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New species and reclassification of the fossil assassin bug *Koenigsbergia* (Hemiptera: Reduviidae: Phimophorinae)

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Abstract

The assassin bug genus *Koenigsbergia* Popov, 2003 is currently monotypic and represented by a female holotype from Baltic Amber (~33.9–55.8 MYA). The genus was originally described within Phymatinae (Phymatine Complex or phymatine clade). However, our literature review reveals that the amber fossil likely belongs to the subfamily Phimophorinae, which is distantly related to the phymatine clade. The recent acquisition of one male and one nymph of *Koenigsbergia* provides the opportunity to reevaluate the systematic placement of this genus. We here examine the new fossils, concluding that the adult male represents an undescribed species, and describe it as *Koenigsbergia explicativa*, **new species.** Our morphological comparison between Phimophorinae, Phymatinae, and *Koenigsbergia* (macro imagining, scanning electron microscopy) shows that the fossil genus shares notable similarities with *Phimophorus* Bergroth, 1886 and *Mendanocoris* Miller, 1956. We therefore formally transfer the fossil genus to Phimophorinae.

Key words

Baltic amber, Eocene, Heteroptera, taxonomy, true bugs

1. Introduction

Koenigsbergia Popov, 2003 is a monotypic assassin bug genus described from the female holotype recovered from Baltic Amber (Eocene, ~33.9–55.8 MYA; Perkovsky et al. 2007). *Koenigsbergia* shares some features with genera in the ambush bug subfamily Phymatinae that led to its original placement within this subfamily. These features include the strongly developed bucculae that en-

close the base of the labium, pronotum with distinct carinae, large membrane of the hemelytron, short antennae and legs, and two-segmented tarsi (Popov 2003). More specifically, this author placed *Koenigsbergia* within the monotypic tribe Themonocorini. Phymatini, Carcinocorini, and Macrocephalini ambush bugs feature synapomorphic subchelate or chelate forelegs, while Themonocorini

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369

have retained the plesiomorphic walking legs similar to those also seen in *Koenigsbergia*. Other features shared between *Koenigsbergia* and *Themonocoris* are the short and stout antennal scape and the two longitudinal pronotal carinae (Popov 2003). He also noted several differences between the two genera, e.g., the length of the anteocular head region, size of the eyes and their prominence in dorsal view, relative length of the antennal segments, and type of vestiture, among others.

However, we noticed that Koenigsbergia in fact shares striking morphological similarities with the assassin bug genera Phimophorus Bergroth, 1886 and Mendanocoris Miller, 1956, which are placed within Phimophorinae Handlirsch, 1897. Among these are two features that were treated by Usinger and Wygodzinsky (1964) as autapomorphic for Phimophorinae, i.e., the subtriangular plates transformed from prosternal processes and a drastically shortened fourth antennomere. Until recently, Phimophorinae (with the two tribes Phimophorini and Mendanocorini) comprised only Phimophorus spissicornis Bergroth, 1886 and two species of Mendanocoris - Mendanocoris browni Miller, 1956 and Mendanocoris milleri Usinger & Wygodzinsky, 1964 (incorrectly named as Mendanacoris). The phylogenetic placement of Phimophorus and Mendanocoris has been enigmatic and controversially discussed as Stenopodainae (Handlirsch 1925), close to the reduviine Aradomorpha Champion, 1899 (Wygodzinsky 1948), or as a distinct subfamily (Phimophorinae) that is part of the phymatine clade (Phymatinae and four related subfamilies) of Reduviidae (Davis 1961). None of the above-mentioned assessments were based on formal phylogenetic analyses, neither morphological nor molecular. The placement suggested by Davis (1961) was accepted in the divergence dating analysis by Hwang and Weirauch (2012), where Koenigsbergia was used as a calibration constraint within the phymatine clade. However, a comprehensive molecular (2268 loci) and morphological (112 characters) phylogenetic analysis of Reduviidae concluded that Phimophorinae are deeply nested within the trichobothrial clade (formerly referred to as "Higher Reduviidae"), the sister group to the phymatine clade (ongoing work by Masonick and colleagues). As part of that study, the concept of Phimophorinae was expanded to include genera formerly treated as Epiroderinae and certain Reduviinae (Aradomorpha Champion, 1899; Marbodus Distant, 1904; Microlestria Stål, 1860; Nalata Stål, 1860; Neostachyogenys Miller, 1953; Sphedanovarus Jeannel, 1919). The biology of Phimophorinae is largely unknown, but Chaverra-Rodriguez et al. (2010) reported that Phimophorus spissicornis were found in the axils of palm fronds. According to the ongoing work by Masonick and colleagues, Phimophorinae are now diagnosed by the following characters: the presence of spatulate setae, trichobothria located distally on the second antennomere, foretibial comb usually located on a subapical spur, 3-3-3 or 2-2-2 tarsal formula, PCu+An1 vein on the forewing long and emanating from the posterior cell apically into the membrane, posterior Cu+An1 closed cell is short, and tergite 8 in females subquadrate, and entirely confined between the connexiva of abdominal segment 7.

The discovery of one male and one nymph of *Koenigs-bergia* provides the opportunity to advance our understanding of the systematics of this unusual fossil assassin bug genus. Our aims are threefold: First, evaluate if the newly acquired fossils represent the described species *Koenigsbergia herczeki* Popov, 2003 or if the adult male should be described as a new species. Second, document the morphology of *Themonocoris*, *Phimophorus* and *Mendanocoris* and compare them with *Koenigsbergia*. Third, formally transfer *Koenigsbergia* to Phimophorinae, should our comparison suggest that the fossil genus indeed belongs to Phimophorinae.

2. Material and methods

The photographs of amber inclusions were taken in the Laboratory of Insect Anatomy and Morphology of the Institute of Biology, Biotechnology and Environmental Protection, the University of Silesia in Katowice (Katowice, Poland) as follows: the focus-stacked color photographs were prepared with a Leica M205C stereo microscope with a high diffuse dome illumination Leica LED5000 HDI, Leica Flexacam C3 digital camera, and LasX ver. 5.1.025593 software (Leica Microsystems, Vienna, Austria). To be photographed, amber pieces were immersed in glycerin to remove most of the optical deformations due to the non-flatness of the surface of the amber. To obtain high-quality figures, fragments of specimens were imaged at high magnifications. Photographs were combined using the Image Composite Editor (panoramic image stitcher). Figures were prepared using Adobe Photoshop CS6 graphic editor. Measurements were made with LasX ver. 5.1.025593 software.

One Mendanocoris milleri specimen was examined: female (private collection of R. Hergovits): Malaysia, Pahang distr., Cameron Highlands, Tanah Rata env. (04°28'25"N 101°22'43"E), 20.3.-7.4.2011, R. Hergovits leg. Color photographs were prepared with a Leica M205C stereo microscope (same settings as for amber inclusion). Scanning electron microscopy (SEM) micrographs were prepared using Phenom XL scanning electron microscope (Phenom-World B.V., Eindhoven, The Netherlands) at 15 kV accelerating voltage with a Back Scatter Detector (BSD). The specimen was cleaned with a micro brush and left uncoated. To obtain high-quality figures, fragments of specimens (for both light microscopy and SEM) were imaged at high magnifications. Photographs were edited and assembled as above. — Three Phimophorus spissicornis specimens were examined: one male (AMNH ENT 00023173), two females (AMNH ENT 00023174; AMNH ENT 00023168) and one nymph (UCR ENT 00127816). Both Phimophorus male (AMNH ENT 00023173) and female (AMNH ENT 00023174) are from the same collection event: Peru: Loreto: Requena Jeraro Herrera 31Aug1987; second female (AMNH_ENT 0002316): Columbia, Antioquia, San Carlos, Vereda Jardín, Finca "El Silencio",

6-Feb-1990; nymph (UCR ENT 00127816): French Guiana: 11Jan2015. — Two specimens of Themonocoris endroedyi van Doesburg and Jacobs, 2011: one female (UCR ENT 00001979) and one nymph (UCR ENT 0010483) from the same collection event (South Africa: Vryheid Hill Nat. Res. 30Jan-2Feb2007). Phimophorus spissicornis and T. endroedyi specimens were assigned 8-digit UCR ENT specimen identifier (USI) labels for databasing (Arthropod Easy Capture database) and 4-digit lab-internal tracking RCW code labels. Voucher specimens of extant taxa are deposited in the Entomology Research Museum at the University of California, Riverside (UCR). Macro images of dorsal and lateral habitus were captured using a Leica Z16 macro imaging system, 1.0x and 2.0x objectives, and LAS v4.3 software. Scanning electron microscopy (SEM) was used to visualize details for P. spissicornis (male) and T. endroedyi (female and nymph) with a Hitachi TM4000Plus II system of uncoated specimens.

Abbreviations used on figures: abd, abdomen; af, antennifer; apl, anterior pronotal lobe; ats, apical tibial setae; bflg, basiflagellomere; bth, bothrium of pedicellar trichobothrium; bucc, buccula; cl, claw; clv, clavus; clvc, claval commissure; cly, clypeus; cor, corium; dflg, distiflagellomere; dlt, dorsal laterotergite; dpsc, dorsal apical processes on scape; fap, femoral apical process; flg, flagellomere; fsp, fossula spongiosa; gcx8, gonocoxa 8; ge, gena; L2-L4, labial segments 2-4; lbr, labrum; mdp, mandibular plate; mesf, mesofemur; mesp, mesopleuron; mest, mesotibia; metp, metapleuron; mett, metatibia; mst, mediosternite; occ, ocellus; par, parempodium; ped, pedicel; pp, pronotal process; ppl, posterior pronotal lobe; prc, pronotal carina; prof, profemur; prop, propleuron; prot, protibia; ptc, protibial comb; prt, proctiger; s1-8, abdominal sternites 1-8; sc, scape; scl, scutellum; sclr, lateral ridge of scutellum; sf, sensory field; smc, submedian carina; spps, subtriangular process of prosternal process; spr, spiracle; tar1, 2, tarsomere 1 and 2; tbs, tuberculate seta; tp, tarsal projection; tpp, pore of tarsal projection; vlt, ventral laterotergite; vpsc, ventral apical processes on scape.

3. Results

3.1. Morphology of Themonocoris, Phimophorus and Mendanocoris

Figures 1-7

We here present for the first time SEM micrographs of *Themonocoris* (Phymatinae), *Phimophorus*, and *Mendanocoris* (Phimophorinae). Similarities between the three genera include the two-segmented tarsi (Figs 3E, 5E, G, 7E, F), antennae placed apically on the head (Figs 1A, C, G, 4A–C, 6A, B, E), long basiflagellomere (Figs 1C, E, G, 2E) or flagellomere in *Mendanocoris* (Fig. 6A, H), a flattened appearance in lateral view (Figs 1B, D, F, H), the presence of bucculae (Figs 2B, 4D, 6B, D, F), and the highly textured integument (Figs 1A–H, 2A–D, 3A–H, 4A–H, 5A–H, 6A–H, 7A–G).

However, differences between the two phimophorine genera and Themonocoris are striking. The antennifers in Mendanocoris and Phimophorus are stout and shieldlike, protecting the antennal insertion (Figs 4C, 6A). In Themonocoris, the antennifers are more slender and do not touch along the midline, and do not shield the antennal insertion (Figs 1B, 2B). The distiflagellomere in Phimophorus is the shortest antennomere, with the basiflagellomere about four times as long as the distiflagellomere (Fig. 4G, H). Basi- and distiflagellomere are not differentiated in Mendanocoris (Fig. 6A, H). In Themonocoris, the basiflagellomere is about three times as long as the distiflagellomere, with the basiflagellomere roughly as long as the pedicel (Fig. 2E, F). The bucculae strongly protrude in Themonocoris (Fig. 2B) but are reduced in Phimophorus (Fig. 4D) and do not strongly protrude in Mendanocoris (Fig. 6B, D). Mendanocoris and Phimophorus possess a subtriangular prosternal process laterally shielding the stridulatory groove (Figs 4B, D, E, 6D, F), while this structure is absent in Themonocoris (Fig. 1B). Themonocoris possesses a previously undocumented dorsal bulbous tarsal projection on all pairs of legs (Fig. 3F), lacks a fossula spongiosa on pro- and mesotibia, but possesses a group of setae on the apex of the protibia (Fig. 3E), here documented for the first time. Phimophorus and Mendanocoris lack the dorsal bulbous tarsal projection and group of tibial setae but possess a fossula spongiosa (Figs 5E-H, 7E, F), here documented for the time for both taxa.

Both phimophorine genera also possess distinctive lateral femoral apical processes on all pairs of legs (Figs 5D, 7C, D). The protibial comb in *Phimophorus* is small and not located on a conspicuous spur (Fig. 5G, H) but is larger in *Mendanocoris* (Fig. 7F). The vestiture of *Themonocoris* consists of elongated tuberculate setae of different lengths and diameters, including both curved, apically widened, and textured setae (black arrow) and erect, smooth setae (white arrow) (Fig. 3C). However, the vestiture of *Phimophorus* and *Mendanocoris* is more uniform, consisting of a dense cover of short and stout setae with distinctive reticulate texture.

3.2. Comparison between *Mendanocoris* and *Phimophorus* (Phimophorinae)

Figures 1, 4-7

Similarities between *Mendanocoris milleri* and *Phimophorus spissicornis* include: a flattened appearance in lateral view (Fig. 1D, F, H), apically inserted and shield-like antennifers (Figs 1C–H, 4A–D, 6A, B, E, F), reduced distiflagellomere (Figs 1C–H, 4H, 6A, H), presence of bucculae (Figs 1D, F, H, 4B, D, E, 6B, D, F), 2nd labial segment (first visible) longer than more apical segments (Figs 4B, D, E, 6B, D, F), possessing subtriangular pros-



Figure 1. Dorsal (A, C, E, G) and lateral (B, D, F, H) view of habitus of extant Themonocorini (Phymatinae) (A, B) and Phimophorinae (C–F). **A**, **B** female (UCR_ENT 00001979) *Themonocoris endroedyi* van Doesburg and Jacobs, 2011; **C**, **D** male (AMNH_ENT 00023173) *Phimophorus spissicornis* Bergroth, 1886; **E**, **F** nymph (UCR_ENT 00127816) of *Phimophorus spissicornis* Bergroth, 1886; **G**, **H** female *Mendanocoris milleri* Usinger & Wygodzinsky, 1964. Scale bar: 1 mm.

ternal process lateral to the stridulatory groove (Figs 4B, D, E, 6B, D, F), legs short and stout (Figs 1C–H, 4B, 6 A, B, 7G), distinct lateral femoral apical process on all legs (Figs 5D, 7C, D), presence of fossula spongiosa on all legs (Figs 5E–H, 7E, F), presence of a protibial comb (Figs 5G, H, 7E, F), and two-segmented tarsi followed by simple claws (Figs 5E, G, 7E, F). Both genera share uniform vestiture comprised of short, stout setae.

There are notable differences between the two genera. Whereas the clypeus in *Mendanocoris* is elongated and projects between the antennifers (Figs 1G, 6A, E), *Phimophorus* possesses a simple clypeus lacking a projection (Figs 1C, E, 4C). The bucculae in *Mendanocoris* are open anteriorly (Fig. 6D, F) but are closed in *Phimophorus* (Fig. 4D, E). The labrum is greatly shortened in *Phimophorus* (Fig. 4B, D) yet is conspicuous in *Mendanocoris* (Fig. 6B, D, F). The 3rd and 4th labial segments in *Mendanocoris* are greatly shortened (Fig. 6D, F) but are not reduced in *Phimophorus* (Fig. 4D). The subtriangular prosternal process in *Phimophorus* covers the apical labi-



Figure 2. Dorsal (A, E–H) and left-lateral (B, C, D) view of head and labium of female (UCR_ENT 00001979) *Themonocoris endroedyi* (A–D) and right antenna of nymph (UCR_ENT 00104834) specimen (E–H). **A–D** Details of head and labium; **E** overview of antenna; **F** basi- and distiflagellomere; **G** detail of base of distiflagellomere; **H** apex of distiflagellomere. — Abbreviations: bflg, basiflagellomere; bucc, buccula; cly, clypeus; dflg, distiflagellomere; ge, gena; mdp, mandibular plate; mxp, maxillary plate; L2–L4, labial segments; occ, ocellus; ped, pedicel; sc, scape; tbs, tuberculate seta.



Figure 3. Dorsal (A, B, F) and lateral (C, D, E, G, H) view of the thorax and abdomen of *Themonocoris endroedyi* (A–G female UCR_ENT 00001979; H nymph UCR_ENT 00104834). A pronotum, scutellum, basal part of hemelytra and base of abdomen covered by wings; **B** detail of hemelytron showing distal margin of corium, base of membrane, and margin of dorsal laterotergite; **C** left foreleg; **D** left side of thorax and anterior part of abdomen; **E** apex of left tibia, tarsus, and pretarsus; **F** distal tarsomere with bulbous tarsal projection; **G** left side of abdomen; **H** right-lateral apex of abdomen. — Abbreviations: abd, abdomen; ats, apical tibial setae; cl, claw; clv, clavus; clvc, clavus commissure; cor, corium; dlt, dorsal laterotergite; gcx8, gonocoxa and abdominal sternite 8; mesp, mesopleuron; metp, metapleuron; mst, mediosternite; par, parempodium; prc, pronotal carina; prop, propleuron; prt, proctiger; s2–s8, abdominal sternites; spr, spiracles; tar1, 2, tarsomere 1 and 2; tp, bulbous tarsal projection; tpp, tarsal projection pore; vlt, ventral laterotergite.



Figure 4. Dorsal (A, C, G, H) and left-lateral (B, D, E, F) view of female *Phimophorus spissicornis* (AMNH_ENT 00023174; AMNH_ENT 00023168). **A** head, thorax, and anterior part of abdomen covered by wings; **B** head and thorax; **C** head showing antennifer and antennal scape; **D** head with buccula and subtriangular prosternal process of prosternum; **E** apex of labium and subtriangular prosternal process of pronotum; **F** detail of scape and pedicel; **G** pedicel showing bothrium of the distalmost trichobothrium; **H** detail of basi- and distiflagellomere. — Abbreviations: af, antennifer; apl, anterior pronotal lobe; bflg, basiflagellomere; bth, bothrium of pedicellar trichobothrium; bucc, buccula; cly, clypeus; clv, clavus; dflg, distiflagellomere; dpsc, dorsal processes; fap, femoral apical process; L2–L3, labial segments; occ, ocelli; ped, pedicel; ppl, posterior pronotal lobe; sc, scape; sclr, lateral ridge of scutellum; spps, subtriangular prosternal process; vpsc, ventral apical processes.



Figure 5. Dorsal (A, D) and lateral (B, C, E–H) of female *Phimophorus spissicornis* (AMNH_ENT 00023174; AMNH_ENT 00023168). A pronotum; **B** left pro-, meso-, and part of metathorax; **C** left-lateral view of scutellum and base of hemelytron; **D** articulation between left profemur and protibia, showing femoral apical processes; **E** two-segmented right protarsus; **F** tenant hairs potentially representing fossula spongiosa at right tibial apex; **G** detail of left foreleg fossula spongiosa and position of protibial comb; **H** detail of protibial comb. — Abbreviations: apl, anterior prontoal lobe; cl, claw; clv, clavus; fap, femoral apical process; fsp, fossula spongiosa; mesp, mesopleurite; metp, metapleurite; par, parempodium; ppl, posterior pronotal lobe; prop, propleurite; ptc, protibial comb; scl, scutellum; smc, submedian carina; tar1, 2, tarsomere 1 and 2.



Figure 6. Dorsal (A, C, E, H) and ventral (B, D, F, G) of female *Mendanocoris milleri*. A antennae, head, and thorax; **B** head and prosternite; **C** details of head; **D** head with buccula and subtriangular prosternal process of prosternum; **E** details of scape and pedicel; **F** details of head and labial segments; **G** left pedicel showing three bothrium of the distalmost trichobothrium; **H** detail of right flagellomere. — Abbreviations: af, antennifer; apl, anterior prontoal lobe; flg, flagellomere; bth, bothrium; cly, clypeus; dpsc, dorsal processes; L2–L4, labial segments; lbr, labrium; occ, ocellus; ped, pedicel; ppl, posterior prontoal lobe; sc, scape; sf, sensory field; smc, submedian carina; spps, subtriangular prosternal process; vpsc, ventral apical processes.

al segment in lateral view, but the apical labial segment is visible in *Mendanocoris* (Fig. 6F). The distiflagellomere is reduced in *Phimophorus* (Figs 1C–F, 4H), but is completely fused with the basiflagellomere in *Mendanocoris* (Figs 1G, H, 6A, H).

While *Phimophorus* only features a single trichobothrium on the pedicel (Fig. 4G), *Mendanocoris* has three, documented here for the first time (Fig. 6G). The structure of the pronotum in *Phimophorus* is simple, with the anterior pronotum as wide as the head (Figs 1C, E, 4A). In *Mendanocoris* the anterior pronotum is wider than the head, with the pronotum distinctly divided into anterior and posterior lobes in dorsal view (Figs 1G, H, 6A, 7A). The fossula spongiosa is reduced in *Phimophorus* (Fig. 5E–H) but fairly well developed in *Mendanocoris* (Fig. 7E, F). The clavus is reduced and posteriorly constricted next to the scutellum in *Mendanocoris* (Fig. 7A) but well developed in *Phimophorus* (Figs 4A, 5A).



Figure 7. Dorsal (A, F), ventral (C, E), and left-lateral (B, D, G) of female *Mendanocoris milleri*. A thorax, and anterior portion of abdomen; **B** pro-, meso, and part of metathorax; **C** ventral view of articulation between left profemur and protibia, showing femoral apical processes; **D** lateral details of left femoral apical process; **E** position of fossula spongiosa and left protibial comb; **F** details of fossula spongiosa and left protibial comb; **G** abdomen. — Abbreviations: apl, anterior prontoal lobe; cl, claw; clv, clavus; cor, corium; dlt, dorsal laterotergite; fap, femoral apical process; fsp, fossula spongiosa; gcx8, gonocoxa and abdominal sternite 8; mesp, mesopleurite; metp, metapleurite; par, parempodium; ppl, posterior pronotal lobe; prop, propleurite; ptc, protibial comb; s2–s7, abdominal sternites; scl, scutellum; smc, submedian carina; tar1, 2, tarsomere 1 and 2.



Figure 8. Adult of *Koenigsbergia explicativa*, **new species** (A–J) and nymph of *Koenigsbergia* sp. (K, L). A dorsal view; **B** ventral view; **C** left-lateral view; **D** overview of left antenna, ventral view; **E** head, dorsal view, **F** head, ventral view; **G** anterior part of body, ventro-lateral view; **H** articulation between right profemur and protibia, showing femoral apical processes; **I** right tibiae apical parts and tarsi of all pairs of legs; **J** right protarsus; **K** dorsal view; **L** ventral view. — Abbreviations: af, antennifer; bflg, basilagellomere; bucc, buccula; cl, claw; cly, clypeus; dflg, distiflagellomere; dpsc, dorsal apical processes on scape; fap, femoral apical process; mesf, mesofemur; mest, mesotibia; mett, metatibia; occ, ocellus; ped, pedicel; pp, pronotal process; prof, profemur; prot, protibia; sc, scape; spps, subtriangular process of prosternal process; tar1, 2, tarsomere 1 and 2; vpsc, ventral apical processes on scape.

3.3. Comparison between Koenigsbergia, Phimophorus, and Mendanocoris

Figures 1, 4-8

Compared to the head in *Phimophorus* (Fig. 4C) and *Koenigsbergia* (Fig. 8E), the head is relatively short in *Mendanocoris* (Fig. 6A). In *Phimophorus*, the antennifer process (Fig. 4C) shields the entire base of the antennal insertion at an oblique angle, and because of this, the view of the small clypeus (Fig. 4C) is obstructed. However, in *Koenigsbergia* and *Mendanocoris*, the antennal process is restricted to the lateral part of the antennifer (Figs 6A, E, 8D–F), making the clypeus easier to see and more prominent than in *Phimophorus* (Figs 6A, 8E). *Phimophorus, Mendanocoris*, and *Koenigsbergia* possess conspicuous bucculae (Figs 4D, 6D, 8G) and a long second labial segment (Figs 4D, E, 6B, F, 8F).

In Koenigsbergia, the pedicel is the longest antennal segment (Fig. 8D, G), over three times the length of the scape (Fig. 8D-F), with both distiflagellomere and basiflagellomere small and ovate (Fig. 8D). In Phimophorus, the basiflagellomere is the longest antennal segment (Fig. 1C), placed between a small, ovate distiflagellomere (Figs 1C, 4H), and a scape that is about the same length as the pedicel (Figs 1C-F, 4A-D). However, in Mendanocoris we found that the apex of the elongated flagellomere possesses a dense setation of sensory structures (sensory field) on the ventral surface and no evidence of a fourth antennal segment (Fig. 6A, H). In Koenigsbergia, the collar of the pronotum is wider than the posterior margin of the head (Fig. 8A), the pronotal process is distinct (Fig. 8A, E-G), and the anterior and posterior lobes are not clearly defined (Fig. 8C). In Phimophorus and Mendanocoris the collar is about as wide as the posterior margin of the head (Figs 1C, D, G, 4A, C, 5A, 6A, C), the pronotum is laterally expanded (Figs 1D, H, 5B, 7B), and the anterior and posterior lobes are clearly defined (Figs 1C, G, 4A, B, 5A, B, 6A, 7A, B). Koenigsbergia (Fig. 8F, G), Phimophorus (Fig. 4B, D, E), and Mendanocoris (Fig. 6B, D, F) possess a subtriangular prosternal process. The scutellar spine is apically expanded in Koenigsbergia (Figs 8A, 9A, B), while it is not apically expanded in Phimophorus or Mendanocoris (Figs 1C, G, 4A, 5A, 7A). The forewing venation in Phimophorus and Mendanocoris includes a slightly rounded anterior cell but lacks a network of veins (Fig. 1C, G). The posterior cell in *Phimophorus* is small and round, but in Mendanocoris, the anterior cell is truncated (Fig. 1C, G). However, in Koenigsbergia the anterior cell is triangular, the anterior and posterior cells are larger in size, the posterior cell is truncated and includes a network of emanating veins (Fig. 8A). Both Koenigsbergia, Phimophorus, and Mendanocoris possess shield-like processes at the apex of the femur (Figs 5D, 7C, 8H), short and stout legs (Figs 4B, 6A, B, 8B, C), and small, two-segmented tarsi (Figs 5E, G, 7E, F, 8J).

3.4. Comparison between Koenigsbergia herczeki and the newly discovered specimens of Koenigsbergia

Figure 9

While the holotype of *K. herczeki* is female, and the newly discovered adult specimen is male, the differences listed in the following are beyond those expected in a sexually dimorphic reduviid species. In the new male specimen, the scape and pedicel are shorter, basiflagellomere and distiflagellomere are longer; the angle between the two shields on the antennifer is much wider, the clypeus is distinctly visible in dorsal view; the head is shorter and wider in dorsal view; and the scutellar spine has a different shape (Fig. 9).

3.5. Taxonomy

Subfamily Phimophorinae Handlirsch, 1897

Tribe Phimophorini Handlirsch, 1897

3.5.1. Genus Koenigsbergia Popov, 2003

Koenigsbergia Popov 2003: 161.

Type species. *Koenigsbergia herczeki* Popov, 2003 (Figs 1–3, 6).

Revised differential diagnosis. Recognized among Phimophorinae by the body being more than twice as long as wide; head, thorax and scutellum densely covered with granules; head more than 1.5 times longer than wide; anteocular portion slightly longer than postocular; lateral portions of antennifers large; in lateral view, eyes not reaching dorsal margin of head; ocelli present; bucculae very prominent, enclosing base of labium; labium stout, second segment (first visible) longest; antennae thickened, pedicel, basi- and distiflagellomeres shortest, densely covered with short adpressed setae; neck indistinct; prothorax with well-developed stridulatory groove; pronotum with two low longitudinal carinae, anterior angles protruding, scutellum subtriangular with strongly elongate apex, without median carina, carinate at sides; hemelytra hyaline, not distinctly divided into corial and membranous parts, costal margins strongly sclerotized; legs densely covered with rows of very short suberect setae, femora and tibiae almost equal in width; tarsi two-segmented, very short, about one-sixth as long as tibiae; abdomen rather wide, egg-shaped, with broad connexivum.



Figure 9. Adults of *Koenigsbergia explicativa*, new species (on the top) and *K. herczeki* (on the bottom). Arrows point to key differences in structure. Original drawing of *K. herczeki* after Popov (2003).

3.5.2. Koenigsbergia explicativa n. sp.

https://zoobank.org/31405D5A-8D80-43BB-B1BF-8607FC5A10D1

Figures 8A-J, 9

Differential diagnosis. Distinguished from *K. herczeki* by the shorter scape and pedicel, longer basiflagellomere and distiflagellomere (Fig. 8D), the much wider angle between the right and left antennifer in dorsal view (Figs 8D, E, 9), the clypeus prominent in dorsal view (Figs 8E, 9; not visible in *K. herczeki*, so likely short), the head shorter and wider in dorsal view (Figs 8E, 9), the spines on the anterior margin of the pronotum shorter and directed more laterad (Fig. 9; longer and directed anteriad in *K. herczeki*), the greater width of the anterior pronotal margin (Fig. 9; much narrower in *K. herczeki*), the rounded elevations posteriorly on the Y-shaped pronotal carinae (Fig. 9), and the scutellar spine with a subapical constriction (no visible constriction in *K. herczeki*).

Description. MALE: Body elongated (Fig. 8A), more than twice as long as wide; head, antennae, pronotum, scutellum and legs densely covered with short tubercu-

late setae. - Head: Elongated (Fig. 8A), 1.7 times longer than wide; anteocular part slightly longer than postocular; neck short, not visible in dorsal view; eyes small, ocelli present; bucculae distinct (Fig. 8G), enclosing base of labium (Fig. 8D, F); antennomeres thick (Fig. 8E), especially scape; pedicel longest (Fig. 8D), 1.3 times longer than other antennomeres together; distiflagellomere shortest (Fig. 8A, D), pointed, covered at the end with distinct hair-like sensilla; all antennal segments narrowed at the base, scape smooth at the base; clypeus clearly visible between the base of the antennae. - Thorax: Trapeze-shaped pronotum (Fig. 8A), 1.5 times as wide as long; lateral spines on anterior pronotal margin directed antero-laterad; humeral angles rounded; anterior pronotal margin slightly rounded, posterior margin almost straight, lateral margins fairly straight; two submedian longitudinal Y-shaped carinae (Fig. 9) between anterior and posterior margins of pronotum, slightly converging in middle part of pronotum, posteriorly expanding into distinct, rounded elevations. Scutellum 1.3 times as long as wide (Fig. 8A), elongated apically, with clear subapical constriction (Fig. 9), resulting in a candle-flame-shaped scutellar spine. Prosternum with two large shield-like structures, probably adjacent to (obscured) stridulatory groove. - Heme-

7.5

3.00

Koenigsbergia herczeki

Table 1. Measurements of Koenigsbergia explicativa, new species (adult), Koenigsbergia sp.iterature). Labial segments I and IV could not be measured.				
	Koenigsbergia explicativa n. sp. (adult)	Koenigsbergia sp. (nymph)		
body length: clypeus to apex of membrane	7.18	4.89		
body maximum width	3.06	1.94		

Table (nymph) and K. herczeki (from the litera

head length	1.32	1.07	1.70
head width including compound eyes	0.95	0.80	1.00
eye length	0.23	_	—
eye width	0.14	_	—
anteocular portion length	0.65	—	—
postocular portion	0.43	—	—
interocular space	0.68	0.39	—
scape length	0.49	0.40	0.50
pedicel length	1.46	1.06	1.50
basiflagellum length	0.31	0.31	0.30
distiflagellum length	0.29	0.31	0.25
labial segment II	0.55	—	—
labial segment III	0.28	_	—
pronotum medial length	1.24	0.61	1.50
anterior width of pronotum	0.98		
maximal width of pronotum	1.90	1.21	1.95
scutellum length	1.18	_	—
scutellum width	0.89	—	—
hemelytra length	4.32	_	4.50

lytron: With sclerotized costal area at base (Fig. 8A), rest membranous; almost 2.5 times as long as wide; not reaching posterior margin of abdomen and not covering abdomen completely; clavus distinct, anterior part covered with single hair-like structures; anterior part of corium also covered with hair-like structures, with two cells – one between radial and medial veins, second between medial and cubital veins, membranous part with two large cells - one between medial and cubital veins, second between cubital and anal vein, and with three veins branching from them. - Legs: Covered with hair-like setae (Fig. 8C, G-I); fore- and middle legs of equal size, shorter than hind legs; ventrally, smooth recess visible between femur and tibia (Fig. 8H); tarsi two-segmented (Fig. 8J), basal segment shorter than apical; claws curved apically (Fig. 8J). — Abdomen: Wide (Fig. 8A-C), almost 1.5 times as long as wide, broadly rounded; connexivum wide, densely covered with hair-like structures; spiracles along connexiva near midlength of sternites. - Measurements (in mm; see also Table 1): body length 7.18; maximum body width 3.06; head length 1.32; head width including compound eyes 0.95; eye length 0.23; eye width 0.14; interocular space 0.68; anteocular portion length 0.65; postocular portion length 0.43; scape 0.49; pedicel 1.46; basiflagellomere 0.31; distiflagellomere 0.29; first labial segment n/a; second labial segment 0.55; third labial segment 0.28; fourth labial segment n/a; pronotum medial length 1.24; anterior width of pronotum 0.98; maximal width of pronotum 1.90; scutellum length 1.18; scutellum width 0.89; hemelytra length 4.32.

Etymology. From Latin explicativus and explico ("to unfold, open out"), in reference to the widened scutellar spine.

Material examined. Holotype: male in $23 \times 14 \times 4$ mm in a piece of Baltic amber. DZUS HE48-700-1-001, coll. Department of Zoology, University of Silesia in Katowice (DZUS) (ex coll. Jonas Damzen, Vilnus, Lithuania, no. 4902). Syninclusion: Hymenoptera: Formicidae: Ponerinae, male, one ex.

Type locality. Unknown locality on the Baltic Sea Coast: Poland, Kaliningrad Oblast or Lithuania.

Type horizon. Baltic amber, mid-Eocene (ca. 44.1±1.1 Ma old according to Wappler 2005; Perkovsky et al. 2007).

Remarks. This new species, with a male holotype, is distinct from K. herczeki which was described from a female specimen based on the characters outlined in the diagnosis and illustrated in Figs 6 and 7. While it might be suspected that sexual dimorphism could account for the differences we observe between these two specimens, we think this to be very unlikely. When describing Phimophorus, Usinger and Wygodzinsky (1964) noted no sexual dimorphism in somatic characters (e.g., antenna, antennifers, head shape, and scutellum) and we confirm this observation based on published descriptions (Usinger and Wygodzinsky 1964) as well as Phimophorus and Mendanocoris specimens we examined.

3.5.3. Koenigsbergia sp.

Figure 8K, L

Description. NYMPH (probably fourth stage): Body elongated (Fig. 8K), more than twice as long as wide; head, antennae, pronotum, abdomen and legs densely covered with short, thick hair-like structures on uniform granules. - Head: Elongated (Fig. 8K), 1.4 times longer than wide; neck short, not seen from above; eyes small; antennomeres thick (Fig. 8K-L), especially scape; pedicel longest (Fig. 8K), 1.1 times longer than other antennal segments together; distiflagellomere shortest (however, slightly compared to basiflagellomere) (Fig. 8K), pointed, covered at the end with distinct sensory hairs; antennal segments narrowed at the base (scape cannot be observed at the base); clypeus small, not protruding beyond antennifers. — Thorax: Trapeze-shaped pronotum (Fig. 8K), 1.75 times as wide as long; both anterior and posterior margin slightly rounded; mesonotum 2.5 times as long as wide (Fig. 8K), anterior margin slightly rounded, posterior margin clearly rounded between the wing pads; wing pads with rounded margin, covered with short, hair-like structures on uniform granules. - Legs: Covered with hair-like structures (Fig. 8K-L); tarsi two-segmented (Fig. 8L), basal segment shorter than second; claws curved apically (Fig. 8L); exact measurements impossible due to dirt in the amber. — Abdomen: Wide (Fig. 8K), almost 1.35 times as long as wide, broadly rounded; connexivum wide, densely covered with hair-like structures; evaporatory areas of dorsal abdominal glands visible between segments III-V (first covered with an air bubble, but visible at an angle; Fig. 8K); spiracles along connexiva near midlength of sternites. — *Measurements* (in mm): body length 4.53; maximum body width 1.89; head length 0.93; head width including compound eyes 0.65; interocular space 0.54; scape 0.33; pedicel 1.0; basiflagellomere 0.3; distiflagellomere 0.28; pronotum medial length 0.53; anterior width of pronotum 0.73; maximal width of pronotum 0.94; mesonotum medial length 0.6; maximum mesonotum width 1.52; dorsal abdomen length 2.5.

Material examined. Nymph in $37 \times 20 \times 7$ mm in a piece of Baltic amber. DZUS HE48-700-1-002, coll. Department of Zoology, University of Silesia in Katowice (DZUS); (ex coll. Jonas Damzen, Vilnus, Lithuania, no. 10033R).

Locality. Rovno region, Ukraine.

Horizon. Baltic amber, mid-Eocene (ca. 44.1±1.1 Ma old according to Wappler 2005; Perkovsky et al. 2007).

Remarks. Popov (2003) also described a nymph (probably fifth stage) that probably represents the genus *Koenigsbergia*. He also indicated that it is somewhat large and may represent another species or simply a larger specimen. It is difficult to compare the two immatures because Popov's description is short and not detailed. Moreover, these are nymphs (larvae are usually used for holometabolous insects) of two different developmental

stages. In Popov (2003), clearly developed wing buds are visible, and the clypeus is also distinct and protrudes beyond the line of antennifers. Apart from these two characters, little can be concluded from the photo posted there.

4. Discussion

Our comparative observations suggest that similarities between Koenigsbergia and Themonocoris are superficial and do not warrant the placement of the fossil taxon within Themonocorini. Some of these similarities are also commonly seen in other subfamilies. Examples include the insertion of the antennae at the apex of the head (also found, e.g., in Salyavatinae and Cetherinae), a flattened appearance in lateral view (also found, e.g., in Phimophorinae), and a highly textured integument (also seen in Phimophorinae and certain Emesinae). However, because of the numerous and striking similarities between Koenigsbergia, Phimophorus and Mendanocoris, we place Koenigsbergia within Phimophorinae. Ongoing work by Masonick and colleagues assembled a morphological and molecular dataset across Reduvioidea that includes Phimophorus spissicornis, but this dataset does not include fossil taxa, including Koenigsbergia or Mendanocoris.

Some of the characters that unite Koenigsbergia, Phimophorus and Mendanocoris are also found in certain other reduviids, but there is phylogenetic evidence in the ongoing work by Masonick and colleagues that they are convergently derived. As an example, bucculae also occur in certain Ectrichodiinae, but that group is placed distantly in phylogenetic hypotheses. Due to the differences we observed between Koenigsbergia, Phimophorus and Mendanocoris outlined above, we recognize the three as separate genera. Interestingly, Usinger and Wygodzinsky (1964) described the 4th antennomere in Mendanocoris as "not free, reduced to a prominence at apex of third article". In contrast, we found that the apex of the flagellomere includes a ventral area of dense sensory structures, but did not find evidence for that area to be a separate antennomere (Fig. 6A, H). We suggest that the unusual antenna of Mendanocoris should be examined using histological techniques.

The morphological differences between the female holotype of *K. herczeki* and the newly discovered male appear distinctive, and we are confident that the male represents a distinct species. However, we decided to not determine the new fossil nymph to either *K. herczeki* or *K. explicativa* **n. sp.** because the features we used in the diagnosis may vary between nymphs and adults (e.g., relative length of antennifers).

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