should be excluded from further analysis until acquisition of further sequences representing members of the group in order to ascertain the cause of this values.

Between groups distances were similar, but lower as in previous grouping.

Distance of *Geocoris*-groups from each other ranged between 9.9–20.0% and 18.4–20.0% from *Piocoris*. In case of *Germalus* the values ranged between 19.9–23.9%. Distance values for *Henestaris* were 21.9–28.5%.

PARK ET AL. (2011) as result of extensive barcoding project published a mean intergeneric distance within families of 19.81% (range: 0-35.8%), however it was concluded that COI divergences in Geocoridae can be considered low compared to other Heteroptera groups: maximum intraspecific distance: 1.39%; mean interspecific distance: 1.79% (range: 0.77–2.82%). Results of the present analysis can be considered as consistent with these findings.

Based on the above interpreted results and the suggestions of former morphological studies the following conclusions are to be formulated:

- a) The morphological characteristics (see chapter 4.3.1. for diagnosis) and above results suggest that the restoration of the status of *Piocoris* as separate genus is warranted. A thorough re-examination of the status of *Eilatatus*, using the same methodology, is recommended.

- b) The taxonomic status of the *Geocoris ater*- and *G. grylloides*-groups are subject of further studies and revision. These groups can be considered phylogenetically coherent based on the results of molecular sequence data analysis and morphological study. However, to clarify their taxonomic status further data are needed.
- c) *Geocoris collaris* and *G. pubescens* are suggested to be studied thoroughly in order to delimit a possible species-group.
- d) The *Geocoris ochropterus*-group is suggested to be recognized as a phylogenetically coherent species group based on previous published results (KÓBOR 2018). The DNA-barcoding of the representatives of this group resulted outlying K2P-values which are possibly result of the presence of nuclear mitochondrial DNA (GAZIEV & SHAIKAEV 2010), thus sequences must be reanalysed.

Summarizing, the preliminary results of molecular sequence data analysis of Geocorinae showed supporting results in terms of the applicability of COI sequences as information source supplementing morphological knowledge to resolve systematic questions. However, it has to be stressed that taxon sampling should be improved, and it is advised to include further non-coding mitochondrial, coding and non-coding nuclear marker sequences in the analysis.

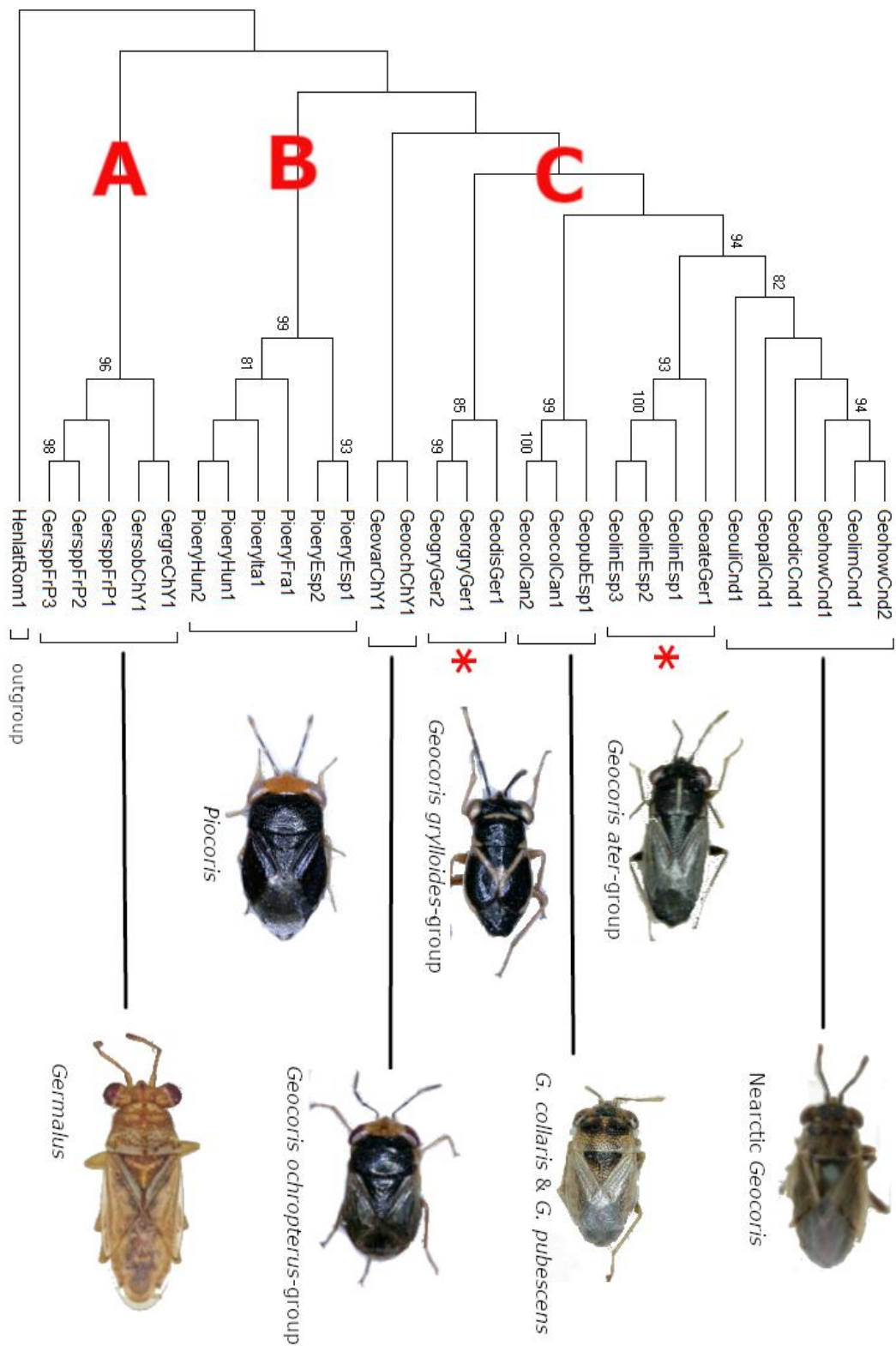


Figure 9. **Species groups within Geocoris based on molecular evidence:** results of Maximum Likelihood reconstruction of cytochrome-oxidase I subunit sequences of Geocoridae taxa (bootstrap consensus of 1000 pseudoreplicates). Bold capitals marking clades mentioned in text, support values indicated below branch. Asterisks marking species-groups recognized by Péricart (1999).

4.2.3. Revisiting the tribal classification of Geocorinae

The concept of tribal classification of Geocorinae was briefly proposed by MONTANDON (1907) and later elaborated in more detail by the same author (MONTANDON 1913a), who separated the two largest genera of the subfamily using the following combination of characters: *Germalus* – eyes stylate with ocular sulcus complete and well-defined; scutellum equilateral, always shorter than pronotum; clavus of hemelytron well-developed, margins parallel, length of claval commissure half of length of scutellum; *Geocoris* – eyes less stylate with ocular sulcus partly or completely reduced; scutellum mostly elongate, shorter than pronotum; clavus of hemelytron narrow, margins converging posteriorly; length of claval commissure less than one fourth of scutellum length. Based on these combinations of characters MONTANDON (1913a) divided the subfamily into two tribes, Geocorini and Germalini. The first tribe consisted of *Geocoris*, *Hypogeocoris* Montandon, 1913 and *Stylogeocoris* Montandon, 1913 and the latter comprised *Germalus*, *Neogermalus* Montandon, 1913 [later synonymized with *Germalus* by BERGROTH (1916)] and *Ninyas* Distant, 1893. However, taxa like *Piocoris*, *Apennocoris* or *Stenophthalmicus* Costa, 1875 were not mentioned by MONTANDON (1913a) and therefore remained unplaced. PARSHLEY (1921) suggested that Montandon's classification needs improvement but he never proposed a revised classification. Montandon's tribes gained no acceptance by the community, and except of the above-mentioned papers they were only mentioned by BARBER (1958). Hereby, preliminary evidence in support of Montandon's concept is presented.

TNT traditional search resulted 10 equally parsimonious trees with values $L = 74$, $Ci = 51$, $Ri = 82$. Majority-rule consensus of trees generated with Mesquite software, support values given in percentage below branch. One tree with same topology as of consensus tree was chosen to explore (Fig. 11). A monophyletic Geocorinae with three main clades and four monogeneric lineages were recovered with branches of support values between 70 and 100%.

Clade A (*C. kurandae* + *U. griseus* + *A. westraliensis* + *G. kinbergi* + *N. dissidens*) is supported by elongate peritremal surface (21: 0) and extended evaporatorium covering most of the metapleurites (24: 0) (non-homoplasious); general arrangement of MTSEA (20: 0) and round ostiole of peritreme (22: 0) (homoplasious). The branching has 100% support value. The terminal branching (*G. kinbergi* and *N. dissidens*) is supported by the uncoiled female spermatheca (27: 0) (non-homoplasious).

Clade B (*G. ater* + *G. collaris* + ... + *P. erythrocephalus* + *P. ochropterus*) is supported by nine non-homoplasious and one homoplasious transformations: ocular sulcus at least partly reduced (5: 1), closed labial trough (11: 2), partial reduction of scutellar trifurcate carina (15: 1), gradually converging margins of clavus with reduced claval commissure (17: 1), ostiole of MTSEA drop-shaped (22:1), vestibular scar closed (23: 1), evaporative area reduced (24: 1), furrow of metapleurites absent, male paramere slender with blade long, curved (28: 1); hamus of metathoracic wing reduced (19: 2). Branch of *G. ater* + *G. collaris* is supported by the plesiomorphic character of completely developed antenniferous tubercle. A subclade formed by *G. bullatus* + *G. punctipes* + *G. flavilineus* shares the homoplasious apomorphy of the presence of median furrow of vertex (7: 1). The subclade *S. fajoumensis* + *P. fallaciosus* + *S. horvathi* is supported by the rectangular pronotum (12: 2).

Clade C is nested within clade B and branches with relatively high support value (90%), supported by the partial reduction of hamus of metathoracic wing (homoplasious). The clade diverging into polytomy containing three minor clades and two lineages each including a single taxon, *M. discifer* and *G. unicolor*. A branch containing *E. chloroticus* + *G. marduk* is supported by combination of the presence of a transversal furrow near ocelli (6: 0) and reduced, flat pronotal callosities (13: 2). *H violaceus* + *G. grylloides* + *G. polytretus* share the presence of wing polymorphism as apomorphy (18: 1). Taxa of terminal subclade (*I. piceus* + *U. kondorosyi* + *P. erythrocephalus* + *G. ochropterus*) share homoplasious apomorphies of median longitudinal furrow of vertex (7: 1) and fused jugal sutures (9: 1).

Besides the clades discussed above four monogeneric lineages were resulted by the reconstruction. *A. pilosulus* was recovered as basal taxon of Geocorinae. *N. deficiens* is closely related to clade A and supported by partly reduced hamus and intervannals of metathoracic wing (19: 1). *S. biroi* and *N. marmoratus* are located between the two major clades.

Results show that the subfamily Geocorinae consists of two major and four minor lineages, the latter each including a single taxon. The major lineages consist of the two most species-rich genera of the subfamily – *Geocoris* and *Germalus* – and allied mono- or oligotypic genera (e.g. *Capitostylus*, *Unicageocoris*, *Mallocoris*). These results suggest that the tribal classification of Geocorinae proposed by MONTANDON (1913a) is plausible. Based on the clades and lineages recovered the following tribes are proposed: Apennocorini trib. nov.,

Germalini Montandon, 1913, Ninyatini trib. nov., Stylogeocorini trib. nov., Nannogermalini trib. nov. and Geocorini Dahlbom, 1851.

Apennocorini, Ninyatini, Stylogeocorini and Nannogermalini are monogeneric. Genera included in Apennocorini and Nannogermalini are monotypic with unusual, highly specialised morphology even in terms of this peculiar subfamily.

Germalini consists of five currently accepted genera, four of them monophyletic.

Nine genera are included in Geocorini. However, *Geocoris* was recovered polyphyletic. This finding is in accordance with suggestion of earlier studies that *Geocoris* is a badly defined group of species belonging to several closely related genera and subgenera (READIO & SWEET 1982, MALIPATIL 1994).

Hereby, preliminary results of the first generic and species-group level phylogenetic analysis of Geocorinae are presented. Homoplasy of characters and the number of polytomies are relatively high which suggests the necessity to improve both character matrix and taxon sampling. This improvement, as it was concluded in previous chapter, should be preceded by delimiting and review of coherent species groups of *Geocoris*.

Further discussion of tribes and taxa including diagnosis, distribution, etc. can be found in the Taxonomy chapter.

4.3. Taxonomy

Tribe **Geocorini** Dahlbom, 1851, revised status

Diagnosis. Morphologically highly heterogeneous tribe; general habitus varying from ovoid to myrmecomorphic. Based on the result of cladistic analysis representatives of the tribe share the following non-homoplasious synapomorphies: reduced ocular sulcus; closed labial trough; reduced trifurcate carina of scutellum; gradually narrowing clavus with reduced claval commissure; rounded ostiole, closed vestibular scar and reduced evaporatorium of MTSEA; absent dorsoventral furrow of metapleurites and male paramere slender with blade long, curved.

Included genera. *Geocoris* Fallén, 1814; (including *Piocoris* Stål, 1872 and *Eilatus* Linnavuori, 1972); *Mallocoris* Stål, 1872; *Hypogeocoris* Montandon, 1913; *Pseudogeocoris* Montandon, 1913; *Stenogeocoris* Montandon, 1913; *Isthmocoris* McAtee, 1914; *Geocoroides* Distant, 1918; *Umbrageocoris* Kóbor, 2019.

Distribution. Distributed worldwide in warm and temperate regions, from South Africa to the Arctic Circle.

Remarks. Based on the re-examination of type and additional materials the above listed genera are all recognized as members of Geocorini as defined above. However, due to the poor definition of some of the genera and a big number of unrevised taxa. no generic level key can be provided to the tribe. Reviewed and revised groups and representatives are discussed separately.

Genus *Geocoris* Fallén, 1814

Type species: *Cimex grylloides* Linnaeus, 1761 (= *Geocoris grylloides grylloides*), fixed by Oshanin, 1912.

LSID: <http://lsid.speciesfile.org/urn:lsid:Lygaeoidea.speciesfile.org:TaxonName:488153>

Remarks. This morphologically heterogeneous group, traditionally recognized as a genus, should be considered as a taxon made up by coherent species groups which possibly merit recognition as taxa of equal rank to currently recognized genera and subgenera of Geocorinae. However, it must be stressed that many representatives of this complex show considerable variability in colouration patterns and morphological characters, making group delimitation

difficult. Thus, it is suggested to perform further studies on the individual groups and their closer relatives before making any taxonomic action.

Geocoris grylloides-group

Diagnosis. Head width always greater than basal width of pronotum; vertex shiny, rugose, elevated between ocelli. Median longitudinal groove of vertex extending from base of head to clypeus. Ocular sulcus partly reduced, slightly visible. Labial trough closed, rounded. Labiomere I not reaching anterior margin of pronotum, labiomeres II shorter than labiomere III. Pronotum trapezoidal with anterior angles strongly rounded. Surface of pronotum with dense punctation; pronotal callosities and humeral angles impunctate, callosities somewhat elevated. Scutellum large, apex sharply pointed; basal width somewhat longer than median length. Trifurcate scutellar carina reduced except apical part. Brachypterous and macropterous morphs are known, in macropterous morph clavus gradually narrowing towards apex, claval commissure reduced; in brachypterous morph clavus indistinguishably fused with corium, claval suture lost. Corium densely punctate in both forms except narrow costal margin. Anterior margin of prosternum narrow. MTSEA “geocorine-type”. Integument of abdominal tergites irregularly wrinkled in their lateral thirds.

Included species. *Geocoris grylloides* (Linnaeus, 1761) (3 valid subspecies); *Geocoris dispar* (Waga, 1839) (2 valid subspecies); *Geocoris itonis* Horváth, 1905.

Distribution. A Palearctic group distributed from the Euro-Mediterranean region to the Japanese Archipelago.

Remarks. A group of characteristic appearance. According to Péricart (1999) this group consists of two species with 5 recognized subspecies. Based on a study of the external morphology of its holotype, *Geocoris itonis* Horváth, 1905 is recognized to be morphologically similar and phylogenetically closely related to *G. grylloides* and *G. dispar*. A study of genital structures would be necessary based on further specimens of *G. itonis*.

Geocoris ater-group

Diagnosis. Head width subequal to basal width of pronotum. Vertex elevated; surface shiny, rugose, with sparse, decumbent pubescence. Clypeus with longitudinal groove; transversal groove anterior to ocelli. Ocular sulcus well-defined to line of ocelli, slightly visible but present for the rest of the head. Labial trough closed, rounded. Labial segment I hardly reaching base of head, segment II shorter than segment III. Pronotum trapezoidal, without lateral impressions, basal width approximately 1.6 times longer than length. Pronotum densely punctate except callosities, median ridge and humeral angles. Basal width of scutellum shorter than median length. Trifurcate carina reduced, inconspicuous. Submacropterous and macropterous morphs known. Clavus with margins diverging, claval commissure missing. MTSEA “geocorine-type”. Anterior margin of prosternum widened medially. Integument of abdominal tergites slightly wrinkled in lateral thirds, with stronger transversal wrinkles medially.

Included species. *Geocoris ater* (Fabricius, 1787) (8 valid subspecies); *Geocoris acuticeps* Signoret, 1881 (2 valid subspecies); *Geocoris lineola* (Rambur, 1839) (4 valid subspecies); *Geocoris phaeopterus* (Germar, 1837).

Distribution. The group distributed mostly in the Palaearctic. However, *G. lineola cognatus* (Fieber, 1861), *G. acuticeps* (both subspecies) and *G. phaeopterus* are present in the Afrotropics (PÉRICART 1999).

Geocoris ochropterus-group

Remarks. Based on the comparison of colouration patterns and morphological structures in course of the description of *Geocoris margaretarum* Kóbor, 2018 it was concluded that related species (*G. ochropterus*, *G. varius* and *G. chinensis*) are highly similar and the scarcity of conspicuous discriminative characters may suggest that these taxa form a coherent group of closely related species. However, this hypothesis should be tested based on a study of longer series of specimens of all included taxa (especially *G. chinensis* and *G. varius*) and thorough comparison with other, similar taxa in the region, e.g. *Geocoris flaviceps* (Burmeister, 1834), preferably with supplementary molecular phylogenies.

Distribution. Species of the group are distributed in the Indomalayan and the easternmost part of the Palaearctic Region.

Hereby, a key to the species of this hypothesized group is provided.

Key to species of the *Geocoris ochropterus*-group

1. Pronotum entirely black or at most with irregular ochraceous spots at humeral angles.
Connexiva entirely black 2
- Pronotum with more extended, irregular ochraceous spots at lateral and posterior margins.
Connexiva with ochraceous markings on lateral margin 3
2. Base of head with blackish marking of various extent. Antennomeres I and IV entirely ochraceous, segments II-III partly fuscous. Humeral angles without ochraceous spots. Corium with sparse, irregular, coarse punctation; punctures and surrounding brownish ..
..... *Geocoris margaretarum* Kóbor, 2018
- Only extreme base of head black, never exceeding the level of ocelli. Antennomere I ochraceous, antennomeres II-IV brownish, antennomeres II-III with apex ochraceous. Humeral angles with irregular ochraceous spot of various extent. Punctuation of hemelytra fine, dense in M-R region. Punctures fuscous without surroundings of the same colour *Geocoris varius* (Uhler, 1860)
3. Antennomeres entirely black or dark fuscous. Hemelytra always translucent; apex of corium undecorated, punctuation with brownish surrounding. Lateral margin of connexiva with smaller, irregular ochraceous spots
..... *Geocoris chinensis* Jakovlev, 1904
- Antennomere I mostly with base ochraceous and apex fuscous or blackish; II-III entirely darker, colouration varies from fuscous to blackish; antennomere IV ochraceous. Hemelytra sometimes opaline with fine brownish punctuation without surroundings of the same colour; apex of corium with irregular fuscous spot. Connexiva margined with ochraceous *Geocoris ochropterus* (Fieber, 1844)

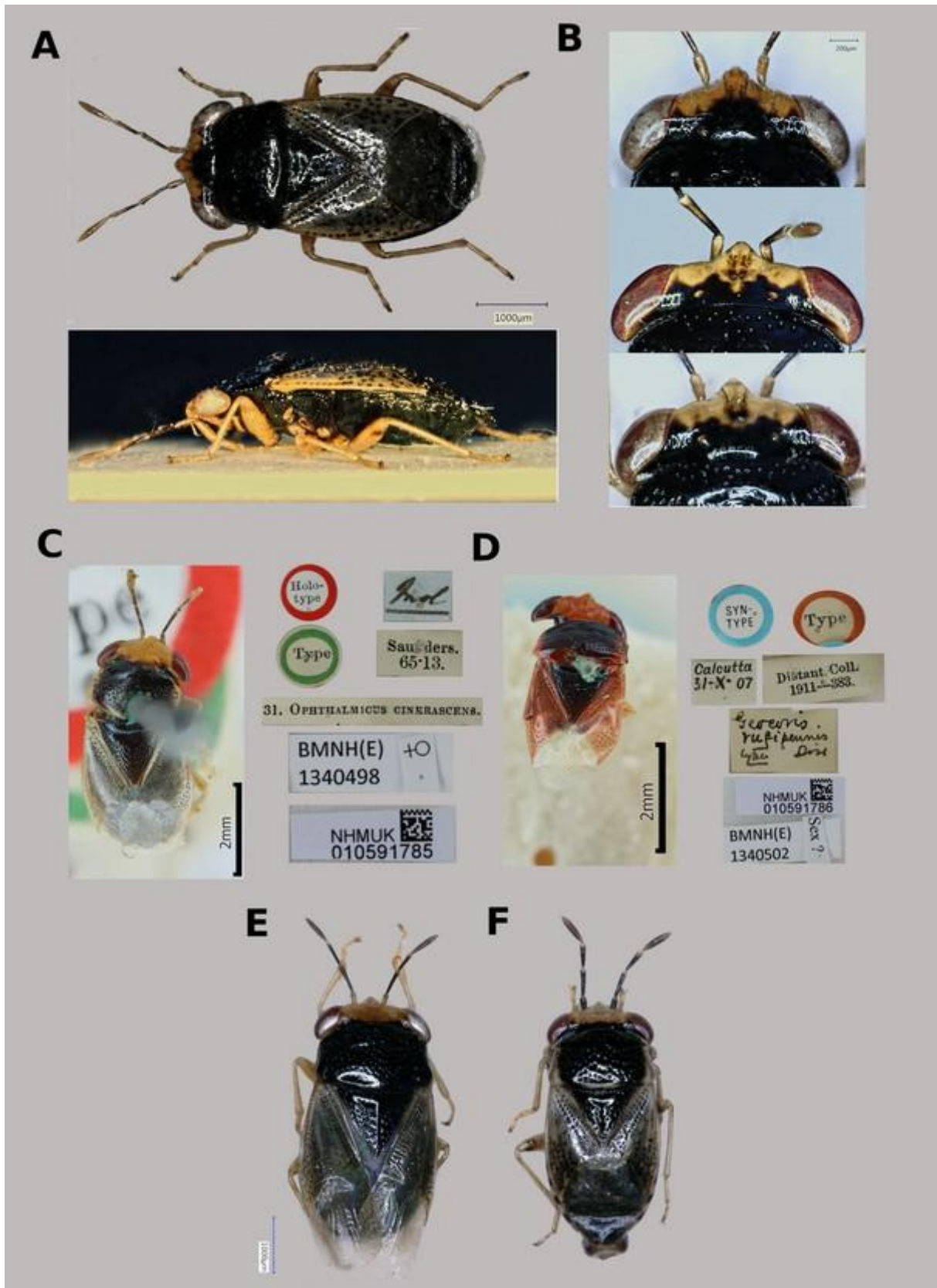


Figure 11. **The *Geocoris ochropterus*-group**: A. *Geocoris margaretarum* Kóbor, 2018: dorsal and lateral habitus (holotype, NHMW); B. Variability of head pattern in *G. margaretarum*; C. Lectotype of *Ophthalmicus cinarescens* Walker, 1872 (design. Kóbor, 2018); D. Lectotype of *Geocoris rufipennis* Distant, 1918 (design. Kóbor, 2018); E. *Geocoris varius* Uhler, 1861; F. *Geocoris chinensis* Jakovlev, 1904.

Genus *Piocoris* Stål, 1872

Type species: *Salda erythrocephala* Lepeletier & Serville, 1825 (= *Geocoris erythrocephalus erythrocephalus*), by subsequent designation.

LSID: <http://lsid.speciesfile.org/urn:lsid:Lygaeoidea.speciesfile.org:TaxonName:488181>

Diagnosis: Mostly broad, dorsally convex species. Head lunate with sulci reduced; labial trough closed without conspicuous suture; clypeus broadens apically; labial segment II longer than segment III. Pronotum with lateral margins subparallel posterior to callosities, anterior edges oblique, callosities small, inconspicuous. Scutellum elongate with trifurcate carina mostly reduced; apex of scutellum always rounded, at least moderately. Basal parts of scutellar trifurcate carina conspicuous, elevated. Only macropterous morphs known. Integument of abdominal tergites with strong longitudinal wrinkles laterally, median part more or less smooth.

Remarks. The rank and position of *Piocoris* has been a subject of debate. LINNAVUORI (1972) recognized it as subgenus of *Geocoris* because the ineligibility of discriminative characters for generic level separation. READIO AND SWEET (1982) disputed this conclusion but did not revise the status of the taxon because it was out of range of study. However, their suggestion is supported by my results including molecular phylogenies, thus *Piocoris* is here suggested to be recognised as a genus of Geocorinae.

Genus *Eilatus* Linnavuori, 1972

Type species: *Piocoris confalonierii* Bergevin, 1932, by original designation.

LSID: <http://lsid.speciesfile.org/urn:lsid:Lygaeoidea.speciesfile.org:TaxonName:488154>

Diagnosis. Representatives of the subgenus are very similar to *Piocoris* species in general appearance. The most remarkable difference is the spinose antennal segment II. This character is observable in larval stages as well (PÉRICART 1999). Another remarkable differences are as follows: vertex with curved transversal groove anterior to ocelli; trifurcate scutellar carina mostly distinct, T-shaped.

Remarks. Due to the spinose antennal segment II, which is to be considered unique in terms of the entire subfamily, and other differences from other *Geocoris* species, it is suggested to consider *Eilatus* as separate genus of Geocorinae similarly as *Piocoris*.

Distribution. Representatives of the genus is associated with desert habitats distributed from the Middle East to Somalia.

Genus *Umbrageocoris* Kóbor, 2019

Type species: *Umbrageocoris kondorosyi* Kóbor, 2019, by original designation.

LSID: <http://lsid.speciesfile.org/urn:lsid:Lygaeoidea.speciesfile.org:TaxonName:506724>

Diagnosis. *Umbrageocoris* can be separated from other geocorines of the Indomalayan and Australasian regions by combination of the following characters: labial trough Y-shaped with suture reaching base of head; labiomere II shorter than III, segment IV longest; clavus gradually narrowing towards apex, claval commissure reduced; corium punctate along veins; peritreme and evaporatorium of metathoracic scent gland as in Fig. 6B; integument of abdominal terga III and IV rugose medially; male paramere slender, blade narrow, curved, surface lacking pubescence.

Remarks. *Umbrageocoris* resembles most strongly the Australian genus *Stylogeocoris* Montandon, 1907, nevertheless there are some remarkable differences separating these genera. Based on MALIPATIL's (1994) revisionary work on *Stylogeocoris* and studying the holotype of *Stylogeocoris biroi* Montandon, 1907 (HNHM), this genus can be diagnosed by the combination of the following characters: labiomeres II and III subequal in length; ocular sulcus complete, distinct; margins of clavus almost parallel, claval commissure developed; abdominal terga III and IV punctate. In *Umbrageocoris* labiomere II is conspicuously shorter than segment III; margins of clavus gradually converging, claval commissure reduced; abdominal terga III and IV rather wrinkly than punctate. Male paramere is stouter, more curved in *Stylogeocoris* compared to *Umbrageocoris*. Furthermore, paramere of *Umbrageocoris* is lacking pubescence. Comparing to species of *Geocoris* distributed in the archipelago (*G. willeyi* Kirkaldy, 1905 and *G. leopoldi* Schouteden, 1933; holotypes examined) the following differences can be observed: the new genus is more slender in general appearance than the other two species; head more pentagonal, ocular sulcus slight, but complete, not reduced; pronotal callosities more developed in *Umbrageocoris*; apical part of trifurcate carina of scutellum slight, but not reduced; corium of hemelytron without punctation in intervannals. The most remarkable differences of *Umbrageocoris* from *Germalus* are the proportions of labiomere II–III (similarly as in the case of *Stylogeocoris*) and the arrangement of peritreme of metathoracic scent gland (Figs. 4A, B).

The completely reduced hamus of hind wing suggests a closer relation to *Geocoris* species of the region.

Distribution. This genus is distributed from the Malay Peninsula to southeastern New Guinea (Fig. 15D).

Key to species and subspecies of *Umbrageocoris*

1. Pronotum entirely dark brownish. Trifurcate carina of scutellum not interrupted by punctures *Umbrageocoris kondorosyi* Kóbor, 2019
- Pronotum with extensive ochraceous regions near humeral angles. Trifurcate carina of scutellum interrupted by punctures at the apices (subspecies of *Umbrageocoris maai* Kóbor, 2019) 2
2. Pronotum anterior to callosities with more than one row of punctures. Pronotum posterior to callosities evenly punctate
..... *Umbrageocoris maai maai* Kóbor, 2019
- Pronotum anterior to callosities with only one row of punctures, surrounding the callosities. Punctures posterior to pronotal callosities forming more or less a transverse band (Fig. 13C) *Umbrageocoris maai timorensis* Kóbor, 2019

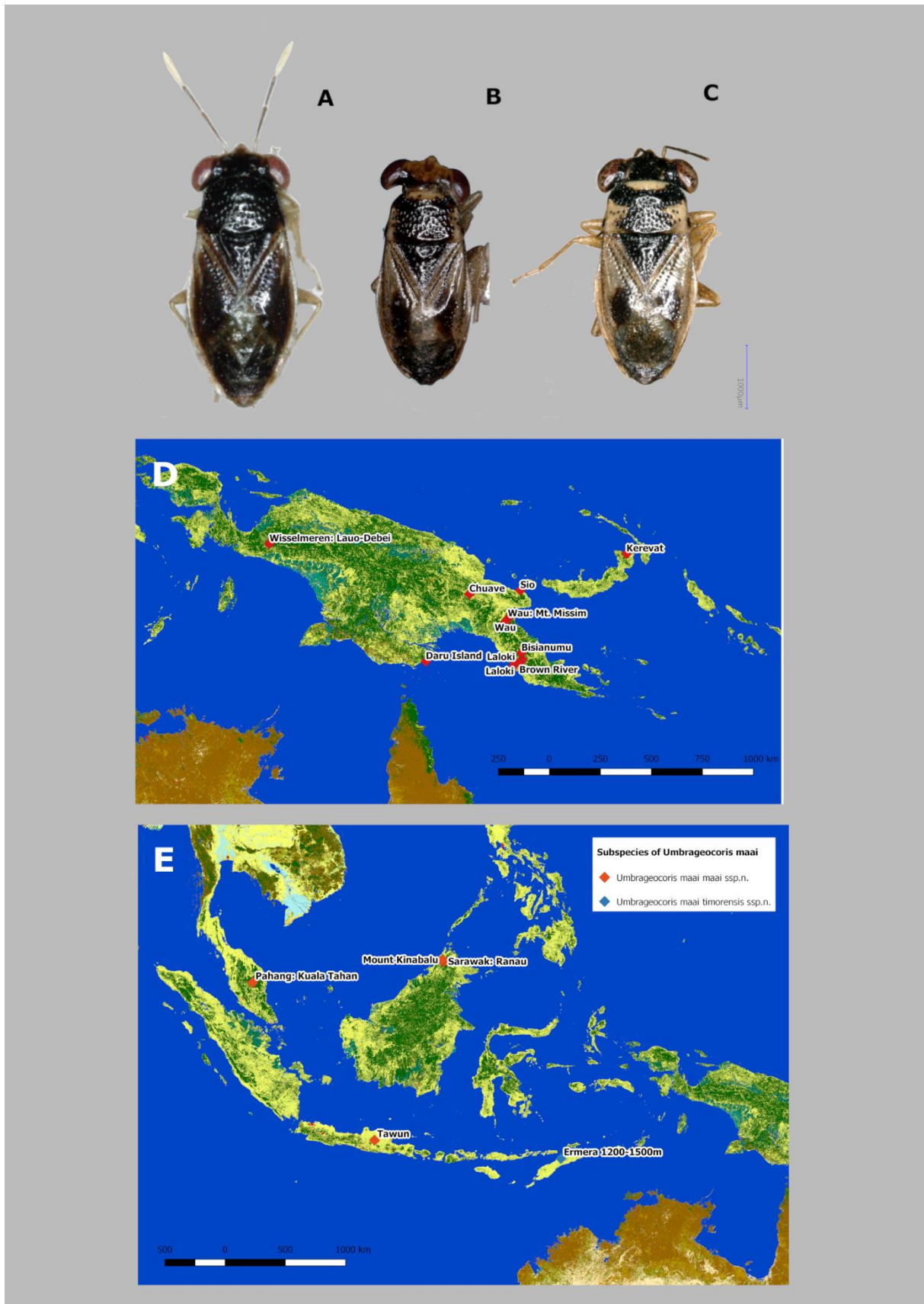


Figure 12. *Umbrageocoris* Kóbor, 2019: A. *U. kondorosyi* (holotype, HNHM); B. *U. maai maai* (holotype, BPBM); C. *U. maai timorensis* (holotype, BPBM); D. Distribution of *U. kondorosyi*; E. Distribution of *U. maai* ssp.

Tribe **Germalini** Montandon, 1913, revised status

Diagnosis. General habitus of included taxa moderately elongate. Eyes moderately stylate, eyesstalks sometimes erect. Wing polymorphism not observed in this group. Representatives of this tribe can be delimited with the combination of following shared synapomorphies: extent of MTSEA reaching the midline of metapleurites (homoplasious); presence of peritremal surface; rounded ostiole of MTSEA; evaporatorium covering most of metapleurites, sometimes reaching line of mesocoxae.

Included genera. *Germalus* Stål, 1862; *Neogermalus* Montandon, 1913; *Ausogeocoris* Malipatil, 2013; *Capitostylus* Malipatil, 2013; *Unicageocoris* Malipatil, 2013.

Distribution. Representatives of the tribe are found from the Afrotropical Region to islands of the Pacific Ocean.

Remarks. MONTANDON (1913a) placed *Germalus*, *Neogermalus* and *Ninyas* into this tribe. However, in contrast to his classification, the present results show that the genus *Stylogeocoris* belongs to this taxon and not to Geocorini. According to the results of phylogenetic reconstruction, the monotypic Australian genera described by MALIPATIL (2013) are to be placed into *Germalini* as well. In the present study only representatives of the tribe reviewed and revised by the author will be discussed due to page restrictions.

Key to genera of Germalini

1. Pronotum with a curved transversal groove across callosities
..... *Unicageocoris* Malipatil, 2013
- Pronotal callosities without groove 2.
2. Vertex coarsely punctate between eyes 3.
- Surface of vertex smooth or at most rugose 4.
3. Body dorsally flat. Head pentagonal, clypeus expressed. Lateral margins of pronotum carinate and explanate. Hemelytron evenly, coarsely punctate
..... *Ausogeocoris* Malipatil, 2013

- Body not flattened dorsally. Head almost lunate, clypeus hardly recognizable. Lateral margins of pronotum partly and slightly carinate, never explanate. Hemelytron densely punctate in M-R region *Capitostylus* Malipatil, 2013
- 4. Antenniferous tubercles armed with tooth-like process laterally
..... *Neogermalus* Montandon, 1913 (revised status)
- Antenniferous tubercles unarmed 5.
- 5. Corial punctation forms an S-shaped line in M-R region *Ninyas* Distant, 1893
- Corial punctation arranged along veins *Germalus* Stål, 1862

Genus *Germalus* Stål, 1862

Type species: *Henestaris kinbergi* Stål, 1858, by subsequent designation

LSID: <http://lsid.speciesfile.org/urn:lsid:Lygaeoidea.speciesfile.org:TaxonName:488770>

Diagnosis. Ovoid, mostly elongate species. Head pentagonal with eyes moderately stylate; eyestalk sometimes erect or prorect. Ocular sulcus complete, well-developed. Labial trough open, U-shaped. Pronotum trapezoidal, lateral margins slightly impressed. Trifurcate carina of scutellum always distinct, developed. Hemelytron punctate along corial veins. MTSEA with oblong peritremal surface of various length and curvature and irregular shaped orifice.

Distribution. The most broadly distributed genus of the tribe, representatives are found from Equatorial Africa to French Polynesia.

Key to Afrotropical and Malagasy species of *Germalus*

1. Body length > 6mm [Madagascar] ... *Germalus benyovszkyi* Kóbor & Kondorosy, 2016
- Body length < 6mm 2.
2. Colouration uniform ochraceous without any markings 3.
- Colouration ochraceous decorated with at least a brownish rounded spot at each humeral angle 4.
3. Dorsal punctation brownish. Corium with fine, sparse punctures between M and R veins [equatorial East Africa] *Germalus telekii* Kóbor & Kondorosy, 2017

- Dorsal punctation concolorous. Corium densely, coarsely punctate between M and R veins [equatorial West Africa] *Germalus oroszi* Kóbor & Kondorosy, 2017
- 4. Colouration dark ochraceous with brownish punctures. Rounded brownish spot at each humeral angle. Abdominal dorsum with broad dark brownish longitudinal bands [Mauritius and Réunion] *Germalus kinbergi* (Stål, 1858)
- Colouration pale ochraceous with at least a median longitudinal dark band exceeding from head to base of scutellum and rounded brownish spots at humeral angles 5.
- 5. An obscure brownish band across each pronotal callosity besides median dark brownish stripe. Abdominal dorsum with narrow longitudinal bands laterally [Madagascar]
..... *Germalus banari* Kóbor & Kondorosy, 2016
- Pronotum with only one, median brownish stripe. Longitudinal bands of abdominal dorsum broad or missing 6.
- 6. Dorsal punctation blackish; corial row of punctures of clavus almost complete. Abdominal dorsum with broad dark longitudinal bands [equatorial East Africa]
..... *Germalus ghesquierei* Schouteden, 1957
- Dorsal punctation mostly concolorous with surface of dorsum; corial row of punctures of clavus reaching to third of length at most. Abdominal dorsum without longitudinal bands laterally [equatorial East Africa] *Germalus conradsii* Schouteden, 1957

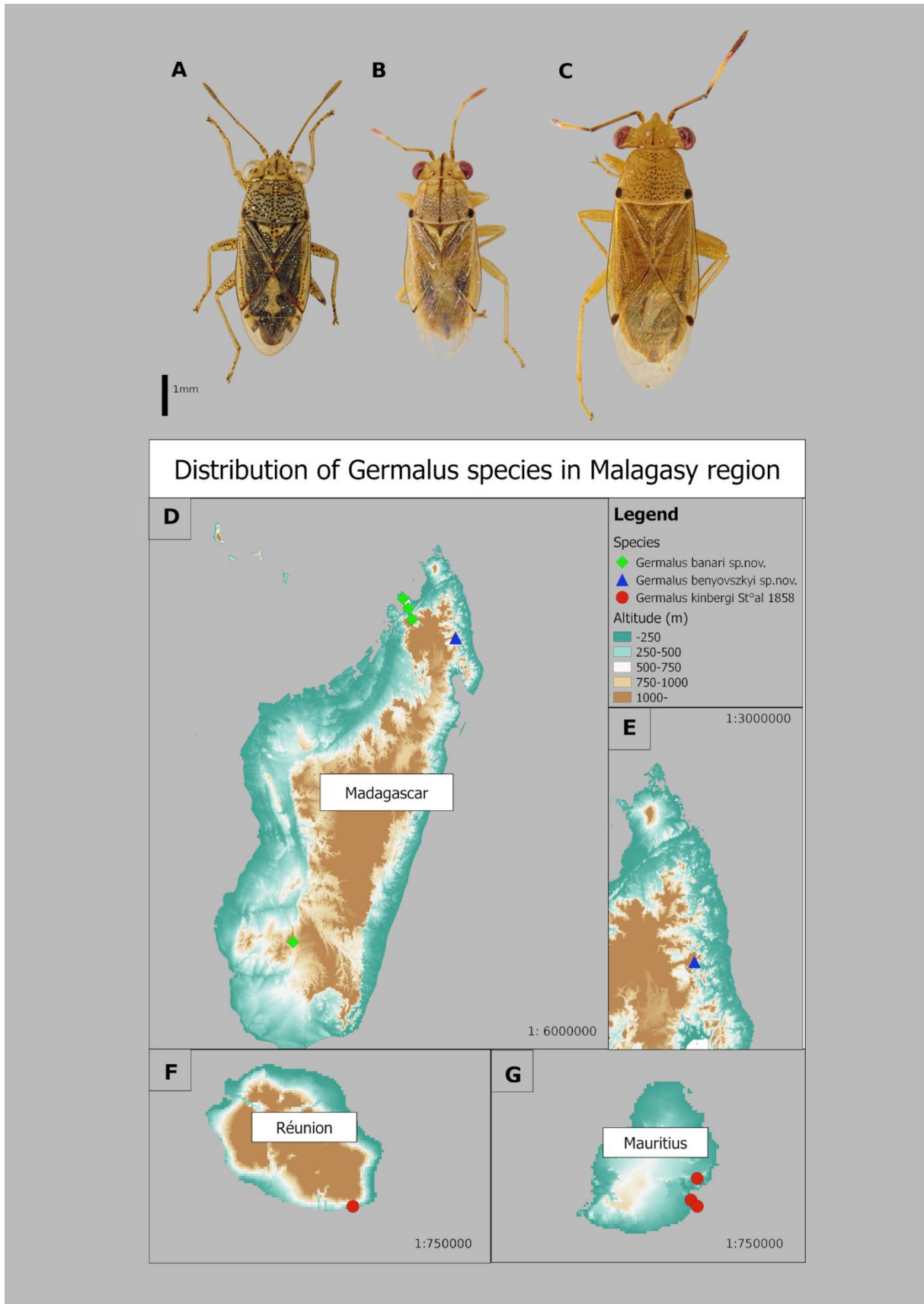


Figure 13. ***Germalus* species of the Malagasy region**: A – *Germalus kinbergi* (Stål, 1858) (NHMW); *Germalus banari* Kóbor & Kondorosy, 2016 (holotype, MZMB); C – *Germalus benyovszkyi* Kóbor & Kondorosy 2016 (holotype, MNHN); D–G distribution of Malagasy *Germalus* species, based on the studied specimens.

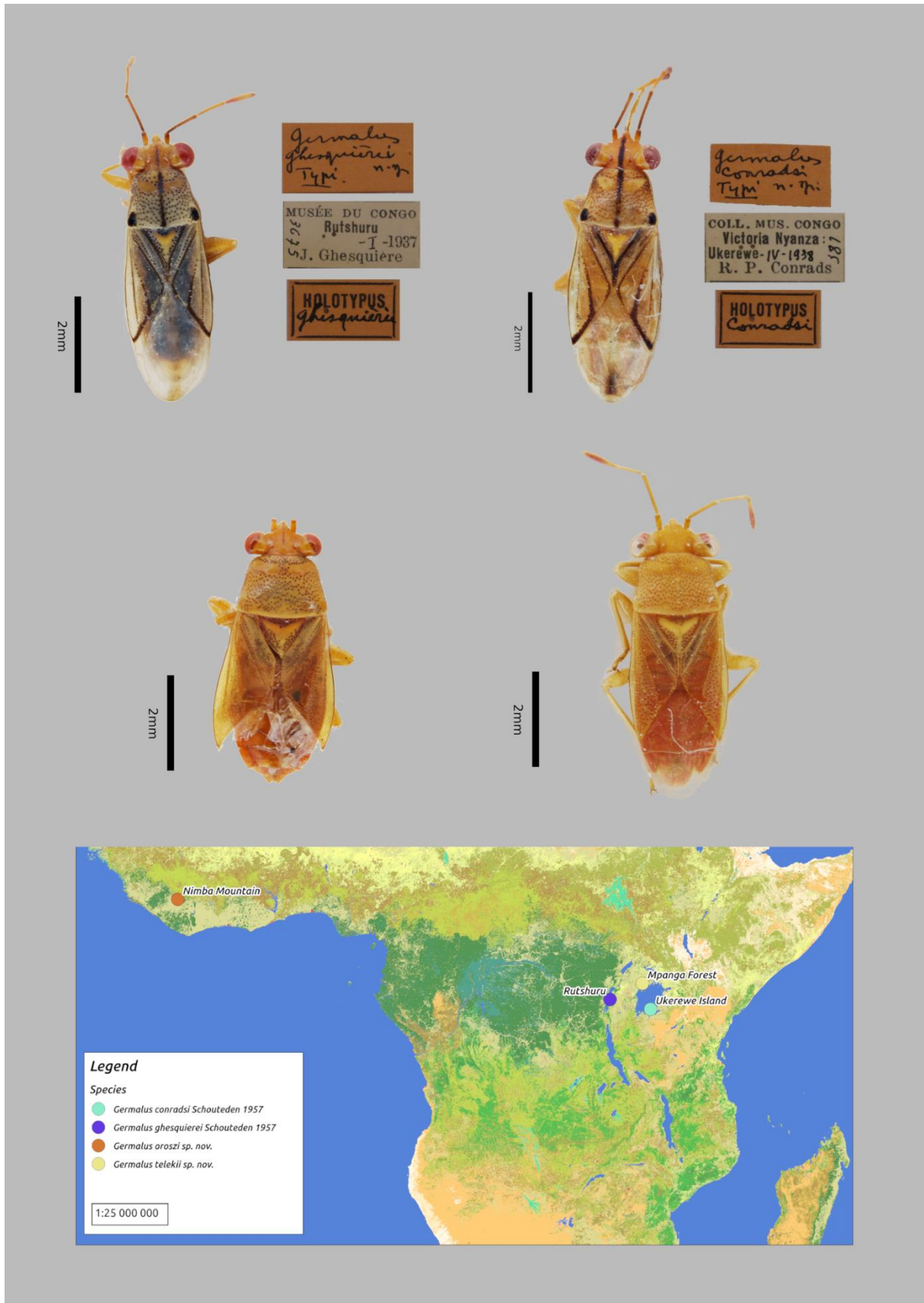


Figure 14. ***Germalus* species of continental Africa**: A. *Germalus ghesquierei* Schouteden, 1957 (holotype, RMCA); B. *Germalus conradsi* Schouteden, 1957 (holotype, RMCA); C. *Germalus telekii* Kóbor & Kondorosy 2017 (holotype, BMNH); D. *Germalus oroszi* Kóbor & Kondorosy, 2017 (holotype, MNHN); E. Distribution map of species based on studied material.

Key to French Polynesian species of Germalini

1. Vertex corrugate, posterior margin of eyes touching the anterior angles of pronotum. Corium with characteristic S-shaped punctation in M-R region
..... *Neogermalus montandoni* (Bergroth, 1916)
- Vertex smooth, posterior margin of eyes not touching anterior angles of pronotum. Corial punctation mostly arranged along veins 2.
2. Hind tarsomere I more than twice as long as tarsomeres II+III combined
..... *Germalus unicolor* Montandon, 1907
- Hind tarsomere I less than twice as long as tarsomeres II+III combined 3.
3. Trifurcate carina of scutellum medially with irregular reddish spot of various extent
..... *Germalus ashlocki* Kóbor, 2020
- Scutellar trifurcate carina without reddish spot, at most infusate 3.
4. Eyes moderately erect in lateral view. Thoracic pleurites and lateral part of abdominal connexiva without longitudinal band-like decoration
..... *Germalus costalis* Van Duzee, 1932
- Eyes slightly or not erect in lateral view. Thoracic pleurites and the lateral part of abdominal connexiva with longitudinal band-like decoration 4.
5. Dorsum with extended fuscous regions or patches 6.
- Dorsum ochraceous with less extensive, mostly pale brownish decorations 7.
6. Dorsum with irregular, pale fuscous “patches” on head, pronotum and hemelytron
..... *Germalus maculatus* Van Duzee, 1932
- Lateral margin of pronotum and hemelytron with large, continuous fuscous regions
..... *Germalus fuliginosus* Van Duzee, 1932
7. Dorsal decoration of head and thorax consists of longitudinal line on vertex, extending from clypeus to line of ocelli and one rounded spot at each humeral angle. Punctation of thoracic dorsum sparse and slight, deeper punctures only present at scutellum
..... *Germalus infans* Van Duzee, 1932

- Dorsum of head and thorax more decorate, longitudinal line on vertex reaching almost base of head, pronotum with irregular spots at callosities and posterior margin. Punctuation of thoracic dorsum strong and dense 8.
- 8. Pronotum with impunctate longitudinal ridge medially. Punctures at corial margin of clavus reaching to half of length *Germalus robustus* Van Duzee, 1935
- Pronotum without impunctate median ridge. Punctures at corial margin of clavus reaching to the third of length *Germalus lateralis* Van Duzee 1932

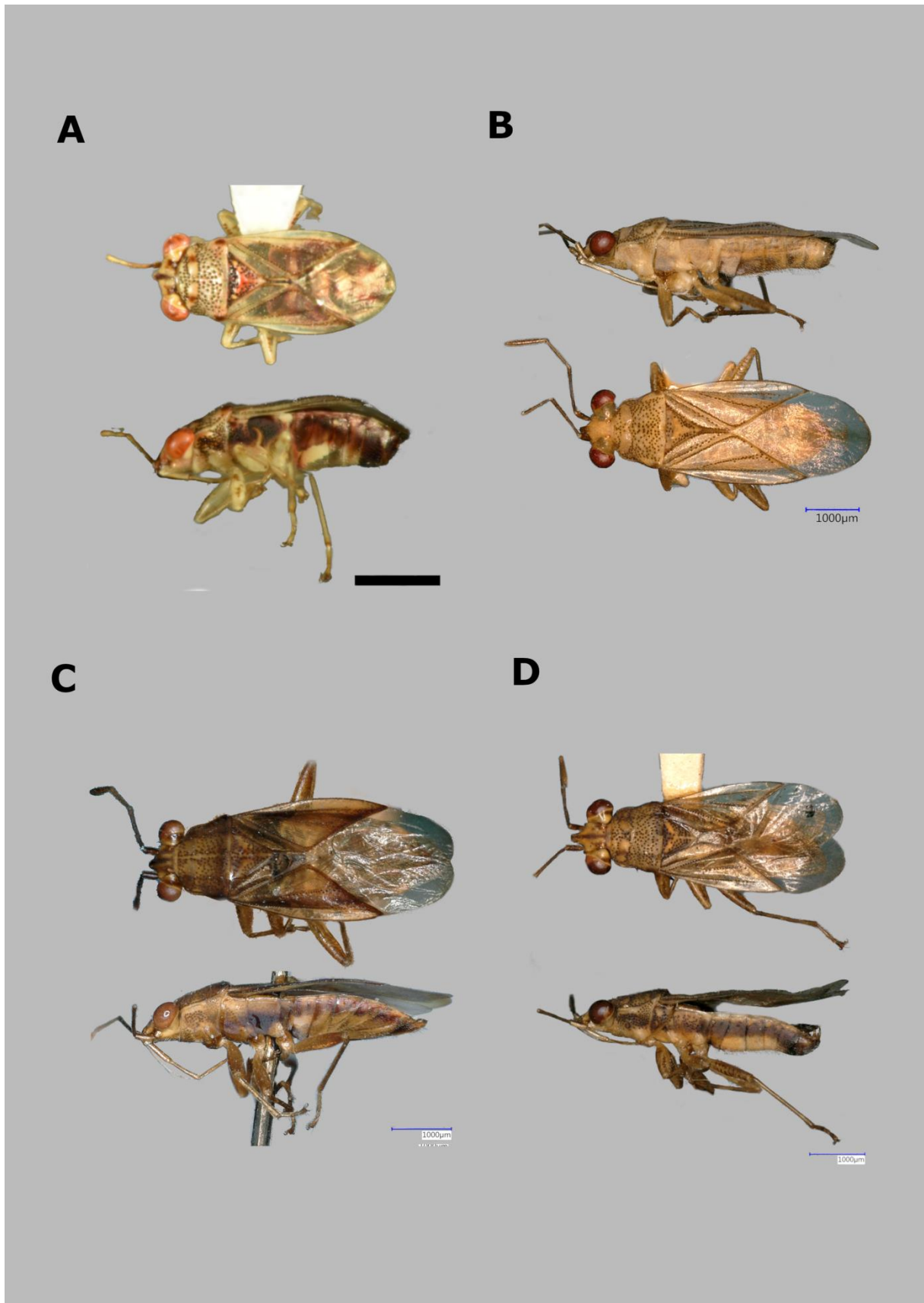


Figure 15. *Germalus* species of French Polynesia I.: *Germalus ashlocki* Kóbor, 2020 (holotype, SEMC); *Germalus costalis* Van Duzee, 1932 (holotype, BPBM); *Germalus fluiginosus* Van Duzee, 1932 (holotype, BPBM); *Germalus lateralis* Van Duzee, 1932 (holotype, BPBM).

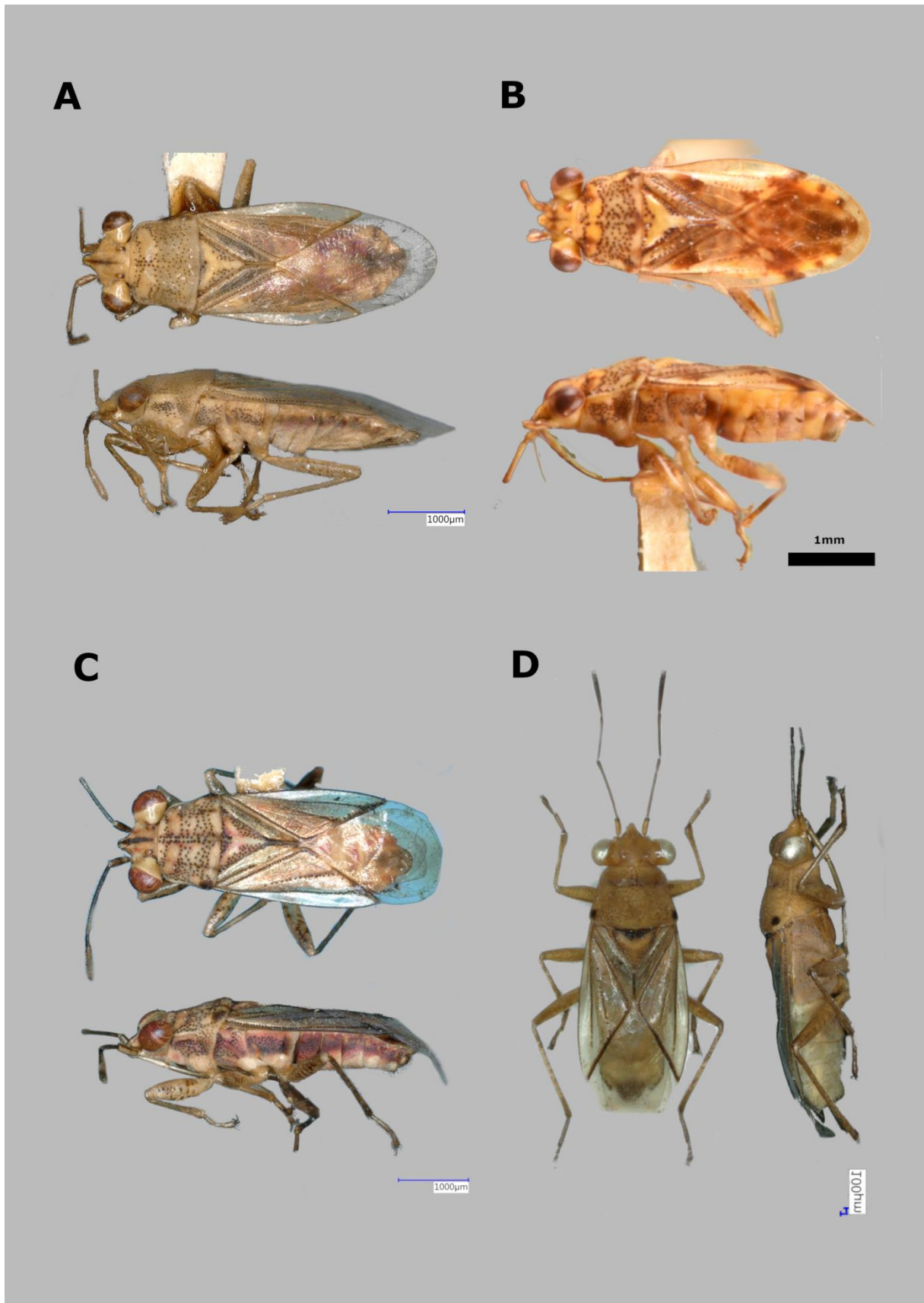


Figure 16. *Germalus* species of French Polynesia II.: A. *Germalus infans* Van Duzee, 1932 (holotype, BPBM); B. *Germalus maculatus* Van Duzee, 1932 (holotype, BPBM); C. *Germalus robustus* Van Duzee, 1935; *Germalus unicolor* (Montandon, 1907) (PCZJ).

Genus *Neogermalus* Montandon, 1907, revised status

Type species: *Ophthalmicus membranaeus* (non Montrouzier, 1861): MONTANDON (1913a) (misidentification) (= *N. montandoni* Bergroth, 1916), by monotypy

LSID: <http://lsid.speciesfile.org/urn:lsid:Lygaeoidea.speciesfile.org:TaxonName:488781>

Diagnosis. This genus can be separated from other geocorines of New Caledonia and other Pacific islands by the combination of following characters: vertex of head corrugate, mostly with decumbent pubescence; antenniferous tubercles armed with tooth like process laterally; scutellum subequilateral with apex sharply pointed; length of claval commissure is approximately half of median length of scutellum; M-R region of corium with S-shaped punctation; hamus of hind wing present, complete; male paramere armed with spine-like process.

Remarks. The characters like trapezoidal pronotum with slight impression on lateral margin, subequilateral scutellum, margins of clavus parallel with claval commissure developed and presence of hamus of hind wing suggest a close relation to *Germalus*. However, general arrangement of head rather resembles to representatives of *Stylogeocoris* and *Geocoris*. MONTANDON (1913a) separated *Neogermalus* from *Germalus* on the basis of the latter character. This was found ineligible for generic level discrimination by BERGROTH (1916).

Results of this study conclude that MONTANDON's (1913a) separation of *Neogermalus* from *Germalus* was sound, though he provided an inadequate differential diagnosis which resulted an erroneous synonymy (BERGROTH 1916). On the other hand, *Ophthalmocoris* (?) *dissidens* was placed in a newly established genus, *Nesogermalus* Bergroth, 1916 on the basis of differences observed. A careful study of types revealed, that *Neogermalus* and *Nesogermalus* share the same structural characteristics as described above. Taking all of the above into account *Neogermalus* Montandon, 1913 proposed to be considered valid and distinct genus of Geocorinae and *Nesogermalus* Bergroth, 1916 should be treated as subjective synonym of the taxon.

Key to *Neogermalus* species:

1. Total body length ≥ 6.5 mm. Colouration purplish with white decoration. Clypeus with bilateral impressions basally
..... *Neogermalus montanus* (Distant, 1920), new combination

- Total body length < 6.5 mm. Colouration ochraceous with fuscous to dark brownish decoration. Clypeus without basal impression 2
- 2. Pronotum trapezoidal with a slight impression on lateral margin, anterior edges strongly rounded *Neogermalus montandoni* (Bergroth, 1916), new combination
- Pronotum quadrangular with a dorsolateral impression medially, anterior edges slightly rounded 3
- 3. Colouration marbled: base colour ochraceous with fuscous to dark brown, irregular decoration. Pronotum with narrow, impunctate median ridge. Trifurcate carina of scutellum interrupted by punctures
..... *Neogermalus spinolae* (Montrouzier, 1865), new combination
- Colouration different. Pronotum without impunctate median ridge. Trifurcate carina uninterrupted by punctures 4
- 4. Colouration mostly monochromatic ochraceous or at most with slightly infuscate regions. Trifurcate carina of scutellum explanate, more or less flat
..... *Neogermalus variegatus*, new species
- Colouration ochraceous with dark brownish longitudinal band on dorsum. Trifurcate carina of scutellum narrow, definitely elevated
..... *Neogermalus membranaeus* (Montrouzier, 1861), new combination

Neogermalus montandoni (Bergroth, 1916) new combination.

LSID: <http://lsid.speciesfile.org/urn:lsid:Lygaeoidea.speciesfile.org:TaxonName:488780>

Germalus minor (Distant, 1920) new subjective synonymy

LSID: <http://lsid.speciesfile.org/urn:lsid:Lygaeoidea.speciesfile.org:TaxonName:488820>

Type material examined: *Germalus montandoni*: holotype, male (HNHM): “Nouméa / N. Calédonie / Delauney // Neogermalus Montandon / type 1913 / membranaeus Montrouz. / det. Montandon 1913 [label handwritten: Montandon]”;

Germalus minor: lectotype, male (BMNH): circular red holotype label; circular red type label; “New Caledonia. / P.D. Montague. / 1918-87 // Neocypus / minor / type Dist. [label handwritten: Distant] // BMNH(E) 1340521 // NHMUK 010591745”.

Diagnosis. The species is easy to recognize by its dark ochraceous general colouration with dark brownish punctures and extended, but narrow and slight infusate spots at posterior margin of pronotum and apical margin of corium combined with reddish colouration of abdominal dorsum. Remarkable structural character is the arrangement of the MTSEA and evaporative area.

Remarks. This species is highly similar to *Germalus minor* (Distant, 1920) in general appearance. After careful study of the available type and non-type specimens of *Germalus minor* it was concluded that no major difference is observable between the species and *N. montandoni*. Comparison of the types showed that the single structural difference is the interruption of pronotal callosities by punctures. However, study of longer series of specimens revealed that this character is variable among specimens and transitions are present. Therefore, the following new synonymy is proposed: *Neogermalus montandoni* (Bergroth, 1916) = *Germalus minor* (Distant, 1920), syn. nov.

In case of *Germalus montrouzieri* the original description mentions the same diagnostic character. However, due to the cursory description and missing type specimen the identity of *G. montrouzieri* is doubtful. MONTANDON (1907) erroneously recognized this species as identical with *Ophthalmicus membranaeus* Montrouzier, 1861, when redescribing it. This error was recognized by BERGROTH (1916) leaving Montrouzier’s species in *Geocoris* and transferring Montandon’s to *Germalus* (as result of synonymy) under the new name *Germalus montandoni* Bergroth, 1916.

Neogermalus membranaeus (Montrouzier, 1861) new combination.

LSID: <http://lsid.speciesfile.org/urn:lsid:Lygaeoidea.speciesfile.org:TaxonName:488576>

Nesogermalus dissidens (Montandon, 1907), new subjective synonymy

LSID: <http://lsid.speciesfile.org/urn:lsid:Lygaeoidea.speciesfile.org:TaxonName:488850>

Type material examined: *Geocoris membranaeus*: syntype, ? (NHMW): “Lifu / Coll. Signoret // membranaeus / det. Signoret [2 labels handwritten: Signoret] // Lygaeus membranaeus (m) / Lifu [label handwritten: [label handwritten: Montrouzier]”.

Nesogermalus dissidens: syntype, 1 male (KNHM): “Nouvelle Calédonie / Gambey // Nouv. Cal. // TYPE // Montandon / Collection / via Parshley // Ophthalmocoris ? / dissidens / Montandon / type 1907 [label handwritten: Montandon] // California Academy / of Sciences / Type No. 7301”.

Diagnosis. Besides its colouration and pattern (fig. 7A), this species is to be recognised by the very short eyestalks compared to other representatives of the genus; narrow, elevated and uninterrupted trifurcate carina of scutellum and band of deep punctures above the peritreme of MTSEA.

Remarks. MONTANDON (1913a) erroneously identified the species he was describing with *Ophthalmicus membranaeus* Montrouzier, 1861. This error was later recognised by BERGROTH when synonymizing *Neogermalus* with *Germalus*. Taking a closer look on the redescription of *Ophthalmocoris* (?) *dissidens* by MONTANDON (1913a) a similarity with Montrouzier’s species is evident. This similarity was ignored by both author and was possibly resulted by the deficient knowledge on taxa described by Montrouzier. BERGROTH (1916) placed *O.* (?) *dissidens* in the newly established, monotypic genus *Nesogermalus* Bergroth, 1916.

In course of the present study a heavily damaged specimen of *O. membranaeus* was found in NHMW, with label data in accordance with the original description, by the handwriting of Montrouzier as identified with the help of HORN’s (1926) work. The remnants of the specimen include the meso- and metathorax with scutellum, hemelytron and legs. Structures of MTSEA can also be studied. These parts provided eligible information to suggest the recognition of this specimen as syntype of *O. membranaeus* and to designate it as lectotype.

Based on the comparison of the structural characteristic of above-mentioned specimens the following synonymy is proposed: *Neogermalus membranaeus* (Montrouzier, 1861) = *Ophthalmocoris* (?) *dissidens* Montandon, 1913.

Neogermalus montanus (Distant, 1920) new combination.

LSID: <http://lsid.speciesfile.org/urn:lsid:Lygaeoidea.speciesfile.org:TaxonName:488793>

Type material examined: holotype, male (BMNH): circular red holotype label; circular red type label; “Mt. St. Arago, / New Caledonia. / 18. VII. 1914. / P.D. Montague. / 1918-87 // Neocypus / montanus / type Dist. [handwritten label: Distant] // BMNH(E) / 1340522 // NHMUK / 010591746”.

Diagnosis. The species is easy to recognize by its conspicuous body size and unique colouration. Structural characteristics: bilateral impression at base of clypeus; fused, slightly elevated pronotal callosities; conspicuously widened trifurcate scutellar carina; evaporative area with a spot of deep punctures situated dorsally to peritreme of MTSEA; three longitudinal furrows at posterior margin of peritreme.

Neogermalus spinolae (Montrouzier, 1865) new combination.

LSID: <http://lsid.speciesfile.org/urn:lsid:Lygaeoidea.speciesfile.org:TaxonName:488505>

Germalus scutellatus (Distant, 1920) new subjective synonymy

LSID: <http://lsid.speciesfile.org/urn:lsid:Lygaeoidea.speciesfile.org:TaxonName:488807>

Type material examined: *Germalus scutellatus*: syntype, male: circular blue syntype label; circular red label: ‘Type H. T’; ‘Rhoou, / Houadou R. / New Caledonia. / 7.X.1914. / P. D. Montague. / 1918-87 // Neocypus / scutellatus / type Dist. [label handwritten: Distant] // BMNH(E) / 1340527 // NHMUK / 010591749’; paralectotype, female (BMNH): circular blue syntype label; ‘♀’; ‘Central / New Caledonia. / 20. XI. 1914. / P. D. Montague. / 1918–87 // NHMUK 010747797”.

Diagnosis. The species is readily recognized by its marbled pattern which is unique among the representatives of the genus. Structural characteristics: peritreme MTSEA with a short stub of reduced peritremal surface; evaporative area evenly covered with coarse, deep punctures.

Remarks. The original description of the species is poorly detailed, and the type material is considered to be lost (SCHOUTEDEN 1933). However, the conspicuously marbled colouration and size of the insect meets the description of *Germalus scutellatus* (Distant, 1920). Therefore, based on the author’s recent knowledge the following new synonymy is proposed: *Neogermalus spinolae* (Montrouzier, 1865) = *Germalus scutellatus* (Distant, 1920), syn. nov.

Neogermalus variegatus new species.

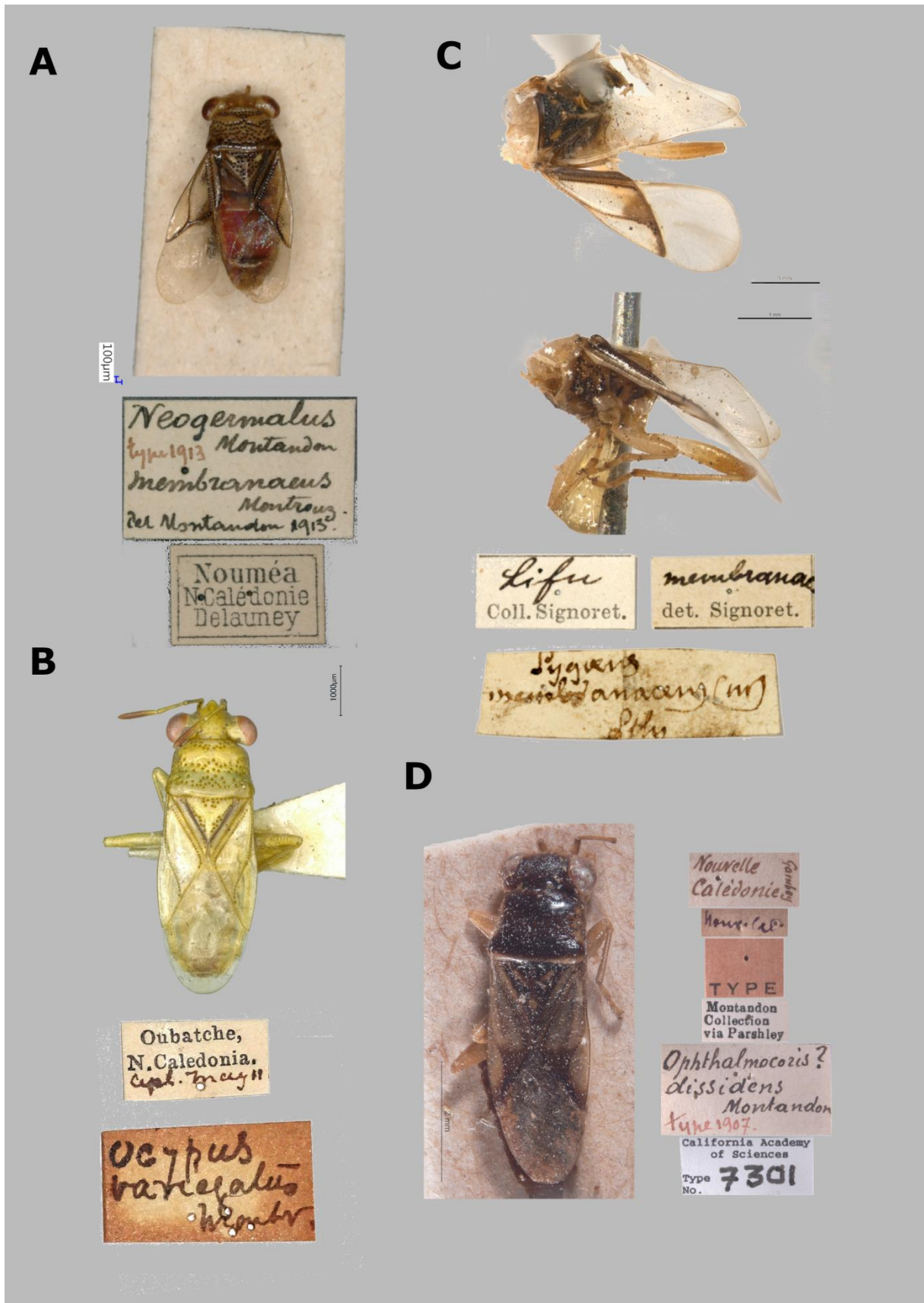
LSID: <http://lsid.speciesfile.org/urn:lsid:Lygaeoidea.speciesfile.org:TaxonName:488782>

Type material examined: lectotype (designated here), female (NHMB): “Oubatche / N. Caledonia. / [unreadable handwritten line] // *Ocypus* / *variegatus* / Montr. [label handwritten: Distant?]”.

Diagnosis. This species is readily recognised by its pale ochraceous colouration with concolorous punctation. Structural characteristics: pronotum with irregular impunctate spots posteriad of pronotal callosities; orifice of MTSEA almost triangular, evaporative area evenly covered with fine, sparse punctures.

Remarks. DISTANT (1914) erroneously identified his available material as *Ocypus variegatus* Montrouzier, 1861, and transferred the species into a newly proposed generic name (*Neocypus*) because *Ocypus* was preoccupied. This error was recognized by VAN DUZEE (1932) who pointed out that Distant described a *Germalus*-related taxon but Montrouzier’s species is a species of Miridae; the latter species is currently known as *Coridromius variegatus* (Montrouzier, 1861) (SCHUH 2013). According to Article 49 of ICZN (1999) names applied wrongly because of misidentification cannot be used as available names thus the species diagnosed and figured by Distant is not to be considered as valid taxon. The species studied by Distant is not conspecific with any described species, therefore it is recognized as an undescribed species and will be described as new.

Etymology. The author would like to name the species respectively to Distant’s intentions in honour of his work on the taxonomy of Geocorinae.



17. Figure New Caledonian Geocorinae I.: *Neogermalus montandoni* (Bergroth, 1916) (syntype, NHNM); *Neogermalus membranaeus* (Montrouzier, 1861) (syntype, NHMW); *Neogermalus variegatus* new species [unpublished] (NHMB); *Nesogermalus dissidens* (Montandon, 1907) (syntype, KNHM).

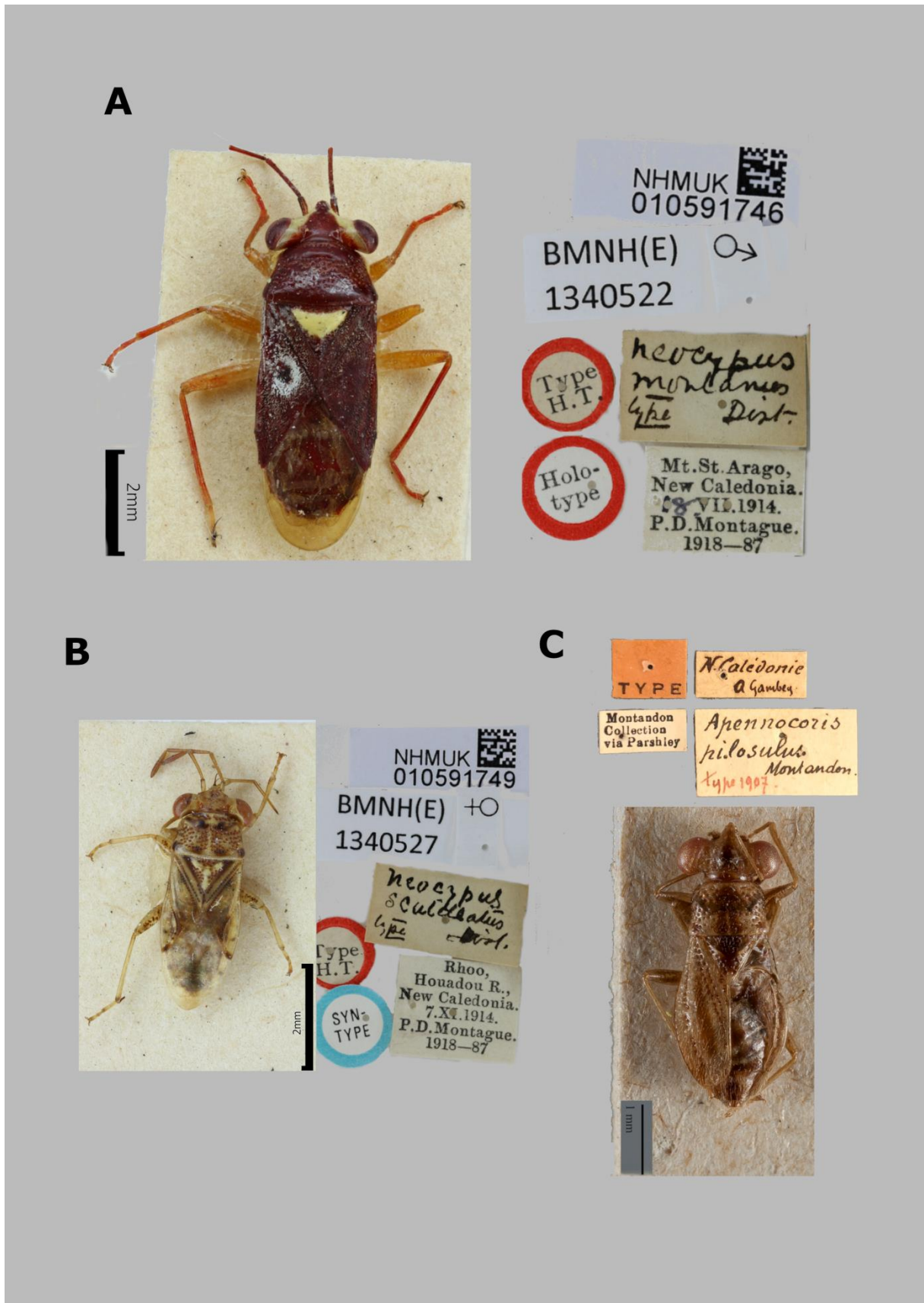


Figure 18. New Caledonian Geocorinae II.: A. *Neogermalus montanus* (Distant, 1920) (syntype, BMNH); B. *Neogermalus spinolae* (Montrouzier, 1865) (syntype, BMNH); *Apennocoris pilosulus* Montandon, 1907 (lectotype, KNHM) (photos: Scott Bundy, NMSU).

Geocorinae incertae sedis

Notes. The following four genera were recovered as separate lineages as result of the generic and species-group level phylogenetic reconstruction of Geocorinae. Based on the topology of tree (fig. 10) it is suggested to recognized these taxa as new tribes of the subfamily. However, the high ratio of homoplasy requires the development of both taxon sampling and study of characters. Taking these into account *Apennocoris*, *Nannogermalus*, *Ninyas* and *Stylogeocoris* are indicated as taxa of uncertain status until the emergence of further evidence supporting their tribal rank. Hereby, notes on taxonomy, distribution and phylogenetic significance of the four genera is provided.

Genus *Apennocoris* Montandon, 1907

Type species: *Apennocoris pilosulus* Montandon, 1907, by monotypy (Fig. 18C)

LSID: <http://lsid.speciesfile.org/urn:lsid:Lygaeoidea.speciesfile.org:TaxonName:488766>

Diagnosis. *Apennocoris* can be separated from other New Caledonian Geocorinae by the combination of the following characters: eyes moderately stylate, eye-stalks slightly erect, ocular sulcus reduced; thoracic dorsum sparsely covered by erect, dark, bristle-like setae; punctuation of corium along M+R less strongly arched than in other taxa; ostiole of MTSEA oblong, oval, evaporatorium covering ventral half of metapleurite; pygophore of male with conspicuous blackish tubercles.

Distribution. Endemic to New Caledonia.

Remarks. *Apennocoris* is the only genus among taxa allied to *Germalus* in which wing polymorphism and a flightless morph is documented. This condition is associated with habitat permanency in Lygaeoidea (SLATER 1977) and relatively common in Afrotropical, Nearctic and Palaearctic representatives of the genus *Geocoris* Fallén, 1814.

Genus *Nannogermalus* Kóbor, 2020

Type species: *Nannogermalus marmoratus* new species (Fig. 1C)

Diagnosis. Besides the minute size compared to other geocorine bugs, *Nannogermalus* can be recognized by the conspicuously declivuous head; furrows of vertex (Fig. 1C); bell-shaped, posteriorly strongly broadened pronotum with furrow-like callosities, and T-shaped carina of scutellum. Characters like pentagonal head with moderately stylate eyes and curved sutures of abdominal tergites IV/V and V/VI clearly indicate that the genus is a representative of the family Geocoridae. The proportion of claval commissure to scutellum and the punctuation of corium suggest a closer relationship to *Neogermalus*.

Distribution: Endemic to New Caledonia

Etymology: The name of the new genus indicates its relationship with the geocorine genus *Germalus* Stål, 1862; the prefix “nanno-” comes from the Greek noun “nanos”, frequently written as “nannos” (meaning “a dwarf”), referring to the fact that these insects are the smallest known representatives of Geocorinae. Gender masculine.

Genus *Ninyas* Distant, 1882

Distribution. Species of *Ninyas* are inhabiting Central and South America, including the Carribean archipelago.

Remarks. *Ninyas* was recovered as separate lineage supported by the homoplasious synapomorphy of partly reduced hamus of metathoracic wing and according to the topology is closely related to tribe Germalini. Taxonomy of the genus was discussed in detail by BRAILOVSKY (2013).

Genus *Stylogeocoris* Montandon, 1913

Distribution. Endemic to Australia.

Remarks. The genus was recovered as separate lineage supported by the extended structures of MTSEA (homoplasious). The taxon was considered as derived representative of Australian Geocorinae by SLATER (1975). Thorough revision of *Stylogeocoris* was published by MALIPAIL (1994).

5. Summary

The big-eyed bugs are moderately species-rich but morphologically rather heterogeneous and characteristic representatives of superfamily Lygaeoidea, comprising nearly 290 species of 30 genera divided into 5 subfamilies. Its largest subfamily is the nominotypical Geocorinae.

Representatives of the taxon are distributed from biomes with moderate climate to deserts and high mountains. Unlikely to most lygaeoids, representatives of Geocorinae are known as predaceous, feeding on agricultural pests e.g. thrips and aphids, making the taxon useful in terms of biological and integrated pest management.

The conspicuous general appearance of this subfamily led to errors and confusions in the systematics of the taxon: early description and diagnoses were mainly based on the study of colouration patterns and the easy-to-observe morphological characters. These errors resulted in inadequate delimitations and diagnostic characters which formed the basis of the taxonomy of Geocorinae for decades. This conclusion is even more valid in terms of the nominotypical genus, *Geocoris*. More recent extensive studies on the taxon suggested that the genus can be considered as “an ill-defined group of species belonging to perhaps several distinct genera” (MALIPATIL 1994) which is in a serious need of thorough revision.

In course of present study collection material of natural history museums and specimens originated from recent field collectings were examined with the implication of morphological study combined with analysis of molecular sequence data.

As result of the investigation

- 1) Afrotropical, Malagasy and French Polynesian representatives of *Germalus* were reviewed and revised, along with the description of five species.
- 2) A new genus, *Umbrageocoris* Kóbor, 2019 was described with its two species and two subspecies.
- 3) Applicability of the subspecies concept was revised based on the evidences acquired from a case study implying an integrated approach, synonymizing one and validating two subspecies of *Piocoris erythrocephalus*.
- 4) Preliminary evidences on coherent species-groups in genus *Geocoris* and the applicability of tribal classification were acquired with the implication of molecular sequence data analysis and cladistic analysis. Preliminary delimitation of a suspected

species group distributed in the Oriental region and description of a new species included in the group.

- 5) A preliminary review made on New Caledonian Geocorinae, along with the description of a new genus and species (*Nannogermalus marmoratus*), resurrection of *Neogermalus* Montandon, 1913 from the synonymy with *Germalus* and clarification of the status of species included, proposing the following synonymies: *Neogermalus montandoni* (Bergroth, 1916) = *Germalus minor* (Distant, 1920); *Neogermalus membranaeus* (Montrouzier, 1861) = *Ophthalmocoris* (?) *dissidens* Montandon, 1913; *Neogermalus spinolae* (Montrouzier, 1865) = *Germalus scutellatus* (Distant, 1920).

This study can provide a firm basis for further systematic studies and action regarding the taxonomy of Geocorinae.

6. References

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7. Theses

7.1. Theses

Based on the results and conclusion of present dissertation I formulate the following theses:

- 1) I performed the first morphological cladistic analysis of subfamily Geocorinae (Heteroptera: Lygaeoidea: Geocoridae). I defined and reviewed the characters included. I defined the main clades within the subfamily. (unpublished)
- 2) I revised the status of the subspecies of *Piocoris erythrocephalus*. I examined the validity of taxa on molecular taxonomic basis, the results provide methodological fundamentals for the revision of other polytypic species. (Kóbor et. al 2018)
- 3) I described a new species, *Geocoris margaretarum* and suggested the recognition of the taxa closely related to *Geocoris ochropterus* as coherent speices-group. (Kóbor, 2018)
- 4) I described a new genus, *Umbrageocoris* including two new species. One of the species consists of two subspecies. (Kóbor 2019a, b)
- 5) I revised the Afrotropical (including Madagascar and the Mascarene Islands) and French Polynesian species of genus *Germalus* based on type materials. I described five new species of the genus. (Kóbor & Kondorosy 2016, 2017; Kóbor 2020)
- 6) I revised the New Caledonian representatives of subfamily Geocorinae based on the type materials. Multiple taxonomic problems were solved in course of the works, new synonymies were proposed, and erroneously synonymised genera were resurrected (unpublished). I described a new genus and species from the region (Kóbor, in press).

7.2. Tézisek

A disszertációban ismertetett eredmények és következtetések alapján a következő tézispontokat fogalmazom meg:

- 1) Elkészítettem a Geocoridae család Geocorinae alcsaládjának első morfológiai alapú kladisztikus elemzését. Az elemzésbe bevont morfológiai bélyegeket definiáltam, átekintettem. Definiáltam a fő kládokat. (publikálatlan)
- 2) Újraértékeltem a *Piocoris erythrocephalus* alfajainak helyzetét. A taxonok érvényességét genetikai alapon is vizsgáltam, amely eredmények további politipikus fajok revíziójában módszertani alapvetésként alkalmazhatók (Kóbor és mtsai 2018).
- 3) Leírtam az orientális elterjedésű *Geocoris margaretarum* fajt és előzetesen lehatároltam került a *Geocoris ochropterus*-fajcsoportot. (Kóbor, 2018)
- 4) Leírtam az indomaláj és új-guineai elterjedésű *Umbrageocoris* genuszt és a genuszba tartozó két új fajt, valamint az egyik fajon belül két új alfajt különítettem el. (Kóbor 2019a, b)
- 5) Típusanyag alapján revideáltam a *Germalus* genusz afrotrópusi (Madagaszkárt és a Mascarenhas-szigetcsoportot is beleértve) és francia-polinéziai elterjedésű fajait. A régiókból öt új fajt írtam le. (Kóbor és Kondorosy 2016, 2017; Kóbor 2020)
- 6) Típusanyag alapján revideáltam a Geocorinae alcsalád Új-Kaledónián előforduló csoportjait. A munka során számos taxonómiai probléma került megoldásra, új szinonimákat javasoltam, tévesen szinonimizált genuszok státusát értékeltem újra (publikálatlan). A régióból leírtam egy új genuszt és fajt. (Kóbor, in press)

Appendices

Appendix 1. – Definition of characters and states used in cladistic analysis

- 0) Head and eyes arrangement: (0) head triangular in dorsal view, eyes never stylate; (1) head pentagonal, eyes at least slightly stylate.
- 1) Sutures of abdominal tergites 4/5 and 5/6: (0) straight; (1) curved.
- 2) Abdominal spiracles II–IV: (0) ventral; (1) dorsal.
- 3) Eye diameter to length of antennal segment I: (0) at most slightly larger; (1) 2–4 times larger.
- 4) Abdominal spiracles: (0) V–VII ventral; (1) V–VII dorsal.
- 5) Ocular sulcus: (0) complete, surpassing line of ocelli; (1) reduced, at most reaching line of ocelli.
- 6) Transversal furrow anterior to ocelli: (0) present; (1) absent.
- 7) Median longitudinal furrow of vertex: (0) absent; (1) present.
- 8) Clypeus: (0) sutures visible; (1) sutures fused with vertex basally; (2) sutures reduced, visible only apically, near jugae.
- 9) Bucculae: (0) jugal suture visible; (1) jugal suture fused.
- 10) Antenniferous tubercles: (0) complete, visible in dorsal view; (1) reduced, not visible in dorsal view.
- 11) Labial trough: (0) open, U-shaped; (1) partly closed, V- or Y-shaped; (2) closed, rounded.
- 12) Pronotum: (0) trapezoidal; (1) broadened; (2) rectangular.
- 13) Pronotal callosities: (0) with furrow; (1) developed, bulging; (2) reduced, flat.
- 14) Scutellum arrangement: (0) subequilateral; (1) elongate
- 15) Scutellar trifurcate carina: (0) complete; (1) basally or apically partly reduced; (2) completely reduced.
- 16) Apex of scutellum: (0) sharply pointed; (1) oblique, rounded.
- 17) Clavus: (0) margins parallel, claval commissure developed; (1) margins converging apically, claval commissure reduced.
- 18) Modification of hemelytron: (0) macropterous or submacropterous forms only; (1) hemelytron shortening observed.
- 19) Hamus of hind wing: (0) complete; (1) partly reduced; (2) completely reduced.
- 20) Extent of MTSEA: (0) reaching or exceeding midline of metapleurite; (1) not reaching midline of metapleurite.

- 21) Peritremal surface: (0) present, elongate; (1) absent, inconspicuous.
- 22) Shape of ostiole: (0) round; (1) oval; (2) drop-shaped
- 23) Vestibular scar: (0) open, reaching dorsum; (1) closed, not reaching dorsum.
- 24) Extent of evaporatorium: (0) covering most of metapleurite, sometimes reaching mesocoxae; (1) reduced to the surroundings of peritreme, not exceeding space between meso- and metacoxae.
- 25) Lateral furrow of metapleurite: (0) absent; (1) present.
- 26) Female ovipositor length: (0) not exceeding the genital capsule; (1) splitting multiple connexiva.
- 27) Female spermatheca: (0) coiled; (1) uncoiled, with bends at most.
- 28) Male paramere: (0) stout, blade short uncurved; (1) slender, blade long, curved.
- 29) Setae at blade of male paramere: (0) present; (1) absent.
- 30) Male gonoporal process: (0) with up to 6 coils; (1) with more than 6 coils.

Appendix 2. – Character matrix of cladistic analysis

Character matrix editor for matrix "morphology"

Type of matrix: Standard Categorical Data (uncompacted)

Number of characters: 31

Number of taxa: 30

Number of characters excluded: 0

Proportion of missing data: 0.00107527

Proportion of inapplicable codings: 0.0

	Head and eye arrangement	Sutures of abdominal tergites IV/V and V/VI				Abdominal spiracles		Abdominal			
	spiracles II-IV	Eye diameter to antennal segment I.					Ocular sulcus				
	Transversal furrow anterior to ocelli	Median longitudinal furrow on vertex				Clypeus					
	Bucculae	Antenniferous tubercles	Labial trough	Pronotum	Pronotal callosities						
	Scutellum	Scutellar trifurcate carina	Apex of scutellum	Clavus	Modification of						
hemelytron	Hamus of hind wing	Extent of MTSEA	Peritremal surface	Shape of							
ostiole	Vestibular scar	Extent of evaporatorium	Lateral furrow of metapleurite	Female ovipositor							
length	Female spermatheca	Paramere	Setae at blade of male paramere	Male gonoporal process							
Apennocoris pilosulus	1	1	1	1	1	0	1	0	1	n	
	0	n	2	1	0	0	n	1	n	1	
	2	0	1	0	0	n	n	n	n		
Austrogeocoris westraliensis		1	1	1	1	1	0	1	0	0	
	0	0	1	0	1	0	0	0	0	0	
	0	0	0	0	0	0	1	0	0	0	
Capitostylus kurandae	1	1	1	1	1	0	1	0	1	0	
	1	1	0	1	0	0	0	0	0	0	
	0	0	0	0	0	1	0	0	0		
Geocoris grylloides	1	1	1	1	1	1	1	1	1	2	0
	0	2	2	1	1	1	0	1	1	1	1
	2	1	1	1	1	1	1	1	1		
Piocoris erythrocephalus	1	1	1	1	1	1	1	1	1	2	1
	1	2	1	2	1	1	1	0	2	1	1
	2	1	1	1	1	1	1	1	1		
Eilatus chloroticus		1	1	1	1	1	1	0	0	2	1
	1	2	1	2	1	0	0	1	0	1	1
	2	1	1	1	1	1	1	1	1		
Geocoris ater	1	1	1	1	1	1	0	0	1	0	0
	2	0	1	1	1	0	1	1	2	1	1
	1	1	1	1	1	1	1	1			2
Geocoris collaris	1	1	1	1	1	1	0	0	1	0	0
	2	0	1	1	1	0	1	0	2	1	1
	1	1	1	1	1	1	1	1			2
Geocoris ochropterus	1	1	1	1	1	1	1	1	1	2	1
	1	2	1	2	1	1	0	1	0	2	1
	2	1	1	1	1	1	1	1	1		

Geocoris bullatus	1	1	1	1	1	0	1	1	0	1
2	0	1	1	1	0	1	0	1	1	2
1	1	1	1	1	1	1	1			
Geocoris punctipes	1	1	1	1	1	1	0	1	2	0
1	2	0	1	1	1	0	1	0	2	1
2	1	1	1	1	1	1	1	1		
Geocoris flavilineus	1	1	1	1	1	1	0	1	2	0
1	2	0	1	1	1	0	1	1	2	1
2	1	1	1	1	1	1	1	1		
Geocorides polytretus	1	1	1	1	1	1	1	0	2	0
1	2	2	1	1	1	0	1	1	n	1
2	1	1	1	1	1	1	1	1		
Geocoris marduk	1	1	1	1	0	0	0	2	0	1
2	0	2	1	1	0	1	0	1	1	2
1	1	1	1	1	1	1	1			
Geocoris unicolor	1	1	1	1	1	1	1	0	2	0
1	2	0	1	1	0	0	1	0	1	1
2	1	1	1	1	1	1	1	1		
Germalus kinbergi	1	1	1	1	1	0	1	0	?	0
0	0	0	1	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0		
Hypogeocoris violaceus	1	1	1	1	1	1	1	0	2	0
1	2	0	1	1	1	0	1	1	1	1
2	1	1	1	1	1	1	1	1		
Isthmocoris piceus	1	1	1	1	1	1	1	1	2	1
1	2	0	1	1	1	0	1	1	1	1
2	1	1	1	1	1	1	1	1		
Mallocooris discifer	1	1	1	1	1	1	1	0	2	0
1	2	0	1	1	1	0	1	0	2	1
2	1	1	1	1	1	1	1	1		
Nesogermalus dissidens	1	1	1	1	1	0	1	0	0	0
0	1	0	1	0	0	0	0	0	0	0
0	0	0	0	1	0	0	0	0		
Ninyas deficiens	1	1	1	1	0	1	0	1	0	1
1	0	1	0	0	0	0	0	1	1	1
0	0	0	0	1	0	0	0			
Pseudogeocoris fallaciosus	1	1	1	1	1	1	1	1	0	1
0	1	2	2	1	1	1	0	1	1	2
1	2	1	1	1	1	1	1	1	1	
Stenogeocoris horvathi	1	1	1	1	1	1	1	0	1	0
1	2	2	1	1	1	0	1	1	n	1
2	1	1	1	1	1	1	1	1		
Stenophthalmicus fajoumensis	1	1	1	1	1	1	1	1	0	1
0	0	1&2	2	1	1	1	0	0&1	0	2
1	2	1	1	1	1	1	0&1	1	1	

Stylogeocoris biroi	1	1	1	1	1	0	0	0	1	0
1	1	0	1	1	0	0	0	0	0	1
1	0	0	0	1	1	0	0	0		
Umbrageocoris kondorosyi		1	1	1	1	1	0	1	1	2
1	1	1	0	1	1	0	1	0	2	1
1	2	1	1	1	1	1	1	1		
Unicageocoris griseus	1	1	1	1	1	0	1	0	0	0
1	1	0	0	0	0	0	0	0	0	0
0	0	0	0	0	1	0	0	0		
Henestaris halophilus	1	1	1	0	0	0	n	n	n	n
n	0	0	0	0	0	0	0	1	n	1
0	n	n	n	0	n	n	n	n		
Engistus boops	1	1	1	0	0	0	n	n	n	n
0	0	0	0	0	0	0	0	1	n	1
n	n	n	0	n	n	n	n			
Heterogaster urticae	0	0	0	0	n	n	n	n	n	n
n	n	n	n	n	n	n	n	n	0	n
n	n	n	n	n	n	n	n	n		