New genus of Enicocephalinae (Hemiptera: Heteroptera: Enicocephalomorpha) from Sabah based on three new species

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Abstract

A new genus and three new species of Hemiptera: Heteroptera: Enicocephalomorpha: Enicocephalidae: Enicocephalinae are described from Malaysia: Sabah, viz. Phaenicocleus n. gen. sabahensis n. sp. (type species), P. schwendingeri n. sp. and P. minor n. sp. (all species male-based). The new genus is macropterous and belongs to that group of Enicocephalinae characterized by presence of large, closed discal cell and absence of basal cell in forewing. The species are distinct in the character states of the median of pronotum, shape of unpaired sclerite of the pro-eusternum, and shape and length of a median keel of meta-eusternum – these are characters previously unemployed as diagnostic in the Enicocephalidae.

Key words: Insecta, Hemiptera, Heteroptera, Enicocephalidae, taxonomy, new genus and species, Malaysia: Sabah, key

Introduction

Southeastern Asia, particularly its insular part, is extremely rich in genera and species of the Enicocephalomorpha, having the same diversity and level of endemism as in Madagascar, New Zealand, New Caledonia, and Fiji. This generic diversity contrasts with the species diversity and generic paucity of New Guinea and Australia (Štys 2008). Revisions of the endemic SE Asian subfamilies Murphyanellinae (Aenictopecheidae), Phallopiratinae and Megenicocephalinae (both Enicocephalidae) are in preparation (P. Štys & P. Baňař) and will include also recently discovered new genera. In this paper we describe a new genus of Enicocephalidae: Enicocephalinae including three new species from Sabah. The new genus belongs to that group of genera characterized by the presence of a closed discal cell and an absence of basal cell in the forewings. All new species are based on single males; further morphological details concerning pterothorax, wings, abdomen, and terminalia will be discussed further in future studies of the abundant new enicocephaline taxa from Sundaland.

Material and methods

The study is based on an examination of three specimens. Two of them are preserved in alcohol (P. schwendingeri n. sp. and P. minor n. sp.); the third one (P. sabahensis n. sp.) is cardmounted. The label data are cited verbatim, using a slash (/) to separate rows on the label. Photographs of legs were provided by SEM, colour photographs by digital camera. The material was borrowed for study from the Museum of Natural History, Geneva. All measurements are given in millimetres.
Phaenicocleus n. gen.

**Etymology.** Anagram of *Enicocephalus*; gender: masculine.

**Type species:** *Phaenicocleus sabahensis* Štys & Baňař, n. sp., by present designation.

**Description** (valid for males only). Small-sized (3.9–5.2 mm), macropterous. Body slender, not depressed.

Texture of cuticle of head and pronotum mostly rugulose, but shiny in *P. schwendingeri*. Some areas of head and pronotum always with setigerous tubercles, at least on posterior lobe of head and collum (*P. schwendingeri*), often also on epicranium, and midlobe, prosupracoxale, and hindlobe of pronotum; cephalic and pronotal tubercles ranging from very minute, lens-shaped, bluntly columnar to large and sharply triangular. Conspicuous setigerous tubercles also on forelegs, on ventral faces of forecoxa, foretrophancer, and forefemur (two tubercles on basalmost part of forefemur in *P. schwendingeri*). Vestiture formed by whitish straight or curly trichoid setae (Figs. 1–3), only sparsely distributed in *P. schwendingeri*. Longer, curly setae occur mostly on foretibiae. Texture of cuticle rugulose to smooth (*P. schwendingeri*). Coloration light brown to blackish, without particular colour patterns.

Head short, antenniferous tubercles diverging immediately in front of eyes, no part of genae visible in dorsal view. Epicranium strongly convex, anteclypeus by ca. half of its length exceeding apices of antenniferous tubercles. Eyes medium-sized, close to a deep postocular constriction, facettes small and separately rounded. Posterior lobe of head transverse, rounded, its posterior margin convex, separated by a sharp constriction from the neck; median shallowly concave, without impression. Ocelli large, mutually widely distant.

Scape with a distinctly separated prescapite. Pedicel slightly and regularly incrassate distalwards, antennal segments III and IV much thinner than pedicel, but not flagelliform, III terete, IV elongately subfusiform. Mutual length ratios of antennal segments II, III, IV variable, but differences small, pedicel shorter to about as long as the first flagellomere.

Labium thin, geniculate, directed posterad, apex reaching basis of posterior lobe of head, segment II strikingly long and thin, about once to 1.3 times as long as III. Labial formula (the longest segment first): II – III – IV – I.

Pronotum of distinct three lobes; collum long and robust, its dorsal architecture species-specific, in lateral outline separated from the midlobe by a deep gulf. Midlobe with a species-specifically constructed central fossette and a pair of indistinct lateral impressions; median species-specific; posterior margin entire, more or less triconvex. Lateral margins of midlobe either free or partly covered by anterolateral extensions of posterior lobe (*P. schwendingeri*). Hindlobe ample, much broader than midlobe, posterior margin broadly concave. Central fosette on midlobe and medians of mid-and hindlobes species-specific.

‘Proepimeral lobes’ reaching about half the length of fore coxa, nearly or fully closing fore acetabula from behind, but their ventralmost apices distant for about a length of fore coxa. Anterior terminations of prosupracoxale shifted mesad, right and left prosupracoxale converging and reaching or nearly reaching the postero medial euprosternal species-specific structure.

Eumesosternum with an impressed, percurrent linear median provided with both anterior and posterior transverse linear bars. Eumetas sternum with a median raised keel, its shape species-specific.

Mesoscutellum triangular, the apex extended in an obtusely rounded and separately convex micro.

Forelegs. Coxa and trochanter without particulars. Femur stouter in *P. sabahensis* and *P. minor*, more slender in *P. schwendingeri*. Slender foretibia markedly dorsoventrally curved in *P. schwendingeri*; stouter and normal shape in *P. sabahensis* and *P. minor*. Tibial armature consists from group of four spiniform setae, situated on apicritical process (very conspicuous in *P. schwendingeri*). Tarsal armature almost missing, with an exception of a slender short spiniform seta in the middle of ventral face of foretarsus. One isolated seta, adjoining the ventralmost seta of the bristle comb always present. Foretarsal claws subequal in length.

Middle and hind legs long and slender, without particulars. Apex of tibiae posterior- and anteroventrally with a short comb of setae each, consisting of 9–10 setae each and provided with two long spiniform setae.
Both middle and hind tarsi with extremely short first tarsal segment, resembling short ringlet only. Claws asymmetrical, the anterior ones much shorter (about one half of length) than posterior ones.

Forewing venation complete, modal, without basal cell and with a strikingly long and narrow, closed discal cell. Clavus with a percurrent AA1+2 separating at its basis from the marginal AA3+4; the latter distinct in the proximal third of clavus only, the distal fusion of both veins and formation of a claval cell absent or indistinct. AP short and distinct on ventral surface only. No macrotrichiae on wing membrane.

Pregenital abdomen. Architecture varying segmentally (as well as occurrence of transverse apodemes), in extreme case (see Discussion) all potential components distinct: mediotergite, pair of dorsal laterotergites, membranous connexival line, pair of ventral spiracle-bearing laterotergites, pair of laterosternites, sternum (sometimes subdivided in two hemisternites). Mediotergites 1 and 2 fused, ventrite 1 large and distinct. Segment 8 without any special modifications.

Terminalia (see Discussion). Pygophore strikingly strongly sclerotized, forming a complete, depressed...

1. See the remark under *P. schwendingeri* and Discussion.
and transverse ring. Guide high, exceeding tergum 10 in posterior view, basally broadest, without a shaft, inversely U-shaped or inversely V-shaped (with rounded apex), always provided with an internal, basomedial sclerotized structure (shape species-specific, minutely triangular to long, tongue-shaped) associated with the ventral margin of posterior foramen. Parameres complex, immobile sclerites, situated beneath and outside the dorsolateral parts of guide arms, associated by apodemes with the guide, pygophore margins and tergum 10. The areas of posterior foramen ventrad to parameres and laterad to the guide sclerotized; no unpaired sclerotized element between the parameres present.

Segment 10 represented by smooth, sclerotized tergum only, the latter free, not fused with the pygophore, lid-shaped, convex, associated with two flaps representing segment 11. Ventral parts of both segments not sclerotized.

**Differential diagnosis.** *Phaenicocleus n. gen.* belongs to that group of genera of Enicocephalomorpha characterized by the absence of a basal cell and the presence of a closed discal cell; and it would fall in Štys’s (2002: 352) group 1.2.1.3 and would key under the couplets 33–37 in his key to the genera of Enicocephalomorpha of the World. The occurrence of this group is restricted to Enicocephalidae: Enicocephalinae: Enicocephalini, *partim.* The diagnosis below is preliminary and rather superficial since all the Eastern Hemisphere genera mentioned will be thoroughly revised in next future; also their relationships will be analyzed at another opportunity.

*Phaenicocleus* differs from the American (Sonorian, broadly conceived) male-based genera *Urnacephala* Wygodzinsky & Schmidt, 1991 and *Lysenicocephalus* Wygodzinsky & Schmidt, 1991 by the normally developed, ample hindlobe of the pronotum and the absence of their diagnostic autapomorphies (Wygodzinsky & Schmidt, 1991; Štys, 2002). It differs from the Australian *Usingeriella* Wygodzinsky, 1950 and a new, closely related Australian genus (Štys in MS) – both strikingly speciose although only one species was formally described – by a normally developed midlobe of the pronotum (not subquadrate), but shares with both of them the presence of many setigerous tubercles over the body and large ‘proepimeral lobes’. The minute species of *Nesenicocephalus* Usinger, 1939 (Australia, Philippines, Oceania, New Guinea – distribution based also on undescribed species) lacks in contrast to *Phaenicocleus* any median and central structures on the pronotum, and their females are universally caducous (unknown in *Phaenicocleus*). The Madagascan *Schenchiella* Villiers, 1969 is based on one female lacking wings, and the general facies (Villiers, 1969; Štys, unpublished) of its minute and depressed type species has nothing in common with *Phaenicocleus*.

*Phaenicocleus* would run in Štys’s (2002) generic key to *Pseudohenschiella* Villiers, 1958, an endemic Madagascan genus with 5 species (Baňař & Štys 2006). The species differ from *Phaenicocleus* species by their smaller size (total length under 3 mm), depressed body, dorsal part of the genae present, flagellum of the antennae filiform, labium directed anterad and its 2nd segment very short, posterior lobe of the pronotum with no indication of a median, discal cell in the forewings strikingly short and claval cell (= anal loop) well developed.

**P. minor n. sp.**

*(Figs. 4–8, 15, 18, 21, 24, 27)*

**Etymology:** *minor*, lat. = smaller.


**Habitat.** Collected in a mountain humid forest of *Lithocarpus*, *Castanopsis*, and tree-ferns.
**TABLE 1. Measurements of Phaenicocleus species (in mm; L = length, W = width).**

<table>
<thead>
<tr>
<th></th>
<th>Phaenicocleus schwendingeri</th>
<th>Phaenicocleus minor</th>
<th>Phaenicocleus sabahensis</th>
</tr>
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<tbody>
<tr>
<td>Antennal segment I, L</td>
<td>0.27</td>
<td>0.18</td>
<td>0.24</td>
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<tr>
<td>Antennal segment II, L</td>
<td>0.45</td>
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<td>Antennal segment III, L</td>
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<td>0.31</td>
<td>0.51</td>
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<tr>
<td>Antennal segment IV, L</td>
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<tr>
<td>Antennal segment II, distal W</td>
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<td>0.05</td>
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<td>Total length antenna</td>
<td>1.77</td>
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<tr>
<td>Head, total L</td>
<td>0.64</td>
<td>0.48</td>
<td>0.56</td>
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<tr>
<td>Width head across eyes</td>
<td>0.39</td>
<td>0.29</td>
<td>0.34</td>
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<tr>
<td>Eye, L</td>
<td>0.15</td>
<td>0.13</td>
<td>0.18</td>
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<tr>
<td>Eye, W</td>
<td>0.11</td>
<td>0.09</td>
<td>0.11</td>
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<tr>
<td>Distance eye-apex of antennifer</td>
<td>0.11</td>
<td>0.07</td>
<td>0.09</td>
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<tr>
<td>Dorsal synthlipsis</td>
<td>0.19</td>
<td>0.16</td>
<td>0.14</td>
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<td>Ventral synthlipsis</td>
<td>0.09</td>
<td>0.04</td>
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<tr>
<td>Intercellular distance</td>
<td>0.09</td>
<td>0.11</td>
<td>0.11</td>
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<tr>
<td>Shortest distance ocellus-eye</td>
<td>0.09</td>
<td>0.03</td>
<td>0.08</td>
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<tr>
<td>Posterir lobe of head, L</td>
<td>0.27</td>
<td>0.19</td>
<td>0.24</td>
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<tr>
<td>Posterir lobe of head, W</td>
<td>0.38</td>
<td>0.27</td>
<td>0.31</td>
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<tr>
<td>Labial segment I, L</td>
<td>0.11</td>
<td>0.08</td>
<td>0.09</td>
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<tr>
<td>Labial segment II, L</td>
<td>0.24</td>
<td>0.22</td>
<td>0.32</td>
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<tr>
<td>Labial segment III, L</td>
<td>0.23</td>
<td>0.17</td>
<td>0.24</td>
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<tr>
<td>Labial segment IV, L</td>
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<tr>
<td>Labial segment II, max dorso-ventral thickness</td>
<td>0.11</td>
<td>0.09</td>
<td>0.09</td>
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<tr>
<td>Labial segment III, max dorso-ventral thickness</td>
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<tr>
<td>Labium, total L</td>
<td>0.74</td>
<td>0.60</td>
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<tr>
<td>Pronotum, max. L</td>
<td>0.71</td>
<td>0.63</td>
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<tr>
<td>Collum, median L</td>
<td>0.15</td>
<td>0.13</td>
<td>0.10</td>
</tr>
<tr>
<td>Pronotum, mid lobe, L</td>
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<td>0.18</td>
<td>0.23</td>
</tr>
<tr>
<td>Pronotum, hind lobe, max L</td>
<td>0.29</td>
<td>0.22</td>
<td>0.30</td>
</tr>
<tr>
<td>Pronotum, hind lobe, median L</td>
<td>0.18</td>
<td>0.16</td>
<td>0.21</td>
</tr>
<tr>
<td>Collum, W</td>
<td>0.33</td>
<td>0.30</td>
<td>0.37</td>
</tr>
<tr>
<td>Pronotum, mid lobe, W</td>
<td>0.69</td>
<td>0.51</td>
<td>0.62</td>
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<tr>
<td>Pronotum, hind lobe, W</td>
<td>1.06</td>
<td>0.80</td>
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<tr>
<td>Forewing, max. L</td>
<td>3.67</td>
<td>2.76</td>
<td>3.51</td>
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<td>Forefemur, L</td>
<td>0.87</td>
<td>0.58</td>
<td>0.73</td>
</tr>
<tr>
<td>Forefemur, W</td>
<td>0.20</td>
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<tr>
<td>Foretibia, L</td>
<td>0.97</td>
<td>0.64</td>
<td>0.71</td>
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<tr>
<td>Foretibia, W</td>
<td>0.19</td>
<td>0.16</td>
<td>0.22</td>
</tr>
<tr>
<td>Foretarsus, L</td>
<td>0.20</td>
<td>0.17</td>
<td>0.18</td>
</tr>
<tr>
<td>Foretarsus, W</td>
<td>0.09</td>
<td>0.07</td>
<td>0.08</td>
</tr>
<tr>
<td>Total length</td>
<td>5.23</td>
<td>3.87</td>
<td>4.96</td>
</tr>
</tbody>
</table>
**Method of collecting.** The specimen was collected by sieving plant residues in a ravine at a forest margin glen.

**Total length:** 3.9 mm. For other measurements see Table 1.

**FIGURES 4–8.** *Phaeciofleus minor* Štys and Baňař n. sp., male, right foreleg, 4, tibial and tarsal armature, ventral view; 5, tibial armature, anterior view; 6, forecoxa, foretrochanter and forefemur, posteroventral view; 7, foretibia, anteroventral view; 8, foretrochanter, ventral view
Distribution of setigerous tubercles on body: setigerous tubercles sharp and conspicuous, situated mostly marginally, some irregularly triangular and larger than others; approximate numbers of tubercles seen (dorsal view, unless specified otherwise): posterior lobe of head 5 small and hardly visible laterally, 9 ventrally; pronotum – lateral sides of collum 6 each (conspicuous; further 5 on the ventral side), midlobe 6 each, hindlobe 5 each, margin of prosupracoxale – a continuous row.

Lateroventral margin of buccular bridge (ventral view) with two large pointed tubercles directed towards the basis of antennifer.

Distribution of setigerous tubercles on forelegs. Forecoxa on distal half of ventral face with 8–10 sharp tubercles, foretrochanter (Fig. 8) on ventral face with 16 such tubercles, situated approximately in a curved double-row. Basal half of ventral face of forefemur with 12 setigerous tubercles, situated in irregular row. Foretibia and foretarsus without tubercles.

**Coloration.** Mostly pale brown; head, pronotum, and ventral part of thorax strongly lustrous, dark brown to black-brown; forewings with brown veins and greyish membrane with smoky hue. Fore knees paler than rest of forelegs.

**Head.** Cuticle on dorsum rugulose. Maximum width of eye 0.56 times width of dorsal synthlipsis, 2.25 times width of ventral synthlipsis. Posterior lobe transverse, regularly rounded laterally, 1.42 times as wide as long, shallowly concave anteriorly and posteriorly, no linear impression. Ocelli large, situated rather laterally, interocellar distance much (3.6 times) longer than shortest distance ocellus – eye.

**Antennal formula** (longest segment first) IV, III = II, I.

**Labium.** Ratio length segment II : III 1.29, II: (III + IV combined) 0.73.

**Pronotum.** Lateral outlines of collum and midlobe not quite distinct owing to large protruding setigerous tubercles. Collum convex, its lateral tubercles visible in dorsal view. Lateral margins of midlobe convex, widest in 4/5 of its length, its posterior margin indistinctly triconvex, the constricted adjacent to posterior lobe much deeper and wider in lateral sectors than mesally. Posterior lobe ample, lateral margins convex, posterolateral angles rounded, subobtusangular, posterior margin broadly and deeply convex. Midlobe with an extensive and not well delimited shallow fossette situated in anterior 3/5 of its length, and a percurrent, linear, impressed median transformed (caudal to fosette) in a linear median ridge continuing across hindlobe (Fig. 15). Midlobe – width : medial length 2.8; hindlode - ditto 5.00.

Prosupraepimeral lobes nearly closing the fore acetabula from behind. Prosupracoxale reaching the euprosternal unpaired postteromesal knob (Fig. 18). Posterior transverse bars of median eumesosternal apodeme simply arcuate, the neighbouring posterior areas of sternum uniformly convex. Eumetasternum with a median, raised, narrowly triangular wedge (Fig. 21) with basis and acutangular apex distant from anterior and posterior sternal margins, respectively; the basis of wedge without transverse arms.

**Foreleg.** Posteroventral face of forecoxa, ventral face of trochanter and the whole of ventral face, ventral half of anterior face and posterior face of forefemur with numerous, lens-like, nonsetigerous tubercles (Fig. 6); for sharp setigerous tubercles see above. Foretrochanter robust, shorter than forecoxa. Forefemur 3.4 times as long as wide, proximal part slender, widening distad, maximum width in 2/3 of its length. Foretibia (Fig. 7) slender, four times as long as wide, without cuticular tubercles. Apex of foretibia protruding as a short process only. Apicitibial armature consists of four spiniform setae (Figs. 4–5, 24), three ventralmost in a short row and the shortest one dorsally. Bristle comb long, consisting of approximately 40 setae, two dorsalmost much stouter and longer. Foretarsus slightly longer than foretibia maximum width, posttarsus formed from two well developed claws, subequal in length. Tarsal armature consists from one short spiniform seta only, situated ventrally, approximately in the two-thirds of foretarsus length.

Guide (Fig. 27) inversely V-shaped, its arms in posterior view narrow; its internal sclerite short, small, triangular, strongly sclerotized.

**Associated enicocephalids in the sample.** Four larvae (some with unusually construed ecdysial line, none congeneric) : (a) 1 spec., larva 2 (?), robust, without wing pads, long genae and short and thick antennae resembling Oncyclocotis sp., but without pronotal impressions characteristic of the genus; (b) 3 spec., nearly "mature" larvae with long, anapterous wing pads and incrassate hind femora, specifically arranged facettes;
possibly two different genera or strongly sexually dimorphic species.

**Differential diagnosis.** See the key and illustrations of diagnostic characters. This is a species easily recognizable owing to its small size and many setigerous tubercles. In most character states (excepting the shape of the guide), it is more similar to *P. sabahensis* than to *P. schwendingeri*.

*P. sabahensis* n. sp.  
(Figs. 1–3, 9–13, 16, 19, 22, 25, 28)

**Etymology:** toponymical adjective derived from Sabah (terra typica).


**Habitat.** Collected in a humid mountain forest of Lithocarpus and Castanopsis.

**Method of collecting.** The specimen was collected by sieving rotten wood, moss, and dead leaves.

**Total length:** 5.2 mm. For other measurements see Table 1.

Distribution of setigerous tubercles on body: epicanrum and the entire posterior lobe covered by numerous minute setigerous tubercles all over (rather inconspicuous marginally).

Lateroventral margin of buccular bridge (ventral view) with two large pointed tubercles directed towards the basis of the antennifer.

Distribution of setigerous tubercles on forelegs. Forecoxa on distal half of ventral face with irregularly distributed 10 sharp tubercles, foretrochanter on ventral face with 14 such tubercles, situated approximately in a curved double-row. Basal half of ventral face of forefemur with 9 setigerous tubercles (Fig. 9), situated in irregular double-row. Foretibia and foretarsus without tubercles.

**Coloration.** Mostly yellowish brown to brown; head, antennal segment I, pronotum and ventral part of thorax strongly lustrous, brownish black; forewings brownish grey (both veins and membrane). Fore knees concolorous with other parts of forelegs.

**Head.** Cuticle on dorsum rugulose. Maximum width of eye 0.79 times width of dorsal synthlipsis, 1.38 times width of ventral synthlipsis. Posterior lobe laterally regularly rounded, widest in the middle, 1.29 times as wide as long, its median formed by broad, shallow, percurrent concavity. Ocelli large, situated sublaterally, interocellar distance 1.4 as long as shortest distance ocellus – eye. Antennal formula (longest segment first) III > IV, II, I.

**Labium.** Ratio length segment II : III 1.33, II: (III + IV combined) 0.84.

**Pronotum.** Collum rather flat, with no median, apparently protruding far laterad because of presence of protruding large lateral, subhorizontal, sharp setigerous tubercles.

Postcostral constriction deep. Midlobe lateral margins rounded, diverging posterad, not at all embraced by posterior lobe (not at all extending anterad); posterior margin moderately convex laterally and medially, the medial convexity obtusely subangular. Posterior lobe: lateral margins in anterior half moderately convex and diverging, in posterior half subparallel, nearly straight, posterolateral angles subrectangular; posterior margin straight in lateral sectors, broadly and shallowly, subangularly excised in mesal sector. Midlobe without median, with an extensive central fossette, hindlobe with a percurrent medial linear ridge (sic!) (Fig. 16). Midlobe – width : medial length 2.7; hindlobe – ditto 4.7.

Proepimeral lobes fully closing fore acetabula from behind. Prosupracoxale meeting mesally onto an euprosternal keel (Fig. 19). Posterior bars of eumesosternal apodemes separately rounded and surrounding posterior parts of sternum separately convex. Median wedge of eu metasternum strikingly narrow, terminating far from posterior margin of sternum, and anteriorly provided with transverse bars (Fig. 22).
Foreleg. Posteroventral face of forecoxa, posteroventral face of trochanter and forefemur, with the exception of dorsal face with numerous, lens-like, nonsetigerous tubercles; for sharp setigerous tubercles see above. Foretrochanter robust, the same length as forecoxa. Forefemur three times as long as wide, proximal part slender, widening distad, maximum width in the middle of its length. Foretibia (Fig. 12) 3.2 times as long as wide, without cuticular tubercles. Apex of foretibia protruding as a short process only. Apicitibial armature
consists of four spiniform setae (Figs. 10–11, 25), three ventralmost in a short row and the shortest one dorsally, similar to *P. minor*. Bristle comb long, consisting of approximately 38–40 setae, two dorsalmost much stouter and longer. Foretarsus slightly shorter than foretibia maximum width (ratio 0.8), posttarsus formed from two well developed claws, subequal in length. Tarsal armature similar to *P. minor*.

Guide (Fig. 28) inversely U-shaped; its internal sclerite moderately long, tongue-shaped, strongly sclerotized, and surrounded by much larger, little sclerotized but similarly shaped structure resembling its halo.

Associated enicocephalids in the sample. Holotype of a macropterous *n. gen., n. sp.* (female) to be described later.

Differential diagnosis. See the key and illustrations of diagnostic characters. This species in most character states (excepting shape of the guide) more similar to *P. minor* than to *P. schwendingeri*, but differing from the former by its larger size and less abundant, smaller, and more rounded setigerous tubercles.

*P. schwendingeri* *n. sp.*
(Figs. 14, 17, 20, 23, 26, 29)

**Etymology:** patronymical adjective; dedicated to Peter Schwendinger (Museum of Natural History, Geneva), our colleague and friend.

**Type material.** Holotype, ♂, ‘11a SABAH (West Coast Residency): / Kinabalu Park, Mt Kinabalu, 2600m, / à proximité de Layang-Layang / forêt brumeuse, tamisage de mousses / et de feuilles mortes très humides / 2.v.1987, leg. D.Burckhardt et I.Löbl’. Preserved in alcohol in a glass tube, together with locality label and red label: ‘HOLOTYPE / Phenicocleus schwendingeri *n. sp.* / Štys & Baňař det. 2009’. Specimens is dissected – head with prothorax separate from the rest of body, both forelegs and right hindleg separately. The left wing with an aberrant venation (see below and Discussion) is missing, being unfortunately lost during preparation of a slide mount. Holotype is deposited in the collections of Museum of Natural History, Geneva.

**Habitat.** Collected in mountain foggy forest on Mt. Kinabalu.

**Method of collecting.** The specimens was collected by sieving moss and very damp leaf litter.

**Total length:** 4.95 mm. For other measurements see Table 1.

Distribution of setigerous tubercles on body: head without setigerous tubercles excepting ca 15 small ones on ventral side of the postocular constriction and posterior lobe. Pronotum: dorsum of collum with minute setigerous tubercles all over, venter with 2 lateral groups of 4 large rounded tubercles each; midlobe without tubercles, lateral margins of posterior lobe with minute tubercles.

Lateroventral margin of buccular bridge (ventral view) with one large black tubercle directed into the gulf between the buccular bridge and antennifer.

Distribution of setigerous tubercles on forelegs. Forecoxa on distal half of ventral face with 10 sharp tubercles, foretrochanter on ventral face with 14 such tubercles, situated approximately in a curved double-row. Basalmost part of ventral face of forefemur with 2 setigerous tubercles only. Foretibia and foretarsus without tubercles.

**Coloration.** Body (inclusive appendages, forewings and its veins) concolorous, uniformly brown.

**Head.** Cuticle on dorsum smooth. Maximum width of eye 0.58 times width of dorsal synthlipsis, 1.22 times width of ventral synthlipsis. Posterior lobe transverse, laterally rounded, slightly pear-shaped, widest behind the middle, 1.41 times as wide as long; median indicated by an indistinct shallow concavity without linear impression but with a median line slightly darker than surroundings. Ocelli very large, situated rather mesally, interocellar distance the same as shortest distance ocellus – eye.

Antennal formula (longest segment first) III = IV, II, I.

**Labium.** Ratio length segment II : III 1.04, II: (III + IV combined) 0.63.

**Pronotum.** Collum with two not very prominent, transverse bulges, medially separated by a shallow, indistinctly delimited concavity, and not protruding laterad; however, lateral outline of collum strikingly

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rounded, postcollar constriction strikingly deep. Lateral outline of midlobe rounded, but free in its anterior half only, posterior part being embraced by an anterolateral extension of hindlobe. Posterior margin of midlobe laterally concave, with three convexities discally. Combined lateral outlines of midlobe and hindlobe nearly straight (with a shallow concavity at the site of termination of free part of midlobe, postrolateral angles of strikingly ample hindlobe broadly rounded, its posterior margin only shallowly and broadly obtusangularly excised. Midlobe with a percurent linear impression starting in anterior 1/3 and passing across a sharply delimited small central fossette provided with a central puncture; the impression continues across all the hindlobe, being there in its anterior third doubled (Fig. 17). Midlobe – width : medial length 2.9; hindlobe - ditto 5.9.

FIGURES 15–23. Diagnostic characters on mesal parts of thorax in *Phaenicocleus* species; schemes without scale. 15, 18, 21, *P. minor*; 16, 19, 22, *P. sabahensis*; 17, 20, 23, *P. schwendingeri*. 15–17, midlobe and hindlobe of pronotum, median, and central structures; 18–20, anterior prosupracoxalia (seen in a strictly ventral view, hence appearing linear) fused with an unpaired euprosternal structure; 21–23, median of meteusternum. Lettering: apcx—anterior prosupracoxale; emtst—eumetasternum; hlpn—hindlobe of pronotum; i—impression; m—median of eumetasternum; mlpn—midlobe of pronotum; ms—medial structure of euprosternum; r—ridge

Proepimeral lobes closing the fore acetabula from behind. Prosupracoxale reaching euprosternal unpaired postomesal rectangular elevation (Fig. 20). Posterior transverse bars of median eumesosternal apodeme simply arcuate, the neighbouring parts of sternum uniformly convex. Eumetasternum with a median, percurent, linear ridge, not quite reaching apex of sternum (Fig. 23).

**Foreleg** (Fig. 14) slender, ventral faces of forecoxa, trochanter, and ventral face, ventral half of forefemur with numerous, lens-like, nonsetigerous tubercles, these sparsely distributed for sharp setigerous tubercles see above. Foretrochanter shorter than forecoxa. Forefemur 4.3 times as long as wide, slender, maximum width in middle of its length. Foretibia slender, more than five times as long as wide, without cuticular tubercles, unusually dorsoventrally curved, slightly S-shaped. Apex of foretibia protruding as a conspicuous process. Apicitibial armature consists of four spiniform setae (Fig. 26), two ventral, one anterior subventral and one
dorsal. Bristle comb very long, consisting of approximately 45 setae, two dorsalmost and two ventralmost much stouter and longer. Foretarsus subequal to foretibia maximum width, posttarsus formed from two well developed claws, subequal in length. Tarsal armature consists from one short spiniform seta only, typical for genus, but seta longer and thinner as in other species.


Right forewing of the holotype normally developed, left wing with an incomplete vein suggesting presence of an incompletely closed basal cell as well (for its significance see Discussion).

Guide (Fig. 29) inversely V-shaped, its arms in posterior view strikingly thick proximally; its internal sclerite long, tongue-shaped, not much distinctly or hardly sclerotized.

**Associated enicocephalids in the sample.** Undescribed genus and species of Enicocephalinae (to be described later), 1 adult female with shed wings and strongly incrassate hind femora.

**Differential diagnosis and comparative notes.** See the key and illustrations of diagnostic characters. This is a species easily recognizable by its smooth texture of its cuticle, its sparse distribution of lens-like tubercles on forefemur, its small amount of setigerous tubercles, its relatively short labial segment II, its uniform coloration, its slender forelegs, particularly the femora, and a peculiar architecture of the pronotum (see Discussion).
Key to *Phaenicocleus* species (males)

1 Posterior part of lateral margins of midlobe of pronotum embraces by anterolaterolateral extensions of the hindlobe. Body unicolorous brown (including appendages), uniformly lustrous. Dorsum of head smooth. Labial segment II subequal in length to III. Lateral margins of head (dorsal view) without setigerous tubercles. Midlobe of pronotum with a percurent median linear impression (Fig. 17) starting at the anterior third and passing across a sharply delimited small central fossette; this impression continuing across all the hindlobe and doubled in its anterior third. Median of eumetasternum formed by nearly percurent sublinear ridge (Fig. 23) not reaching its posterior margin. Foretibia dorsoventrally curved, sightly S-shaped (Fig. 14). (Guide inversely V-shaped (Fig. 29))... *P. schwendingeri* n. sp. (4.95 mm)

- Lateral margins of midlobe of pronotum free. Head, pronotum, and ventral parts of thorax darker than rest of body, dark-brown to blackish, contrastingly strongly lustrous. Dorsum of head rugulose. Labial segment II about 1.3 times as long as III. Lateral margins of posterior lobe of head (dorsal view) with distinct setigerous tubercles. Median of eumetasternum formed by an elevated wedge distant from both its anterior and posterior margins. Foretibia not dorsoventrally curved............................................................................................................. ............................................ 2

2 Small species. Fore knees paler than rest of forelegs. Forewing veins darker than forewing membrane. Lateral cephalic setigerous tubercles few, large and pointed. Antennal segment II as long as III. Midlobe of pronotum with a percurent linear impression (Fig. 15) starting in its anterior third and passing across a sharply delimited small central fossette; this impression continuing across entire hindlobe. Basis of eumetasternal wedge with transverse arms (Fig. 21). Guide inversely V-shaped................................. .................................................................................. *P. minor* n. sp. (3.9 mm)

- Much larger species. Fore knees concolorous with rest of forelegs. Forewing veins concolorous with its membrane. Lateral cephalic setigerous tubercles small, numerous, rounded. Antennal segment II slightly shorter than III. Midlobe of pronotum lacking a median, provided with extensive central fossette (Fig. 16); median of hindlobe formed by percurent linear ridge (sic!). Basis of eumetasternal wedge without transverse arms (Fig. 22). Guide inversely U-shaped. (Fig. 28). ............................................................................................................. *P. sabahensis* n. sp. (5.2 mm)

Discussion

Homoplasic pronotal architecture in *Trichopirates* and *Phaenicocleus schwendingeri*

The hindlobe of the pronotum in *Phaenicocleus schwendingeri* extends anterolaterad along the midlobe; this character is among all the Enicocephalinae shared with species of the endemic Madagascan genus *Trichopirates* Villiers, 1958 only. This similarity is homoplasic, because it is incongruent with other genus-specific characters; particularly the shape of head and pattern of forewing venation are strikingly different (Villiers 1958, 1969; Štys 2002). However, we cannot exclude the possibility that *P. schwendingeri* does not actually belong to the *Phaenicocleus* clade, and the architecture of the pronotum jointly with many other autapomorphies of the species casts doubts on the correctness of its present generic classification.

Discal cell in the forewing of *Phaenicocleus schwendingeri*

Although the venation of the right forewing of *P. schwendingeri* ((holotype F) is basically identical with that of other *Phaenicocleus* species (crossvein closing the basal cell is missing, and hence the basal cell is absent), its left forewing is different. Its discal cell is provided with an incomplete vein at the site of vein delimiting distally the basal cell. The latter vein and the cell are present in most Enicocephalomorpha (see Štys 2002), but absent in the group of genera similar to *Phaenicocleus* (see differential diagnosis of this genus as well as, in Štys 2002).

Many authors (last Wygodzinsky & Schmidt 1991; Štys & Baňař 2008) pointed out and illustrated great variation of forewing venation in the Enicocephalomorpha, which may often affect even those character states which are usually rather stable and characteristic of large groups of genera. Sometimes even losses of a “crossvein” (whatever its real nature is) closing the basal cell or the discal cell are involved. For this reason, Štys (2002) downgraded some African and Madagascan monotypic “genera” based on such forewing reductive mutations to subgenera of monophyla (more broadly conceived genera) congruent in sets of other characters. Type species of all the above downgraded genera were based on single specimens.

A similar and more convincing case is to be found in the enicocephaline genus *Hoplitocoris* Jeannel, 1942
whose subgenus *Iphlotocoris* Štys, 1981, endemic to the Philippine Islands and known from many individuals, differs from other *Hoplitocoris* subgenera by absence of crossvein delimiting the basal cell from all other members of this specious genus (Štys 1981).

Simply, the presence or absence of some crossoveins of great diagnostic importance are unstable. Sometimes these may characterize large groups of genera, sometimes small monophyla, sometimes it is individually variable but clearly recognizable as a rare mutated forewing phenotype. In *Phaenicocleus schwendingeri* the situation resembles a transitional fluctuating variation and shows that the gene for the expression of crossovein delimiting the basal cell was not lost but is only sleeping in the genus.

**Species-specific diagnostic characters**

A heteropterist studying the alpha-taxonomy of species of Enicocephalomorpha often gets an impression that the morphospecies within a genus are greatly variable and nearly amorphous entities differing largely by general facies, vestiture, texture of cuticle, absolute and relative dimensions, and similar characters whose states are difficult to define and communicate. Paraphrasing the famous phrase by Remane (1955, in German) used for differentiation of a new species of the Miridae, the species of enicocephalids are usually recognizable by a “set of character states inexpressible by words and affecting our sensory system as a complex.” The exceptions are species with rich male genitalia or clear-cut differences in colour patterns and/or vestiture.

The illustrations (Figs. 15–23, 27–29) of diagnostic characters of *Phaenicocleus* species, with their descriptions and key, show that there is an array of characters (structure of median or mesal part of the hindlobe of head, median and central structures on the midlobe and hindlobe of pronotum, mode of association of anterior prosupracoxalia with a species-specifically shaped mid-structure of euprosterum, median of eumetasternum, shape of male guide and its internal sclerite), which can be used for precise species diagnostics and which have been overlooked by former authors, or used (medians of head and pronotum, shape of the guide) spotwise and *ad hoc* only.

Precisely the same situation we have found when revising the species of the endemic Madagascan specious genus *Proboscidopirates* Villiers, 1958 (Štys & Baňař, MS). The diagnostics of the species of the Enicocephalidae, even those with reduced male genitalia, do not thus seem fundamentally different from that of other groups of Heteroptera; only one must look more for the neglected sources of qualitatively different character states.

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**References**

