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Taxonomy of Oriental Enicocephalidae (Heteroptera: Enicocephalomorpha) and morphological novelties of new taxa

Ph.D. Thesis

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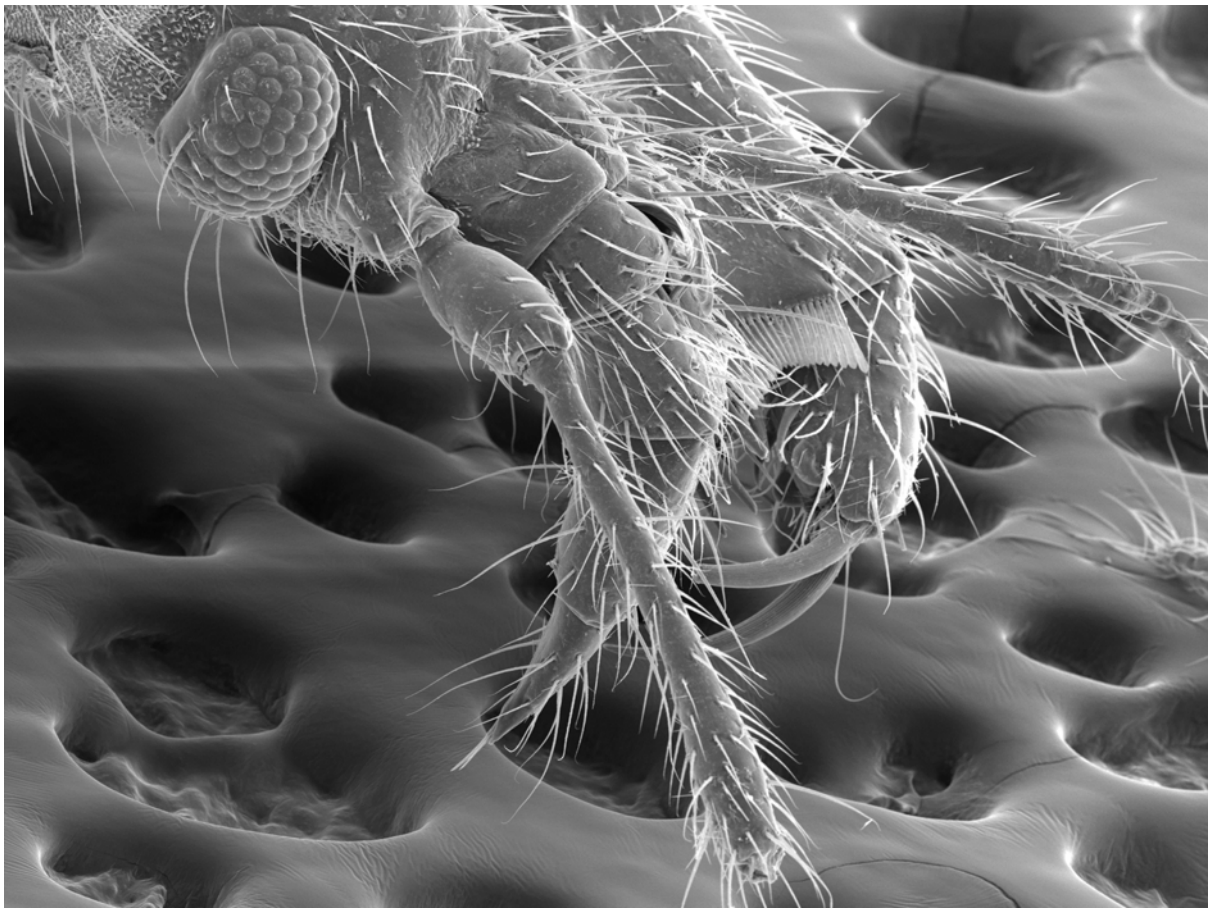

Declaration: I hereby declare that I have written this thesis independently, using the mentioned references; or in cooperation with other paper co-authors. I have not submitted this thesis, or any of its parts, to acquire any other academic degree.

In Prague, September 2013 Petr Baňař

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Abstract

The infraorder Enicocephalomorpha represents the basalmost group of Heteroptera, the sister group of all remaining Heteroptera (= Euheteroptera) (ŠTYS 1989). The infraorder, whose unique phylogenetic position was recognized by most modern authors (ŠTYS & KERZHNER 1975), is currently divided into two families, Aenictopecheidae and Enicocephalidae.

Some new taxa are described (Results: **Parts A–H**) and special attention is paid to newly discovered or overlooked morphological characters of the group, some of them important for all the Heteroptera.

In **Part A** is described first member of worldwide distributed genus *Systelloderes* from the Oriental region, *S. loebli* Štys & Baňař, 2007 and the term **neopatella** is established for for sclerites within the femoro-tibial intersegmental membrane. *Xenicocephalus josifovi* Štys & Baňař, 2008 is described in **Part B**, representing first known complete adult of this peculiar genus. **Unique type of raptorial foreleg** among all Enicocephalomorpha is described and illustrated and its function by predation is assumed. In **Part C** is described new genus *Phaenicocleus* Štys & Baňař, 2009 from northern Borneo, based on males of three species. **New diagnostic characters** in Enicocephalomorpha are used. *Phaenicocleus granulosus* Baňař & Štys, 2011 is described in **Part D**, based on the first known female of the genus and **autapomorphies** of the are stressed and discussed. A new **key to genera** of Enicocephalidae with forewing basal cell absent and closed discal cell present is provided. In **Part E** is *Oncylocotis inexpectatus* Štys, Baňař & Drescher 2010 is described and his association with very aggressive invasive yellow crazy ant, *Anoplolepis gracilipes* (Smith, 1857) is studied and described. **Myrmecophily** of Enicocephalomorpha is reviewed, list of species found in inquilines of *A. gracilipes* in Sabah is included. Some plesiomorphic anatomical features of the *O. inexpectatus* are discussed and illustrated. Taxonomy and nomenclature of *Enicocephalus flavicollis* Westwood, 1837 is solved in **Part F**, status of type series of this crucial species is published and **lectotype** and **paralectotype** are signed and described. In **Part G** new genus of Aenictopecheidae is described, **lack of cephalic neck** is described and discussed, new term **epimeroid** is established for so called 'epimeral lobe'. Part H is unpublished revision of the genus *Megenicocephalus* Usinger, 1945, **unique type of foreleg**, as well as some apomorphies of the genus are described and group is newly upgraded to family status.

Contents

1. Introduction

1.1. Characteristics of the infraorder Enicocephalomorpha

1.1.1. Short morphological characteristics

Enicocephalomorphans range in length between 2 and 16 millimetres and are somewhat reduviid-like in appearance.

Head elongate, in most genera subdivided into anterior (preocular) and posterior (postocular) lobes by conspicuous, sometimes very deep, postocular constriction. Anterior lobe in some genera very long, cylindrical. Eyes usually medium sized, in macropterous forms sometimes very large, in extreme cases holoptic (Madagascan and Seychellan *Cocles* Bergroth, 1905 species); in flightless taxa sometimes extremely reduced (single ommatidium in New Zealandian and Tasmanian apterous *Nymphocoris* Woodward, 1956 species; 0–5 ommatidia in apterous females of Caribbean *Alienates* Barber, 1953 species).

Ocelli, if present, are situated on posterior lobe, often sitting on more or less visible ocellar tubercles. Posterior lobe of head in some cases (*Ulugurocoris grebennikovi* Štys & Baňař, 2013; some undescribed Aenictopecheinae) without differentiated neck, typical for all heteropterans. Absence of the neck may represent a symplesiomorphy shared with non-heteropteran Hemiptera (ŠTYS & BAŇAŘ 2013).

Labium four segmented, always shorter than head, usually robust (extremely robust in all Aenictopecheidae: Aenictopecheinae and some Enicocephalidae – *Henschiella* Horváth, 1888 species).

Antennae four segmented, flagelliform to terete.

Forewings always completely membranous (tegminal), sometimes reduced, females of many genera often micropterous or brachypterous, pterygopolymorphism very common. Forewing base in macropterous and brachypterous forms with anchor (e.g. ŠTYS & BAŇAŘ 2008b, ŠTYS *et al.* 2010) – crossvein-like structure connecting the costal complex of veins with basal sectors of R and M+Cu stem, anchor missing in some micropterous forms with remnants of venation (e.g. ŠTYS & BAŇAŘ 2013). Wings of macropterous and submacropterous females of some genera (*Stenopirates* Walker, 1873, *Nesenicocephalus* Usinger, 1939) often caducuous, with short remnants of costal vein after forewing loss.

Fore legs usually raptorial with apicitibial and fore tarsal armature formed from various number of spiniform setae, with two exceptions: 1) *Nymphocoris* species with fossorial forelegs with many spiniform seate on femora and tibiae of all pairs of legs and 2) *Megenicocephalus* Usinger, 1945 species with cursorial forelegs, without specialized apicitibial and fore tarsal armature (ŠTYS 1989; ŠTYS & BAŇAŘ in prep.). Raptorial fore tibia is disto-ventrally produced, bristle comb always present on anterior face of fore tibial apex. In males of Phallopiratinae fore tibia compressed in two different planes (ŠTYS, 1985).

ŠTYS & BAŇAŘ (2008a) described a new type of raptorial fore leg in *Xenicocephalus josifovi* Štys & Baňař, 2008 from Suriname, unique within all Enicocephalomorpha (see Results: **Part B**).

Pronotum formed from three lobes, posterior lobe often shortened, in Aenictopecheidae: Aenictopecheinae strongly reduced, but always present. Most Enicocephalidae with distinct three lobes, collum in *Megenicocephalus* very short, narrowly ring-like (ŠTYS & BAŇAŘ in prep.), overlooked in the past in *Megenicocephalus chinai* Usinger, 1945; apterous females of *Alienates* with two (collum and middle lobe) lobes only.

Phallus in Aenictopecheidae typically heteropteran, inflatable or not, with mobile parameres, male terminalia in primitive Enicocephalidae very complicated, unlike that of other Heteroptera (Phallopiratinae, Phthirocorinae), in Enicocephalinae greatly reduced and simplified, usually formed by racquet-shaped guide, paired parameral sclerotizations and simple, plate shaped-supradistal lobe.

Ovipositor in Aenictopecheidae: Nymphocorinae and Aenictopecheinae fully developed (reduced only in *Aenictopechys* Breddin, 1905), in Aenictopecheidae: Maoristolinae almost completely reduced, females of Murphyanellinae unknown; in Enicocephalidae external female genitalia absent or retained as remnants in some taxa (Systelloderini, *Megenicocephalus*) or females unknown (Phallopiratinae).

1.1.2. Biology of Enicocephalomorpha

The biology of enicocephalomorphans is insufficiently known. Most species are found in leaf litter of tropical forests, or in loose soil, mosses, and also in rotting wood. The author repeatedly sifted many specimens in such man-made places as dry furrows, dry water courses along roads and similar excavated field depressions with remnants of various plant material. He also collected apterous females of an undescribed species of *Nesenicocephalus* under the

bark of a dead tree close to colony of thrips and collected some specimens by beating living and dead branches of trees, covered with mosses, lichens and primitive fungi. In arid areas they most probably live in soil crevices with remnants of humidity.

The most effective collecting method is sifting leaf litter and the upper level of the soil in tropical and temperate forests of the Southern Hemisphere with subsequent extraction of sifted material using a Winkler apparatus. Use of Berlese funnels is also possible and could be effective, but many macropterous specimens are attracted to the light used in the funnel and often die because of the hot microclimate under the lamp.

All enicocephalomorphans are generalized predators (probably with some specialization in *Xenicocephalus*, see also **Part B**). The best review of biology of the group was published by WYGODZINSKY & SCHMIDT (1991). The author has kept a group of living adults of Enicocephalidae three times in tropical countries, and tried to offer various potential prey (e.g. collembolans, larvae of holometabolan insects, adults of various insect groups, small earthworms) found together with the enicocephalomorphans in the litter sample. The results are still not summarized nor published, but these experiments clearly show that enicocephalomorphans prefer weakly sclerotized prey, often the same body size as themselves, but in three cases the author recorded a small group (5 to 8) adults of undescribed *Oncylocotis* Stål, 1856 species and *Euchelichir geniculatus* Jeannel, 1942, feeding on an approximately 5 cm long earthworm.

Mating and the developmental cycle is almost unknown in enicocephalomorphans, WYGODZINSKY & SCHMIDT (1991) described oviposition and hatching in captivity in *Hymenocoris formicinus* Uhler, 1892 and HICKMAN & HICKMAN (1981) published some biological aspects of *Oncylocotis tasmanicus* (Westwood, 1837) with description of the immature stages of this species.

Myrmecophily has been described in several cases and this special behavior was summarized by several authors (JEANNEL 1942; USINGER 1932, 1945; WYGODZINSKY & SCHMIDT 1991; ŠTYS *et al.* 2010). ŠTYS *et al.* (2010) described *Oncylocotis inexpectatus* from Borneo, from colonies of the invasive "yellow crazy ant", *Anoplolepis gracilipes* (Smith, 1857), a species ranked among the 100 most devastating invaders worldwide.

1.1.3. Ethology of Enicocephalomorpha

Ethology of enicocephalomorphans is very poorly known. Typical for the infraorder and absolutely unique among Heteroptera is swarming. ŠTYS (1981) summarized known cases of swarming, WYGODZINSKY & SCHMIDT (1991) added cases of swarming of some New World taxa. The swarms are mixed or unisexual, consisting from several to many thousands of specimens (unpublished huge swarm of *Stenopirates* species from Taiwan). The author personally collected a swarm of an undescribed *Systelloderes* species in the mountains of Ecuador, composed of 11 males, a small swarm of an undescribed *Oncylocotis* species in Malaysia containing 20 males, and a larger swarm of *Euchelichir hymaeneus* (Bergroth, 1905) containing 156 males and a single female in central Madagascar.

Recent intensive studies of the author using SEM photography show numerous unusual sensilla, gland openings, cuticular processes and denticulations, some of them possibly acting as plectrum and minute mechanoreceptors illustrating a very rich spectrum of communication and/or defensive behaviours.

1.2. Taxonomy of Enicocephalomorpha

The Infraorder Enicocephalomorpha is the basalmost group of Heteroptera, sister to all remaining Heteroptera (=Euheteroptera) (ŠTYS 1989). The infraorder, whose unique phylogenetic position was recognized by most modern authors (ŠTYS & KERZHNER 1975) is currently divided into two families, Aenictopecheidae (with four subfamilies) and Enicocephalidae (five subfamilies).

WESTWOOD (1837) described the first four species of enicocephalomorphans (all as *Enicocephalus* in family Reduviidae, with the type species *Enicocephalus flavicollis* Westwood, 1937), STÅL (1860) established the new family Enicocephalidae for existing species. Major classical students of the group were BERGROTH (e.g. 1903, 1905a, b, 1906, 1915), BREDDIN (e.g. 1899, 1905, 1912), DISTANT (e.g. 1902, 1903, 1911), ENDERLEIN (1904) and STÅL (1856, 1860, 1866). JEANNEL (1942) monographed the group, USINGER (1945) provided the first higher classification. VILLIERS (1958) monographed the fauna of Madagascar, and later (VILLIERS 1969) the fauna of the Afrotropical and Madagascan Regions. USINGER & WYGODZINSKY (1960) revised the fauna of Micronesia; MIYAMOTO (1965) revised the fauna of Taiwan. KRITSKY (1977, 1978, 1979) established and revised

some New World genera; WYGODZINSKY & SCHMIDT (1991) revised the fauna of the New World.

ŠTYS (1969) revised the extinct Enicoceophalomorpha and subsequently established many new higher taxa (e.g. ŠTYS 1981 – Monteithostolinae; ŠTYS 1985 – Phallopiratinae). The same author later established the modern classification of Enicocephalomorpha (ŠTYS 1989, 1995), and published a key to genera with some taxonomic changes (ŠTYS 2002).

Recently, ŠTYS & BAŇAŘ (2006, 2009, 2013) established some new genera and prepared a revision of the genus *Megenicocephalus* (ŠTYS & BAŇAŘ in prep.) with an elevation of this genus to separate family status (see also **Part H**).

1.3. Family Enicocephalidae in Oriental Region

Enicocephalomorphans are distributed worldwide, but are most diverse in the tropics and temperate zones of the Southern Hemisphere. The zoogeography of the Enicocephalomorpha was summarized by ŠTYS (2008). The Oriental Region, mainly its insular part, comprising the Great Sundas and Philippines, Indochina and Malay Peninsula, is generally declared as one of the richest biodiversity hot spots of the World. The number of genera and higher taxa of enicocephalomorphans, very often endemic to this region, support this view.

For purposes of this work the term 'Oriental' Region includes the following areas: 1) southernmost East Palaearctic to South-east Asia (from Tibet, Nepal, south China, Taiwan and Japan), species living here are undoubtedly derived from the fauna of South-east Asia; 2) Indian region; 3) South-east Asia (= SE Asia) to Wallacea, including Philippines; 4) Papuan region (Moluccas, New Guinea and Melanesia) and 5) Pacific regions (Polynesia, Micronesia, Hawai).

The fauna of the Enicocephalidae of this region is very rich, in contrast with a relatively untold number of Aenictopecheidae, with high generic endemism, mainly in SE Asia. The Aenictopecheidae is represented by three monotypic genera: *Aenictopechys necopinatus* Breddin, 1905 from Great Sundas; *Murphyanella aliquantula* Wygodzinsky & Štys, 1982 and *Timahocoris paululus* Wygodzinsky & Štys, 1982, both from Singapore and in the Far East also *Boreostolus sikhotalinensis* Wygodzinsky & Štys, 1970, which is the northernmost living enicocephalomorphan. Recently, a third species (and second from the Old World) of *Boreostolus* was collected in southern Tibet (RÉDEI, ŠTYS & BAŇAŘ in prep.).

The most diverse (100 described species totally) genus of Enicocephalidae is *Oncylocotis* Stål, 1860, occurring in the Old World except New Zealand, with 28 described and many hundreds of undescribed species. Other genera occurring in this region are Old World (except of Oceania): *Henschiella* (12 described species) with the Taiwanese *H. saigusai* Miyamoto, 1965 and *H. capillicornis* (Bergroth, 1918), second species of doubtful position (ŠTYS 1968); *Hoplitocoris* Jeannel, 1942 (5 species from 32), genus of 'Oriental' and African distribution; *Nesenicocephalus* Usinger, 1939 with three described and many undescribed species, so far known from Oceania and Philippines, recently discovered throughout SE Asia (Malaysia, Taiwan, Great Sundas), Papua and Australia; *Stenopirates* Walker, 1873 with eight described species from SE Asia, East Palaearctic fringes, Japan, Taiwan and dozens of undescribed species; subfamily Phallopiratinae Štys, 1985, endemic to SE Asia with *Phallopirates* Štys, 1985, with four species and several undescribed genera and species from SE Asia, subfamily Megenicocephalinae Štys, 1989, endemic to SE Asia with so far monotypic *Megenicocephalus* Usinger, 1945, eight new species will be described and the group elevated to family status (see **Part H**); the monotypic *Phthirocorisella* Štys, 1986 from New Guinea; *Monteithostolus* Štys, 1981 (two species); the monotypic *Ciucephalus* Štys, 1982, both genera endemic to New Caledonia; *Phaenicocleus* Štys & Baňař, 2009 recently with four species described from northern Borneo, Sabah province (ŠTYS & BAŇAŘ 2009, ŠTYS & BAŇAŘ & ŠTYS 2011. ŠTYS & BAŇAŘ (2007) described *Systelloderes loebli*, from New Caledonia, the first species of this Cosmopolitan genus described outside of the New World and Afrotropical, Madagascan, and New Zealand Regions (additional species will be described).

1.4. Aims of the thesis

Objectives of the thesis were to 1) describe new important taxa of Enicocephalidae from the Oriental region; 2) study their external morphology and clarify some inconsistently used terms; 3) describe and comment newly discovered morphological characters.

2. Results

General comments. Results are presented as seven separately published papers (**Parts A–G**) and one unpublished manuscript, prepared for submission (**Part H**). Some published papers not dealing with the Oriental fauna are also included to **Results** of this Thesis, because contain general information important for infraorder Enicocephalomorpha or whole Heteroptera.

In **Part A,** *Systelloderes loebli* Štys & Baňař, 2007 is described, the first species of this Cosmopolitan genus described outside New World and Afrotropical, Madagascan, and New Zealand regions. We described and illustrated erect ventral scales on the ventral face of the forecoxa, a character unique among the Enicocephalomorpha, and established the term **neopatella** for sclerites within the femoro-tibial intersegmental membrane at the site of the lost patellar limb segment. We also interpreted a rasp-like structure on the fore coxa as a **stridulitrum** rubbing against the edges of the prosternum, which acts as a **plectrum**.

In **Part B**, *Xenicocephalus josifovi* Štys & Baňař, 2008, is described based on a single male from Suriname. This genus has been known from a single incomplete female (with head, pronotum and fore legs missing) and fifth instar larva of *Xenicocephalus giganticus* Wygodzinsky & Schmidt, 1991. A **new type of raptorial foreleg**, unique in the entire infraorder is described, adaptedfor holding rounded, potentially strongly sclerotized prey. We assume that *Xenicocephalus* is trophically specialized and catches the prey by a unique method. The method of capture and type of the foreleg and potential prey could be an analogy of the feeding strategies of some specialized groups of assassin bug (Reduviidae: Ectrichodiinae) hunting millipedes.

Part C describes three species of a new genus *Phaenicocleus* Štys & Baňař, 2009, which is endemic to northern Borneo (Sabah): *P. sabahensis* Štys & Baňař, 2009, *P. schwendingeri* Štys & Baňař, 2009 and *P. minor* Štys & Baňař, 2009. **New diagnostic characters** in Enicocephalomorpha are used – median of the pronotum, shape of unpaired sclerite of the pro-eusternum, and shape and length of a median keel on the meta-eusternum.

Phaenicocleus granulosus Baňař & Štys, 2011 is described in **Part D**, based on the first known female of the genus. **Autapomorphies** of the genus – particularly reduced apicitibial and fore tarsal armature, interrupted claval vein AA3+4, striking occurrence of large setigerous tubercles (shared with Australian *Usingeriella* Wygodzinsky, 1950) are

stressed and discussed. A new **key to genera** of Enicocephalidae with the basal cell of the forewing absent and closed discal cell present is provided.

In **Part E** *Oncylocotis inexpectatus* Štys, Baňař & Drescher 2010 is described. This species was found in Borneo (Sabah) in association with very aggressive invasive 'yellow crazy ant', *Anoplolepis gracilipes* (Smith, 1857). This ant species is ranked among the 100 most devastating invaders worldwide. In total, twenty adults of *O. inexpectatus* were found in two *A. gracilipes* supercolonies (ca. 100,000 ants sampled). Specimens of *O. inexpectatus* were never attacked by ants, and were able to live in a laboratory colony for at least two months. **Myrmecophily** of Enicocephalomorpha is reviewed, list of species found in inquilines of *A. gracilipes* in Sabah is included. Some plesiomorphic anatomical features of the *O. inexpectatus* are discussed and illustrated, e.g. the clypeus subdivided into a well delimited **anteclypeus** and **postclypeus**, presence of **prescapite**, unmodified male abdominal segment 8.

ŠTYS & BAŇAŘ (2012) resolved the taxonomy and nomenclature of *Enicocephalus flavicollis* Westwood, 1837 in **Part F**. The status and location of the type series of this important species (type species of the *Enicocephalus* Westwood, 1837, the type genus of Enicocephalidae) from St. Vincent Island (Lesser Antilles) is discussed, and instead of two formerly assumed different 'holotypes', used by several authors, a **lectotype** and **paralectotype** are designated. The species is redescribed, the fifth instar larva is described for the first time. A list of modern *Enicocephalus* species is also given in the paper, the correct spelling of *Enicocephalus dominica* Bruner, 1924 is published and **pterygopolymorphism** in *Enicocephalus* is discussed.

Part G describes a new genus and species of Aenictopecheidae, *Ulugurocoris grebennikovi* Štys & Baňař, 2013, the first member of the family in continental Africa, based on micropterous females. Some general aspects of *Ulugurocoris* morphology are discussed in a broader context: presence of **cephalic trichobothria**, suggested to be a groundplan character of Heteroptera; presence of '**gular sulci**', suggested to have an ecdysial function; **lack of cephalic neck**, symplesiomorphy with other non-heteropterous Hemiptera; association of posterior lobe of pronotum with the **epimeroid** (a new term for so called 'proepimeral lobe'); presence of **notopleural sulcus** on propleuron. Short morphological characteristics of the obviously monophyletic subfamily Aenictopecheinae as well as its distributional data are given.

Part H is an unpublished manuscript of the revision of the genus *Megenicocephalus* Usinger, 1945 that was included by ŠTYS (1989, 1995) in a new subfamily of Enicocephalidae. The only known species, *Megenicocephalus chinai* Usinger, 1945, is redescribed and an additional seven species are described as new. All species are described in detail and illustrated. The unique type of foreleg, as well as many apomorphies of the group are described. The group is newly elevated to family status for many reasons, e.g.: 1) cursorial foreleg (unique in Enicocephalomorpha); 2) minute, ring-like collum of pronotum (unique situation in Enicocephalomorpha); 3) apicitibial and tarsal armature on fore leg missing (character shared with *Nymphocoris*, which has fossorial legs); 4) forewing with weak, but conspicuous costal fracture (shared with Aenictopecheidae); 5) fore trochanter of female with specialized armature (unique in Enicocephalomorpha, similar situation in Neotropical *Xenicocephalus* only known) and 6) unique male and female genitalia (see Results: **Part H**)

3. Future perspectives

The fauna of the Enicocephalomorpha of the Oriental Region is one of the richest in the World. The author, in cooperation with Pavel Štys, sorted out many thousands of undetermined specimens of Enicocephalomorpha from important institutional collections during the last decade. We assume that the total number of described species of this infraorder (slightly more than 300) represents at most 5% of the species available for study. For example, the author has more than 300 undescribed species of the genus *Oncylocotis* in his collection (own and borrowed material) only from the South-east Asia. The enicocephalomorphans of the Oriental Region, together with those of Madagascar and the tropical New World represent a reservoir of work for many taxonomists for several decades.

Richness and availability of unstudied enicocephalomorphans collected in the last three decades is caused by several factors, namely by more frequently used quantitative methods of collecting (sifting of leaf litter in tropics, followed by extraction in Berlese funnels and Winkler apparatus, collecting in Malaise traps and flight interception traps) and the community-wide sharing of residual collections of people studying other taxa, like semi-edaphic and litter inhabiting spiders, mites, beetles, hymenopterans, springtails etc.

It is possible to assume, that the two basalmost heteropteran infraorders Enicocephalomorpha and Dipsocoromorpha, so far more or less overlooked by most heteropterists, belong to the most specious groups of true bugs.

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