Species, Phylogeny and Evolution 1, 3 (30.9.2008): 147-170.

The genus *Metallyticus* reviewed (Insecta: Mantodea)

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Abstract

Metallyticus Westwood, 1835 (Insecta: Dictyoptera: Mantodea) is one of the most fascinating praying mantids but little is known of its biology. Several morphological traits are plesiomorphic, such as the short prothorax, characters of the wing venation and possibly also the lack of discoidal spines on the fore femora. On the other hand, *Metallyticus* has autapomorphies which are unique among extant Mantodea, such as the iridescent bluish-green body coloration and the enlargement of the first posteroventral spine of the fore femora.

The present publication reviews our knowledge of *Metallyticus* thus providing a basis for further research. Data on 115 *Metallyticus* specimens are gathered and interpreted. The Latin original descriptions of the five *Metallyticus* species known to date, as well as additional descriptions and a key to species level that were originally published by Giglio-Tos (1927) in French, are translated into English. The only published records of *Metallyticus*' behaviour by Shelford (1903, 1916), as well as personal observations by several people and data on the distribution of *Metallyticus*, its biology, phylogeny and classification, are cited and compared.

A brief introduction to the morphology of *Metallyticus*, including detailed morphological drawings, a distribution map and a plate of historical drawings, is presented. Furthermore, photographs of living *Metallyticus* specimens in their natural habitat are furthermore published for the first time.

Zusammenfassung

Metallyticus Westwood, 1835 (Insecta: Dictyoptera: Mantodea) gehört zu den faszinierendsten Gottesanbeterinnen, allerdings ist über die Biologie der Gattung kaum etwas bekannt. Mehrere morphologische Merkmale sind plesiomorph, beispielsweise der kurze Prothorax, Merkmale der Flügeladerung und vermutlich das Fehlen der Discoidaldornen auf den Vorderfemora. Andererseits weist *Metallyticus* Autapomorphien auf, die innerhalb der rezenten Mantodea einzigartig sind, wie zum Beispiel die metallisch schillernde, blau-grüne Färbung des Körpers und die Vergrößerung des ersten posteroventralen Dorns der Vorderfemora.

Die vorliegende Veröffentlichung fasst das Wissen über *Metallyticus* zusammen, um eine Grundlage für weitere Forschung zur Verfügung zu stellen. Die Daten von 115 *Metallyticus*-Exemplaren werden zusammengeführt und interpretiert. Die lateinischen Originalbeschreibungen der fünf bisher bekannten *Metallyticus*-Arten sowie zusätzliche Beschreibungen und ein Bestimmungsschlüssel zu den Arten, von Giglio-Tos (1927) in Französisch veröffentlicht, werden ins Englische übersetzt. Die einzigen publizierten Berichte zum Verhalten von *Metallyticus* von Shelford (1903, 1916), persönliche Sichtungen mehrerer Beobachter sowie Daten über die Verbreitung von *Metallyticus*, die Biologie, Phylogenie und Klassifikation werden zitiert und miteinander verglichen.

Eine kurze Einführung in die Morphologie von *Metallyticus* einschließlich detaillierter morphologischer Zeichnungen, einer Verbreitungskarte sowie einer Tafel mit historischen Abbildungen wird präsentiert. Erstmals werden Fotografien lebender *Metallyticus*-Exemplare in ihrem natürlichen Lebensraum publiziert.

1 Introduction

Mantodea (praying mantises, praying mantids) are a subordinate taxon of the Polyneoptera. Together with Blattodea (cockroaches and termites), they form the monophyletic Dictyoptera (Hennig 1969; Kristensen 1991, 1995; Klass 1995, 1997, 2003; Maekawa et al. 1999; Beutel & Gorb 2001, 2006; Wheeler et al. 2001; Bohn & Klass 2003; Kjer 2004; Grimaldi & Engel 2005; Terry & Whiting 2005; Cameron et al. 2006; Kjer et al. 2006; Klass & Meier 2006; Inward et al. 2007; Ware et al. 2008).

About 2,300 extant species of Mantodea have been

described so far (Ehrmann 2002). They are thermophilic and therefore distributed predominantly in the subtropical and tropical regions (e.g. Handlirsch 1930; Beier 1968; Balderson 1991; Balderson et al. 1998; Ehrmann 2002; Klass & Ehrmann 2003) where they inhabit all kinds of environments from the tropical wet forests to the savannahs and deserts (e.g. Balderson et al. 1998; Ehrmann 2002; Klass & Ehrmann 2003). Only few species exceed 45-46° latitude on either hemisphere (e.g. *Mantis religiosa* Linné in Europe, *Empusa pennicornis* (Pallas) in Russia, and *Orthodera novaezealandiae* (Colenso) on New Zealand's South Island (Beier 1939: 5, 1968: 13; Ramsay 1990: 19 and map 1; Ehrmann 2002: 30; Klass & Ehrmann 2003: 193).

Praying mantises are predatory, although pollen-feeding as additional protein source has been described (Beckman & Hurd 2003). They usually feed on other arthropods but have also been observed devouring small vertebrates such as small birds, lizards, frogs, or small snakes and mammals (e.g. Chopard 1949; Beier 1968; Ridpath 1977; Froesch-Franzon 1982; Balderson 1991; Ehrmann 1992; Bohn & Klass 2003; Grimaldi & Engel 2005). In connection with their predatory lifestyle, the mantodeans have evolved powerful raptorial forelegs that carry two ventral rows of sturdy spines on femur and tibia in most species and a strong tibial spur ("claw") in all mantodeans except for *Chaeteessa* Burmeister in which the tibial spur is missing. Derived Mantodea have strongly elongated prothoraces which help to increase the radius of action for catching prey.

Many studies on Mantodea from various scientific fields have been published, the greater part of them listed by Ehrmann (2005). Most of these publications treat highly derived species, mostly from derived taxa (e.g. Levereault 1936, 1938; La Greca & Raucci 1949; Liske 1982, 1989; Rossel 1996; Moran & Hurd 1998; Poteser et al. 1998; Bullaro & Prete 1999; Gonka et al. 1999; Maxwell 1999, 2000; Fagan & Folarin 2001; Yamawaki & Toh 2003; Beckman & Hurd 2003; Hurd et al. 2004; Gemeno et al. 2005; Perez 2005). The most primitive mantodeans have only been considered in few publications (e.g. Shelford 1903, 1916; Hubbell 1925; Beebe et al. 1952; Crane 1952; Smart 1956; Deyrup 1986; La Greca & Lombardo 1989; Klass 1995, 1997; Wieland 2003, 2006; Svenson & Whiting 2004; Salazar 2005; Klass & Meier 2006; Inward et al. 2007; Ware et al. 2008), probably due to their extremely rare occurrence. *Mantoida* Newman, *Chaeteessa* and *Metallyticus* together comprise no more than 19 species described to date (Ehrmann 2002; Salazar 2004, 2005); they are quite small (1-3.5 cm) and seldom collected. Even museums with extensive Mantodea collections often possess only few specimens. Nonetheless, these basal mantids are insects and exhibit many interesting - often plesiomorphic - morphological traits.

This study is an attempt to illuminate the knowledge of one of these basal lineages, the genus *Metallyticus*. Although this is not a taxonomical revision of the genus, this synopsis will hopefully lay a valuable basis for further research and lead to a better understanding of these fascinating insects.

2 Synopsis of the knowledge about *Metallyticus*

2.1 Classification

The taxonomic history of the basal Mantodea, including *Metallyticus*, was briefly summarized by Salazar (2005: 265). The latest classification of Mantodea was published by Ehrmann and Roy in Ehrmann (2002: 374). Fossils showing the characteristic autapomorphies of the genus are unknown to date. The "family" rank for this monogeneric group is redundant and will not be used here.

The genus was described by Westwood in 1835 with *Metallyticus splendidus* as typus generis. It comprises five species:

M. splendidus Westwood, 1835
M. violaceus (Burmeister, 1838), originally described as *Metalleutica violacea*
M. semiaeneus Westwood, 1889
M. fallax Giglio-Tos, 1917
M. pallipes Giglio-Tos, 1917

The synonyms of *M. splendidus* and *M. violaceus* are listed by Ehrmann (2002: 221).

Taxonomical descriptions

In the following, the original Latin descriptions of the species and additional data by Giglio-Tos (1927) in French are cited. The corresponding English translations directly follow the original text passages. The terms "testaceous", "yellowish", and "brownish" by different authors refer to the same type of coloration: the yellowish-brown areas of *Metallyticus*' body that do not show an iridescent coloration (as, for instance, on the mid and hind femora of the late instar nymph in Fig. 20).

Metallyticus Westwood, 1835

> "Corpus oblongo-ovatum, depressum, metallicolor. Prothorax latitudine vix longior, (quartam partem longitudinis abdominis vix aequans,) lateribus fere rectis, absque dilatatione laterali, antice haud angustatus. Oculi maximi rotundati. Caput muticum, vertice plano. Pedes antici maximi; femoribus brevibus crassimis; femora 4 postica simplicia, quam in Mantide crassiora. Abdomen versus apicem acuminatum, apice eius tegminibus alisque perfectis haud obtecto. Antennae simplices.
>
> Nota. Generi Mantidi (ut a Servilleo restricto) affinis. Differt prothoracis brevitate, abdominis apice detecto, coloreque metallico."

Translation: Body oval and elongated, flat, of metallic colour. Prothorax hardly wider than long, (hardly reaching a quarter of the length of the abdomen), its sides almost straight and without lateral expansions, anteriorly not very narrow. Eyes strongly rounded. Head blunt, vertex flat. Anterior legs very large; the short femora sturdy; the four posterior femora simple as in

Key to species level

Giglio-Tos (1927: 39) provided a key to the species in French. The English translation reads as follows:

1 - Coxae of the raptorial forelegs metallic green _____ 2
- Coxae of the raptorial forelegs testaceous (i.e. yellowish-brown, not metallic) _____ 3

2 - Alae smoky _____ *M. splendidus*
- Alae hyaline _____ *M. semiaeneus*

3 - Femora of the raptorial forelegs almost entirely black _____ 4
- Femora of the raptorial forelegs almost entirely testaceous _____ *M. pallipes*

4 - Femora of the raptorial forelegs testaceously hemmed on the edge of the dorsal rim; pronotum carrying two testaceous marks on its posterior rim _____ *M. violaceus*
- Femora of the raptorial forelegs entirely black, pronotum black, without marks _____ *M. fallax*

more corpulent mantodeans. Abdomen caudally pointed, its apex not exactly well covered and protected by the tegmina and alae. Antennae simple.

Note. Similar to the mantodean genera (as restricted by Serville). Distinguishable by the shortness of the pronotum, the bare abdominal apex and the metallic coloration.

Giglio-Tos (1921: 3) provided additional data in Latin that he later translated into French (Giglio-Tos 1927: 39):

"♂.♀. Corps aplati. Ecussion frontal très étroit, le bord sup. saillant, sinué au millieu. Vertex sillonné de chaque côté près des yeux. Sommet du vertex dépassant un peu les yeux, la partie entre les sillons juxtaoculaires large, un peu arquée. Yeux globuleux, très saillants en avant, un peu pedonculés. Ocelles petits chez ♂♀. Pronotum aplati, un peu plus long que large, les bords parallèles lisses ou parfois à peine un peu convergents en avant, le sillon transversal bien marqué. Elytres et ailes développés chez ♂♀. Elytres des ♀ souvent opaques, métalliques, ceux des ♂ souvent hyalins. Hanches ant. larges. Cuisses ant. très dilatées et courtes, triangulaires, le bord sup. arqué à la base, 4 épines externes dont la 1e à partir de la base très longue, très forte et un peu arquée en avant; pas des épines discoïdales; le sillon de la griffe tout-à-fait à la base mais placé sur le bord inf. des cuisses entre les épines internes et externes. Tibias ant. avec 6-7 épines externes fortes. Les pattes post. fortes et courtes. Prosternum caréné au milieu sur la métazone. Cerci longs, grêles, poilus."

Translation: ♂.♀. Body flattened. Scutellum very slender, the upper edge protruding, curved in the middle. Vertex furrowed on either side close to the eyes. Top of the vertex a little bit higher than the eyes, the area between the furrows located near the eyes large, slightly arched. Eyes round, strongly protruding towards the anterior, slightly pedonculated. Ocelli small in both sexes. Pronotum flat, slightly longer than wide, edges smooth and parallel or sometimes slightly convergent in the front, the transverse furrow strongly marked. Tegmina and alae developed in both sexes. Tegmina in ♀ often opaque, metallic, those of the ♂ often hyaline. Anterior coxae large. Anterior femora very wide and short, triangular, the upper rim arched at the base, 4 outer spines of which the first from the base is very long, very sturdy and slightly arched in the front; discoidal spines missing; the claw groove at the very base but located on the inside of the femora between the inner and outer spines. Anterior tibiae with 6-7 sturdy external spines. Posterior legs sturdy and short. The prosternum carries a median ridge on the metazona. Cerci long, slender, hairy.

Metallyticus splendidus Westwood, 1835

"Viridis nitidissimus; tegminibus cupreo-nitentibus; femoribus anticis macula centrali fulva.

Variat colore purpureo, femoribus 4 posticics antice subfulvis.

Long. corp. lin. 14. Expans. tegminum lin. 22.

Habitat in Malabaria."

Translation: Strongly green gleaming; tegmina copper-gleaming; anterior femora with a brownish-yellow mark in the middle. Changes colour to purple, the four posterior femora almost brownish-yellow towards the anterior.

Body length lin. 14. Width of tegmina lin. 22.

Inhabits Malabar.

The unit of measurement used by Westwood is probably the "Ligne" (line; linea in Latin) that was used in France in the 18th and 19th century. The French foot ("Pied de Roi") measured 32.48394 cm, the Pied de Roi contained 144 lignes (Trapp 1998: 230). Accordingly, the measurements given by Westwood can be calculated as follows: Body length: 3.16 cm (Westwood probably described a female), width of tegmina: 4.96 cm (the measurement of the tegmina therefore probably comprises the entire wingspan including the width of the thorax; compare data by Giglio-Tos below).

Giglio-Tos (1927: 39) provided a more complex description of the species:

"♂.♀. D'un beau vert doré (♀) ou bleu violacé (♂) à reflets métalliques, avec une tache jaune au milieu du sommet du vertex, une autre au bout de la face externe des hanches ant. et 2 autres l'une au milieu l'autre au bout du bord sup. des cuisses ant. La base des 4 cuisses post. chez ♂ et parfois chez ♀ ferrugineuse. Elytres des ♂ dépassant l'abdomen, noirâtres à beaux reflets viola-

cés, ceux des ♀ aussi longs que l'abdomen d'un beau vert métallique opaque. Ailes enfumées, l'aire costale noire opaque. Hanches ant. avec 4-6 cils. - L. du corps mm. ♂ 21, ♀ 31. L. du pron. mm. ♂ 5, ♀ 7. Larg. du pron. mm. ♂ 3,5, ♀ 5. L. des élytr. mm. ♂ 18, ♀ 22."

Translation: ♂.♀. Of a beautiful golden-green (♀) or blue-violet (♂) reflecting metallic, with a yellow mark on the middle of the highest point of the vertex, another one at the end of the outer surface of the anterior coxae and two others, one of them at the middle, the other at the end of the upper rim of the anterior femora. The base of the four hind legs of the ♂ and sometimes of the ♀ of a yellowish brown. The tegmina of the ♂ protrude beyond the abdomen, blackish with beautiful violet reflections, those of the female as long as the abdomen, of a beautiful metallic opaque green. Alae smoky, costal area blackish opaque. Anterior coxae with 4-6 setae. - Body length ♂ 21 mm, ♀ 31 mm. Pronotum length ♂ 5 mm, ♀ 7 mm. Pronotum width ♂ 3.5 mm, ♀, 5 mm. Length of tegmina ♂ 18 mm, ♀ 22 mm.

Metallyticus violaceus (Burmeister, 1838)

"Chalybea, verticis macula, alteris duabus pronoti in margine postico femoribusque testaceis. Long. corp. 1″ 2‴.
Aus Java, vom Hrn. Hagenbach als *M. violacea* geschickt; die Vorderbeine fehlen."

Translation: Metallic, testaceous mark on vertex, two further on the posterior rim of the pronotum and the posterior femora. Body length 1″ 2 ‴.
From Java, sent as *M. violacea* by Mr. Hagenbach; fore legs are missing.

It is unclear which measurement system Burmeister used at the time. Giglio-Tos (1927, see below) provides his data in metrical units, therefore an attempt to re-calculate Burmeister's data is omitted here.

Giglio-Tos (1927: 40) provided a more detailed description of the species:

"♂.♀. D'un bleu luisant à reflets violacés. Une tache au milieu du sommet du vertex, 2 sur le bord post. du pronotum, les hanches ant. sauf leur base, les 4 cuisses post. sauf leur bout et und bande le long du bord sup. externe des cuisses ant. jaunes. Elytres des ♂ hyalins, les veines costales, médiastines et la radiale ant. noirâtres, les autres blondes. Elytres des ♀ opaques, à beaux reflets violacés. Ailes des ♂ hyalines, celles des ♀ subhyalines, l'aire costale et le bout enfumés. - L. du corps mm. ♂ 27, ♀ 31. L. du pron. mm. ♂ 6, ♀ 6,5. Larg du pron. mm. ♂ 4,5, ♀ 5. L. des élytr. mm. ♂ 24, ♀ 22."

Translation: ♂.♀. Of a gleaming blue with violet reflections. One mark on the middle of the highest point of the vertex, two on the posterior rim of the pronotum, the anterior coxae except for their base, the four posterior femora except for their distal ends, and a band along the upper outer rim of the anterior femora yellow. Tegmina of the ♂ hyaline, the costal, medial and anterior radial veins blackish, the others yellow. Tegmina of the ♀ opaque, with beautiful violet reflections. Alae of the ♂ hyaline, those of the ♀ subhyaline, the costal area and the tip smoky. - Body length ♂ 27 mm, ♀ 31 mm. Length of pronotum ♂ 6 mm, ♀ 6.5 mm. Width of pronotum ♂ 4.5 mm, ♀ 5 mm. Length of tegmina ♂ 24 mm, ♀ 22 mm.

Metallyticus semiaeneus Westwood, 1889

"Nigro-metallice tinctus, capite aureo-viride, prothorace nigro-violaceo vix nitido, meso- et metanotis aeneo-violaceis, abdominis apice nitide violaceo; tegminibus brunneis; violaceo-nitidis; costa obscuriori; alis hyalinis nitidis costa angusta nigra; pedibus anticis viridibus; posticis violaceis, tibiis tarsique nigris.
Long. corp. lin. 10; expans. tegm. lin. 19."

Translation: Black-metallic coloured, head golden-green, pronotum black-violet scarcely gleaming, meso- and metanotum of a metallic violet, apex of abdomen gleaming violet; tegmina brown; violet gleaming; costal area darker; alae hyaline, the costal area narrow and black; anterior legs green; posterior legs violet; tibiae and tarsi black.
Body length lin. 10; width of tegmina lin. 19.

For an explanation of the measurement units, see the description of *M. splendidus* above. The data of Westwood can be calculated as follows: Body length: 2.26 cm, width (i.e. length) of tegmina: 4.29 cm.

The description of this species (only male known) by Giglio-Tos (1927: 40) is a direct translation of the original description by Westwood (1889) as cited before. Additionally, Giglio-Tos (1927: 40) provided the following data:

"L. du corps mm. 13. L. du pron. mm. 5. Larg. du pron. mm. 3,5. L. des élytr. mm. 22."

Translation: Body length 13 mm; length of pronotum 5 mm; width of pronotum 3.5 mm; length of tegmina 22 mm.

Giglio-Tos's data differs from the re-calculated measurements of Westwood by several millimetres. As there are no reliable data on variation in body size for *Metallyticus*, it is of no value to speculate about the differences between these measurements.

Metallyticus fallax Giglio-Tos, 1917

"♀. Caput nigrum, vix nitens, macula flava in medio summi verticis. Pronotum subquadratum, nigrum. Elytra abdomine longiora, sordide hyalina, venis flavis, macula dilute nubeculosa flavescente in medio areae discoidalis. Alae perfecte hyalinae, vix dilute infumatae ad marginem internum areae analis. Coxae anticae flavae. Femora, tibiae et tarsi antici nigri, violaceo nonnihil nitentes. Pedes 4 postici infuscati, femoribus basim versus pallidioribus, apicem versus violaceo nitentibus. Abdomen nigricans. Long. corp. mm. 23; long. pron. 5,5; lat. pron. 4; long. elytr. 20."

In his later publication Giglio-Tos (1927: 41) repeated this description in French.

Translation: ♀. Head black, hardly gleaming, yellowish mark in the middle of the highest point of the vertex. Pronotum almost square, blackish. Tegmina protruding tip of abdomen, smoky, veins yellowish, a faded, blurred yellowish mark near the middle of the discoidal area. Alae perfectly hyaline, hardly diluted smoky near the anterior margin of the anal area. Anterior coxae yellowish. Anterior femora, tibiae and tarsi black, relatively gleaming violet. The four posterior legs brownish, the femora proximally slightly paler, distally slightly violet gleaming. Abdomen black. Body length 23 mm; length of the pronotum 5.5 [mm]; width of the pronotum 4 [mm]; length of the tegmina 20 [mm].

Metallyticus pallipes Giglio-Tos, 1917

"♂. Superne niger, inferne testaceus. Caput flavum, vertice inter oculos fascia nigra, summo vertice in medio macula flava. Pronotum nigrum, opacum, antrorsum nonnihil angustatum. Elytra abdomine longiora, subopaca, area costali inter venam mediastinam et marginem anticum albicante, area discoidali ultra basim nonnihil violaceo nitente. Alae nonnihil infumatae, area costali nigricante, opaca. Pedes testacei. Femora antica spinis brunneis, macula brunnea inter basim et sulcum unguicularem. Abdomen brunneum. Long. corp. mm. 23; long. pron. 6; lat. pron. 4; long. elytr. 21."

In his later publication Giglio-Tos (1927: 40) translated his description into French.

Translation: ♂. Black on the dorsum, venter testaceous. Head yellowish, vertex with a black band between the eyes, the highest point of the vertex with a yellowish mark. Pronotum black, matte, slightly narrowing towards the anterior. Tegmina projecting beyond the tip of the abdomen, subopaque, costal area whitish between the Media and the anterior margin, discoidal area beyond the base gleaming slightly violet. Alae a little smoky, costal area blackish, opaque. Legs testaceous. Spines of the anterior femora brown, brownish mark on the ventral side between the proximal apex and the suture of the tibial spur. Abdomen brown. Body length 23 mm; length of pronotum 6 [mm]; width of pronotum 4 [mm]; length of the tegmina 21 [mm].

Giglio-Tos (1927: 40) added the following information:

"Trochantères ant. un peu brunâtres en dessous."

Translation: Anterior trochanters ventrally slightly brownish.

2.2 Phylogeny

The internal phylogenetic relationships of the Mantodea are virtually unknown. The typological classification by Ehrmann and Roy (in Ehrmann 2002) is based mainly on the work of Beier (1968) and several other publications (for a summary of authors see Ehrmann 1997: 6) with only little changes. In contrast to Beier (1968), several "subfamilies" were raised to "family" rank (Liturgusidae, Tarachodidae, Iridopterygidae, Thespidae, Toxoderidae, Sibyllidae) and a new "subfamily" Dystactinae was created.

The first approaches to mantodean phylogeny, strictly following the methods of phylogenetic systematics *sensu* Hennig (1950), were published only recently. Klass (1995, 1997) and Klass & Meier (2006) shed light on the relationships among the most primitive extant Mantodea *Chaeteessa*, *Mantoida*, and *Metallyticus* by evaluating the genital structures, the proventricle morphology and further traits of the three dictyopteran lineages. Resulting from their analyses, Klass (1995: 186, 191 and diagr. 6, 1997: 279 and diagr. 1) and Klass & Meier (2006: 16) found evidence for a basal split between *Mantoida* and all remaining extant mantodeans, followed by *Chaeteessa* as the sister of the other groups and *Metallyticus* as the adelphotaxon of the remaining taxa of the classification by Ehrmann and Roy (in Ehrmann 2002), i.e. Amorphoscelidae + Eremiaphilidae + Acanthopidae + Hymenopodidae + Liturgusidae + Tarachodidae + Thespidae + Iridopterygidae + Mantidae + Toxoderidae + Sibyllidae + Empusidae. In contrast, Roy (1999: 37) stated that *Metallyticus* may be the most basal extant praying mantid due to the lack of discoidal spines on the fore femora and due to the strongly branched anterior cubital vein (Cu1) and anal veins (A) in the tegmen (see Fig. 14). The primitive wing venation of *Metallyticus* was also pointed out earlier by Handlirsch (1925: 498, 1930: 813) who emphasized the morphologically isolated position of the genus within Mantodea (Handlirsch 1925: 498) and the resemblance of the wing venation with certain "Protoblattoids" (Handlirsch 1925: 498, 1930: 813). Smart (1956: 552) stated that, without knowing its head and forelegs, *Metallyticus* could be mistaken for a cockroach. Until recently, *Chaeteessa* was believed to be the most primitive extant mantodean due to the possession of setae-like spines, the lack of the tibial spur, and the terminal insertion of the tarsus of the forelegs (e.g. Beier 1968). Neither of these characters can be found in any other extant Mantodea. However, Klass (1995: 193) and Klass & Meier (2006: 17) discussed and rejected the value of these characters for an argumentation in favour of *Chaeteessa* being the sistergroup of all remaining extant Mantodea. A phylogenetic discussion of the basal Mantodea can be found in Klass & Meier (2006: 17).

The first extensive molecular analysis of Mantodea (Svenson & Whiting 2004) supported *Mantoida* as sistergroup to all remaining Mantodea, but included neither *Metallyticus* nor *Chaeteessa*. The molecular analysis of Dictyoptera by Inward et al. (2007), on the other hand, included *Mantoida* and *Metallyticus*. In their study, a sister-group relationship between *Mantoida* and the remaining Mantodea is supported. The following dichotomy, however, is between *Ichromantis*, a Madagascan member of the derived traditional Iridopterygidae, and the remaining taxa. Only the third dichotomy is between *Metallyticus* and the remaining Mantodea, suggesting that *Metallyticus* may be more derived than previously assu-

med. The analyses by Ware et al. (2008) included all three genera. While the basal position of *Mantoida* as sister-group of all remaining Mantodea found support therein, the positions of *Chaeteessa* and *Metallyticus* varied considerably among the different analyses (Ware et al. 2008: Figs. 2, 3). Data on mantodean phylogeny is scarce, and the clarification of the phylogenetic position of *Metallyticus* certainly needs further data.

Autapomorphic characters of *Metallyticus* are the bluish-green iridescent body coloration and the strong enlargement of the first posteroventral ("outer") spine of the fore femora (Figs. 1, 7, 8-10, 22). Characters that are likely to be plesiomorphic are the shortness of the pronotum (less than twice as long as wide, see Figs. 1, 7, 22), both sexes being fully winged, tegmina with short costal area (area between C and ScP), strongly branched anterior cubitus (Cu1) and anal veins (Fig. 14), the asymmetrical subgenital plate of the males (Fig. 16), which can be found in many mantodean species as well as in cockroaches (e.g. Wieland 2006: 52, see also discussion of abdominal morphology in 2.6 below), and probably also the lack of the discoidal spines on the fore femora as well as the anal area of the hind wings being turned down under the discoidal area without being folded several times. An extensive phylogenetic analysis of Mantodea based on morphology is still missing but is in preparation.

Apart from the dispute about the most basal extant mantodean, it is highly probable that many of the remaining traditional groupings are non-monophyletic. First evidence for this was presented by Svenson & Whiting (2004). Their phylogenetic trees emphasize the para- or polyphyly of several "families" and "subfamilies" of Ehrmann & Roy's classification (in Ehrmann 2002). This was also confirmed by Ware et al. (2008). On the other hand, some classical taxa may be monophyletic, e.g. Empusidae, because the members share synapomorphic morphological characters, such as a special anteroventral spination-pattern on the fore femora and the pectinated antennae of the males (Roy 1999, 2004).

2.3 *Metallyticus* specimens

This chapter lists information gained from 85 museum specimens (see Tab. 1), 9 specimens cited in literature (see Tab. 2) and 21 sightings by biologists, insect collectors and insect traders or data from specimens in private collections (see Tab. 3). As most of the museum specimens have not been examined by the author, no certainty of the correct determination of the species mentioned can be given. Sexes are indicated if known.

The identification of location names from the past two centuries faces many difficulties. In addition to the possible change of place-names, some locations, such as mountains, volcanoes, plateaus, districts and villages, may carry identical names. For the reconstruction of the current names of the collecting sites, online sources such as Google™, Google Earth™, Google Maps™, geographical websites, as well as historical and modern world atlases and other publications were used. Although the identification was done with great care, the possibility remains that some of the collecting sites have been misinterpreted. The "Remarks" column contains remarks concerning the sampling locations and discussions (in the case of ambiguous data) as well as additional data on the specimens.

The "Data" column contains notes cited from the specimens' labels or information that was kindly provided by the curators or by colleagues who visited the museums. Slashes separate data of several labels belonging to the same specimen, question marks replace numbers or letters that could not be identified, if not specified otherwise. Furthermore, data provided by people who personally observed *Metallyticus* or who were able to pass on data regarding collected specimens are listed therein.

Evaluation of the data

Metallyticus is restricted to the Oriental region (e.g. Giglio-Tos 1927; Beier 1939, 1968; Ehrmann 2002). Most of the specimens collected in the more than 170 years since the description of the genus were found throughout the Malayan and Indonesian regions.

According to their labels, four specimens were collected in India. Three specimens (*M. splendidus* and *M. violaceus*, currently in the Museums of Berlin (Tab. 1, No. 31), Oxford (Tab. 1, No. 78), and London (Tab. 1, No. 3)) are from "Malabar", which correlates to Malabar Coast, the south-western coast of India, and which is the locus typicus for *M. splendidus* as published by Westwood (1835: 442). The presence of *M. splendidus* in India has been stated, for instance, by Mukherjee et al. (1995: 204) and Ehrmann (2002: 221). However, the presence of *M. violaceus* in India has not been mentioned before. If the data of the Oxford specimen (Tab. 1, No. 78) is correct and belongs to the specimen that currently carries the label, this may confirm the presence of *M. violaceus* in India. A further *M. splendidus* specimen from the Oxford collection (Tab. 1, No. 72) is from Mysoore, a town in southern India about 125 km southwest of Bangalore (Bengaluru).

Two nymphs of unidentified *Metallyticus* specimens in the Natural History Museum in London (Tab. 1, No. 7, 8) are labelled "Matiana". It was possible to locate two places in Asia that carry this name: one is in northern Pakistan, the other one in northern India. Being a tropical mantid, *Metallyticus* is likely to be delicate in terms of cold weather conditions. Pakistan has a dry climate and cold winters. In northern India there are areas with a humid, sub-tropical climate. Therefore, it is more likely that "Matiana" refers to northern India rather than Pakistan. Due to the ambiguous data both locations were set as green question marks in the distribution map (Fig. 31), but until the locations are clearly identified, the specimens will be listed for India.

One specimen of *M. violaceus* (Tab. 2, No. 92) was mentioned from Tavoy (Myanmar) by Giglio-Tos (1927: 40). Two specimens of *M. violaceus*, collected in 1836 in "Mari, Indes orientales" (Tab. 1, No. 39, 40), are located in the Musée National d'Histoire Naturelle in Paris. Several locations named "Mari" were found: several towns in

Tab. 1. *Metallyticus* specimens from museum collections. Abbreviations and German terms (unless stated otherwise in the remarks column): Roman numbers (e.g. II, VII) refer to months (e.g. II = February; VII = July); Berge = mountains; coll. = collection; det. = determined by; E and O = east; Fluss = river; Gebiet = area, region; Gebr. = brothers; Insel = island; leg. = collector or collected by; Mai = May; Mus. Berol. = Latin abbreviation for "Museum of Berlin"; N = north; Ober- = upper; Ost = east; S = south; W = west.

Museums	Species, specimens	Data	Remarks	Specimen No.
Natural History Museum, London (United Kingdom)	*M. splendidus*	*M. splendida* Westw.	No further data.	1
	M. splendidus	Kuching, December 1898	Kuching is the capital of Sarawak.	2
	M. violaceus	Zool. Journal, Malabar	Malabar coast is a strip of coast in Southwest India between Goa and Cape Comorin, 845 km long and between 48 and 113 km wide. In the East it is bordered by the Western Ghats. The former district Malabar now belongs to the state of Kerala.	3
	M. violaceus	*Metalleutica violacea*, Burm.; M. splendidus	No further data.	4
	Metallyticus sp. (adult)	Padang, Malaysia, Miss Pascoe 96-41	Padang is a city on the mid-western coast of Sumatra, it is questionable if "Malaysia" is correct. The specimen will be listed for Sumatra. 96 may stand for 1896, 41 is probably an internal collection number.	5
	Metallyticus sp. (adult)	*fallax*? Sarawak, E.A. Lewis, 1910-116	1910 is probably the year, 116 an internal collection number.	6
	Metallyticus sp. (2 nymphs)	J.E.A. Lewis, 1910-116, Matiana, Mai 09	Two years are mentioned. It is likely that 1909 stands for the collecting date and that 1910 is the year in which the specimens were catalogued in the museum. Two places named Matiana were found: one in Pakistan (N 31°37' / E 73°19'), the second in northern India (N 31°13' / E 77°24'). As the climate in Pakistan is much drier, it is more likely that the location is in northern India where large forests remain. Both locations are marked with green question marks in Fig. 31.	7, 8
	Metallyticus sp. (nymph)	G. Bryant coll., 1919-147, Penang Is., Oct. 1913, G.E. Bryant	Two years are mentioned. It is likely that 1913 stands for the collecting date and that 1919 is the year in which the specimen was catalogued in the museum. Pulau Penang (Pulau Pinang), island on the north-western coast of the Malay Peninsula (Georgetown N 5°25' / E 100° 19').	9
	Metallyticus sp. (nymph)	Dindings, 96-85	Dindings is the name of a river on the west coast of the Malay Peninsula. It is also the name of the ruins or a Dutch fortress on Pangkor Island, an island facing the delta of the Dindings river. 96 probably stands for 1896, 85 may be an internal collection number.	10
	Metallyticus sp. (nymph)	Negri Sembilan, Malay Penins., H.N. Ridley	Negri Sembilan is a state in Malaysia, on the west coast just south of Kuala Lumpur.	11
Naturhistorisches Museum Wien (Austria)	*M. splendidus*	Ternate	Ternate is a small island west of the island Halmahera, Maluku Utara province, and belongs to the Moluccan Islands (east of Sulawesi). It is at the same time a town in the southern part of the islet.	12
	M. splendidus	Sumatra, Stevens	No further data.	13
	M. splendidus	O. Borneo, Batan Bessi	Eastern Borneo may be a false label. The name Batang Bessi (Padangbessi, Padang-Bessie, Padangbessie) occurs as an old collecting site in few publications, but in there it is listed for Sumatra. However, a current location with this name could neither be identified for Borneo nor for Sumatra. It will be listed for Sumatra in here.	14
	M. splendidus	Borneo, Frivaldsky	No further data.	15
	M. splendidus	Kina Balu	Mountain and national park in Sabah (Borneo).	16
	M. splendidus	Borneo, Boucard	No further data.	17
	M. violaceus	Gunong Angsi, Negri Sembilan	Negri Sembilan is a state in Malaysia, on the west coast just south of Kuala Lumpur. Gunong Angsi is the name of a mountain in Negri Sembilan. There is a public park at its base (Ulo Bendol Recreation Park).	18
	M. violaceus	Kota Tinggi, Jahore	Johor is a Malaysian state, at the south-eastern tip of the Malay Pensinsula. Kota Tinggi is a small town north-east of Johor-Bahru.	19
	M. violaceus	Goeneng Malang	Goenoeng or Gunung is the Indonesian name for mountain. There is a mountain with this name in western Java, and a hill of the identical name in eastern Java (both indicated by blue question marks in Fig. 31).	20
Staatliches Museum für Naturkunde, Karlsruhe (Germany)	*M. splendidus* (♂ nymph)	Java-W: Sukabumi (6.55S-106.56E), 2000 m, leg. C. Mülburg, X. 1977	Western Java, Sukabumi lies about 80 km south of Jakarta.	21
	M. splendidus (♀)	Sumatra-NW: Padangpanjang (0.27S-100.25E), 600 m, leg. Gebr. Rautenstrauch, VII. 1991.	Padangpanjang is a town on the west coast of Sumatra, about 50 km northwest of Padang.	22
	M. violaceus (1♂, 1♀)	Borneo-E: Insel Poeloe-Kiang, leg. Graber, XII. 1987.	This location could not be determined. It will be listed under "Borneo".	23, 24
	Metallyticus sp. (♂)	Thailand-S: Ban Yang Chum (12.04N-99.36E), S Bilauktaung Berge, leg. H. Lehmann jun. & S. Steinke, II. 1985.	The Bilauktaung-range extends from the south-eastern Dawna-range to the Isthmus of Kra along the border between Thailand and Myanmar (about 400 km).	25
Biozentrum Grindel und Zoologisches Museum der Universität, Hamburg (Germany)	*M. splendidus* (2 nymphs)	Malakka-Gebiet: Camp Jor, leg. A. Grubauer.	Malacca (Melaka) area, Malay Peninsula.	26, 27
Museum für Naturkunde der Humboldt-Universität, Berlin (Germany)	*M. splendidus* (♀)	Cat. No. 536 / Pulo Penang Wetterin [Westerin?]. / *Metalleutica splendida* Westw. Burm. / Mus. Berol. / *Metallyticus splendidus* Westw. E. Giglio-Tos, det.	Pulau Penang (Pulau Pinang), island on the north-western coast of the Malay Peninsula (Georgetown N 5°21'49" / E 100° 18'35"). Wetterin or Westerin may refer to the collector's name, however, no reference could be found.	28

Museums	Species, specimens	Data	Remarks	Specimen No.
Museum für Naturkunde der Humboldt-Universität, Berlin (Germany)	*M. splendidus*	*Metallyticus splendidus* Westw. Sumatra / Deli auf Sumatra, Hartert / Mus. Berol. / *Metallyticus splendidus* Westw, E. Giglio-Tos, det.	Deli was a historical sultanate in northern Sumatra and still is the name of a river near Medan.	29
	M. splendidus (♂)	Ober-Langkat, Deli, Sumatra 1894 M. Ude S. / *Metallyticus splendidus* Westwood / *Metalleutica*	Langkat is a district in the eastern part of the province of northern Sumatra (Sumatera Utara). Deli was a historical sultanate the same area and still is the name of a river near Medan. "M. Ude. S." may stand for "collector M. Ude" (collector is "Sammler" in German).	30
	M. splendidus (♀)	536 / Malabar Melly / *splendida* Westw. Burm. / Mus Berol. / *Metallyticus splendidus* Westw., E. Giglio-Tos, det.	Malabar coast is a strip of coast in Southwest India between Goa and Cape Comorin, 845 km long and between 48 and 113 km wide. In the East it is bordered by the Western Ghats. The former district Malabar now belongs to the state of Kerala. 536 refers to the catalogue number.	31
	M. violaceus (♀)	Cat. No. 537 / Java, Hagenb. / *Metalleutica violacea* Burm. Charp. / *violacea* Burm. Charp., ♂ *vitripennis* Burm., ♀ *Mant. chalybea* Serv. / Type	No further data on the location. Type specimen.	32
	M. violaceus (♂)	537 / Java, Hagenb. / Type	No further data on the location. 537 refers to the catalogue number. Type specimen.	33
	M. violaceus (nymph)	Cat. No. 537 / Java, Hagenb. / *Metalleutica violacea* Burm. Charp.	No further data on the location.	34
	M. violaceus (♂)	538 / *Metallyticus violaceus* Burm., E. Giglio-Tos, det. / Java, Charp. / *Metalleutica violacea* Burm. Charp. / Mus. Berol. / Type	No further data on the location. 538 refers to the catalogue number. Type specimen.	35
	M. violaceus (♀)	Cat. No. 538 / *Metallyticus violaceus* Burm., E. Giglio-Tos, det. / Java Charp. / *Metalleutica violacea* Burm. Charp. / Mus. Berol. / Type	No further data on the location. Type specimen.	36
Muséum National d'Histoire Naturelle, Paris (France)	*M. splendidus* (♂)	Borneo, 1891	No further data.	37
	M. splendidus (♀)	Java, 1873	No further data.	38
	M. violaceus (1♂, 1♀)	Mari, Indes Orientales, 1836	Mari may stand for one of several towns in Pakistan. A second Mari was found in northern Myanmar about 2,300 m a.s.l. (N 27°28' / E 98°30'). Another Mari is in eastern Papua New Guinea (S 4°24' / E 142°58'). However, this location is unlikely to be correct because the location is termed "Indes orientales" (East Indies). Papua New Guinea was geographically never part of the East Indies but of Melanesia. The remaining forests in Pakistan are rather dry whereas there are tropical wet forests in Myanmar. Therefore the Myanmar location is likely to be correct. Both locations are marked with red question marks in Fig. 31.	39,40
	M. violaceus (1♂, 2♀♀)	Java, 1852	No further data.	41-43
	M. violaceus (nymph)	1891	No further data.	44
Eidgenössische Technische Hochschule, Zürich (Switzerland)	*Metallyticus* sp.	Java occident., Mons Gede, 4000 1896, H. Fruhstorfer	Mount Gede is part of a twin volcano (together with Mount Pangrango) in western Java. 4000 stands for 4,000 feet (equals 1,219 m).	45
Institut Royal des Sciences Naturelles de Belgique, Brussels (Belgium)	*M. violaceus* (2 specimens)	No data available	No further data.	46, 47
	M. violaceus	Borneo, Kina Balu	Kinabalu is the name for a coastal strip, a mountain, and a national park in north-western Sabah (Borneo).	48
	M. violaceus (3 specimens)	Java	No further data.	49-51
	M. violaceus	Borneo Waterstradt	John Waterstradt is the collector's name (Constant, pers. comm. 2006).	52
	M. splendidus	Borneo Pontianac 1910	Pontianak is the capital of Kalimantan Barat, the western province of Kalimantan (Borneo).	53
Smithsonian Institution, National Museum of Natural History, Washington D.C. (USA)	*M. violaceus* (3 specimens)	The Philippines: Mindanao, Davao	Mindanao is a southern Philippine island. Davao is the biggest city on Mindanao and the second biggest in the Philippines.	54-56
	Metallyticus sp.	Ost-Sumatra	No further data.	57
Nationaal Natuurhistorisch Museum, Leiden (Netherlands)	*M. splendidus*	Pladjoe	Pladjoe or Pladju is a village slightly north of Palembang in South-Eastern Sumatra.	58
	M. splendidus (nymph)	Sumatra, Padang	Padang is a city on the mid-western coast of Sumatra.	59
	M. violaceus	Java	No further data.	60
	M. violaceus	Borneo, Mahakkam	Mahakkam (Mahakam) is a river in East Kalimantan.	61
	Metallyticus sp.	Sumatra, Dolokmerangir	Dolok Merangir is a rubber plantation in northern Sumatra, about 100 km south of Medan near Pematang Siantar.	62
Zoologisches Institut und Museum, Greifswald (Germany)	*M. splendidus* (1♂, 1♀(juv.))	Sumatra-Bedagei	Bedagei is a small state in north-eastern Sumatra, substate of the historical Deli sultanate (area around Medan in the Sumatera Utara province today). The name occurs in Dutch economic publications from the late 19th century in which the import calculations of tobacco from Sumatra to Europe are listed.	63-64
	M. violaceus (2♀)	Jawa-Sukabumi-W	The city is located about 80 km south of Jakarta in western Java.	65, 66
Zoologische Staatssammlung München, Munich (Germany)	*M. violaceus*	No data available.	No further data.	67

Museums	Species, specimens	Data	Remarks	Specimen No.
Naturhistorisches Museum Basel (Switzerland)	*M. splendidus*	No data available.	No further data.	68
Oxford University Museum of Natural History, Oxford (United Kingdom)	*M. splendidus* (♂)	Johore, W.	Johor is a Malaysian state, at the south-eastern tip of the Malay Pensinsula. W is likely to stand for the western part of the state.	69
	M. splendidus (♀)	Sumatra, Wallace / C. Lomer Collection /	No further data.	70
	M. splendidus (♀)	SING / Wallace / Singapore, Wallace, Coll. Saund. / E. Coll (1830-73) W.W. Saunders. Purchased and pres '73 by Mrs F.W. Hope	Specimen from Singapore, bought and probably collected in 1873.	71
	M. splendidus (♀)	Mysoore	Mysoore (Mysore) is a town in southern India, about 125 km southwest of Bangalore (Bengaluru).	72
	M. splendidus (♀)	Borneo / E. Coll (1830-73) W.W. Saunders. Purchased and pres '73 by Mrs F.W. Hope	Specimen from Borneo. This specimen was purchased in 1873.	73
	M. splendidus (♀)	N.W. Borneo, Kuching. Coll. 18.iii.99. Pres 1905 by H.H. the Rajah of Sarawak / 1905 613 / Kuching Mar 18 1899	Kuching is the capital of Sarawak. 1905 613 represents the accession number of the specimen.	74
	Metallyticus sp. (different from previous specimens)	N. Borneo, Brunei. Capt. Waterstradt. Van der Poll Coll. Bought Janson 1909 / 1909 414	Specimen from Brunei. 1909 414 represents the accession number of the specimen.	75
	M. violaceus (♀)	Sumatra, Wallace / Sumatra Wallace Coll Saunders Bates MS p. 14. *Metalleutica chalybea* Serv. Orthop p. 202	Specimen from Sumatra. *Metalleutica chalybea* is a synonym of *M. violaceus* under which Serville described the species in 1839 on page 202 (Ehrmann 2002: 221).	76
	M. violaceus (♀)	Johore, W.	Johor is a Malaysian state, at the south-eastern tip of the Malay Pensinsula. W may stand for the western part of the state.	77
	M. violaceus (♀)	Malabar / *Metalliticus splendodus*. Westw. Zoch?? no 20 / W	Malabar coast is a strip of coast in Southwest India between Goa and Cape Comorin, 845 km long and between 48 and 113 km wide. In the East it is bordered by the Western Ghats. The former district Malabar now belongs to the state of Kerala. The W is written on a blue rhomboid paper which indicates that this specimen belonged to Westwood. The specimen is identical with the previous two, which have been put as *M. chalybea* (= *violaceus*) in the drawer. It differs distinctly from the females of *M. splendidus*, therefore it is likely to belong to *M. violaceus*. If the data is correct and corresponds to this specimen, this may be the first record of *M. violaceus* for India.	78
	Metallyticus sp. (nymph)	No data available.	No further data.	79
	M. violaceus, ♂	Sumatra, Wallace / Sumatra, Wallace, Coll. Saund / *Metall. Vitripennis*. Burm. ?2-527	In this case the question mark has been taken over from the original label. 527 is the page on which Burmeister described *M. vitripennis* in 1838 (Ehrmann 2002: 221).	80
	M. splendidus	*Metallyticus splendidus* Westwood / *Metalleutica splendida* Westw. 3.9. Bates MS' p 12, Sarawak / Wallace / SAR.	Type specimen. "Bates MS p 12" probably refers to a page in a manuscript by Bates. The manuscript could not be identified.	81
	M. violaceus (♀)	Serville. *Mantis chalybea*. Hist. Nat. Ins. Orth. 1839, p. 202 / *Mantis chalybea* Serville / Java	Type specimen (1 of 2). Refers to Serville's description of *Mantis chalybea* (see also Ehrmann 2002: 221).	82
	M. violaceus	Serville. *Mantis chalybea*. Hist. Nat. Ins. Orth. 1839, p. 202 / *Mantis chalybea* Serville / Java	Type specimen (2 of 2). Refers to Serville's description of *Mantis chalybea* (see also Ehrmann 2002: 221).	83
	M. semiaeneus	PL 14 f 3, Sarawak, coll. Saunders, *Metalleutica semiaenea*, Bates MS p. 13. *Metallyticus semiaeneus* Westwood	Type specimen of *M. semiaeneus*. "Bates MS p. 13" probably refers to a page in a manuscript by Bates. PL14 f3 probably refers to a plate and a footnote (or perhaps figure) in a publication. Both manuscript and plate could not be identified.	84
Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt (Germany)	*M. violaceus* (late instar nymph)	*Metallyticus violacea* / Brunner v. W. determ. / *chalybea* Serv. / Borneo, Baramfluss, Kükenth. 94	Baram is a river in Northwest Borneo. It's the second longest river of Sarawak (400 km) and it flows into the South China Sea near Kuala Baram. The specimen was collected by Kükenthal, 94 indicates 1894 as date.	85

Pakistan, another one in Myanmar and a third in Papua New Guinea. "Indes orientales" does certainly not correlate with Papua New Guinea which has never belonged to the East Indies geographically nor politically, but rather to Melanesia. The climate in Myanmar is tropical whereas in northern Pakistan it is much drier and colder during winter. Therefore the location in Myanmar is the most plausible alternative. Due to the doubtfulness of the correct site, both locations are set as red question marks in the distribution map (Fig. 31), but until the locations are identified, the specimens will be listed for Myanmar.

If these interpretations are correct, the "Indian Matiana", Malabar coast, and Mysoore would be the westernmost locations from where *Metallyticus* has been reported. "Indian Matiana" and the "Myanmar Mari" would in this case represent the northernmost locations. The eastern borders of *Metallyticus*' distribution that have been found so far are confirmed by the finds of four *M. violaceus* (three from Davao (Tab. 1, No. 54-56) and one from Zamboanga (Tab. 2, No. 89) on the island of Mindanao, southern Philippines) and by a *M. splendidus* specimen from Ternate (Halmahera, Moluccan Islands east of Sulawesi; Tab. 1, No. 12). The specimen from Halmahera, together with a recent finding of an undetermined *Metallyticus* from north-western Sulawesi (Klank, pers. comm. 2005; Tab. 3, No. 100), are the only locations east of the

Tab. 2. *Metallyticus* specimens additionally found in the literature. Abbreviations and German terms see Tab. 1.

Authors	Species, specimens	Data	Remarks	Specimen No.
Shelford (1903: 299)	*M. semiaeneus*	Sarawak	No further data.	86
Giglio-Tos (1917: 79)	*M. fallax*	Borneo	No further data.	87
Giglio-Tos (1917: 78)	*M. pallipes*	Borneo	No further data.	88
Werner (1922:147)	*M. violaceus* (♀)	Mindanao, Zamboanga	Philippine Islands, Island of Mindanao, located on the tip of the island's western peninsula; this is the second evidence for *Metallyticus violaceus* from Mindanao.	89
Werner (1923: 388)	*M. violaceus* (♂)	Palaboean Ratoe (West-Java)	Pelabuhan Ratu, a small coastal town on the southern coast of western Java (province Java-Barat).	90
Werner (1925: 477)	*M. violaceus* (♀)	Kapala Roessa, Bindjei-Deli (Sumatra), August 1922, 400', leg.: L. J. Toxopeus	Probably the area around Binjai, near Medan. Deli was a historical sultanate in northern Sumatra (province Sumatera Utara today) and still is the name of a river near Medan. 400' probably stands for 400 feet, which equals nearly 122 m.	91
Giglio-Tos (1927: 40)	*M. violaceus*	Tavoy	Tavoy is a city in southern Myanmar.	92
Ehrmann (2002: 221)	*M. violaceus*	Pulau Sinkep	Pulau Sinkep is a small island east of Sumatra.	93
Ehrmann (2002: 221)	*M. splendidus*	Pulau Sinkep	Pulau Sinkep is a small island east of Sumatra.	94

Tab. 3. *Metallyticus* specimens from sightings by biologists, insect collectors and insect traders or data from specimens in private collections. Abbreviations and German terms see Tab. 1.

Observers	Species, specimens	Data	Remarks	Specimen No.
Dennon, pers. comm. 2004	*Metallyticus* sp.	Tapah Hills, 800 m, April , probably found in 2004.	Tapah Hills Forest Reserve is located on the foot of the Cameron Highlands near Tapah, state of Perak, Malay Peninsula.	95
Dennon, pers. comm. 2004	*Metallyticus* sp.	Trus Madi, 900 m, January, probably found in 2004	Sabah (Borneo).	96
Williams, pers. comm. 2006	*Metallyticus* sp. (2 specimens, Figs. 19 and 21)	Khao Sok National Park, March 2005	Thailand.	97, 98
Williams, pers. comm. 2006	*Metallyticus* sp. (1 nymph, possibly different species than above, Fig. 20)	Khao Sok National Park, March 2005	Thailand.	99
Klank, pers. comm. 2005	*Metallyticus* sp.	Toro Village, June / July 2004	Kulawi Valley, borders the Lore Lindu National Park on its western side, south of Palu, north of Gimpu, Central Sulawesi. National Park primary forest.	100
Beck, pers. comm. 2004 / 2005	*Metallyticus* sp.	Sukau, July 2003, about 200 m a.s.l. or less, appr. 8:00 p.m.	Sabah (Borneo), attracted by light outside a village meeting house.	101
de Groof, pers. comm. 2004, 2005, 2006; Salazar, pers. comm. 2004, 2005	*M. splendidus* (4 ♂♂, 4 ♀♀)	Jambi, March, April & June 2004	Central Sumatra, forests outside the city.	102-109
de Groof, pers. comm. 2004, 2005	*M. fallax* (2 ♀♀)	Jambi, March, April & June 2004	Central Sumatra, forests outside the city.	110, 111
Béthoux, pers. comm. 2007	*M. splendidus* (4 ♀♀)	Cameron Highlands, August 2006	Malaysia, Cameron Highlands.	112-115

Wallace Line (indicated as a green line in Fig. 31). The southern border of *Metallyticus*' distribution is marked by findings from Sumatra and Java.

Detailed collecting dates, such as location, altitude or exact time of the year, are rare. Only few specimens are labelled completely. The *Metallyticus* specimens listed under Tab. 1 almost certainly represent just a small part of the specimens that may be stored in many of the museums around the world. In the following, an evaluation of the biological facts gained from the data listed in Tabs. 1-3 is given.

Number of specimens of each species

45 specimens were labelled as *M. violaceus*, 44 specimens as *M. splendidus*, 3 as *M. fallax*, 2 specimens belong to *M. semiaeneus*, and 1 to *M. pallipes*. The remaining 20 specimens are unidentified nymphs or adults.

Locations

India: 6 specimens (No. 3, 7, 8, 31, 72, 78: *M. violaceus*, *M. splendidus*, *Metallyticus* sp., including the assumed "Matiana" specimens). Given collecting date: May 1909.

Myanmar: 3 specimens (No. 39, 40, 92: *M. violaceus*, including the assumed "Mari" specimens). Given collecting date: 1836.

Thailand: 4 specimens (No. 25, 97-99; the latter two possibly two different species, see Figs. 19-21). Given collecting dates: February 1985, March 2005.

Malay Peninsula (including Singapore): 16 specimens (No. 9-11, 18, 19, 26-28, 69, 71, 77, 95, 112-115: *M. violaceus*, *M. splendidus*, several undetermined specimens). Given collecting dates: 1873, 1896, October 1913, April 2004, August 2006.

Borneo (Sarawak, Sabah, Brunei, Kalimantan): 23 specimens (No. 2, 6, 15-17, 23, 24, 37, 48, 52, 53, 61, 73-75, 81, 84-88, 96, 101: *M. splendidus*, *M. semi-aeneus*, *M. violaceus*, *M. fallax*, *M. pallipes*). Given collecting dates: 1873, 1891, 1894, December 1898, March 18th 1899, 1909, 1910, December 1987, July 2003, January (probably 2004).

Sumatra: 28 specimens (No. 5, 13, 14, 22, 29, 30, 57-59, 62-64, 70, 76, 80, 91, 93, 94, 102-111: *M. violaceus*, *M. splendidus*, *M. fallax*, several undetermined speci-

mens). Given collecting dates: 1894, 1896, August 1922, July 1991, March, April and June 2004.
Java: 21 specimens (No. 20, 21, 32-36, 38, 41-43, 45, 49-51, 60, 65, 66, 82, 83, 90: *M. violaceus*, *M. splendidus*, several undetermined specimens). Given collecting dates: 1852, 1873, 1891, 1896, October 1977.
Sulawesi: 1 specimen (No. 100: undetermined). Given collecting date: June / July 2004.
Philippines: 4 specimens (No. 54-56, 89: *M. violaceus*). No dates mentioned.
Moluccan Islands: 1 specimen (No. 12: *M. splendidus*). No dates mentioned.
The labels of eight specimens do not indicate any location. The distribution map (Fig. 31) shows the locations that were identified. Uncertain sites have been indicated by question marks.

Altitude data (available from seven locations only)

M. violaceus from Sumatra: 122 m a.s.l. (No. 91)
Metallyticus sp. from Sukau (Sabah): lowland, appr. 200 m a.s.l. or less (Beck, pers. comm. 2005) (No. 101)
M. splendidus from Padangpanjang (Sumatra): 600 m a.s.l. (No. 22)
Metallyticus sp. from Tapah Hill (Malaysia): 800 m a.s.l. (No. 95)
Metallyticus sp. from Trus Madi (Sabah): 900 m a.s.l. (No. 96)
Metallyticus violaceus from Java: 1,219 m a.s.l. (No. 45)
M. splendidus from Sukabumi (Java): 2,000 m a.s.l. (No. 21)

Collecting months

India: May
Thailand: February, March
Malay Peninsula: April, August, October
Borneo (Sarawak, Kalimantan, Sabah, Brunei): January, March, July, December
Sumatra: March, April, June, July, August
Java: October
Sulawesi: June / July

2.4 Biology

Only little is known about the biology of *Metallyticus*. The only two publications that provide insight into its behaviour are those by Shelford (1903, 1916). He was the curator of the Sarawak Museum in Kuching from 1897 until 1905 and was obviously a keen observer of the mantodean fauna around him. In his descriptions of the behaviour of several Mantodea species he observed in captivity, two paragraphs (Shelford 1903: 299, 303) are devoted to *Metallyticus semiaeneus*:

> "A very curious and interesting species is *Metallyticus semiaeneus*; it is metallic-green and blue-black, is much flattened dorso-ventrally, and has many other uncommon characteristics; unlike all other Mantidae with which I am acquainted, it runs with great swiftness, and with the gait of a cockroach, i.e. literally *ventre à terre*, the body not being raised well off the ground as it is the case with its relations. The species is found generally on the bark of trees, but often underneath the bark, and it preys on cockroaches. I endeavoured, with ill-success, to keep specimens of this Mantis in captivity before I discovered that its natural prey was cockroaches; butterflies, flies, termites were never touched, but if a cockroach was introduced into a cage containing this Mantid, it was either pounced on at once or else captured after a long and exciting chase all over the cage." (p. 299).
>
> "The young of *Metallyticus semiaeneus* are chequered on the meso- and meta-notum and on the dorsal surface of the abdomen with white, and the legs are red. Unlike all the other larvae and pupae of Mantidae that I am acquainted with, this does not carry the abdomen turned up over the back of the thorax." (p. 303).

Chopard (1938: 277) cited the information from these paragraphs but assigned them to Wood-Mason. The only paper by the latter author listed in Chopard's references for the corresponding paragraph is Wood-Mason (1878) in which, however, *Metallyticus* is not mentioned at all. Wood-Mason published seven articles in 1878 (Ehrmann 2005: 221) but *Metallyticus* was not treated in any of them. Therefore it is most likely that Chopard (1938) confused Shelford (1903) with the Wood-Mason (1878) publication.

In his book "A Naturalist in Borneo", Shelford (1916: 141) gave a further description of his observations on *Metallyticus semiaeneus* including details he had not mentioned in 1903:

> "I mentioned above that nearly all the Mantidae had a very uncertain gait when walking, and that consequently they could not run down prey. The members of the genus *Metallyticus*, however, are an exception. These are brilliant metallic green, with red reflections, or bluish-black insects inhabiting the Malayan islands and peninsula; they are flattened like Cockroaches, and with their long legs they scurry along on the floor of the jungle or over the bark of trees at a great pace; the young, which are chequered with white or orange on the back, I have taken in decaying wood. These Mantids prey almost entirely on Cockroaches, and they pursue their victims with great vigour, as I was amused to witness when I placed Cockroaches in a cage in which was confined a specimen of *M. semiaeneus*. This creature was quite indifferent to Butterflies put in its cage, and I was puzzled how to feed it until it occurred to me that the lack of protective coloration and the swiftness of the insect might be associated with active predatory habits. A diet of Cockroaches was much appreciated by my captive, and the pace at which a despairing Cockroach and its relentless enemy careered all over the cage had to be seen to be believed."

Metallyticus has been found on old, large trees, such as, for instance, Durian (*Durio zibethinus* L.) in Sumatra. The specimens run up and down the trunk and occasio-

nally fly up (de Groof, pers. comm. 2006). Living specimens observed in Thailand were not easily disturbed and could be approached quite closely before they scurried off (Williams, pers. comm. 2006). When disturbed, however, *Metallyticus* tends to quickly run up the tree trunk it was resting on in a zigzag motion (de Groof, pers. comm. 2006).

Malayan natives have stated that *Metallyticus* can be found in the morning sitting in the sun on the upper foliage of tea plants in the local plantations, under fallen tree-trunks or even under stones (Materna & Schulze, pers. comm. 2005). However, several people who live close to the tea plantations and even work there do not seem to know *Metallyticus* (Materna, Schulze & Mehl, pers. comm. 2006). Therefore the reliability of this information remains doubtful and a confusion with other iridescent insects (e.g. Chrysomelidae) is possible (Mehl, pers. comm. 2006).

2.5 *Metallyticus* illustrations in literature

Pictures of *Metallyticus* are rare. Westwood (1835: Pl. 22, Fig. 1; Fig. 27 herein) depicted a female *M. splendidus*. A drawing of a male *M. semiaeneus* was published by Westwood in 1889 (Pl. 14, Fig. 3; Fig. 25 herein). Handlirsch (1908: Pl. 2, Fig. 8, 1925: Fig. 418, 1930: Fig. 845; Fig. 26 herein) published the left pair of wings of *M. splendidus* and the posteroventral spination of the foreleg of the same species (Handlirsch 1925: Fig. 422, 1930: Fig. 849/2; Fig. 29 herein). Giglio-Tos (1921: Pl. 1, Fig.1; Fig. 24 herein) presented a coloured drawing of a female *M. splendidus* in the Genera Insectorum. On the same plate (Giglio-Tos 1921: Pl. 1, Fig. 1a; Fig. 28 herein) a line drawing of a right foreleg of the same species was depicted. Chopard presented a drawing of the anteroventral view of a right foreleg of *M. splendidus* (Chopard 1938: Fig. 296, 1949: Fig. 77d; Fig. 30 herein), as well as a habitus-drawing of a female *M. splendidus* (Chopard 1938: Fig. 298; Fig. 23 herein). Chopard's drawing of the raptorial foreleg was re-published several times with slight alterations, e.g. by Ehrmann (2002: Fig. 25), Klass & Ehrmann (2003: Fig. 13.4g), and Salazar (2005: Fig. 2). Salazar also presented a drawing of the prothorax, head and forelegs of a female *M. splendidus* (Salazar 2005: Fig. 1; Fig. 1 herein) and two photographs of a dried pair of the same species (Salazar 2005: Fig. 3). The right foreleg of *Metallyticus* sp. was shown by Brues et al. (1954: Fig. 78). Loxton & Nicholls (1979: Fig. 6M.v.) depicted the anterior view of the left foreleg of *M. violaceus* on their plate of forelimb variation in Mantodea. Steinmann & Zombori (1985: Fig. 291) presented a rather schematic drawing of the anterior view of a *Metallyticus* foreleg. Klass (1995: Figs. 20-27, 1997: Figs. 20-27) published detailed schematic drawings of the male genitalia of *M. violaceus*. The cervical sclerites of a female *M. splendidus* were drawn by Wieland (2006: Fig. 5). A photograph of a living specimen of *M. splendidus* in captivity was published by Schütte (2007).

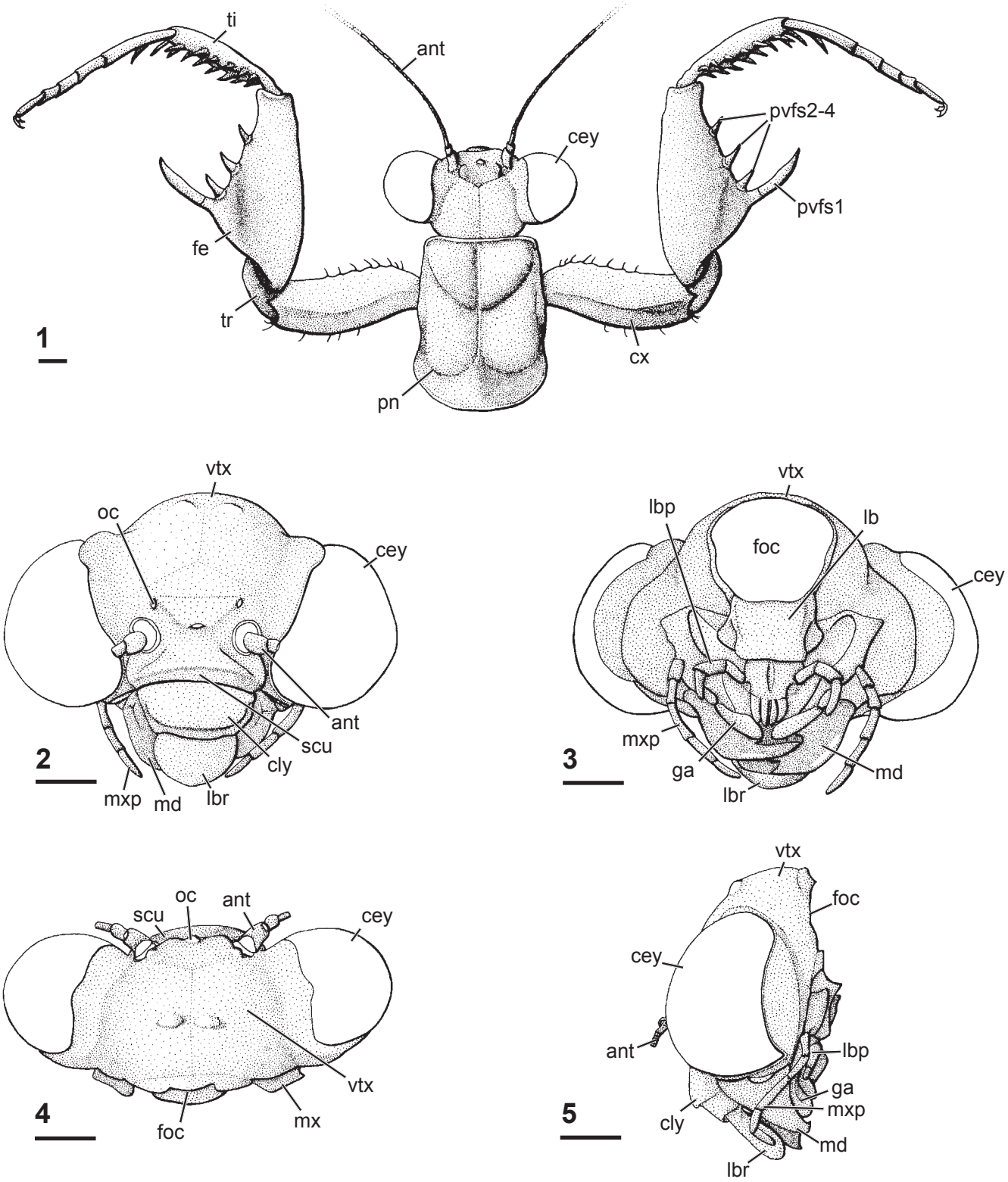
2.6 Morphology (Figs. 1-18)

Metallyticus has unique morphological characters. The iridescent coloration of the entire body cannot be found in any other Mantodea to this extent (e.g. Beier 1968: 4; Grimaldi 2008: 236). Only one other, very rare, species of Iridopterygidae, *Nemotha metallica* (Westwood, 1843), has been described to have a blackish colour with blue reflections (Westwood 1843: Pl. 62, Fig. 3; Wood-Mason 1884: 35; Roy 1999: 34). The body of *Metallyticus* is dorso-ventrally flattened which gives it a cockroach-like appearance (see also Shelford 1903: 299, 1916: 141).

Head (Figs. 2-5). The head is carried in a prognathous position (Figs. 19-21). This can also be found in other tree-dwelling taxa (e.g. *Amorphoscelis*, *Dactylopteryx*, *Humbertiella*, and *Liturgusa*). The compound eyes are large and exophtalmic. Compared to other mantodeans, the three ocelli are small in both sexes and far apart from each other. The vertex is bulging and posteriorly slightly covered by the anterior part of the pronotum. Both the short scutellum and the clypeus are transversely folded at a right angle. Together they form a step-like structure. Compared to more derived taxa (e.g. *Deroplatys*), the antennal foramina are farther separated from each other.

Cervical region (Fig. 6). The neck region or cervix of Mantodea was studied by several authors (Crampton 1926; Levereault 1936, 1938; La Greca & Raucci 1949; Matsuda 1970; Wieland 2006). Wieland (2006: Fig. 5) studied the cervical sclerites of *Metallyticus splendidus*. Ventral cervical sclerites are missing. The lateral cervical sclerites are bulging. They are caudally subdivided into a medial part and a lateral part by a short groove. The intercervicalia are medially separated, which has been stated to be the plesiomorphic condition as compared to the medially connected intercervical sclerites in more derived Mantodea (Wieland 2006: 70). Separated intercervicalia can also be found in other basal mantids (e.g. *Chaeteessa*, *Mantoida*, Amorphoscelidae, Eremiaphilidae), cockroaches and termites (Wieland 2006). In more derived Mantodea, the intercervicalia are medially close to each other or even connected (e.g. *Sphodromantis* sp., Wieland 2006: Fig. 1B). This feature may be autapomorphic for Mantoidea (Wieland 2006: 70), an assumed monophyletic group comprising Hymenopodidae + Mantidae + Empusidae *sensu* Beier 1968 (e.g. Roy 1999; Grimaldi 2003; Grimaldi & Engel 2005, Wieland 2006). The dorsal cervical sclerites and the small, slender sclerites, hidden underneath the intercervicalia (Levereault 1936: Pl. 11, Fig. 7; La Greca & Raucci 1949: Fig. 1; Beier 1968: Fig. 20; Wieland 2006: Fig. 2), have not been studied in *Metallyticus*.

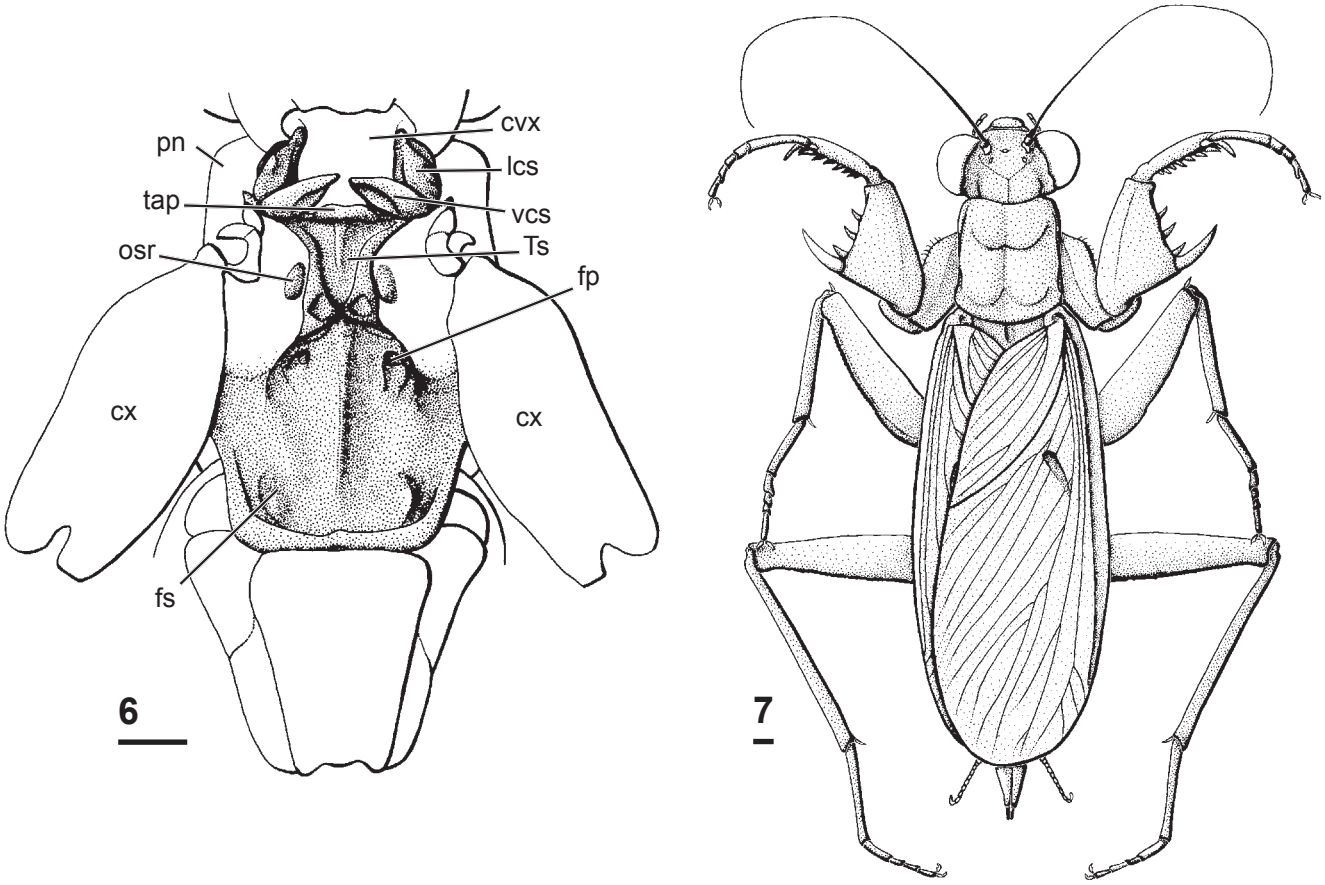
The ventral prothorax (Fig. 6). The mantodean ventral prothorax, especially the area anterior to the coxae of the raptorial legs, has been studied by Crampton (1926: Fig. 85), Levereault (1936: Pl. 11, 1938: Pl. 71), Chopard (1949: Figs. 75, 86), and Wieland (2003). Wieland (2003 and herein) studied the prothoracic sternites and their value for the phylogenetic reconstruction of mantodean



Figs. 1-5. *Metallyticus splendidus*, ♀. **1.** Prothorax, head and raptorial legs. **2.** Head in anterior view. **3.** Head in posterior view. **4.** Head in dorsal view. **5.** Head in lateral view (left side). Abbreviations see appendix. Scale bar 1 mm. Drawings by the author.

relationships. He stated that in basal Mantodea a slender structure ("basisternal clasp" in Wieland 2003) can be found between the intercervicalia and the coxal foramina which, in fact, is the transverse anterior part (tap in Fig. 6) of a T-shaped sclerite (Ts in Fig. 6). The T-shaped sclerite probably consists of the basisternite and the preepisternites (Levereault 1936; Beier 1968; Matsuda 1970). In more derived Mantodea, the transverse anterior part of this assembly became longer and evolved into a plate ("basisternal plate", Wieland 2003) during the elongation of the entire prothorax, whereas the posterior part became more slender.

Metallyticus shows the plesiomorphic condition. The transverse anterior part of the T-shaped sclerite (tap in Fig. 6) is not elongated craniad. The posterior part of the T-shaped sclerite is rather wide. Its lateral edges are thickened and it carries an anterior medial ridge. A small oval sclerotized region (osr in Fig. 6) is present on either side of the T-shaped sclerite. The function of these structures is unclear.



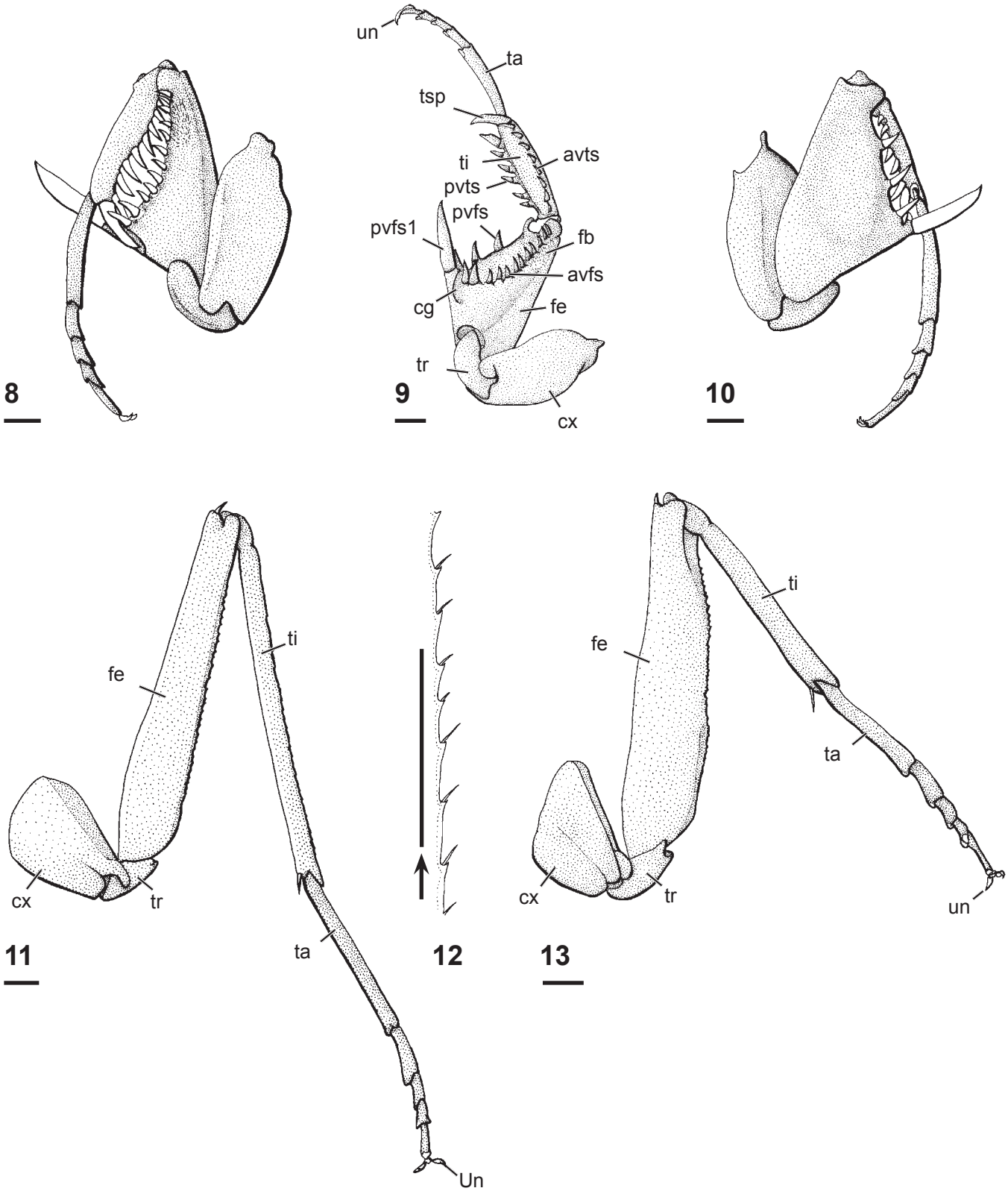
Figs. 6, 7. *Metallyticus*. **6.** *M. splendidus*, ♀, prothorax in ventral view. **7.** *M. fallax*, ♀, in dorsal view. Abbreviations see appendix. Scale bar 1 mm. Drawings by the author.

Posteriorly, the furcasternite (fs in Fig. 6) covers the remaining ventral prothorax. The furcal pits (fp in Fig. 6) are indented hollows shortly posterior to the T-shaped sclerite. The furcasternite carries a median ridge (as described by Giglio-Tos 1921: 3, 1927: 39), and its posterior rim is bent ventrad.

Pronotum (Figs. 1, 7). The pronotum is less than twice as long as wide which is assumed to be a plesiomorphic trait (e.g. Klass & Ehrmann 2003: 183; Grimaldi & Engel 2005: 229, 255). The prozona is slightly shorter than the metazona. A longitudinal groove runs throughout the anterior three quarters of the pronotum. The prozona therefore appears to be medially divided. On the metazona, an additional transverse groove separates two bulges from the posterior part of the pronotum. The lateral edges slope down ventrad in the posterior third and rise again to form a wider, posterior edge of the sclerite, thus giving it a saddle-like structure. In contrast to Ehrmann's generic diagnosis (2002: 221), the metazona is not keeled. This character has probably been misinterpreted because of Giglio-Tos' descriptions (1921: 3, 1927: 39) who, however, described the medially carinated prosternite of the metazona ("prosternum in metazona medio carinatum", Giglio-Tos 1921: 3; "prosternum caréné au milieu sur la métazone", Giglio-Tos 1927: 39; i.e. the prothoracal furcasternite) instead of the metazona itself (see generic description of *Metallyticus* in 2.1).

Raptorial legs (Figs. 1, 7, 8-10). The forelegs of *Metallyticus*, as in all Mantodea, are adapted to a raptorial lifestyle. They can be held up and folded against the ventral prothorax when at rest (hence the trivial name: praying mantis). The raptorial legs of *Metallyticus* are sturdy and massive. The coxa is about as long as the femur. The tibia is shorter than the femur. The femur is proximally enlarged ventrad thus gaining a triangular appearance in lateral view. Both tibia and femur carry two rows of sturdy spines.

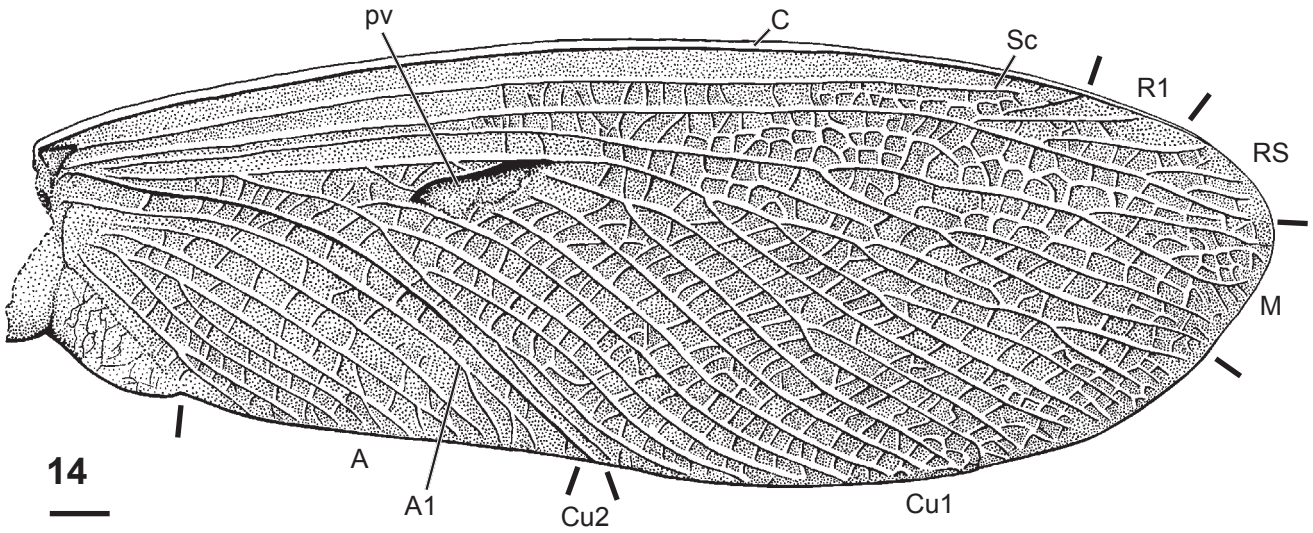
The tibia (Figs. 8-10) has eight anteroventral and six posteroventral spines. In either row, the spines grow gradually longer distad. The tibial spur is robust. There are 12 anteroventral spines of nearly equal length on the femora, except for the first two which are slightly longer and thicker. *Metallyticus* has four posteroventral femoral spines, the second to fourth of which are of equal length, unlike shown in the drawing by Westwood (1835: Pl. 22, Fig. 1; Fig. 27 herein). The first one, however, is strongly enlarged and is three to four times as long as the remaining spines (pvfs1 in Figs. 1 and 9, see also Figs. 7, 8, 10, 22, 28-30). This character is autapomorphic for *Metallyticus*, and the function of the enlarged spine is unknown. Loxton & Nicholls (1979: 197 ff.) argued that, considering the putative specialization for hunting cockroaches as mentioned by Shelford (1903, 1916), the spine might be used like "the prongs of a fork-lift truck" in order to lift

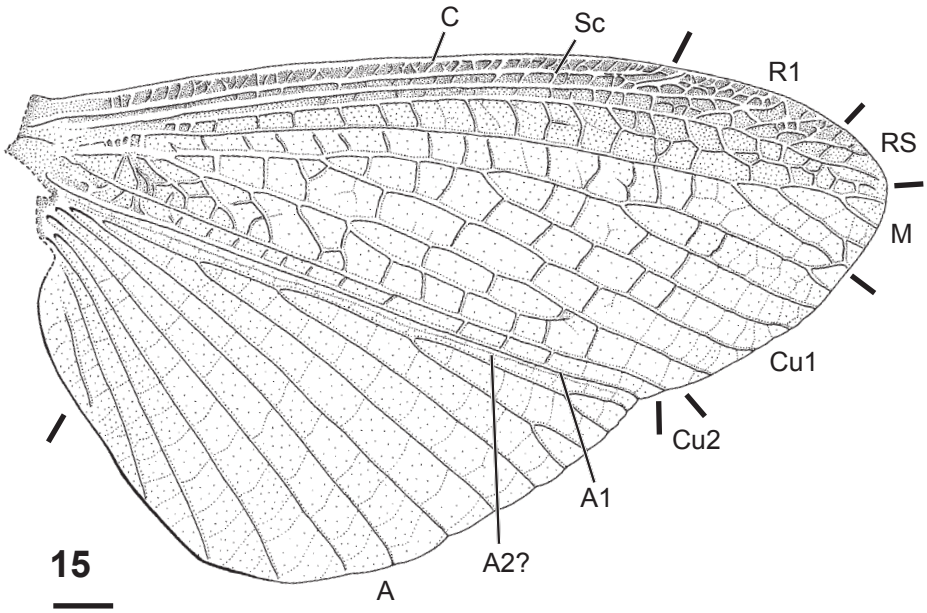


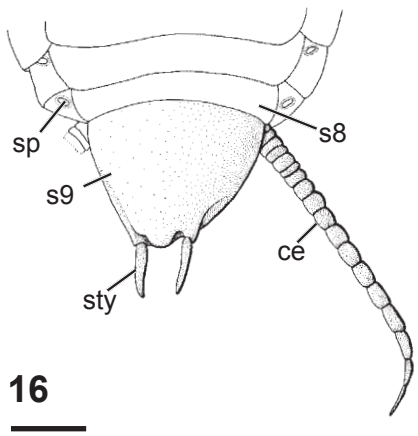
Figs. 8-13. *Metallyticus splendidus*, ♀. **8.** Right raptorial foreleg, anterior view. **9.** Right raptorial foreleg, oblique view of opened leg. **10.** Right raptorial foreleg, posterior view. **11.** Left metathoracal leg, anterior view. **12.** Detail of ventral socketed setae on metathoracal femur. ↑ = distad. **13.** Left mesothoracal leg, anterior view. Abbreviations see appendix. Scale bar 1 mm. Drawings by the author.

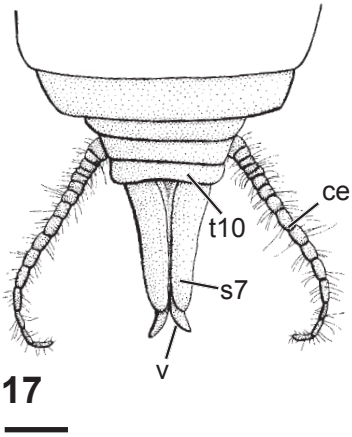
cockroaches off the bark. Furthermore they mentioned the possibility of *Metallyticus* using the enlarged spine "as a spear or as a pin to winkle cockroaches out of crevices". These assumptions, however, are highly speculative and cannot be verified without the study of living specimens.

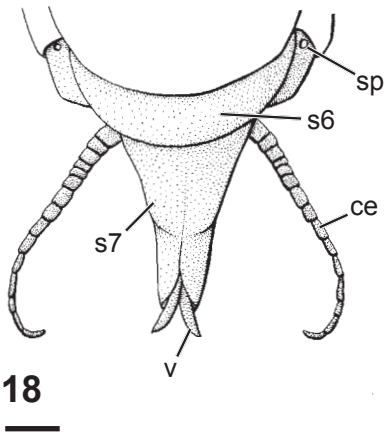
Metallyticus lacks discoidal spines, which is unique within the extant Mantodea (see also 2.2 and Fig. 9). However, some species from Cretaceous amber without discoidal spines were described or revised by Grimaldi (2003: 39 and Figs. 8a, 9b, 14). This character has to be investigated more closely because it remains unclear whether the lack of discoidal spines is a plesiomorphic cha-











Figs. 14-18. *Metallyticus splendidus*. **14.** Right tegmen of ♀. **15.** Left ala (mirrored) of ♀. **16.** Male external genitalia, ventral view, showing asymmetrical subgenital plate (s9); right cercus and cercal setae omitted. **17.** Female external genitalia, dorsal view. **18.** Female external genitalia, ventral view, cercal setae omitted. Abbreviations see appendix. Scale bar 1 mm. Drawings by the author.

racter for *Metallyticus* or if it is a secondary trait due to reduction (in prep.).

As typical of Mantodea, a fore-femoral grooming device ("femoral brush") is present in *Metallyticus*. It is positioned in the antero-distal third of the femur.

Cursorial legs (Figs. 11-13). The meso- and metathoracal legs are used, as is usual in mantodeans, for running. According to Shelford (1903: 299, 1916: 141), *Metallyticus* is a swift runner. The lengths of the leg segments show the usual condition for Mantodea. The tibiae of the mesothoracal legs are shorter than the corresponding femora, those of the metathoracal legs are slightly longer than the corresponding femora. The femora of both legs are ventrally serrated (Figs. 11, 13). What appears to be small spines are actually the pointed bases of small setae (Fig. 12).

The tarsi of both leg pairs are about as long as the tibiae. They have five tarsomeres, a trait that is characteristic of all Mantodea, except for *Heteronutarsus* (Eremiaphilidae), which has reduced numbers of tarsomeres, probably as an adaptation to its lifestyle in desert environments (e.g. Giglio-Tos 1921: 11; Chopard 1941: 25 and Fig. 7; Klass & Ehrmann 2003: 185). The basitarsomere of the mesothoracal leg of *Metallyticus* is about as long as the remaining tarsomeres altogether. In the metathoracal leg, the basitarsomere is even longer than the rest. The second and terminal tarsomeres are slightly elongated, whereas the almost equally long third and fourth are the shortest. The euplantulae are small and restricted to the distal parts of the tarsomeres. The fourth tarsomere has a subdivided euplantulum. In more derived mantodeans, the latter may become strongly enlarged (e.g. *Odontomantis*, Wieland, pers. obs.).

The ungues do not differ from the typical mantodean type. Arolia are missing as in all Mantodea (Holway 1935: 8; Beutel & Gorb 2001: 180, 2006: 14; Klass & Ehrmann 2003: 185).

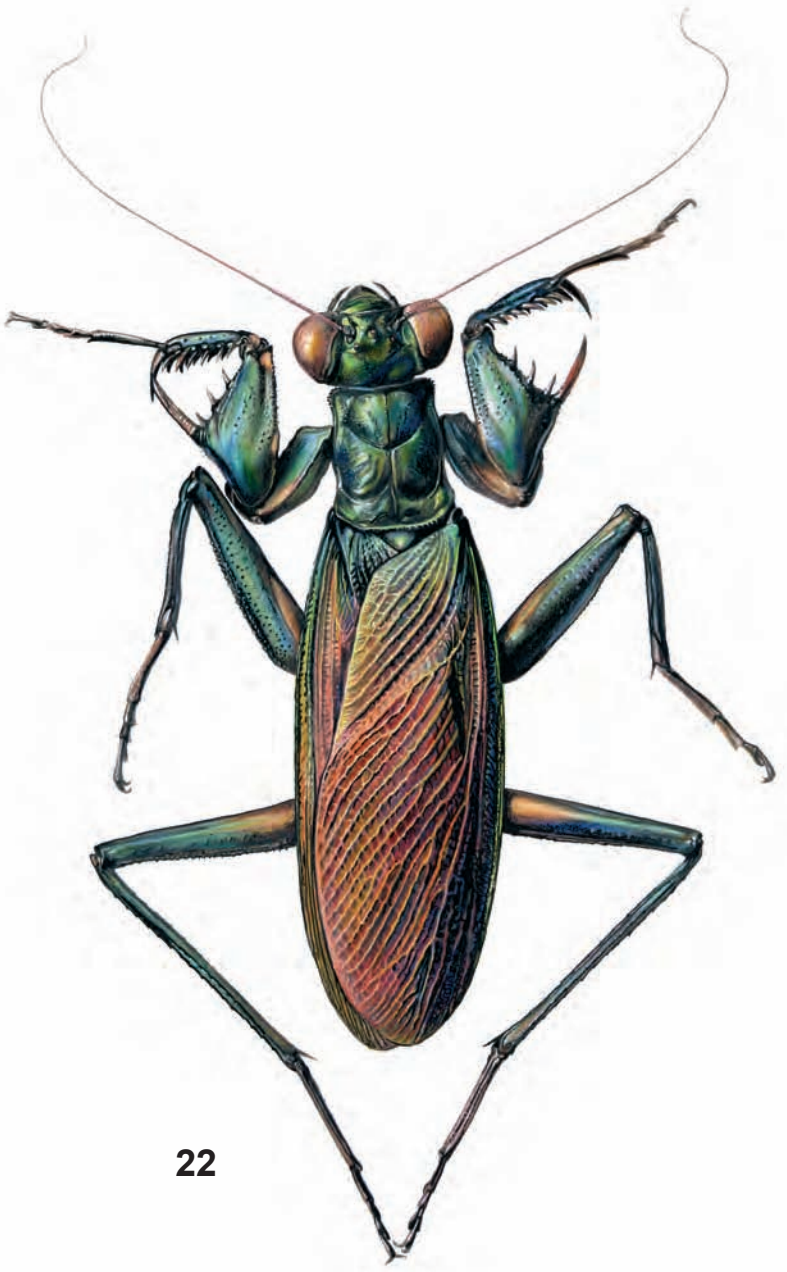
Wings (Figs. 14, 15). The wings of *Metallyticus* have been the subject of discussion whenever it came to the topic of mantodean wing venation. Some authors (e.g. Roy 1999: 37) assumed *Metallyticus* to be the most basal extant Mantodea due to the cockroach-like venation of the wings. Both sexes show the plesiomorphic macropterous condition. The wings project the abdomen caudally in the male, whereas in the female, the external genitalia are more or less free, depending on the state of feeding and gestation.

Forewings (Fig. 14). The nomenclature of the wing venation follows Ragge (1955: 131). The forewings are strongly sclerotized and therefore termed tegmina. The same condition can be found in cockroaches, saltatorians and several other Neoptera. The tegmina of *Metallyticus* reflect in metallic red, yellow or blue colours (e.g. *M. splendidus*) or may be darker. They can even be hyaline, as in the males of *M. violaceus* (see also 2.1 for description by Giglio-Tos 1927).

The Costa (C) runs along the anterior edge of the tegmen. It is followed by the unbranched Subcosta (Sc). The costal area (the area between these two veins) is very narrow in *Metallyticus*, as it is in other basal mantodeans (e.g. *Chaeteessa*, *Mantoida*, Amorphoscelidae). It becomes wider in the more derived taxa and may be about half as wide as the entire wing (e.g. *Deroplatys*, *Choeradodis*). The Radius consists of the anterior Radius (R1) and the radial sector (RS). It dismisses four or more parallel veins to the Costa. Such parallel veins between R1 and C, as well as between Sc and C, are also typical for cockroach wings (Bohn 2003: 199). Therefore this character is assumed to be plesiomorphic for *Metallyticus*. The tegminal Media (M) branches three to four times. The anterior Cubitus (Cu1) has more than 12 terminal branches, a situation that is also characteristic of cockroaches (Bohn 2003: 199) and unique for *Metallyticus* among extant Mantodea (Roy 1999: 38). The posterior Cubitus (Cu2) runs in or very closely to the claval furrow (Cu2 in Fig. 14). The latter, as characteristic of Dictyoptera, is strongly curved (Bohn & Klass 2003: 181) and runs into the posterior rim of the wing. In cockroaches and in basal Mantodea including *Metallyticus*, the claval furrow is distinct and deeply indented. More derived Mantodea have a more shallow and indistinct claval furrow. The first Anal vein (A1) in *Metallyticus* has a single origin and is terminally bifurcated (Roy 1999: 32; A1 in Fig. 14 herein) and runs towards the posterior rim of the wing. The remaining Anal veins originate from a common stem. None of the Anal veins run parallel to the posterior rim and meet Cu2, as can be frequently noticed in more derived Mantodea.

A special structure in the forewing of *Metallyticus* is the so-called "pseudovein" (Handlirsch 1930; Grimaldi 2003; Grimaldi & Engel 2005; pv in Fig. 14), an oblique indented area with interrupted veins between M and Cu1. It is distinct in *Metallyticus*, *Chaeteessa*, and several fossil Mantodea (e.g. Nel & Roy 1996: Figs. 1-3, Grimaldi 2003: Figs. 4c, 5b,c, 6, 20c, 23, 24). In *Metallyticus*, it is strongly indented. Its function is unclear. Grimaldi (2003: 6, 38) homologises it with the so-called "stigma" or "pterostigma" on the tegmina of many other mantids. The "stigma" is an often calloused area in approximately the same wing area where the veins are sometimes interrupted (e.g. Ramsay 1990: 41). Handlirsch (1930: 807), however, apparently thought of the "pseudovein" and the "stigma" as two independent structures.

Hind wings (Fig. 15). The hind wings are less sclerotized and more or less hyaline or smoky. They are shorter than the forewings and they have a much larger anal area than the forewings. C is marginal, as in the tegmina. Sc follows shortly behind it leaving no enlarged costal field between the two. Sc ends in the distal third of the wing. R1 is branched once and distally dismisses several indistinct, parallel branches to the costa. RS branches off R1 near the wing base and shows a terminal splitting into several parallel branches. M is distally split into four branches. Cu1 reaches the posterior rim of the hind wing with six branches. Cu2 is a single, almost straight vein. A1 is single and runs parallel to Cu2 up to the posterior rim of the wing. A2 is missing as in most Mantodea, except *Chaeteessa* in which it is completely present (Smart 1956: 552; Klass & Ehrmann 2003: 185). Smart (1956: 552) stated that



Figs. 19-21. Photographs of living specimens of *Metallyticus* sp., taken in Thailand (© Dave Williams). Photographs courtesy of Dave Williams (http.//www.paddleasia.com). **22.** Drawing of *Metallyticus splendidus* (© Klaus Fabian). Artwork courtesy of Klaus Fabian (contact: kna-fabian@t-online.de; more pictures by the artist: http://www.salix-art.de).

A2 (his 1V) is reduced (also mentioned by Beier 1968: 4; Klass & Ehrmann 2003: 185) and does not reach the posterior margin of the wing in *Metallyticus*. Smart suggests this vein is the remnant of a true vein due to the cross-veins that reach it from A1 and A3 (his Pcu and 2V). A thin line, about as thin as the cross-veins and running parallel to A1 in the area mentioned, could be identified (A2? in Fig. 15). It resembles a folding line more than a true vein and almost reaches the posterior rim of the wing, but indeed inconspicuous cross veins are present as observed by Smart (1956: 552). A similar structure is present in other Mantodea in the same area: the anal fold (e.g. Klass 1995: Af in Fig. 346b for *Mantis religiosa*), which is used during the wing folding process. Therefore it remains unclear whether the structure in *Metallyticus* is a remnant of a reduced A2 or a folding line or maybe both. The following Anal vein is branched six times.

The anal area is not folded several times during wing

folding, as in other Mantodea, but flapped entirely under the anterior part of the wing (Ehrmann 2002: 17; Klass & Ehrmann 2003: 185). This also occurs in some cockroaches and therefore is probably a plesiomorphic trait (e.g. Martynov 1925: 495; Handlirsch 1930: 806). Within Mantodea, this feature can also be found in Eremiaphilidae (Ehrmann 2002: 17; Klass & Ehrmann 2003: 185) in which, however, it might be a secondary trait due to the strong reduction of the wings.

Abdomen. Ten tergites are visible as typical for Mantodea. The abdomen is strongly flattened. This may be artificial due to desiccation and preparation, but the dorso-ventrally flattened body was also emphasized for living specimens by Shelford (1903: 299, 1916: 141). The supra-anal plate (t10 in Fig. 17) is formed by the 10th tergite in both sexes. In *Metallyticus* it is short, transverse and almost rectangular in both sexes. The first abdominal sternite is strongly reduced, as in all Mantodea (Klass & Ehrmann 2003: 186).

In the female, there are six visible sternites. The last (seventh) sternite forms the female's subgenital plate (s7 in Figs. 17, 18) which shapes the genital vestibulum and encloses the vestigial ovipositor. The tips of the valvulae of the latter protrude the subgenital plate apically (v in Figs. 17, 18).

The male abdomen has eight visible abdominal sternites. Sternite 9 (the eighth being visible) forms the male's subgenital plate (s9 in Fig. 16) which ventrally encloses the male genitalia. In *Metallyticus,* the male subgenital plate is asymmetrical (s9 in Fig. 16), a feature that is more or less distinct within several lineages of Mantodea (e.g. *Tarachodula pantherina* (Tarachodidae), *Pseudocreobotra wahlbergii* (Hymenopodidae), *Galinthias amoena* (Hymenopodidae) (Wieland 2006: 52; Wieland, pers. obs. 2006; see also Klass 1997: 266)) and Blattodea (e.g. *Ectobius* sp., Klass 1997: 266; Wieland 2006: 52) and therefore is probably plesiomorphic (Wieland 2006: 52).
The multisegmented cerci are long and pointed in both sexes (ce in Figs. 16-18) and carry long setae (see Fig. 17, setae omitted in Figs. 16 and 18). The male has two unsegmented styli on its subgenital plate (sty in Fig. 16).

3 Discussion and conclusions

Metallyticus can easily be distinguished from any other extant Mantodea due to its unique characters. However, the phylogenetic position of the genus within the group is not satisfactorily resolved. Although *Mantoida* shows the most plesiomorphic character states as far as the genital apparatus is concerned, both *Chaeteessa* and *Metallyticus* exhibit several characters of different body regions that are likely to represent the plesiomorphic states (short prothorax, cockroach-like wing venation, both sexes being fully winged, lack of discoidal spines, and medially separated intercervicalia in *Metallyticus*; short prothorax, both sexes being fully winged, separated intercervicalia, and possibly the lack of a tibial spur and the terminal insertion of the basitarsomere on the fore tibia in *Chaeteessa*). On the other hand, molecular data implicate that *Metallyticus* may be more derived than previously assumed. Extensive morphological and molecular datasets in the future will hopefully be able to settle the question of the relations of *Metallyticus* to other Mantodea.

M. violaceus and *M. splendidus* appear to be the most abundant species of the genus. Their ranges cover the entire Southeast Asian region from India in the West via Myanmar, Thailand, Malaysia and Indonesia up to the Moluccan Islands and the Philippines in the East and Sumatra and Java in the South. As some location names are more than one hundred years old and have remained ambiguous, the correctness of some of them (for instance Mari and Matiana) has to be verified.

Metallyticus can be found in different regions of Southeast Asia throughout the year. However, the data gathered so far are too scarce to deduce any ecological interpretations, such as seasonality in different regions.

Many specimens have been collected during the recent years, therefore the population of *Metallyticus* in certain areas may be larger than the rare findings in the past implicate. A high danger of extinction caused by logging of the natural habitats, however, is likely.

The highest numbers of specimens have been found in Sumatra followed by Borneo (comprising Sarawak, Kalimantan, Brunei and Sabah), Java, and the Malay Peninsula.

Several specimens have been found in altitudes between 600 m and 2,000 m above sea level. Tea plantations are also usually located in the higher regions due to the need of tea plants for a comparatively cool climate. If the information given by Malayan natives is correct, this may indicate a tolerance of *Metallyticus* for cooler climate conditions. As sightings from the lowlands of Sabah and Sumatra have also been recorded, this may indicate a wide temperature tolerance of *Metallyticus*, but further studies and observations are required to support this assumption.

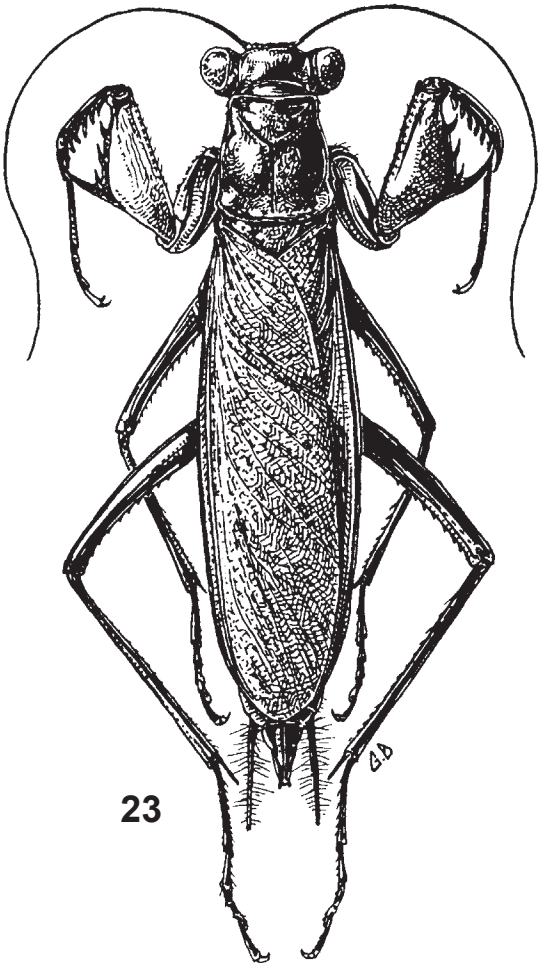
Metallyticus is an active hunter that goes directly after its prey in contrast to many other mantodeans that are lurking hunters.

It may be specialized in the hunt for cockroaches as indicated by Shelford (1903, 1916), dwells the bark of trees and may occasionally be found running on the ground. It is possible that *Metallyticus* hunts cockroaches even under loose bark, as Shelford (1903) emphasizes that it is "often" found there. This could provide an explanation for the considerable dorso-ventral flattening of the body. The description of a tree-dwelling lifestyle has been supported by photographs of living specimens (Williams, pers. comm. 2006; Figs. 19-21 herein).

Nymphs of *Metallyticus* can be found in or on decaying wood. Their coloration apparently differs from the adults as indicated by Shelford (1903, 1916).

Metallyticus is a swift runner that, by keeping its body and legs close to the ground, has a cockroach-like appearance while moving.

If the information given by the Malayan natives is reliable, then *Metallyticus* hunts in a wider environment than previously assumed. Additionally, the report of *Metallyticus* in tea plantations may be a first indication for the genus being able to adapt to secondary forests or even monocultural plantations, although this is rather unlikely.



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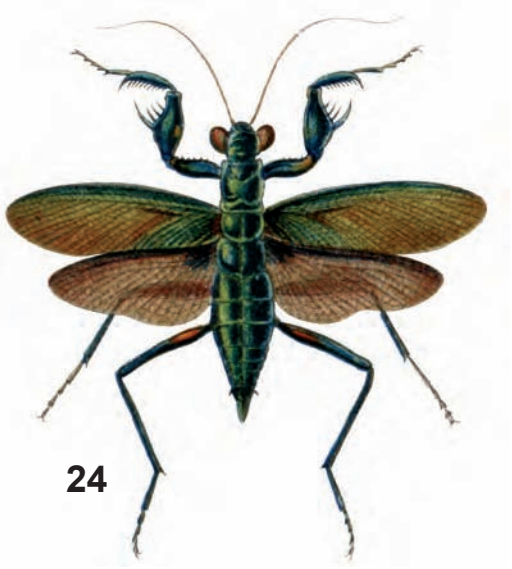

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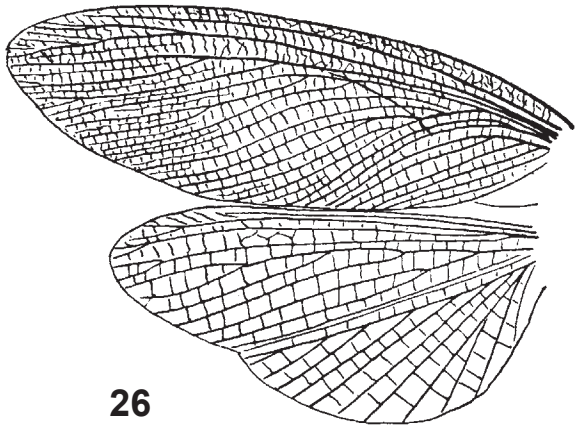

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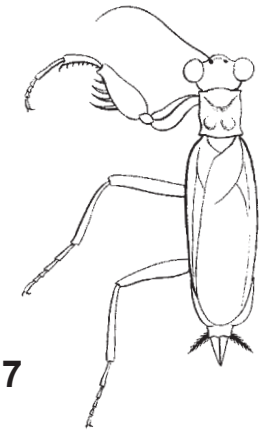

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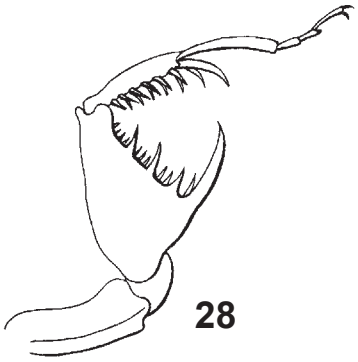

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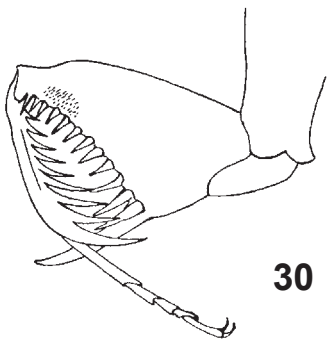

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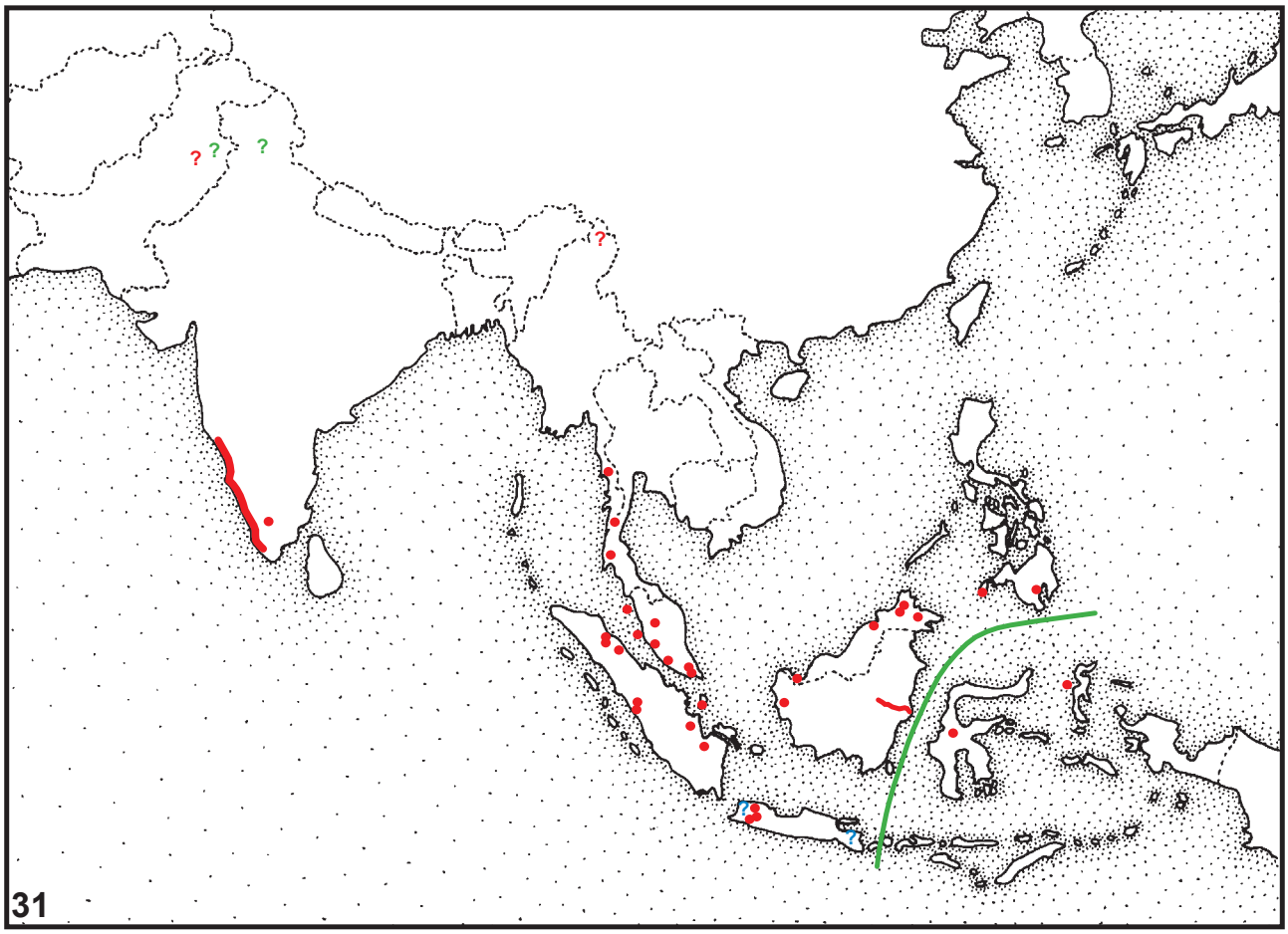

Fig. 31. Map of Southeast Asia, showing locations of *Metallyticus*-findings as listed herein. Wallace's Line is shown in green. Question marks represent ambiguous data, pairs of alternative locations are indicated by the same colour (see text for explanation).

Many more data have to be evaluated before this can be regarded as sufficiently supported.

Some species, namely *M. splendidus* and *M. violaceus*, probably occur sympatrically. It remains to be studied whether they compete for the same kind of niches or if any ecological or behavioural specializations exist. The observations of these mantises hunting their prey on trees as well as possibly under decomposing logs and stones (if true) may indicate a specialization for several niches or just a wide environmental tolerance.

It remains unclear whether *Metallyticus* is actually specialized in hunting cockroaches or if the Lepidoptera, Diptera, and Isoptera offered as prey by Shelford (1903: 299) simply did not fit its preferred prey spectrum.

Many parts of Southeast Asia have almost entirely lost their primary forests. However, *Metallyticus* seems to be still rather widespread, at least in some regions of Sumatra, Borneo, Java, and the Malay Peninsula. Therefore the question remains how specialized they actually are in relation to their environment, and whether the species tolerate secondary forestation or if they just survived in small remnants of the original vegetation.

More data on the abundance of the genus are required, not least of all for reliable information on a possible threat of extinction for a single species or even the entire genus.

Most of the open questions, of course, cannot be solved until observations of these amazing insects in their natural environment, as well as observations of living specimens under laboratory conditions, can be undertaken.

4 Acknowledgements

I would like to thank everyone who helped me gathering data on *Metallyticus* specimens from museums and collections all over the world, who told me about personal sightings of *Metallyticus* or about people they knew had observed specimens personally, or who have provided me with pictures or other data. My special thanks in alphabetical order go to: Nancy Adams † (Smithsonian Institution, Washington D.C., USA), Pieter Baas (Nationaal

Figs. 23-30. Historical drawings of *Metallyticus*. **23.** *M. splendidus*, ♀ (taken from Chopard 1938: Fig. 298). **24.** *M. splendidus*, ♀ (from Giglio-Tos 1921: Pl. 1, Fig. 1). **25.** *M. semiaeneus*, ♂ (from Westwood 1889: Pl. 14, Fig. 3). **26.** *M. splendidus*, left pair of wings (from Handlirsch 1908: Pl. 2, Fig. 8, 1925: Fig. 418, 1930: Fig. 845). **27.** *M. splendidus*, ♀ (from Westwood 1835: Pl. 22, Fig. 1). **28.** *M. splendidus*, ♀, right foreleg, posterior view (from Giglio-Tos 1921: Pl. 1, Fig. 1a). **29.** *M. splendidus*, right foreleg, posterior view (from Handlirsch 1925: Fig. 422, 1930: Fig. 849/2). **30.** *M. splendidus*, right foreleg, anterior view (from Chopard 1938: Fig. 296, 1949: Fig. 77d).

Herbarium Nederland, Leiden, Netherlands), George Beccaloni (Natural History Museum, London, United Kingdom), Olivier Béthoux (Staatliche Naturhistorische Sammlungen, Museum für Tierkunde, Dresden / Freiberg University, Freiberg, Germany), Jan Beck (University of Basel, Switzerland), Matthias Borer (Université de Neuchâtel, Switzerland), Jerome Constant (Royal Belgian Institute of Natural Sciences, Brussels, Belgium), Didier Drugmand (Royal Belgian Institute of Natural Sciences, Brussels, Belgium), Reinhard Ehrmann (Staatliches Museum für Naturkunde, Karlsruhe, Germany), Klaus Fabian (Essen, Germany, www.salix-art.de), Benny de Groof (Lier, Belgium), Alfred Kaltenbach † (Naturhistorisches Museum, Vienna, Austria), Charlotte Klank (Eidgenössische Technische Hochschule, Zürich, Switzerland), Darren Mann (Oxford University Museum of Natural History, Oxford, United Kingdom), Sören Materna (Erlangen, Germany), Jürgen Mehl (University of Erlangen, Germany), Michael Ohl (Museum für Naturkunde der Humboldt-Universität, Berlin, Germany), Niels Raes (Nationaal Herbarium Nederland, Leiden, Netherlands), Roger Roy (Musée National d'Histoire Naturelle, Paris, France), Julián Salazar (Museo de Historia Natural, Caldas, Colombia), Kai Schütte (University of Hamburg, Germany), Tobias Schulze (Berlin, Germany), Christian Schwarz (University of Würzburg, Germany), Zoe Simmons (Oxford University Museum of Natural History, Oxford, United Kingdom), Jürg Sommerhalder (Volketswil, Switzerland), Jan van Tol (Nationaal Natuurhistorisch Museum, Leiden, Netherlands), Frank Weigelt (University of Göttingen, Germany), Peter C. van Welzen (Nationaal Herbarium Nederland, Leiden, Netherlands), Dave Williams (www.paddleasia.com, Thailand).

For helpful comments on the manuscript, I am grateful to Julia Goldberg (Massey University, AWC, Palmerston North, New Zealand), Rebecca Klug (University of Göttingen, Germany), and Rainer Willmann (University of Göttingen, Germany).

This project was partly funded by the Deutsche Forschungsgemeinschaft (German Research Foundation, DFG Wi 599/12).

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Appendix

Abbreviations in figures

A anal veins
A1 first anal vein
A2? putative remnant of the second anal vein in hind wing
ant antenna
avfs anteroventral femoral spines
avts anteroventral tibial spines
C costa
ce cercus
cey compound eye
cg claw groove
cly clypeus
Cu1 anterior cubitus
Cu2 posterior cubitus
cvx cervix
cx coxa
fb femoral brush
fe femur
foc occipital foramen
fp furcal pit
fs furcasternite
ga galea
lb labium
lbp labial palp
lbr labrum
lcs lateral cervical sclerite
M media
md mandible
mx maxilla
mxp maxillary palp
oc ocellus
osr oval sclerotized region
pn pronotum
pv pseudovein
pvfs posteroventral femoral spines
pvts posteroventral tibial spines
R1 anterior radius
RS radial sector
s6-s9 sternite 6 - sternite 9
Sc subcosta
scu scutellum
sp spiracle
sty stylus
t10 tergum 10
ta tarsus
tap transverse anterior part of T-shaped sclerite
ti tibia
tr trochanter
Ts T-shaped sclerite
tsp tibial apical spur / claw
un ungues
v valvulae of vestigial ovipositor
vcs ventral cervical sclerite
vtx vertex