A new genus and species of Mantophasmatidae (Insecta: Mantophasmatodea) from the Brandberg Massif, Namibia, with notes on behaviour

Article · January 2003

Source: OAI

CITATIONS
21

READS
740

7 authors, including:

Oliver Zompro

58 PUBLICATIONS **617** CITATIONS

SEE PROFILE

Piotr Naskrecki

Harvard University

72 PUBLICATIONS **703** CITATIONS

SEE PROFILE

Kathy Meakin

Gloucestershire Wildlife Trust

8 PUBLICATIONS **111** CITATIONS

SEE PROFILE

A new genus and species of Mantophasmatidae (Insecta: Mantophasmatodea) from the Brandberg Massif, Namibia, with notes on behaviour

Oliver Zompro[1], Joachim Adis[1], Philip E. Bragg[2], Piotr Naskrecki[3], Kathy Meakin[4], Martin Wittneben[5] &Victoria Saxe[6]

[1]Max-Planck-Institute for Limnology, Tropical Ecology Working Group, 24302 Plön, Germany; e-mail: o.zompro@sungaya.de; adis@mpil-ploen.mpg.de

[2]8 The Lane, Awsworth, Nottinghamshire, NG16 2QP, UK.

[3]Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA; e-mail: p.naskrecki@conservation.org

[4]The University of Leeds, Leeds LS2 9JT, UK; e-mail: bgykm@leeds.ac.uk

[5]Institut für Ökologie und Evolutionsforschung IFOE, Universität Bremen, 28359 Bremen, Germany; e-mail: witti@uni-bremen.de

[6]P.O. Box 148, Woodacre, CA 94973, USA; website: www.victoria-saxe.com

A new genus and species of Mantophasmatidae, namely: *Tyrannophasma gladiator* Zompro, gen. nov. sp. nov., is described and figured based on material from the Brandberg Massif, Omaruru District, Namibia. A key to fossil and extant genera of Mantophasmatodea and new observations on the bionomics and behaviour of *T. gladiator* sp. nov. and *Mantophasma zephyra* Zompro *et al.*, 2002, are included. 'Gladiator-bugs' is here proposed as the vernacular name for the order Mantophasmatodea. A standardised set of defined measurements for the description of species is proposed.

INTRODUCTION

The first described representative of the insect order Mantophasmatodea was the fossil species †*Raptophasma kerneggeri* Zompro, 2001, described from Baltic amber. This species was described as 'Orthoptera *incertae sedis*' in the original publication, although taxonomic differences from known orders were discussed, and it was pointed out that a new order was necessary to accommodate the described taxon, plus two extant species from Namibia and Tanzania. This latter step was achieved in a subsequent publication, in which the order and the included taxa were named (*vide* Klass *et al.* 2002). The two extant species were named *Mantophasma subsolana* Zompro *et al.*, 2002 (Tanzania), and *M. zephyra* Zompro *et al.*, 2002 (Namibia) respectively.

In the formal published description of the new order, the first described since 1915, Mantophasmatodea Zompro *et al.*, 2002 *in* Klass *et al.* 2002: 1456, includes only a single family: Mantophasmatidae (*ibid*), with the single genus *Mantophasma* (*ibid*). Some months later, a new genus and species *Praedatophasma maraisi* Zompro & Adis, 2002 *in* Zompro *et al.* 2002, was described from southern Namibia. Unfortunately, the symbols for 'male' and 'female' were reversed in that publication. More recently, first records of three further new species from South Africa have been published (Picker *et al.* 2002). For a review of the history of the discovery *vide* Zompro & Zompro 2001. A second new extant genus and species from Namibia, collected on the Brandberg Massif on the edge of the Namib Desert, is here described.

Tyrannophasma gladiator sp. nov. described herein, was the subject of numerous media reports in 2002 and represents the 'Gladiator' referred to in the press and figured on a Namibian stamp by Helge Denker. Journalists and the general public frequently request a vernacular name for this group of insects, and 'Gladiator-bugs' (German: 'Gladiator-Schrecken') is here proposed. Further information on the insect and pictures of the order Mantophasmatodea and the material discussed here is available on the Internet (Adis & Hirschel 2002a, 2002b; Zompro & Zompro 2001).

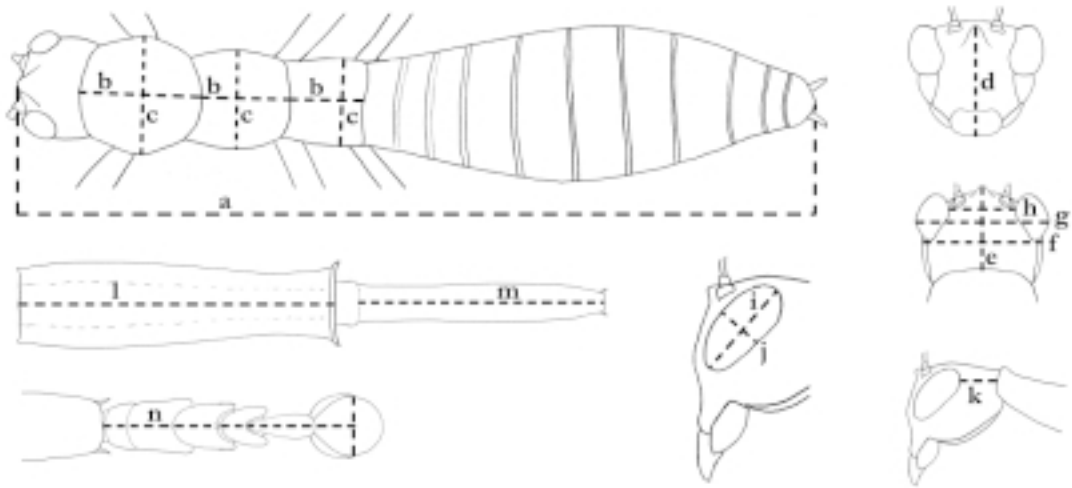

Figure **1**. Diagrammatic proposed standardised measurements for Mantophasmatodea. Letter codes: **a** = total length; **b** = length of notum; **c** = width of notum; **d** = height of head; **e** = length of head; **f** = width of head; **g** = width over eyes; **h** = width between eyes; **i** = height of eye; **j** = length of eye; **k** = length between eye and anterior margin of pronotum; **l** = length of femur; **m** = length of tibia; **n** = length of tarsus.

MATERIAL & METHODS

Most of the material used in this study was collected alive on the Brandberg Massif, Namibia, and was kept in criation chambers at Plön, Germany prior to subsequent preservation in 96% ethanol. Further material of *Mantophasma zephyra*, on which behavioural studies were based, was found to occur in more humid conditions than the Brandberg species described herein, and was obtained from the Erongo Mountains, Namibia.

Examination was undertaken using a Zeiss-Citoval-2 stereoscope microscope. Illustrations were completed using a drawing-tube attached to the same microscope. V. Saxe prepared the habitus illustrations. Photographs were taken by attaching a Pentax-Super-A camera. Measurements were taken using a Russian-made MBC-9 stereoscope and a special scale ocular.

Measurements (*vide* Figure 1): It seems helpful to propose standard measurements that are recommended for the descriptions of species of Mantophasmatodea. Measurements are taken at least to a tenth of a millimetre. The total length (*vide* Figure 1, a) is taken from the most anterior point of the tubercle between the antennae (here termed 'frontal tubercle') and the middle of the posterior margin of the tenth tergite.

Head: The length of the head (Figure 1, e) is defined as the length from the posterior margin of the head to the tip of the frontal tubercle. The width over the eyes (Figure 1, g) is taken from the most exterior point of the eyes, while the width of the head (Figure 1, f) is measured at the posterior margin of the genae seen from dorsal aspect directly behind the eyes. The height of the head (Figure 1, d) is measured from the middle of the ventral margin of the labrum to the most dorsal point of the frontal tubercle. The height of the eye (Figure 1, i) is measured at the longest distance from the dorsal to the ventral margin of the eye. The length (Figure 1, j) is taken in a right angle at the middle of the previous axis. The width between the eyes (Figure 1, h) is measured dorsally at an imaginary line directly behind the bases of the antennae. To describe the dimension of the eyes, their length should be compared to the length of the longitudinal length of the vertex between the eyes and the anterior margin of the pronotum.

The length of the antennae is taken from the most basal point of the scapus to the apex of the terminal antennomere. It is recommended that the number of the antennomeres be included in the description.

Thorax: The length of the pronotum, mesonotum and metanotum is taken at the middle of the nota, while the width is taken at the widest part in a right angle to the longitudinal axis.

Extremities: It is recommended that the length of the extremities should be provided for all three pairs of legs. The length of the coxa is defined as the length at the exterior edge. The reason for this is that this edge is also visible in dried specimens without them being softened. The length of the femur (Figure 1, l) is defined as the length of a dorso-median line from the most basal part of the basal margin to the most basal part of the impression between the antero-lateral spines of the femur. Tibia length (Figure 1, m) is measured in dorsal aspect from the middle of the impression marking the knee to the apex of the tibia. The length of the tarsus (Figure 1, n) is taken from the most basal part of the first tarsomere to an imaginary line between the apices of both claws when the whole tarsus is pressed flat. The arolium has a tendency for shrinkage, especially in dried specimens, and is, therefore, not suitable for measurements.

Abdomen: As the demarcations of the sclerotised parts and the inter-segmental membranes are often difficult to discern in preserved specimens, it is more applicable to describe the relations of the lengths and widths of the single segments to one another. It is recommended that the abdominal segments should be numbered with the Roman numbers I to X.

Holotype label data are quoted as they appear, a slash (/) indicates the end of a line of print, two slashes (//) signify data on a further label. Significant supplementary or qualifying information is presented in square brackets when considered necessary. For conservation reasons, the latitude and longitude coordinates are withheld. Terminology used in this paper follows Zompro *et al.* (2002). Abbreviations used in the text: ANIC = Australian National Insect Collection, CSIRO Canberra, Australian Capital Territory, Australia; MHNG = Muséum d'Histoire Naturelle, Geneva, Switzerland; MZSP = Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil; NMNW = *Namibian National Insect Collection*, National Museum of Namibia, Windhoek; UMO = Hope Entomological Collections, Oxford University Museum of Natural History, Oxford, UK; UPLBMNH = Museum of Natural History, University of the Philippines, Los Baños, Philippines; ZMUC = Zoological Museum, University of Copenhagen, Copenhagen, Denmark; ZMUK = Zoologisches Museum der Christian Albrechts-Universität, Kiel, Germany.

SYSTEMATICS

Mantophasmatodea Zompro, Klass, Kristensen & Adis, 2002 *in* Klass *et al.* 2002: 1456.
Mantophasmatidae Zompro, Klass, Kristensen & Adis, 2002 *in* Klass *et al.* 2002: 1456.

KEY TO FOSSIL & EXTANT GENERA OF MANTOPHASMATODEA

1. Profemora with spines ventro-laterally (Figure 4) 2
- Profemora without spines ventro-laterally .... †*Raptophasma* Zompro
2. Eyes large, smallest diameter longer than shortest distance of vertex behind eyes; body spinose 3
- Eyes smaller, smallest diameter shorter than shortest distance of vertex behind eyes; body not spinose ..... *Mantophasma* Zompro *et al.*
3. Head round in anterior aspect .... *Praedatophasma* Zompro & Adis
- Head triangular in anterior aspect (Figure 3) . ..... *Tyrannophasma* gen. nov.

Tyrannophasma Zompro, **gen. nov.**

TYPE-SPECIES: *Tyrannophasma gladiator* sp. nov., by present designation.

DIAGNOSIS: Large Mantophasmatidae, adults of the only known species longer than 3 cm. Body and extremities spinose. Head triangular in anterior aspect, transverse (over eyes 4:2.5) in dorsal aspect. Eyes prominent, kidney-shaped, horizontal length longer than vertex behind eyes.

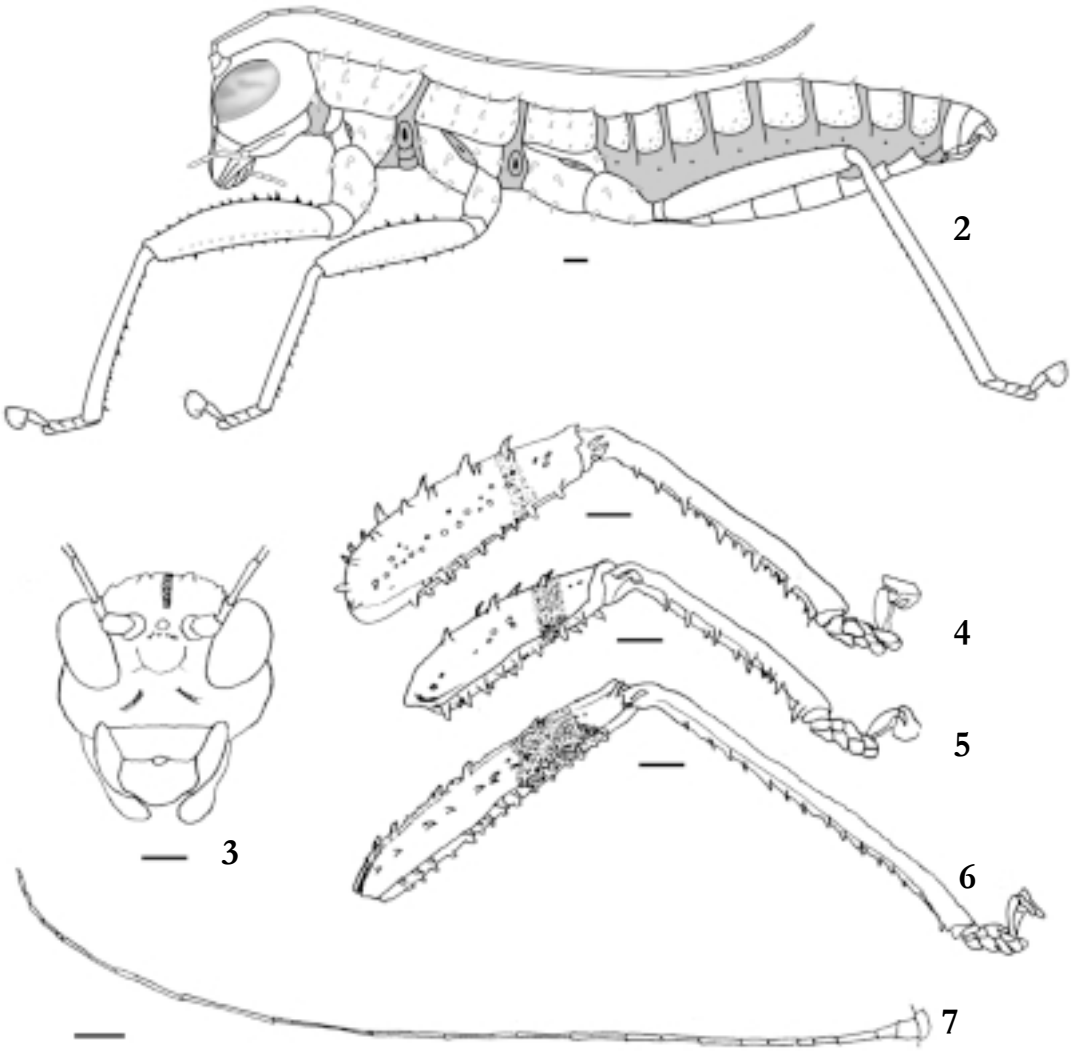

Figure **2-7**. *Tyrannophasma gladiator* sp. nov. **2**, habitus ♀ (lateral aspect); **3**, head (anterior aspect); **4**, right foreleg (lateral aspect); **5**, right midleg (lateral aspect); **6**, right hind leg (lateral aspect); **7**, right antenna (dorsal aspect). Scale bars = 1 mm.

Pronotum and mesonotum hexagonal. Pro and mesofemora stout, strongly broadened. Ventro-lateral edges of femora and tibiae spinose. Number of spines not constant, individual spines sometimes reduced, or additional spines present.

DIFFERENTIAL DIAGNOSIS: *Tyrannophasma* gen. nov. differs from the fossil †*Raptophasma* in the presence of ventro-lateral spines on profemora and tibiae, from *Mantophasma* in the size of the eyes, of which the width is shorter than the vertex behind the eyes in *Mantophasma*, while it is distinctly longer in *Tyrannophasma* gen. nov., further the strong forelegs and the more robust, spinose body and the dorsally spinose extremities, and from *Praedatophasma* by the triangular head. *Tyrannophasma* gen. nov. agrees with *Praedatophasma* in the structure of the legs and the armament of

the body and extremities, but differs strikingly in the triangular head, which is completely circular in *Praedatophasma*. It is also triangular in †*Raptophasma*.

ETYMOLOGY: The generic epithet *Tyrannophasma* is composed of the first part of the generic name of one of the largest carnivorous dinosaurs *Tyrannosaurus rex* and *-phasma*, a common ending in Mantophasmatodea. *Tyranno* refers to the impressive feeding habits of this insect, which is able to kill and consume insects of its own size.

DISTRIBUTION: To date, the genus is only known from the type locality of the type species.

Tyrannophasma gladiator Zompro, **sp. nov.**

Figures 2-16

MATERIAL: In ethanol. The type-series includes the three specimens recorded by Zompro *et al.* (2002). Holotype: adult ♂ (no. 1), 'Brandberg / Mason Shelter, 1800m / [coordinates] / 20.iv.2001 / M. Wittneben / sandy riverbed [white label]' // *Tyrannophasma gladiator* ♂ Zompro, n. sp. HOLOTYPUS det. O. Zompro III.2001 [red label]' [abdominal segments I-VII rotten, but loose parts included] (NMNW # T492). Paratypes: 1 nymph (no. 8), length 5.6 mm; 1 nymph (no. 10), length 12.1 mm; 1 nymph (no. 16), length 10.6 mm; 1 nymph (no. 18), length 13.1 mm; 1 nymph (no. 19), length 15.0 mm, 'Namibia, Erongo Prov., Brandberg / Monument, Mason Shelter, [coordinates] / [coordinates], 1730m, 05.-13.III.2002, leg. O. / Zompro *et al.* [white label] // *Tyrannophasma gladiator* Zompro, n. sp. PARATYPUS det. O. Zompro III.2001 [red label]' (all NMNW type series # T492); 1 nymph (no. 12), length 6.3 mm; 1 nymph (no. 21), length 13.0 mm: same data (all ANIC); 1 nymph (no. 7), length 5.0 mm; 1 nymph (no. 11), length 6.9 mm: same data (both ANSP); 1 nymph (no. 14), length 9.1 mm: same data (UMO); 1 nymph (no. 13), length 8.0 mm: same data (MZSP); 1 nymph (no. 9), length 5.1 mm: same data (MHNG); 1 nymph (no. 4), length 5.3 mm; 1 nymph (no. 3), length 4.8 mm, 'Namibia: Brandberg, Hungarob [*sic*! = Hungorob] / ravine at: [coordinates] / 1170m, 07.iv.2000 K. Meakin / / Raleigh Int. Malaise Trap Mal H036 // *Tyrannophasma gladiator* Zompro, n. sp. PARATYPUS det. O. Zompro III.2001 [red label]' (both NMNW); 1 nymph (no. 5), length 14.1 mm: same data (UPLBMNH); 1 nymph (no. 17), length 15.0 mm: same data (ZMUC); 1 nymph (no. 6), length 4.5 mm; 1 nymph (no. 15), length 10.2 mm; 1 nymph (no. 20), length 15.6 mm: same data; 1 subadult ♂ nymph (no. 2), length 17.2 mm [tip of abdomen broken-off], 'Namibia: Brandberg / Falls Rock Ravine woodland at: / [coordinates] / 1920m, 24.v.2000 / K. Meakin/Raleigh Int. / Malaise Trap / Mal F068 // *Tyrannophasma gladiator* Zompro, n. sp. PARATYPUS det. O. Zompro III.2001 [red label]' (all ZMUK). Individuals of this species were further observed at Wasserfallfläche, on the Brandberg, at 1 960 m.

DESCRIPTION: Overall colour of body and extremities light brown, thoracic segments reddish brown, postero-lateral edges and posterior margin darker. Measurements in mm. Holotype ♂: Total length: *ca.* 32 (parts of abdomen rotten); length of head: 3.8, width: 5.0; width over eyes: 7.3, height: 5.6; length of antennae: 21.4; length of eyes: 2.5, width: 1.3, between eyes: 2.75; length of pronotum: 5.1, width: 4.75; length of mesonotum: 5.1, width: 4.3; length of metanotum: 3.3, width: 3.8; procoxae: 2.9; profemora: 6.9; protibiae: 7.2; protarsi: 2.3; mesocoxae: 2.4; mesofemora: 5.7; mesotibiae: 6.1; mesotarsi: 2.4; metacoxae: 1.7; metafemora: 7.7; metatibiae: 10.3; metatarsi: 2.2. The nymphs are smaller, but proportions of the body and extremities do not show noteworthy differences to the adults.

Head (*vide* Figure 3): Triangular in anterior aspect, edges rounded, vertex with black stripe medially and one black stripe behind each eye. Frons reddish brown. Frontal tubercle prominent. Clypeus dirty white, transverse trapezoid. Labrum rounded pentagonal, slightly longer than clypeus (ratio: 1.5:1). Genae with prominent raised margin ventrally, its margin with three small spines medially and one prominent spine posteriorly. Mandibles black, molae with two denticles, basal incisivus distinctly shorter than distal one. Submentum trapezoid, dirty white, mentum transverse rectangular, also dirty white. Labial palpi, glossae and paraglossae dirty white. Lacinia brownish black, furcate anteriorly. Antennae projecting beyond

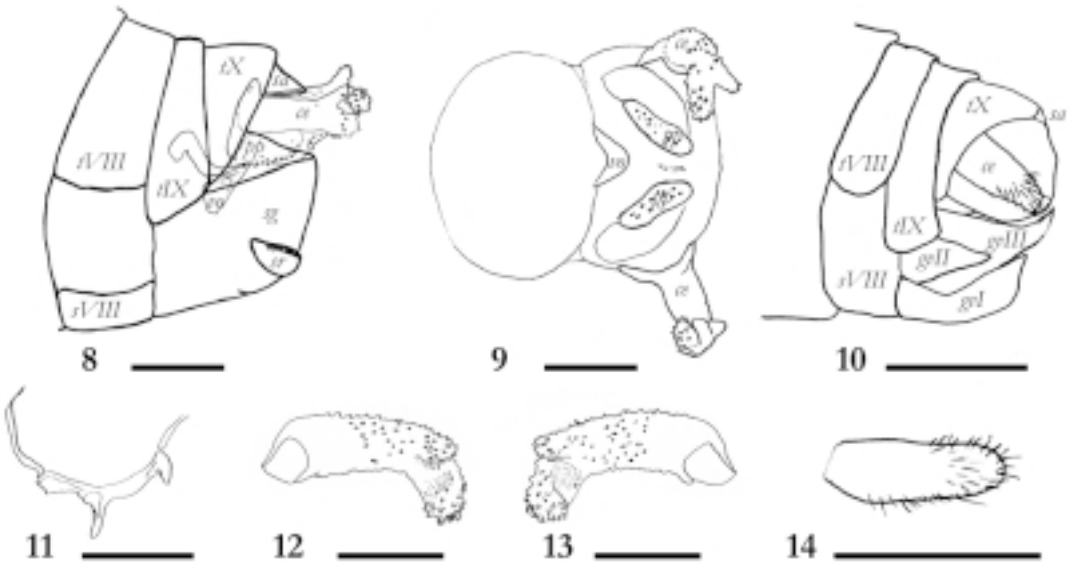

Figure **8-14**. *Tyrannophasma gladiator* sp. nov. genitalia. **8**, sclerotised parts of genitalia of ♂ (lateral aspect); **9**, genitalia of ♂, subgenital plate removed (ventral aspect); **10**, terminal abdominal segments of ♀ nymph (lateral aspect); **11**, vomer of ♂ (postero-lateral aspect); **12**, left cercus of ♂ (interior aspect); **13**, right cercus of ♂ (interior aspect); **14**, left cercus of ♀ nymph (dorsal aspect). Abbreviations: *ce* = cercus; *gvI*, *II*, *III* = genital valves 1, 2, 3; *pp* = paraproct; *sVIII* = sternite 8; *sa* = supra-anal plate; *sg* = subgenital plate; *sr* = subgenital ridge; *tVIII*, *IX*, *X* = tergite 8, 9, 10; *vo* = vomer. Scale bars = 1mm.

abdominal segment VII, consisting of 24 antennomeres (less in nymphs) (Figure 7). Scapus cylindrical, short, about as long as wide, impressed extero- and intero-laterally. Pedicellus club-shaped, as long as scapus, about half as wide. Third antennomere considerably longer than scapus and pedicellus combined, about as long as next two segments combined, following antennomeres increasing in length, brown, dirty white basally and apically. Terminal six antennomeres much shorter. Eyes prominent, kidney-shaped.

Pronotum: Hexagonal, as long as wide posteriorly, with broad, flat margin anteriorly. Anterior margin with two large spines sub-laterally and two smaller ones sub-medially. Lateral margins with two large spines medially and two smaller ones posteriorly. Postero-lateral corners rounded. Posterior margin overlapping over anterior margin of mesonotum, bearing six large spines. Disc with indistinct median line and transverse impression medially. Anterior half with row of four large spines, posterior half with two large spines and a smaller one adjacent to them. Proepimerum I with single spine. Prosternum with median ridge and two small excavations postero-submedially.

Mesonotum: Hexagonal, as long as pronotum with distinct darker line medially, broadening posteriad. Anterior margin hidden beneath posterior margin of pronotum. Lateral margin with one spine anteriorly and one posteriorly. Two large spines placed adjacent to margins medially. Postero-lateral corners rounded. Posterior margin with six large spines. Disc with four large spines arranged in trapezoidal fashion. Mesoepisternum with row of five spines of irregular size dorsally, row of three spines ventrally and two large spines posteriorly. Mesoepimerum with large and small spines. Mesosternum with impressed median line and two rows of three spines beside this median line.

Metanotum: Transverse, considerably shorter than mesonotum (ratio: 1:0.8), also broadening posteriad, with distinct, dark median line. Anterior margin spineless, hidden beneath posterior margin of mesonotum. Lateral margin with one small spine before rounded postero-lateral corners. Above lateral margin with two large spines medially. Posterior margin with six large spines. Disc with four spines standing in trapezoidal fashion. Metaepisternum with row of five spines dorsally, two smaller spines ventrally and two large spines posteriorly. Metaepimerum with two minor spines. Metabasisternum with four large spines posteriorly, metafurcasternite with deep incision anteriorly.

Legs (*vide* Figures 4-6): Femora with black stripe in distal third. Procoxae elongate, depressed cylindrical, with some large spines antero-dorsally, few smaller ones antero-ventrally and some minor spines directed mediad. Profemora broad and stout, rectangular in cross-section, dorso-lateral edges rounded, with several prominent spines, ventro-lateral edges prominent, elevated, with variable number of equally-sized spines. Exterior margin of profemora with several small spines, inner margin with several large spines. Protibiae long and slender, round in cross-section, with alternating rows of large and small spines extero- and intero-ventrally. In protarsi, first three tarsomeres transverse, U-shaped, fourth segment V-shaped. Fifth tarsomere as long as first three tarsomeres combined. Claws directed outwards, surrounding basal half of the large arolium. Dorsal process of third tarsomere very short. Mesocoxae less elongate than procoxae, spination as in procoxae. Mesofemora, mesotibiae and mesotarsi structured as in forelegs. Metacoxae shorter than mesocoxae, with same structure as mesocoxae. Mesofemora structured as profemora, but much more elongate and slender. Tibiae and tarsi as in foreleg.

Abdomen: Tergites I, II & V darker in colour than the remaining body. Abdominal segments I-VI increasing, VII-VIII decreasing in length and width. Segment I with a row of four large spines posteriorly. II-VI with four large spines posteriorly and one large spine sub-medially, the spines decreasing in size in the following segments. Sternites simple, not armed, in middle often with broad, black stripe.

Genitalia (*vide* Figures 8-14): In males, abdominal tergite VIII shorter than VII, slightly longer than IX and considerably shorter than X. X rounded posteriorly. Paraprocts slightly kidney-shaped, weakly granulated. Vomer elongate and slender, with a small, triangular process at the left and a prominent process in the middle; this process triangular in lateral aspect. Left side more or less smooth, and the right slightly serrated. Cerci elongate and furcate, spinose. Main branch of furca curved inwards, with prominent spines apically; these spines distinctly smaller in the shorter dorsal appendices. Sub-genital plate swollen, broadly marginated dorsally. Process of sub-genital plate, here termed as 'sub-genital ridge', broad, slightly projecting. Supra-anal plate small, slightly projecting, half oval in shape. In females, tergite IX slightly shorter than VIII. IX strikingly extended laterally. X almost as long as VIII and XI combined, with rounded apex posteriorly. Supra-anal plate small, projecting, rounded triangular. Cerci about cylindrical, slightly narrowed towards apex, with several whitish-transparent bristles. Genital valves I broad, slightly curved, narrowest in middle, extending apicad, apex acute. Valves II short, flat, triangular. Valves III large, elongate triangular, with acute apex, the latter curved upwards.

NYMPHS: The spines on the extremities and body are not produced in the early nymphal instars and increase in size with each moult. In the stage preceding maturity, the spines are almost produced as in adults. The thoracic nota are more trapezoid in the young to half adult nymphs; the hexagonal form becomes distinct within the last four moults. In males, the furca of the cerci becomes visible within the three stages preceding maturity.

ETYMOLOGY: Provisionally named 'Gladiator' by the first author, inspired by a character in the Universal Pictures & Dreamworks motion picture *Gladiator*. As the media have subsequently used this name to denote the species, for the sake of consistency the name is here adopted as the specific epithet of the new species.

HABITAT (Figure 17): The Brandberg is a single, large, isolated massif of granite rising dramatically to a plateau at approximately 2 000 m a. s. l.,

1 500 m above the flat peneplain of the central Namib Desert. Königstein is the highest peak within the massif and at 2 573 m is the highest mountain in Namibia. The sides of the massif are extremely steep and almost devoid of vegetation. Overland access to the study sites involves a difficult climb following boulder-strewn ephemeral watercourses. This has further compounded the Brandberg's isolation, and numerous endemic flora and fauna have been documented (Kirk-Spriggs & Marais 2000).

Precipitation is extremely variable under the influence of the Namib climate, with an average of 100 mm p.a. at Uis, 30 km east of the Brandberg (Olszewski 2000). The prevalence of rain decreases markedly to the west of the massif, but the plateau of the Brandberg is expected to receive more rainfall than the surrounding plains through the orographic effect (Olszewski 2000). During the 'wet season' (February - April), run-off is very rapid, often resulting in flash floods with little water retained. Soils of varying depths between boulders, in cracks and depressions rise markedly in clay content and age with increasing altitude (Wittneben in prep.). Surfaces at various scales - from stones to extensive rock faces – serve to locally concentrate water and provide a sheltered habitat for various plant communities at all altitudes.

Vegetation below 1 800 m is sparse, with woody perennials usually confined to watercourses and ravines. From 1 600 to 2 300 m, the massif is complemented by a more mesic flora in a mosaic landscape of plains and *koppies* (small peaks) of the plateau as found at Mason Shelter. Falls Rock valley below Wasserfallfläche is a tributary to the Hungorob River, and not a plain such as Wasserfallfläche itself. Phaenerophytic vegetation is primarily xerophytic, whilst chameaophytes (shrubs) tend to show a suffrutex habit, capable of prolific shoot growth in a good rainy season. Ephemeral flora (forbs and grasses) contributes substantially under favourable conditions (Wittneben in prep.). Tree species such as *Acacia hereroensis* Engl. (Fabaceae) and *Dombeya rotundifolia* (Hochst.) Planch. (Sterculiaceae) indicate isolated pockets of highland savanna, whilst the upper plateau is dominated by a karoid dwarf shrub vegetation (Craven & Craven 2000).

At Mason Shelter, the plateau (*ca.* 1 800 m) is crossed by a sparsely vegetated riverbed, which is surrounded by clumps of *Triraphis ramosissima* Hack. (Poaceae), a tussock grass typically 15-30 cm in height. This grass is endemic to arid south-western Africa. The grass clumps extend up the more gentle slopes and also occur on steeper slopes at the base of large rock outcrops. Owing to their profuse branching habit and condensed structure, these plants attain markedly higher levels of humidity than bare sand, thus providing a relatively moist microclimate. On the slopes they are partially sheltered from direct sunlight, thus retaining more moisture than plants in the open. The majority of *Tyrannophasma gladiator* sp. nov. specimens were found in clumps of *Triraphis ramosissima* on sloping areas near the base of outcrops. Collecting was mainly undertaken at night by beating clumps of grass and searching by torchlight. Previously, nymphs had been collected as an incidental result of Malaise trapping around *Acacia* trees in the Hungorob and Falls Rock ravines. One specimen was observed clinging to the underside of the roof of Malaise trap (P.E. Bragg), indicating that individuals may climb to considerable heights.

BIONOMICS: *Tyrannophasma gladiator* sp. nov. is nocturnal in habits. First observations on the bionomics of nymphs under laboratory conditions are provided by Adis *et al.* (2002). Animals are solitary and appear to chiefly lie in wait for prey, continuously waving their long antennae. The antennae are usually held straight forward, with the distal segments slightly turned downwards; in Figures 2, 16 and 19, the antennae are arranged backwards to achieve a larger image of the body without cutting off the antennae. The arolia of all legs are mostly held in an upright position. These are frequently cleaned by drawing them through the mouthparts (*vide* Adis & Hirschel 2002a). Other body parts are also cleaned, and this is achieved by bending the relevant part towards the mouthparts, while the animal is frequently fastened upside-down by one or two legs only. Moults take place in the early evening, when temperatures are still

high, exuviae being ingested by all nymphal stages. Size measurements of 12 specimens in rearing chambers at Plön (Germany) at 30/18°C (8 hrs. day/16 hrs. night) indicate eight, possibly 10 developmental stages. Uptake of water after moulting is observed as common, and hatched nymphs reach adulthood after 3.5-4 months.

Mantophasma zephyra Zompro, Klass, Kristensen & Adis, 2002 *in* Klass *et al.* 2002: 1456.

Figures 18-19

Live specimens collected in the Erongo Mountains, Namibia, in March 2002 (*vide* Figure 20), have the body green with a lateral stripe. This stripe is yellow in males and dirty white in females. Females occur in a green and a pale brown form (Adis *et al.* 2002). A detailed anatomical study of both sexes, including the description of the male, is in progress and shall be published elsewhere.

BIONOMICS: *Mantophasma zephyra* is diurnal in habits. For most of the day animals sit solitarily on twigs, on blades of grass, or at the base of trees, constantly waving their antennae (*vide* Adis & Hirschel 2002b). Adis *et al.* (2002) briefly described the feeding and hunting behaviour of the species. Males and females were repeatedly observed 'drumming' during daylight hours. Every 30-35 seconds animals 'drum' the abdomen seven times onto the ground for the duration of 12-15 seconds. Only during this 'drumming' the arolia are placed on the ground, suggesting these to be important for sound reception. When the two sexes meet, they maintain a distance of several centimetres, their flickering antennae not making contact. The smaller male (body length: 17.8±0.6 mm, wet weight: 0.07±0.01 g; n=10) of a sudden then rapidly mounts the pronotum or abdomen of the larger female (body length: 19.7±0.8 mm, wet weight: 0.14±0.02 g; n=10), possibly to avoid cannibalism. If females appear agitated, males retreat by jumping, often landing some 10 centimetres away. If the male's head is initially directed towards the tip of the female's abdomen, the male quickly rotates until the heads are aligned (*vide* Adis & Hirschel 2002b). The male abdomen is then bent down to the right side to facilitate copulation, while the female in turn projects the abdomen upwards. Connection of genitalia on the left side of the body was not observed. Under laboratory conditions the duration of copulation was measured as 12-72 hours (n=12), with the arolia being held upright. Intense pumping movements were observed in the tip of the male's abdomen, after which a spherical eversion of the male's genitalia occurred during the first 1-2 minutes of copulation to be later observed at least three times during the first hour of copulation (*vide* Adis & Hirschel 2002b). This action is taken to indicate the direct transfer of sperm from male to female.

Males do mate with other females already two days later, and females generally copulate with two different males. Within two weeks, the abdomen of females grows significantly, the body length attains 23 mm and wet weight 0.22 g. In nature, females lay eggs encased in protective foam deep in the soil. Adults do not moult.

DISCUSSION

The true position of the order Mantophasmatodea within the classification of insects remains a puzzle, although the structure of the thoracic terga, which overlap one another and decrease in length caudad, together with the structure of the egg, indicate closer affinities to the order Grylloblattodea.

Dallai *et al.* (2003) described the ultrastructure of the spermatozoa of Mantophasmatodea. A cladistical analysis based on these sperm features indicates a close relationship with the order Mantodea. This also agrees with the structure of the egg. Klass *et al.* (2002) suggest a possible closer affinity to Phasmatodea or Timematodea. The mantophasmatodean egg, however, lacks the apomorphies of Phasmatodea, including the hard eggshell, an external and internal micropylar plate, and the presence of an operculum, which is discarded by the hatching nymph (Zompro 2004). The order also differs considerably from Timematodea in the lack of a detachable operculum in the egg (Zompro 2004).

The discovery of further species of Mantophasmatodea in South Africa by Picker *et al.* (2002) indicates that there are presumably many more species to be discovered, possibly each mountain

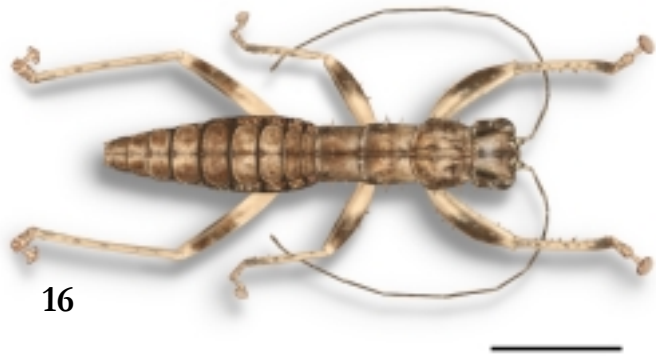

Figure **15**. Habitus of living *Tyrannophasma gladiator* sp. nov. ♂. Figure **16**. Habitus of *Tyrannophasma gladiator* sp. nov. ♀ (dorsal aspect, antennae laid back). Figure **17**. The habitat of *Tyrannophasma gladiator* sp. nov. on the Brandberg Massif, Namibia. Scales bars: 15-16 = 10 mm

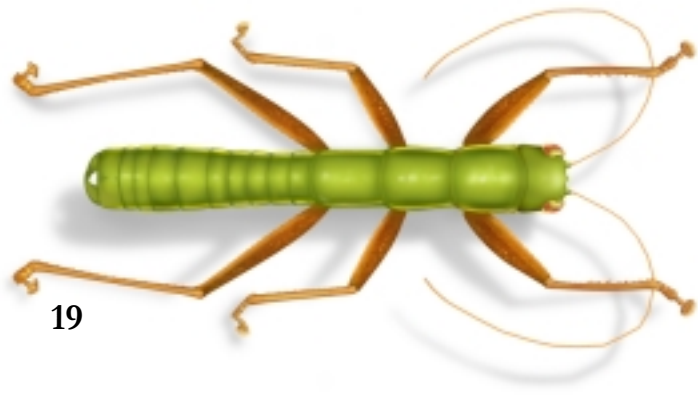

Figure **18**. *Mantophasma zephyra* Zompro *et al.*, pair in *copula*. Figure **19**. *Mantophasma zephyra* Zompro *et al.*, ♂ (dorsal aspect, antennae laid back). Figure **20**. The habitat of *Mantophasma zephyra* Zompro *et al.* in the Erongo Mountains, Namibia. Scale bars: 18-19 = 10 mm.

range featuring endemic species. The occurrence of Mantophasmatodea in South Africa was predictable, as natural barriers to dispersal do not divide the area. More interesting is how far to the north the order is distributed, if species of the order also occur at lower altitudes and more humid climates, and finally, if the order is actually restricted to the African Continent.

ACKNOWLEDGEMENTS

Scientific members of the Brandberg Expedition were Philip E. Bragg, Seth Eiseb (NMNW), John Irish (Namibian National Biodiversity Programme, Windhoek, Namibia), Ashley H. Kirk-Spriggs (NMNW), Thomas Kujawski (ASA-Multimedia, Flintbek, Germany; www.asa-multimedia.de), who also supplied the photographs, Darren Mann (UMO), Eugène Marais (NMNW), Wolfram Mey (Museum für Naturkunde, Berlin, Germany), Piotr Naskrecki, Louis Scott (University of the Orange Free State, Bloemfontein, South Africa) and the first author. Anke Teschke (Kiel, Germany) digitised the detailed figures. The writers wish to acknowledge the following individuals for their kind support: Stefanie and Reinhard Mosich (Omaruru, Namibia), Roger Butlin (University of Leeds, UK); Esther Moombolah-/Goâgoses (NMNW); Judith Marshall (British Museum, Natural History, London, UK); Sigfrid Ingrisch (Bad Karlshafen, Germany); Wolfgang Junk, Berit Hansen and Irmgard Adis (Max-Planck-Institute for Limnology, Plön, Germany); Wolfgang Dreyer and Friedrich Sick (Zoological Institute, Christian-Albrechts-University of Kiel, Germany); Kurt Hirschel (Oberriexingen, Germany); Linda de Jager (Strings Productions, Johannesburg); Andreas Zompro (Elmshorn, Germany). The National Museum of Namibia and the Max-Planck-Institute for Limnology coordinated the expedition to the Brandberg. Conservation International sponsored helicopter support and the Max-Planck-Institute for Limnology sponsored assistance by the Brandberg Mountain Guides. The British Ecological Society provided funding to support P.E. Bragg's participation in the expedition. Permission to conduct the expedition was kindly granted by the National Monuments Council of Namibia.

REFERENCES

ADIS, J. & HIRSCHEL, K. 2002a. "Gladiator" - a new insect order. Videoclip 4/2002 (99 sec), available at: http.// www.mantophasmatodea.de

ADIS, J. & HIRSCHEL, K. 2002b. *Mantophasma zephyra* - a new insect order. Videoclip 4/2002 (144 sec), available at: http.//www. mantophasmatodea.de

ADIS, J., ZOMPRO, O., MOOMBOLAH-/GOÂGOSES, E. & MARAIS, E. 2002. Gladiators: a new order of insects. *Scientific American* **287**(5): 60-67.

CRAVEN, P. & CRAVEN, D. 2000. The flora of the Brandberg, Namibia (pp. 49-67). In KIRK-SPRIGGS, A. H. & MARAIS, E. (eds). *Dâures - biodiversity of the Brandberg Massif, Namibia.* Cimbebasia Memoir **9**, National Museum of Namibia, Windhoek, 1-389 pp.

DALLAI, R., FRATI, F., LUPETTI, P. & ADIS, J. 2003. Sperm structure of *Mantophasma zephyra* (Mantophasmatodea, Insecta). *Zoomorphology* **122**: 67-76.

KIRK-SPRIGGS, A. H. & MARAIS, E. (eds). *Dâures - biodiversity of the Brandberg Massif, Namibia.* Cimbebasia Memoir **9**, National Museum of Namibia, Windhoek, 1-389 pp.

KLASS, K. D., ZOMPRO, O., KRISTENSEN, N. P. & ADIS, J. 2002. Mantophasmatodea: a new insect order with extant members in the afrotropics. *Science* **296**: 1456-1459.

OLSZEWSKI, J. D. S. 2000. Brandberg climatic considerations (pp. 39-48). In KIRK-SPRIGGS, A. H. & MARAIS, E. (eds). *Dâures - biodiversity of the Brandberg Massif, Namibia.* Cimbebasia Memoir **9**, National Museum of Namibia, Windhoek, 1-389 pp.

PICKER, M. D., COLVILLE, J. F. & VAN NOORT, S. 2002. Mantophasmatodea now in South Africa. *Science* **297**: 1475.

WITTNEBEN, M. in prep. *Eine Beschreibung und Klassifikation der Vegetation und Habitate entlang eines Höhentransektes auf dem Brandbergmassiv in der Wüste Namib, Namibia.* Diploma dissertation, Institute of Ecology & Evolutionary Research, University of Bremen, Germany.

ZOMPRO, O. 2001. The Phasmatodea and *Raptophasma* n. gen., Orthoptera *incertae sedis*, in Baltic Amber (Insecta: Orthoptera). *Mitteilungen des Geologisch-Paläontologischen Institutes der Universität Hamburg* **85**: 229-261.

ZOMPRO, O. 2004. Revision of the genera of the "Areolatae", including the status of *Timema* and *Agathemera* (Insecta: Phasmatodea). *Abhandlungen des Naturwissenschaftlichen Vereins in Hamburg*: in press.

ZOMPRO, O., ADIS, J. & WEITSCHAT, W. 2002. A review of the Order Mantophasmatodea (Insecta). *Zoologischer Anzeiger* **241**(3): 269-279.

ZOMPRO, O. & ZOMPRO, A. 2001. Mantophasmatodea - a new order of insects, available at: http://www.mantophasmatodea.de

Received December 2002; accepted May 2003.