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Revision of the genus *Heliomantis* Giglio-Tos 1915 (Insecta: Mantodea: Hymenopodidae)

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**Summary.** The little-known flower mantis genus *Heliomantis* Giglio-Tos 1915 (Hymenopodidae) distributed in South and South-Eastern Asia is revised. All species are redescribed. New data on the morphology, distribution and ecology are given, and all known specimens are listed. The lectotype of *H. elegans* (Navás 1904) is designated. Due to highly divergent morphology, *H. latipennis* Werner 1930 from Sarawak, Bornéo, is transferred to *Werneriana* **n. gen.**, leaving the genus *Heliomantis* with the only species, *H. elegans* (Navás, 1904).


http://www.zoobank.org/urn:lsid:zoobank.org:pub:DDA3941B-1A65-4576-8E92-570B0C9B2FFE

**Keywords:** Dictyoptera; Anaxarchini; taxonomy; revision; new genus; Oriental region

**Mots clés:** Dictyoptera; Anaxarchini; taxonomie; révision; nouveau genre; région de l’oriental

Hymenopodidae (the flower mantises) is a diverse praying mantis family including at least 38 genera distributed in Africa and Asia (Svenson et al. 2015). The group is extremely heterogeneous. While many of its genera are famous for supposed plant mimicry, including flowers (O’Hanlon et al. 2014), others do not exhibit such peculiar features – they have a very short or absent vertex process, possess a long prothorax, slender fore femora, very short middle and hind leg lobes (if any) and are not particularly colourful; in other words, they resemble the “typical green mantis” ecomorph.

Among such genera is *Heliomantis* Giglio-Tos 1919, a rarely collected genus, which has been placed in Hymenopodinae Anaxarchini in the recent revision of the flower mantises and allied families (Svenson et al. 2015). The genus includes two species with widely separated distributions, *H. elegans* (Navás 1904) and *H. latipennis* Werner 1930. They also differ considerably by their morphology, making both the old key of Giglio-Tos (1927) and the new key by Svenson et al. (2015) insufficiently clear for identification of the genus: the former was constructed before the description of *H. latipennis*, while only *H. elegans* was investigated for the latter. By a thorough examination of the type material and the original descriptions, it became evident that the two species of the genus *Heliomantis* actually belong to different genera.

**History of the genus**

Navás (1904) described the species *Polyspilota elegans* Navás 1904 on the basis of a pair, a male and a female, collected in Kurseong (now a town in Darjeeling district of West Bengal, India). The description was detailed, but without figures. Later, the female was sent to I. Bolivar and the male was sent to E. Giglio-Tos for further studies.

Bolivar (1914) erected the genus *Paraspilota* Bolivar 1914 for *P. elegans* on the basis of the female sent to him. In his opinion, the species is close to *Polyspilota* Burmeister 1838, *Prohierodula* Bolivar 1908 and *Sphodromantis* Stål 1871 (Mantidae), with which he compared the new genus.

Giglio-Tos (1915) erected the genus *Heliomantis* Giglio-Tos 1915 for *Polyspilota elegans* on the basis of the male sent to him, placing the new genus in Acromantinae. Giglio-Tos provided no description and figures for the erected genus, only noting that it “closer resembles” *Anaxarcha* Stål 1877 (“assai affine a Anaxarcha”; Giglio-Tos 1915, p. 2).

Giglio-Tos (1919) placed the genus *Heliomantis* in Acromantinae Acromantes, noting, however, that it is almost

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intermediate between the groups Acromantes and Anaxarchae (i.e. Anaxarcha, the only genus in the group at that time). He mentioned the work of Bolivar and possible synonymy of Heliomantis and Paraspilota Bolivar 1914. He admitted that he had no access to the work and no communication with I. Bolivar, so the true status of Paraspilota elegans was unknown to him. Apparently, both Giglio-Tos and Bolivar didn’t know that Bates (1888) described Paraspilota Bates 1888 as a subgenus of the genus Anomala Samouelle 1819 (Coleoptera: Scarabaeidae: Rutelinae). According to Articles 23, 52 of ICZN, that makes Paraspilota Bolivar 1914 a junior homonym and invalid name. Werner (1916) described the genus Deiroharpax Werner 1916 with two species: D. viridis Werner 1916, based on a male from Sikkim, India and D. hyalina Werner 1916, based on a female from Sumatra. He provided figures of the pronotum and forewings along with the descriptions.

Giglio-Tos (1927) treated the genus Heliomantis in the group Acromantes and briefly described the male that was sent to him, again with no figures. Werner (1930) described the second species of Heliomantis, H. latipennis Werner 1930, during his work on the Asian Mantodea from the collection of NRM. A brief description on Latin was based on a female from Sarawak, a photograph of which was also in the paper. Werner noted its proximity to D. viridis, but provided no differential diagnosis. On the page 6 of the same paper Werner placed a note about a letter from Max Beier, who recognized that D. hyalina belongs to the genus Oligomantis Giglio-Tos 1915, while D. viridis is identical to H. elegans.

Beier (1934), in his catalogue of Hymenopodidae, formally synonymized D. viridis with H. elegans (simultaneously, the genus Deiroharpax became junior synonym of Heliomantis) and transferred D. hyalina to the genus Oligomantis. While he left H. latipennis Werner 1930 under Heliomantis in the catalogue, he marked it with “?”, indicating his uncertainty.

Lombardo (1993) reported H. elegans from Nepal.

Mukherjee et al. (1995) complemented the description of H. elegans, provided figures for the male and reported the species from additional locations in India.

Mukherjee et al. (2014) listed additional location for H. elegans in Nepal.

Ehmann and Borer (2015) reported H. elegans from Bhutan.

Svenson et al. (2015) transferred H. elegans and the whole genus from Hymenopodidae Acromantinae to Hymenopodidae Anaxarchini, placing it sister to the genus Odontomantis Saussure 1871.

Material and methods

Abbreviations

BMNH: The Natural History Museum, London, UK

ICZN: International Code on Zoological Nomenclature (ICZN 1999)

MNCN: Museo Nacional de Ciencias Naturales, Madrid, Spain

NHMW: Naturhistorisches Museum, Vienna, Austria

NRM: Naturhistoriska Riksmuseet, Stockholm, Sweden

SMNK: State Museum of Natural History, Karlsruhe, Germany

ZSI: Zoological Survey of India, Kolkata, India

ZSM: Zoologische Staatssammlung, München, Germany

Examined material of Heliomantis elegans (Navás 1904) used in this study is deposited in the collections of SMNK, NMB and ZSM. The male genitalia were prepared according to the standard protocol for Mantodea (e.g. Shcherbakov & Savitsky 2015).

Photographs of specimens of the main material were taken with a Canon PowerShot A630 digital camera (Tokyo, Japan) and processed using software Adobe Photoshop 8.0.1 (Adobe Systems, San Jose, CA, USA). Photographs of the male genitalia were taken with Keyence VHX-2000 digital microscope (Osaka, Japan). Photographs of the lectotype of H. elegans were kindly provided by Mercedes Paris (MNCN), made with a Nikon D700 camera (Tokyo, Japan) and Tamron 90 mm macro lens (Saitama, Japan). Photographs of the holotype of Deiroharpax viridis were kindly provided by Harald Bruckner (NHMW), made with Nikon D60 camera, equipped with Nikon AF-S Micro Nikkor 105 mm 1:2.9 G ED lens and Sigma EM-140 DG flash (Kawasaki, Japan).

High resolution photographs of the type of H. latipennis Werner 1930, made with Canon EOS Utility 5D and Zerene Stacker software (http://zerenesystems.com/cms/home) were studied, due to courtesy of Gunvi Lindberg (NRM).

All figures were processed using Adobe Photoshop CS5 by the first author.

Terminology of the external features is given according to Wieland (2013) and Svenson et al. (2015), of the male genitalia according to Klass (1997).

Results and discussion

Even at first glance, the two species of Heliomantis appear to be very different from each other. H. latipennis differs from H. elegans in several important morphological characters. It lacks meso- and metafemoral preapical lobes (Figure 7C) and the fore coxal apical black band (Figure 5). The pronotum (Figure 6D) is shorter and bulkier, with weakly defined supracoxal extension, not strongly contracting in the metazon. The forewings are lanceolate, barely exceeding the end of abdomen, and the hind wings have partially pink coloration (Figure 5). In contrast, in H. elegans the pronotum is slender, with well-developed supracoxal extension and the metazon noticeably constricting in the middle, while the forewings are oval and well exceed the end of the abdomen, even in female. Other genera of Anaxarchini, Anaxarcha and Odontomantis, do not have meso- and metafemoral lobes. Species of Anaxarcha have slender pronotum similar to the pronotum of H. elegans (Figure 6A, B), while Odontomantis (except O. rhysa Werner 1930) has very short pronotum with (Figure 6E) or without (Figure 6F) strongly pronounced supracoxal extension; even in the latter case lateral edges of the prozone start to noticeably converge immediately
anteriad the point of maximum width, which is not the case in *H. latipennis*.

Another notable character lies in female forewing venation. Most mantises have a quite simple structure of cross-veins pattern posteriad RP+M: straight or very slightly curved cross-veins form double rows of more or less rectangular cells between the main veins (Figure 9C; Wieland 2013, fig. 334). In other instances, the cross-veins, while still nearly perpendicular to the main veins at their base, form irregular cells, which sometimes can be very dense, resembling archedictons (Figures 8A, 9A). The cells themselves are generally not elongated in any particular direction. The third state, resembling at first glance the second one, has in fact a totally different structure: dense cross-veins form elongated, mostly longitudinal cells, or longitudinal themselves (Figure 8B, C).

Females of most Hymenopodidae, including the majority of Acromantinae genera, are characterized by the first state (*e.g.* *Oligomantis*, Figure 9C). The second state is rarer and can be observed in most Hymenopodini, *Psychomantis* Giglio-Tos 1915 and in considerable number of species of *Acromantis* Saussure 1870. Inside Anaxarchini it can be observed in *Heliomantis elegans* (Figure 8A) and most species of *Odontomantis* (*e.g.* *O. foveafrons* Zhang 1985, Figure 9A), the only two exceptions to our knowledge being *O. planiceps* (De Haan 1842) possessing the first state (the common “double rows” pattern), and *O. rhyssa*, which has only a single row of cells between each two main veins (Figure 9B). This state is rarely encountered outside Hymenopodidae. It should be noted that *O. rhyssa* has many other interesting characters separating it from other *Odontomantis* species (*e.g.* relatively elongated pronotum, densely covered by tubercles, Figure 6G) and probably deserves its own genus. The third state can be found in *Heliomantis latipennis* (Figure 8B) and all species of *Anaxarcha* (Figure 8C) and appears to be unique at least among Hymenopodidae and allies, further stressing morphological differences between two species of *Heliomantis*. Based on these differences we suggest to erect a new genus for *H. latipennis*, rendering the genus *Heliomantis* monotypic.

**Genus Heliomantis Giglio-Tos 1915**


**Type species.** *Polyspilota elegans* Navás 1904 (by monotypy).

**Diagnosis.** *Heliomantis* differs from *Anaxarcha* (Figures 6A, B, 7D, 8C) by presence of ventral meso- and metafemoral preapical lobes (Figure 7B), strongly curved main forewing veins and dense, irregular cross-vein pattern (Figure 8A); from *Odontomantis* (Figures 6E–G, 9A, B) by elongated pronotum with pronounced supracoxal extension (Figure 6C) and presence of ventral meso- and metafemoral preapical lobes (Figure 7B); from *Werneriana* n. gen. (Figures 5, 6D, 7C, 8B) by elongated pronotum with pronounced supracoxal extension (Figure 6C), presence of ventral meso- and metafemoral preapical lobes (Figure 7B), long wings and irregular cells in female forewing venation (Figure 8A); from *Oligomantis* (Figure 9C) by dense forewing venation (Figure 8A) and more dorsoventrally compressed pronotum; from *Psychomantis* by absence of median process on the head vertex (Figure 4A, B), more dorsoventrally compressed pronotum, smooth surface of pronotum, straight dorsal edge of fore femora and only one ventral lobe on middle and hind femora (Figure 7B); from *Rhomantis* by absence of median process on the head vertex (Figure 4A, B), shorter and more dorsoventrally compressed pronotum and dense forewing venation (Figure 8A); from *Acromantis* (Figure 7A) and *Citharomantis* by rounded apices of hind wings (Figures 1–3); from *Ambivia* by absence of median process on the head vertex (Figure 4A, B), smooth surface of pronotum, straight dorsal edge of fore femora, only one ventral lobe on middle and hind femora (Figure 7B) and dense forewing venation (Figure 8A); from *Majangelia* by absence of median process on the head vertex (Figure 4A, B), smooth surface of pronotum and straight dorsal edge of fore femora.

**Systematic position.** Giglio-Tos (1927) clearly separated Acromantes from the other tribes of his Acromantinae, including Anaxarchae, by a presence of preapical lobes on middle and hind femora (Figure 7A), absence of a long median head process, spherical eyes and smooth pronotum. *H. elegans* (Figures 1–4, 6C, 7B, 8A) corresponds to this diagnosis of the tribe. Externally, it is similar to the acromantine genera *Psychomantis*, *Rhomantis* Giglio-Tos 1915 and *Oligomantis* in slender pronotum (Figure 6C), with metazone strongly narrowing in the middle, and fore coxae with contiguous apical lobes and same coloration as in these genera, including a black preapical band (Figures 4A, B). However, it lacks vertex process; prozone of its pronotum is more gently convex, not strongly laterally compressed; its fore femora are without a trace of dorsal lobes, and the meso- and metafemoral lobes are widely oval (Figure 7B) and not triangular like in the rest of Acromantes (*e.g.* Figure 7A). Nevertheless, the position of *Heliomantis* inside Acromantes (= tribe Acromantini) was not disputed by later authors, until recently.

Svenson et al. (2015) conducted phylogenetic analyses of all genera included in Hymenopodidae *sensu* Ehrmann
Figure 1. Heliomantis elegans (Navás 1904), habitus. A, male, SMNK #12622, dorsally; B, female, SMNK #03625, dorsally; C, female, ventrally; D, male, ventrally. Photos: R. Ehrmann, © SMNK, published with permission.
2002, Empusidae, Mantidae: Sibyllinae and Mantidae: Phyllotheliinae, using molecular data from 10 gene fragments, as well as morphology. *H. elegans* was used as the representative of the genus *Heliomantis*. Since a sample of DNA of *H. elegans* was unavailable, only morphological data were used to determine its place on the phylogenetic tree. In the equally weighted analysis of morphology under maximum parsimony (see Svenson et al. 2015, fig. 6A), *H. elegans* was recovered in large basal polytomy. Next, Svenson et al. reconstructed ancestral states on the total evidence topology (recovered through Bayesian inference with Mk1 model for morphology), identified “synapomorphies” of the respective clades and increased the weight of corresponding characters in morphological dataset up to 6, motivating it by poor resolution of the strict consensus tree in case of equally weighted characters (Svenson et al. 2015, p. 12). In the upweighted morphological analysis under maximum parsimony (see Svenson et al. 2015, fig. 6B) as well as in the total evidence analysis (see Svenson et al. 2015, fig. 7) *H. elegans* was recovered deep in Anaxarchini as the sister taxon to *Odontomantis*, while Anaxarchini as a clade was very distant from Acromantinae sensu Svenson et al. (2015) in both analyses. The only apomorphy unifying *H. elegans* and *Odontomantis* in the analysis is “the costal area width is 10–24% of the width of discoidal area of female fore wing” (state 1 of character 61; see Svenson et al. 2015, table S3), contrary to plesiomorphic state found in *Anaxarcha*, where the ratio is supposedly 25–50%. However, this character is essentially continuous and no argumentation in favour of delineating these character states in such a way was provided in the paper. Therefore, there is no evidence of the clade uniting *Heliomantis* and *Odontomantis*.

Figure 2. *Heliomantis elegans* (Navás 1904), lectotype female in dorsal and ventral perspective and its labels. Photos: M. Paris, © M. Paris, MNCN, published with permission.
Figure 3. *Deiroharpax viridis* Werner 1916, holotype male in dorsal, lateral and ventral perspective and its labels. Photos: H. Bruckner, © NHMW, NOaS Image Collection, published with permission.
Though there is currently no counterevidence to the monophyly of Anaxarchini including *Heliomantis*, we believe that addition of molecular data from the fresh material to the analysis is important for reliable phylogenetic placement of the genus. Moreover, it is desirable to reinvestigate external morphological characters, as well as the male genitalia across Anaxarchini and possibly even Hymenopodidae, to ensure correct homologization of all phylogenetically informative characters, usable for phylogenetic assessment of *Heliomantis* and its presumed sister taxa.

*Heliomantis elegans* (Navás 1904) ([Figures 1–4, 6C, 7B, 8A])


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**Figure 4.** *Heliomantis elegans* (Navás 1904), details of morphology. **A,** anterior part of the male, ventrally; **B,** anterior part of the female, ventrally; **C,** asymmetrical variation of the subgenital plate, ventrally; **D,** male genitalia, preparation of SMNK #12622, ventrally; **E,** variation of the phalloid apophysis.


Deiroharpax viridis Werner 1916: 283–284, fig. 6 (male) (India-NE: Sikkim) (syn. by Beier 1934: 11); Giglio-Tos 1927: 524; Werner 1930: 6.

**Type material.** Of two syntypes, male and female, the male could not be located. The second sytype, female, is

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**Figure 5.** *Werneriana latipennis* (Werner 1930), holotype female in dorsal and ventral perspectives and its labels. Photos: G. Lindberg, © NRM, published with permission.
Figure 6. Pronotum of female. A, Anaxarcha limbata Giglio-Tos 1915; B, A. acuta Beier 1963; C, Heliomantis elegans (Navás 1904); D, Werneriana latipennis (Werner 1930); E, Odontomantis foveafrons Zhang 1985; F, O. planiceps (De Haan 1842); G, O. rhyssa Werner 1930. Scale bar 1 mm.

Figure 7. Apex of middle femur of female, dorsally, arrow marks the preapical lobe. A, Acromantis sp.; B, Heliomantis elegans (Navás 1904); C, Werneriana latipennis (Werner 1930); D, Anaxarcha limbata Giglio-Tos 1915.
Figure 8. Proximal half of forewings in females, dorsally. A, *Heliomantis elegans* (Navás 1904); B, *Werneriana latipennis* (Werner 1930); C, *Anaxarcha limbata* Giglio-Tos 1915. Part of the cross-veins network highlighted. See the text for details.
deposited in the collection of MNCN under the code MNCN Ent 140643 and designated herein as the lectotype (Figure 2). It is satisfactorily preserved. Head without both flagella, with eyes and frons partially destroyed. Prothorax with large longitudinal gap dorsally and ventrally. Distal parts of the fore coxae glued to the prosternum and the pin. Parts of mesothorax, middle and hind coxae destroyed; right middle leg from the femur glued to right hind coxa apart from the right middle coxa. Left pair of wings spread; anal fan of the hind wing posteriorly torn. The lectotype has following labels: handwritten “Polyspilota elegans + Nav. Kurseong

Table 1. Depositaries with known specimens of Heliomantis elegans (Navás 1904).

<table>
<thead>
<tr>
<th>Depositary</th>
<th>Number of specimens</th>
<th>Country of origin</th>
<th>Previous publications</th>
</tr>
</thead>
<tbody>
<tr>
<td>BMNH</td>
<td>3 males, 1 female</td>
<td>India</td>
<td>Svenson et al. (2015)</td>
</tr>
<tr>
<td>MNCN</td>
<td>1 female (lectotype)</td>
<td>India</td>
<td>Navás (1904) and Bolivar (1914)</td>
</tr>
<tr>
<td>NHMW</td>
<td>2 males (including the holotype of D. viridis)</td>
<td>India, India?</td>
<td>Werner (1916)</td>
</tr>
<tr>
<td>NMB</td>
<td>1 male</td>
<td>Bhutan</td>
<td>Ehrmann &amp; Borer (2015)</td>
</tr>
<tr>
<td>SMNK</td>
<td>1 male, 1 female</td>
<td>Bhutan, Nepal</td>
<td>Mukherjee et al. (2014) and Ehrmann &amp; Borer (2015)</td>
</tr>
<tr>
<td>ZSI</td>
<td>4 males, 1 female</td>
<td>India</td>
<td>Mukherjee et al. (1995)</td>
</tr>
<tr>
<td>ZSM</td>
<td>3 males</td>
<td>India, Nepal</td>
<td>Lombardo (1993) and Ehrmann &amp; Borer (2015)</td>
</tr>
</tbody>
</table>

Figure 10. Distribution of Heliomantis elegans (Navás 1904) and Werneriana latipennis (Werner 1930).
Re-examination of the holotype of *Deiroharpax viridis* Werner 1916 (Figure 3) confirms its synonymy with *H. elegans*.


India: 2 ♂, West Bengal, Darjeeling env. (ZSM).

There are very few specimens in the collections worldwide: only 18 are known to the authors, including cited in various literature (Table 1).

**Redescription.** Female (Figures 1B, C, 2, 4B, 6C, 7B, 8A). Medium sized (body length 47–54 mm).

Head triangular. Vertex straight, smooth, without any process. Parietal furrows deep, but lateral tubercles absent. Ocelli small, with diameter less than that of scapae, forming triangle, not elevated. Scutellum transverse, pentagonal, nearly smooth, anterior margin concave, posterior margin forming wide, triangular medial process projecting anteriorly. Clypeus rectangular. Labrum almost as wide as clypeus, widely rounded at apex.

Pronotum (Figure 6C) moderately slender, with distinct oval, elongated supracoxal dilatation, dorsally smooth. Prozone narrowing anteriorly, with rounded anterior edge, dorsally slightly bulged, with shallow median groove. Prozone separated from metazone by distinct supracoxal sulcus, medially straight, laterally curved toward the anterior. Metazone 2.6–2.7 times longer than prozone, constricted posterior supracoxal dilatation, with edges parallel and diverging again only near posterior edge. Dorsal surface of metazone medially with very shallow groove and low, short, less than 1/3 of metazone’s length, carina inside the groove. Lateral margins of pronotum slightly lamellar, in prozone covered by short, blunt spines, in supracoxal dilatation almost smooth, with only a few barely noticeable low tubercles, in metazone covered by very spaced, long, apically rounded tubercles.

Forelegs typical of praying mantises (Figure 4B). Coxae slightly shorter than metazone of pronotum, triangular in cross-section, with anterior apical lobes adjacent. Dorsal margin with 7–9 relatively large denticles inclined toward the apex of coxa, with 1–3 smaller denticles between them. Ventral margin with numerous small, very short spines. Dorsal margin of femora straight or very slightly concave in the middle; ventral margin with 13–14 alternating in length anteroventral spines, 4 posteroventral spines, 4 discoidal spines and small genicular spines on each side. Tibiae with 11–12 anteroventral spines and 9–10 posteroventral. Posteroventral tibial spines strongly inclined, but their bases clearly separated from each other. Middle and hind femora with small, very elongated preapical lobe (Figure 7B). Middle and hind tibiae shorter than femora, apically with triangular elongation and two short spines. Hind metatarsus slightly longer than all other tarsomeres combined.

Both pair of wings far surpassing the end of abdomen (Figure 1B, C). Forewings wide, gradually narrowing and narrowly rounded at apex. Costal field wide, main veins strongly curved posteriorly, venation between them very dense; irregular (Figure 8A). Stigma very elongated, not well defined. Hind wings slightly shorter than forewings, wide, more or less triangular. Anterior edge curved posteriorly near apex, apex narrowly rounded.

Abdomen wide, tergites and sternites simple, without lobes. Anal plate transverse, widely rounded. Cerci circular in cross-section, simple.

Main life colour green. Anterior surface of fore coxae with black band in apical third, not reaching the end of apical lobes. Anterior surface of fore femora with irregular black spot at the base of first two anteroventral spines, almost reaching the middle of femora’s width. Forewings subopaque with yellowish costal field. Wings transparent, hyaline with yellowish main veins, except yellowish-brownish costal field.

Male (Figures 1A, D, 3, 4A, C–E) very similar to female, but smaller (body length 32–37 mm). Comparing to female, eyes bulging, pronotal and coxal spines relatively shorter, femoral spot less distinct. Anal plate slightly more triangular than in female, cerci with 13–14 cerceromes. Genital plate wide, in some specimens more or less semicircular, in others unusually asymmetrical (Figure 4C), with small and short styli. Male genitalia (Figure 4D) weakly sclerotized, similar in shape and structure to *Anaxarcha*. Sclerite L4A elongated, without any kind of process. Sclerite L4B very narrow and elongated. Sclerite L2 mostly membranous, its titillator short and rounded. Sclerite L1 anteriorly curved, very long and narrow, posteriorly (phalloid apophysis) sclerotized, more or less rounded, with little variation of shape (Figure 4E). Sclerite R1A triangular, its apex abruptly curved dorsoventrally. Sclerite R3 in distal 2/3 widened, more or less rectangular in shape.

**Measurements (in mm).** Total length male 32–37, female 47–54; head width male 5.0, female 6.9; pronotum length male 11–12, female 16; metazone length male 7.2, female 11.0; pronotum maximum width male 3.6–4.0, female 5.2–
5.5; fore coxa male 7.8, female 11.0; fore femur male 9.1–9.2, female 12.0; fore wing length male 37–39, female 48.0–48.4; fore wing width male 10.0–10.1, female 14.3.

**Distribution.** India-NE, Nepal, Bhutan (Figure 10). Apparently the species prefers mountain forests: there are no specimens recorded from elevation lower than 1600 m, while some were collected as high as 2000–2150 m.

**Genus Werneriana n. gen.**

**Type species.** *Heliomantis latipennis* Werner 1930.

**Diagnosis.** *Werneriana n. gen.* differs from *Heliomantis* (Figures 1–4, 6C, 7B, 8A) by shorter, much more robust pronotum with much less pronounced supracoxal dilatation (Figure 6D), by absence of ventral lobes on middle and hind femora (Figure 7C), by much shorter, lanceolate forewings, barely covering the apex of abdomen (Figure 5) and in female by very elongated cells in forewing venation (Figure 8B); from *Anaxarcha* (Figures 6A, B, 7D, 8C) by shorter, much more robust pronotum with much less pronounced supracoxal dilatation (Figure 6D), by much shorter, lanceolate forewings, barely covering the apex of abdomen (Figure 5) and by hind wings clearly shorter than forewings; from *Odontomantis* (Figures 6E–G, 9A, B) by almost parallel edges of supracoxal extension in prozone (Figure 6D), by narrow separation of ScP and RA and very elongated cells in female forewing venation (Figure 8B) and by complete absence of dark pattern on hind wings of females (Figure 5).

**Systematic position.** The genus fits the diagnosis of Anaxarchini. Unique character of forewing cross-vein pattern shared with *Anaxarcha* suggest that the latter is a sister-group of *Werneriana n. gen.*. However, as in the case of *Heliomantis*, a thorough study of morphology (including male genitalia) as well as obtaining DNA sample is necessary to test this hypothesis.

**Etymology.** The genus is named in honour of the author of its type species, Austrian zoologist Franz Werner. The name gender is feminine. Monotypic, therefore the generic characteristics are those of the type species.

**Werneriana latipennis** (Werner 1930), n. comb. (Figures 5, 6D, 7C, 8B)

*Heliomantis latipennis* Werner 1930: 7, Taf. 2, fig. 2 (female) (Borneo: Sarawak); Sjöstedt 1930: 13; Beier 1934: 11; Ehrmann 2002: 169; Otte & Spearman 2005: 76; Schwarz & Konopik 2014: 142.

**Type material.** Holotype: ♀, Malaysia: Borneo, Sarawak, Murad Mt., 6500 f, 17.XI, Mjöberg leg. (NRM-MANT 0002699)

**Redescription.** Female (Figure 5). Medium sized (body length 29 mm).

Head triangular. Vertex slightly convex, without process. Posterior lateral tubercles between compound eyes and parietal furrows small, but noticeable. Between vertex bump and each parietal furrow noticeable depression, thus five small bumps in total between compound eyes. Ocelli small. Scutellum (without apical spine) strongly transverse, anterior border concave, posterior border very strongly angular, its middle extended into a narrow spine with rounded apex.

Prothorax (Figure 6D) elongated. Length of pronotum 2.28 times its maximum width. Anterior edge of prozone widely rounded. Metazone of pronotum 2.2 times the length or prozone, separated from the latter by shallow supracoxal sulcus. Supracoxal dilatation weak, widely oval. Pronotum dorsally with a median groove, covered by low tubercles in prozone, otherwise smooth. Lateral edges of pronotum covered by large obtuse tubercles, except anterior and posterior edges; in prozone tubercles short, stout, densely arranged, in supracoxal dilatation very small and flat, in metazone longer, rounded and more spaced than in prozone.

Forelegs typical of praying mantises. Coxa longer than metazone of pronotum; anterior apical lobes contiguous; dorsal edge with numerous short, sharp, irregularly alternating larger and smaller spines; ventral edge with very short sharpened tubercles. Femur wide, with dorsal edge straight. Anteroventral row with 14 spines total plus genicular spine, first 10 spines in the row long and short, alternating, penultimate 3 spines short, last spine long; posteroverentral row with 4 spines plus genicular spine, most distal spine a little shorter than others; discoidal row with 4 spines, the 1st much shorter than the rest, the 2nd as the 4th, the 3rd more than twice the 2nd. Claw furrow in proximal half of fore femur. Tibia approximately half the length of fore femur, anteroventral row with 12 distally elongating spines, posteroverental row with 11 strongly inclined and packed spines plus very long and curved tibial claw.

Middle and hind legs short, simple. Ventral edges of middle and hind femora slightly lamellar (Figure 7C), each apex of femur with very short genicular spine.

Forewings barely cover end of abdomen, wide, lanceolate, with narrowly rounded apex and very dense venation (Figure 8B). Jugal area very small. Stigma small, very elongated, highly indistinct. Hind wings shorter than forewings, anterior edge curved near apex.

Abdomen wide. Cerci simple, circular, with 12 noticeable cercomeres.

Coloration. Overall life colour green. Forelegs unicolor, except for completely black large femoral spines and small femoral and all tibial spines with dark-brown apices. Forewings greenish, semi-transparent, veins green, costal field and cells in proximal half of discoidal field light-brown
in preserved specimen. Hind wings transparent, brownish along anterior edge, bright rose centrally.

Male not known.

**Measurements (in mm).** Total length 29, pronotum length 8, metazone length 5.5, maximum width 3.5, fore femur 8.5, forewing length 18, width 6.5.

**Distribution.** The only known specimen is the holotype female, collected by Eric Mjöberg 85 years ago on the highest mountain of Sarawak, Mt Murud (Gunung Murud, 2423 m), at the elevation of 1830 m (Figure 10). No new specimens were reported since then (Schwarz & Konopik 2014). Given the short wings and high elevation at which the specimen was collected, it may be hypothesized that this species (and, probably, the genus as well) is endemic to Borneo. Presently, the mountain is part of Pulong Tau National Park.

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**References**


