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***Titanodula* gen. nov., a new genus of giant Oriental praying mantises (Mantodea: Mantidae: Hierodulinae)**

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Front cover: Live photograph of *Titanodula attenboroughi* sp. nov. male holotype, Kon Chu Rang Nature Reserve, Vietnam, July 2018. © Xavier Vermeersch.

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Abstract

Recent taxonomic expeditions that were made possible within the framework of the Global Taxonomic Initiative project “A step further in the entomodiversity of Vietnam” resulted in the collecting of large and robust *Hierodula*-like praying mantises with a unique morphology of the male genitalia for which the new genus *Titanodula* gen. nov. is created. All collected specimens were very similar in external morphology, but an in-depth analysis of the male genitalia revealed the existence of two distinct species in Vietnam. One species was matched with *Hierodula fruhstorferi* Werner 1916, previously only known by the holotype female, hereby transferring it to *Titanodula* gen. nov. The other species is new to science, endemic to the Annamite mountain range in the Vietnamese Central Highlands, and is described as *Titanodula attenboroughi* sp. nov. in tribute to Sir. David Attenborough. Additionally, two other Oriental species, *Hierodula grandis* Saussure, 1870 and *Hierodula formosana* Giglio-Tos, 1912 are discussed and transferred to *Titanodula* gen. nov.

Keywords: Annamite mountains, Global Taxonomic Initiative, *Hierodula*, Vietnam

Introduction

The very speciose genus *Hierodula* Burmeister, 1838 has served as a wastebasket taxon since its creation and accommodates the vast majority of Oriental praying mantises with a typical praying mantis appearance. These species all share in common a generally large size, are usually coloured green or brown, have a large triangular head without processes, filiform antennae in both sexes, a smooth and elongated pronotum without lateral expansions, legs without lobes and a smooth fusiform abdomen without lobes or other projections. However, although many species share common traits in their external morphology, the male genitalia in *Hierodula* are incredibly diverse and a strong indication of the polyphyletic nature of the genus. Amongst the species currently placed within *Hierodula* one group can clearly be set apart, both by their large size and robustness, and by the unique morphology of the male genitalia which have no equal within the subfamily Hierodulinae. The combination of distinctive morphologic characters and the unique genitalia justify generic separation, for which the new genus *Titanodula* gen. nov. is created. *Titanodula attenboroughi* sp. nov. from the Annamite mountain range in the Vietnamese Central Highlands is described and the new combination *Titanodula fruhstorferi* (Werner, 1916) comb. nov. is proposed for its close relative from Northern Vietnam. A diagnosis and additional information on the species are given. Although both species share a great resemblance in external appearance they can easily be differentiated by the unique morphology of the male genitalia. Furthermore, *Hierodula grandis* Saussure, 1870 and *Hierodula formosana* Giglio-Tos, 1912 also belong to *Titanodula* gen. nov. based on their external morphology and male genitalia, resulting in the new combinations *Titanodula grandis* (Saussure, 1870) comb. nov. and *Titanodula formosana* (Giglio-Tos, 1912) comb. nov. Future research is still needed to identify which other species of *Titanodula* gen. nov. might have been

erroneously described within *Hierodula* in the past and to investigate the existence of other unknown species of *Titanodula* gen. nov. across the Oriental region.

Material & methods

FIELD COLLECTING AND PREPARATION

Specimens were collected during the day by visually inspecting the vegetation and at night by the same method using a hand torch and/or a head torch. The specimens were euthanized by ethyl acetate fumes shortly after capture and stored in an airtight plastic “zip”-bag, embedded in fine wood chips and sprinkled with ethyl acetate to prevent rotting, moult growth and to keep the specimens flexible during storage and transport. The bags were frozen at -18°C upon arrival, the specimens were dry mounted at a later time.

For genitalia preparations the tip of the abdomen was separated from the specimens and macerated in a 10% potassium hydroxide (KOH) solution for ca. 45 minutes at ~70°C, then rinsed with distilled water and placed in 70% ethanol for further dissection to isolate the genitalia and the last abdominal tergite and coxosternite. All the dissected parts were placed in small hermetically sealed plastic vials filled with glycerine for long-term preservation and subsequently pinned under the specimen. Each genitalia preparation received a unique identifier following the GENXXYY template used by the author, with GEN being short for ‘Genitalia’, XX being the year in which the preparation was made, and YY the follow up number of the preparation.

ILLUSTRATIONS

Photographs were taken with a Canon EOS 700D DSLR camera mounted with a Sigma AF 50mm f/2.8 EX DG macro lens and two Yongnuo Speedlite YN 460-II off-camera flashes. The photographs were stacked and processed in Adobe® Photoshop CS5.

DESCRIPTIVE CONVENTIONS AND MORPHOLOGICAL CHARACTERS

The morphological nomenclature follows BRANNOCH *et al.* (2017) and VERMEERSCH (2018), genital terminology is according to SCHWARZ & ROY (2019). The formula to express the spine count of the raptorial legs follows BRANNOCH *et al.* (2017). Spine numbering is always performed from the proximal end towards the distal end.

OBSERVATIONS AND MEASUREMENTS

Observations were done using a Leica EZ4W stereo-microscope. The description of the colouration is based on live specimens. Measurements were taken on dry-pinned collection specimens using an electronic calliper as detailed and illustrated in SHCHERBAKOV (2017) and VERMEERSCH (2018) and are expressed in millimetres. The measurement ‘Body Length’, from the vertex to the tip of the abdomen is added. ‘Total Length’ is here measured from the vertex to the tip of the tegmina or alae, whichever is the longest as it is done for species in which the wings extend further than the tip of the abdomen. [Note: This measurement is identical to ‘Body Length’ for short winged species]. For paired appendages the given value represents the mean of both measurements with exception of the tegmina where only the overlapping tegmen is taken into account. In addition to the twenty-four detailed measurements provided in Table 1, all dry-pinned specimens of the Vietnamese species were measured for total length (TL), body length (BL), pronotum length (PL), pronotum width (PW), and tegmen length (TgL) to assess intraspecific variability across specimens (Table 2).

ABBREVIATIONS:

Asl	=	Above sea level
AvS	=	Anteroventral spine
DS	=	Discoidal spine
HT	=	Holotype
N.P.	=	National Park
N.R.	=	Nature Reserve
PT	=	Paratype
PvS	=	Posteroventral spine
PzL	=	Prozone length
MzL	=	Metazone length.

COLLECTION ACRONYMS:

RBINS	=	Royal Belgian Institute for Natural Sciences, Brussels, Belgium
MNHN	=	Muséum National d'Histoire Naturelle, Paris, France
NHMW	=	Naturhistorisches Museum Wien, Vienna, Austria
UniFI	=	Università degli Studi di Firenze, Florence, Italy.

Taxonomy

Order Mantodea Burmeister, 1838

Family Mantidae Burmeister, 1838

Subfamily Hierodulinae Brunner von Wattenwyl, 1893

Genus *Titanodula* gen. nov.

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(Figs 1–3, 5–6)

Type species: *Titanodula attenboroughi* by present designation.

DIFFERENTIAL DIAGNOSIS. *Titanodula* gen. nov. can be distinguished from all other genera within Mantidae by the combination of the following characters:

- 1) Large and robust praying mantis.
- 2) Lower frons with two vertical margins within, interrupted in the middle, forming two small but distinct tubercles at its anterior margin.
- 3) Ventral coxal lobe darkened or black ventrad.
- 4) Darkened or black spots at the base of 2nd, 10th and 15th profemoral AvS.
- 5) All protarsal segments black anteriorly.
- 6) Male genitalia as described below.

DESCRIPTION. Large and very robust praying mantises. Females macropterous, tegmina cover the abdomen completely. Male macropterous, tegmina extend beyond the abdomen.

Head: triangular, broader than high, with large rounded eyes. Antennae filiform. Long but robust pronotum, with smooth dorsal surface, without projections or lateral expansions.

Thorax: pronotum very finely denticulate along the margins of the prozone without denticulations in the metazone in females, entirely smooth edges in males. Dorsal side of the pronotum covered by a very thin whitish waxy layer in adults of both sexes that can easily be removed by direct contact. Profemora with 4 discoidal spines, 15 anteroventral spines and 4 posteroventral spines. Protibiae with 13–14 (rarely 15) anteroventral spines and 10 posteroventral spines. Protarsus (all segments) entirely black anteriorly, concolour with rest of the forelegs (green in all studied specimens) on the posteriorly. Ratios: ♂ MzL/PzL: 3.2; ♀: MzL/PzL: 3. All known species have darkened or blackish spots on the anterior side of the profemora located at the base of the 2nd, 10th and 15th anteroventral spine.

Male genitalia: with left phallic complex elongated and relatively narrow, lobe L4A projecting anteriorly; afa with small tubercle-shaped aafa and larger pafa with spear shaped projection oriented posteriad; distal processes (sdp) adjacent, relatively short but very strongly curved and about the same size.

ETYMOLOGY. The genus name is derived from the ‘Titans’ in Greek mythology, who were a mythological race of giants, thus emphasizing the large size and strength of the species belonging to this genus. The second part of the genus name “-dula” is a reference to the genus *Hierodula* in which some species were previously described.

DISTRIBUTION. *Titanodula* gen. nov. has a confirmed presence in Bangladesh, Southern China, Taiwan and Vietnam. It appears that the genus has a wide distribution across the Oriental region but remains limited to suitable forested habitats, making these giant praying mantises vulnerable to habitat loss and deforestation as a result of expanding human activities.

SPECIES INCLUDED:

Titanodula attenboroughi sp. nov.

Titanodula formosana (Giglio-Tos, 1912) **comb. nov.**

Titanodula fruhstorferi (Werner, 1916) **comb. nov.**

Titanodula grandis (Saussure, 1870) **comb. nov.**

***Titanodula attenboroughi* sp. nov.**

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(Figs 1–3, 5–6)

DIAGNOSIS. Very large and robust praying mantis. Head triangular, antennae filiform. Long but robust pronotum, with smooth dorsal surface. Pronotum very finely denticulate along the margins of the prozone in female, without denticulations in the metazone, entirely smooth edges in males. Spinal formula: F = 4DS/15AvS/4PvS; T = 13–14AvS/10PvS. Ratios ♂: MzL/PzL: 3.2; ♀: MzL/PzL: 2.9. With black spots on the anterior side of the profemora located at the base of the 2nd, 10th and 15th anteroventral spine. Protarsus (all segments) entirely black on the anterior side. Both sexes macropterous. Phalloid apophysis (afa) with two sclerotised processes, anterior process (aafa) small and tubercle-shaped, broad and dome-like at the base with a smaller rounded projection on top of it, located posteriorly from the middle. Posterior process (pafa) spear-shaped, with weakly developed base, almost straight, long and heavily sclerotised, projecting straight or slightly diagonally posteriad.

TYPE MATERIAL. Holotype ♂ (Figs 1, 3 A–C): Vietnam, Gia Lai Province., Kon Chu Rang N.R., 14°28'28"N; 108°32'27"E, 13–20.VII.2018, At Light, leg. J. Constant, J. Bresseel, X. Vermeersch, Genitalia prep. Vermeersch Nr. GEN1840, GTI Project, I.G.: 33.769 (RBINS).

Paratypes (3♂♂, 6♀♀): 2♀♀ (Fig. 2): same data as holotype, Night Collecting. Paratypes (2♂♂): Vietnam, Gia Lai Province, Kon Chu Rang N.R., 15 km from HQ, 1110 m asl, 14°31'13"N; 108°28'12"E, 27–28.V.2019, At Light, leg. L. Bartolozzi, S. Bambi, A. Bandinelli, E. Orbach. Stored in ethanol (UniFI); 1♂, 4♀♀: Vietnam, Quang Tri Province, Da Krong N.R., 16°37'N; 106°47'E, 5–10.VII.2011, Day Collecting, leg. J. Constant, J. Bresseel, Genitalia prep. Vermeersch Nr. GEN1910, GTI Project, I.G.: 31.933 (RBINS).

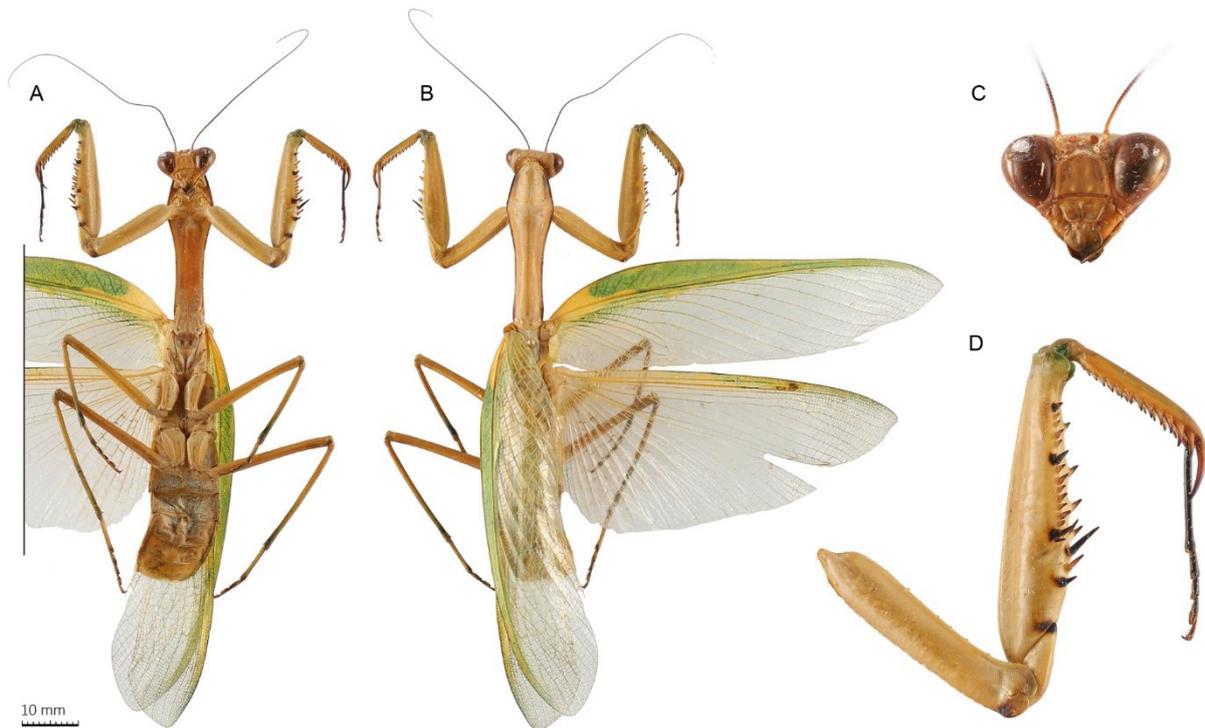


Fig. 1. *Titanodula attenboroughi* sp. nov., holotype ♂ (RBINS). A, habitus, dorsal view. B, habitus, ventral view. C, head, frontal view. D, left prothoracic leg, anterior view. C, D not to scale.

DESCRIPTION. MALE (Figs 1, 3 A–C). Measurements (see Tables 1–2). Colouration (Figs 1, 3A–C): All known male specimens of *T. attenboroughi* sp. nov. feature a uniformly green colouration without any variations in darkness or tone between individuals. The dorsal side of pronotum is green and covered in both sexes with a whitish waxy secretion that is easily removed by touch. Underside of pronotum is entirely reddish-brown with a hint of magenta (purplish-red colour, sometimes also referred to as *Fuchsia*), but posterior end of pronotum is mostly magenta and is consistently covered with same whitish waxy secretion as on dorsal side. Ventral side of meso and metanotum are also magenta. Meso- and metacoxa are bright green but their trochanters are magenta while rest of legs are green.

Head (Figs 1 C; 3 A–C): Wider than long with large, rounded compound eyes. Vertex flat. Ocellar tubercle not visible, in same plane as frons, without protruding ridges. Ocelli small, all about same size. Lower frons transverse with external margins posteriorly and laterally, no margin anteriorly, with two faintly defined vertical ridges internally that run from posterior end towards middle where they are abruptly interrupted. Two more clearly defined tubercles are placed in their extension and border anterior part of lower frons. Clypeus and labrum smooth.

Thorax (Figs 1 A–B; 3 A–C): Pronotum long, straight and robust. Margins smooth, without denticulations or projections. Dorsal surface also entirely smooth, with a darker spot at each side laterally adjacent to the posterior margin of pronotum. Largest width before one third of pronotum, narrowest width located after middle of pronotum. Cervix with strongly sclerotized lateral and intercervical sclerites, merged in the middle. Postcervical plate and posterior ventral part of pronotum entirely smooth. Ventral lateral margins concolour with rest of pronotum.

Table 1. Detailed measurements [mm] of *Titanodula attenboroughi* sp. nov. and *Titanodula fruhstorferi* comb. nov. From left to right: *T. attenboroughi* holotype ♂, *T. attenboroughi* paratype ♀, *T. fruhstorferi* male, additional specimen 1, *T. fruhstorferi* female, additional specimen 2.

Measurements	<i>T. att</i> HT (♂)	<i>T. att</i> PT (♀)	<i>T. fru</i> AS1 (♂)	<i>T. fru</i> AS2 (♀)
Total length	99.6	102.2	107	93.7
Body length	-	97.3	88.4	91.9
Head width	10.3	12.5	10.5	11.9
Head height	8.6	11.2	8.2	10.6
Pronotum length	29.3	35	30.2	33.2
Pronotum width	8.2	10.4	8.9	10.2
Pronotum narrow width	4.7	6	4.9	5
Prozone length	7	8.9	7.3	8.3
Metazone length	22.3	26.1	22.9	24.9
Tegmen length	69	61.2	73.8	59.2
Ala length	62.2	55.5	-	-
Procoxa length	16.8	22.5	18.5	21.4
Profemur length	20.4	25.6	21.2	23.1
Protibia length	12.9	17.3	13.8	16.1
Protarsus length	14	13.3	13.6	15.1
Mesofemur length	19.2	24.2	21.2	21.9
Mesotibia length	16	20.6	17.3	17.8
Mesotarsus length	10.7	10.8	11.4	11.3
Metafemur length	22.3	28	25.8	25.2
Metatibia length	21.8	28.6	24.4	25.5
Metatarsus length	12.9	14.6	14.6	13.9
Anteroventral femoral spine count	15/15	15/15	15/15	15/15
Anteroventral tibial spine count	13/13	14/14	14/14	14/14
Posteroventral tibial spine count	10/9	10/10	10/10	10/10

Prothoracic legs (Figs 1 A–B, D; 3 A–C): Coxa with 8–10 very small more or less blunt spinules of more or less equal size with same colour as coxa. Dorsal and ventral coxal lobes rounded, equal in length and adjacent, both lobes equally as broad. Black spot at proximal edge of ventral coxal lobe. Trochanter with black spot at anterior tip, adjacent matching black spot of same size on anterior side of femur. Femur with gently convex but straight dorsal margin, surface entirely smooth. Femoral brush ellipse-shaped, starting from 12th or 13th AvS and

ending just a little distally of 15th AvS. Genicular lobes large and rounded, with minute, almost invisible genicular spur. Colouration of prothoracic legs green posteriorly, yellow anteriorly. Tibial spine groove proximally placed from middle of femur. AvS 1, 2, 10 and 15 black, black only along the distal and proximal edges or strongly apically infuscate (variable colouration between specimens) with black spot at base of AvS 2, 10 and 15 that slightly extends on anterior surface of femur; other AvS concolour with femur, only apically infuscate; AvS 10 and 12 large, but with 2 much smaller spines of equal size between them. Large and medium spines alternate between AvS 1 and 12, first spine being a medium one; medium spines subtly inclined towards anterior side of femur. PvS 4 smaller than others, PvS 1, 2 and 3 about equal in size; all concolour with femur and slightly apically infuscate. DS 1 and 4 more or less equal in size, DS 2 slightly longer than DS1, DS 3 longest and about 2x size of DS 2; DS 1 and 3 entirely black on anterior side (note: in some specimens only DS1 entirely black and DS3 apically infuscate), apically infuscate on posterior side, others apically infuscate on both sides. DS1 with black spot at base on anterior side. Protibiae smooth with longitudinal groove across entire length of posterior side. Tibial AvS gradually elongated towards tibial spur, all concolour to tibia but apically infuscate. PvS slightly more procumbent, spines gradually longer towards distal end. Tibial spur apically infuscate. Protarsi apically darkened posteriorly, entirely black anteriorly; first tarsomere longer than others combined. Spinal formula: F = 4DS/15AvS/4PvS; T = 13–14AvS/10PvS.

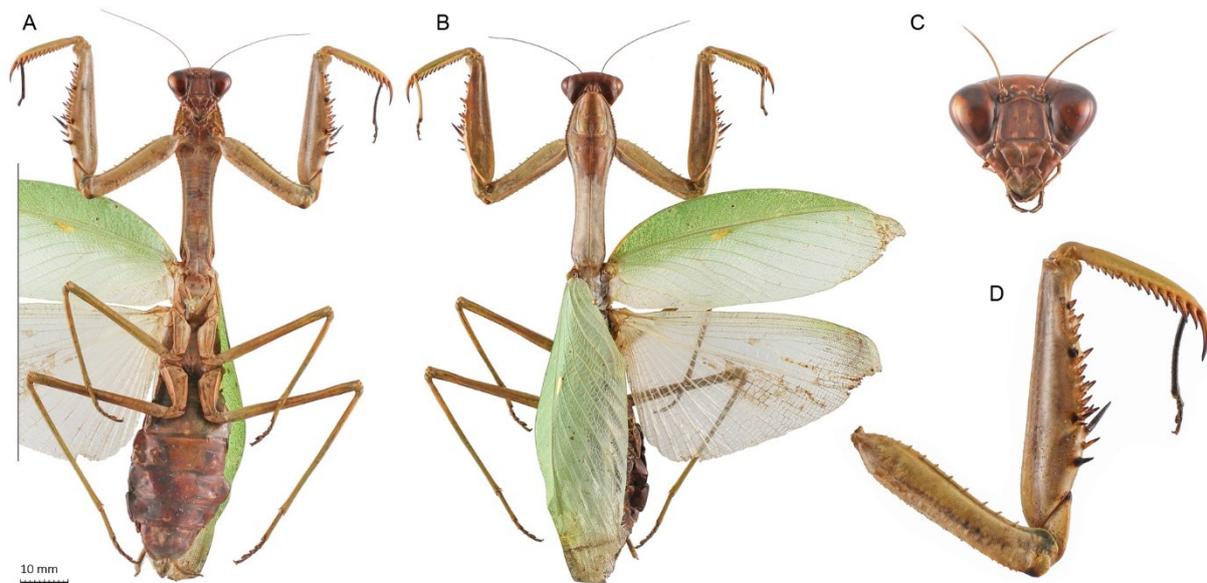


Fig. 2. *Titanodula attenboroughi* sp. nov., paratype ♀, [PT1] (RBINS). A, habitus, dorsal view. B, habitus, ventral view. C, head, frontal view. D, left prothoracic leg, anterior view. C, D not to scale.

Meso- and metathoracic legs (Figs 1 A–B; 3 A–C): Long and slender, without dilatations or projections. Femora with rounded genicular lobes and a short genicular spur. Tibiae with two apical spurs. Tarsi 5-segmented, green and slightly darkened apically. First tarsomere of mesotarsus shorter than remaining segments combined, first tarsomere of metatarsus about equal in length compared to remaining segments combined.

Tegmina and alae (Figs 1 A–B; 3 A–C): Tegmina uniformly green on costal area, hyaline in discoidal area, longer than tip of abdomen when folded in rest. Veins green, stigma white with strong hue of yellowish-green. Stigma located anteriorly from middle of tegmen. Alae fully developed, hyaline with only greenish anterior margin.

Abdomen (Fig. 1 A–B): Fusiform, uniformly green ventrally, yellowish-green dorsally. Cerci setose, not flattened, with 22–23 segments, proximal segments being merged together and difficult to distinguish.

Table 2. Measurements [mm] of *Titanodula attenboroughi* sp. nov. and *Titanodula fruhstorferi* comb. nov. to assess intraspecific variability.

<i>Titanodula attenboroughi</i> sp. nov. (♂) - from 2 specimens					
	TL	BL	PL	PW	TgL
Average	95.6	-	28.9	8.2	65.4
Standard Deviation	4	-	0.45	0	3.6
Max value	99.6	-	29.3	8.2	69
Min value	91.6	-	28.4	8.2	61.8
<i>Titanodula attenboroughi</i> sp. nov. (♀) - from 6 specimens					
	TL	BL	PL	PW	TgL
Average	105.1	99.8	36.3	10.8	64
Standard Deviation	7	9.2	2.6	0.7	4.8
Max value	115	115	39.6	12	71.3
Min value	97.7	88.4	33.8	9.9	59.2
<i>Titanodula fruhstorferi</i> comb. nov. (♂) - from 14 specimens					
	TL	BL	PL	PW	TgL
Average	105.4	90.46	30.7	8.8	71.9
Standard Deviation	4.5	3.8	1.5	0.4	3.3
Max value	110.3	96.8	33.5	9.3	75.5
Min value	95	81.7	27.8	8.1	64.5
<i>Titanodula fruhstorferi</i> comb. nov. (♀) - from 1 specimen [AS2]					
	TL	BL	PL	PW	TgL
Value	93.7	91.9	33.2	10.2	59.2

Male genitalia (Fig. 5 B–D): Ventral phallomere of left phallic complex elongated, much longer than broad, with two short and strongly sclerotised distal processes (sdp) of about the same length with acute apex. Median process (sdpm) bend at the middle and pointing sideways, lateral process (sdpl) much more strongly bend and pointing upwards, with broader base than sdpm. Apical process of left phallomere (paa) complex in shape, with sclerotised apex and sclerotizations near the base, but membranous in the middle. Apex abruptly projecting dorsally and to the left, the apex sharply curved in a 90° hook with narrower but rounded tip. Phalloid apophysis (afa) with two sclerotised processes, anterior process (aafa) small and tubercle-shaped, broad and dome-like at the base with a smaller rounded projection on top of it, located posteriorly from the middle. Posterior process (pafa) spear-shaped, almost straight from the base onwards, long and heavily sclerotised, projecting straight or slightly diagonally posteriad. Membranous lobe loa rounded and small. Genital lobe goa strongly developed, extending laterally over its whole length. Right phallomere with sclerite R1A more or less triangular. Sclerite R3 shovel-shaped, very wide at its anterior end. Ventral process (pia) triangular with many longitudinal grooves on its surface, sclerified ventral process (pva) strongly sclerotized,

finger-shaped, ending in a blunt hook. Coxosternite IX (subgenital plate) with small black spikes on the right lateral edge, sometimes also in the middle of the distal edge.



Fig. 3. *Titanodula attenboroughi* gen. nov. et sp. nov., live photographs of holotype ♂ (A, B, C) and paratype ♀ [PT1] (D, E) at Kon Chu Rang N.R., VII. 2018.

FEMALE (Figs 2, 3 D–E). Measurements (see Tables 1–2). Similar to male, with following differences:

Thorax (Figs 2 A–B, 3 D–E): Margins of pronotum finely denticulated anteriorly, fading out after pronotal supracoxal dilatation, absent in posterior end.

Prothoracic legs (Figs 2 A–B, D, 3 D–E): Coxae with 8–10 small sharp and regularly interspaced spinules of more or less equal size with same colour as coxa, spinules larger and more pronounced than in the male.

Tegmina and alae (Figs 2 A–B, 3 D–E): Tegmina uniformly green in costal area, partly hyaline in discoidal area, being green anteriorly, then quickly becoming hyaline in a gradient posteriorly. Tegmina reaching tip of abdomen when folded in rest. Alae fully developed, hyaline with faintly green anterior margin.

Abdomen (Figs 2 A, 3 D): Elongated ovaliform, much broader than in male, uniformly green ventrally, bright yellowish dorsally with a hint of green near the edges.

NOTE: The shape of the pronotum in females appears to be somewhat variable between different locations. Females from Da Krong N.R. have a noticeably more pronounced supracoxal dilatation and a metazona that appears thinner, while females from Kon Chu Rang N.R. have a more subtle sinusoidal transition of the pronotal edge between these parts. Male genitalia are the same between different locations and provide the most stable and reliable characters to correctly identify the species.

ETYMOLOGY. The species epithet is a patronym dedicated to Sir David Attenborough, one of the world's most beloved naturalists, in acknowledgment for his life-long endeavours to disseminate knowledge on all the beings that are part of the natural world and to advocate for their protection and conservation.

DISTRIBUTION. *Titanodula attenboroughi* sp. nov. appears to be an endemic of undisturbed forests in the Vietnamese Annamite mountains. However, forests in the known distribution area are highly threatened and continue to disappear at an alarming rate. More distribution data are needed to evaluate the conservation status according to the IUCN Red Lists assessment guidelines, in the meanwhile the species is considered DD (Data Deficient).

***Titanodula fruhstorferi* (Werner, 1916) comb. nov.**

(Figs 4–6)

DIAGNOSIS. *Titanodula fruhstorferi* comb. nov. is very similar to *T. attenboroughi* sp. nov. in external appearance although profemoral AvS 1, 2, 10 and 15 and the basal spots of AvS 2, 10 and 15 are noticeably less dark or pronounced compared to *T. attenboroughi* sp. nov. However, both species can be readily differentiated by the unique morphology of male genitalia.

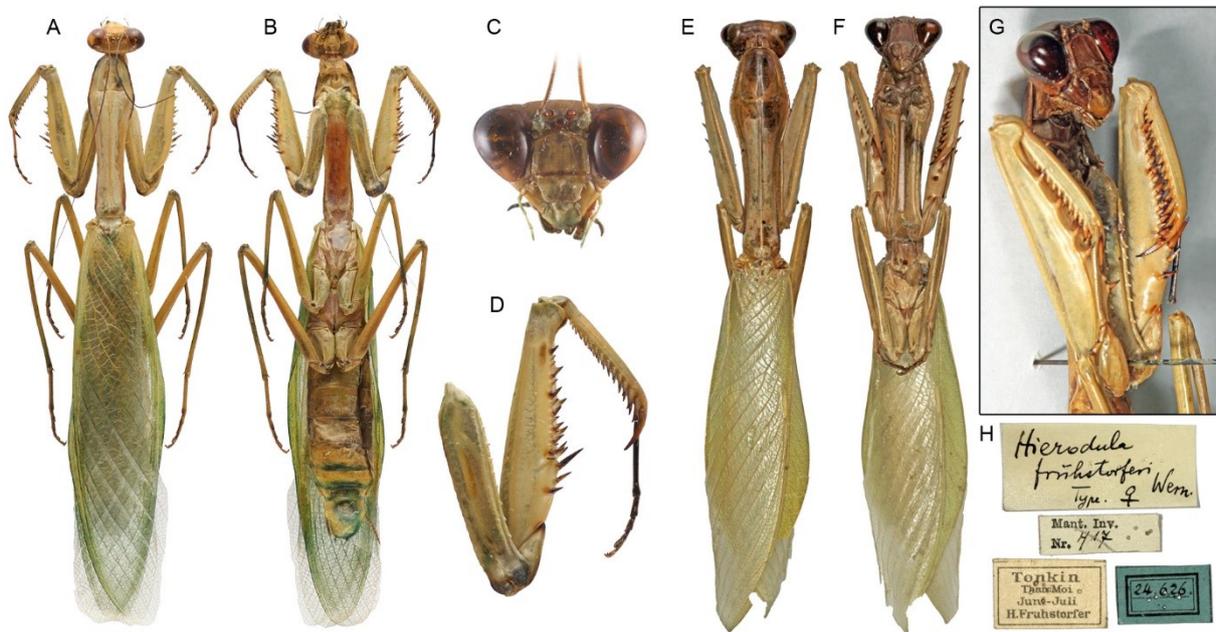


Fig. 4. *Titanodula fruhstorferi* comb. nov., additional specimen ♂ [AS1 – Tam Dao N.P.] (RBINS). A, habitus, dorsal view. B, habitus, ventral view. C, head, frontal view. D, left prothoracic leg, anterior view. *Titanodula fruhstorferi* comb. nov., holotype ♀ (NHMW). E, habitus, dorsal view. F, habitus, ventral view. G, detail of head and prothoracic legs. H, labels. © A–D, Xavier Vermeersch and E–H, Harald Bruckner)

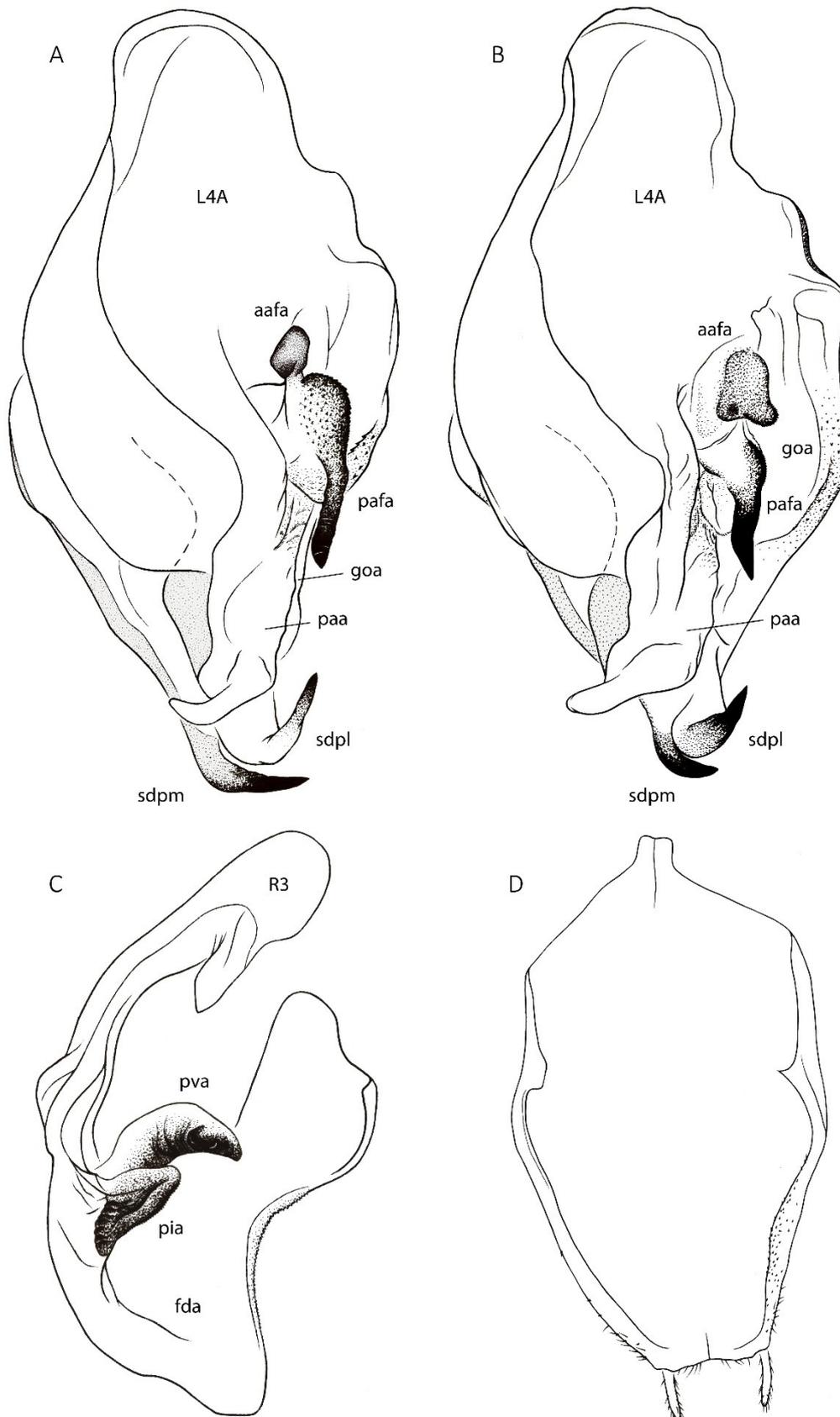


Fig. 5. *Titanodula fruhstorferi* comb. nov., additional specimen ♂ from Cuc Phuong N.P. (RBINS). A, Genitalia prep. Vermeersch Nr. GEN1839, left phallic complex, dorsal view. *Titanodula attenboroughi* sp. nov., holotype ♂ (RBINS). B, genitalia prep. Vermeersch Nr. GEN1840, left phallic complex, dorsal view. C, right phallic complex, ventral view. D, coxosternite IX (subgenital plate), dorsal view. Drawings © Mado Berthet.

MATERIAL EXAMINED. TYPE MATERIAL (examined from detailed photographs): Holotype ♀ (Fig. 4 E–F): Vietnam, Tonkin, Than Moi, VI–VII, leg. H. Fruhstorfer (NHMW).

NOTE: Holotype damaged, abdomen and metathoracic legs are missing.

ADDITIONAL MATERIAL (14♂♂, 1♀): (1♂): Vietnam, Cham Chu N.R., 22°12'N; 105°06'E, 8–12.VII.2015, Night Collecting, leg. J. Constant, J. Bresseel, Genitalia prep. Vermeersch Nr. GEN1833, GTI project, I.G.: 33.092 (RBINS). (3♂♂): Vietnam, Tam Dao N.P., 21°31'N; 105°33'E, 25–30.VII.2011, leg. J. Constant, J. Bresseel, Genitalia prep. Vermeersch Nr. GEN1909, GTI project, I.G.: 31.933 (RBINS). (10♂♂): Vietnam, Cuc Phuong N.P., 20°19'00"N; 105°36'30"E, 19–23.VII.2011, Light Trap, leg. J. Constant, J. Bresseel, Genitalia prep. Vermeersch Nr. GEN1839, GTI project, I.G.: 31.933 (RBINS). (1♀): Vietnam, Tay Yen Tu N.R., 21°11'10"N; 106°43'26"E, 7–11.VII.2013, Day Collecting, leg. J. Constant, J. Bresseel, I.G.: 32.454 (RBINS).

REDESCRIPTION. Measurements (see Tables 1–2). Very large and robust praying mantis. Head triangular, antennae filiform. Long but robust pronotum, with smooth dorsal surface. Pronotum very finely denticulate along the margins of the prozone in female, without denticulations in the metazone, entirely smooth edges in males. Spinal formula: F = 4DS/15AvS/4PvS; T = 14AvS/10PvS. Ratios ♂: MzL/PzL: 3.1; ♀: MzL/PzL: 3. With black spots on the anterior side of the profemora located at the base of the 2nd, 10th and 15th anteroventral spine. Protarsus (all segments) entirely black on the anterior side. Both sexes macropterous.

Male genitalia (Fig. 5 A): Ventral phallomere of left phallic complex elongated, much longer than broad, with two short and strongly sclerotised distal processes (sdp) of about the same length with acute apex. Median process (sdpm) bend at the middle and pointing sideways, lateral process (sdpl) much more strongly bend and pointing upwards, with much broader base than sdpm. Apical process of left phallomere (paa) complex in shape, with sclerotised apex and sclerotizations near the base, but membranous in the middle. Apex abruptly projecting dorsally and to the left, the apex sharply curved in a 90° hook with narrower but rounded tip. Phalloid apophysis (afa) with two sclerotised processes, anterior process (aafa) small and flat, tubercle-shaped, without additional projections or extensions. Posterior process (pafa) spear-shaped, with very strongly developed base, bulging anteriorly, strongly curving towards an almost straight, very long and heavily sclerotised structure, projecting straight posteriad. Membranous lobe loa rounded and small. Genital lobe goa membranous, sometimes well-developed anteriorly but in some specimens also completely collapsed, and much weaker and wrinkled in appearance posteriorly, running almost parallel to pafa posteriad. Right phallomere with sclerite R1A more or less triangular. Sclerite R3 shovel-shaped, very wide at its anterior end. Ventral process (pia) triangular with many longitudinal grooves on its surface, sclerified ventral process (pva) strongly sclerotized, finger-shaped, ending in a blunt hook. Coxosternite IX (subgenital plate) with small black spikes on the right lateral edge, sometimes also in the middle of the distal edge.

ETYMOLOGY. This species was described in 1916 by the Austrian taxonomist Franz Werner (1867–1939) in honour of Hans Fruhstorfer (1866–1922), a German explorer, insect trader and Lepidoptera specialist.

DISTRIBUTION. *T. fruhstorferi* comb. nov. inhabits the closed canopy forests of the North Vietnamese lowlands (Fig. 6). Forests in this area are highly threatened due to a high rate of

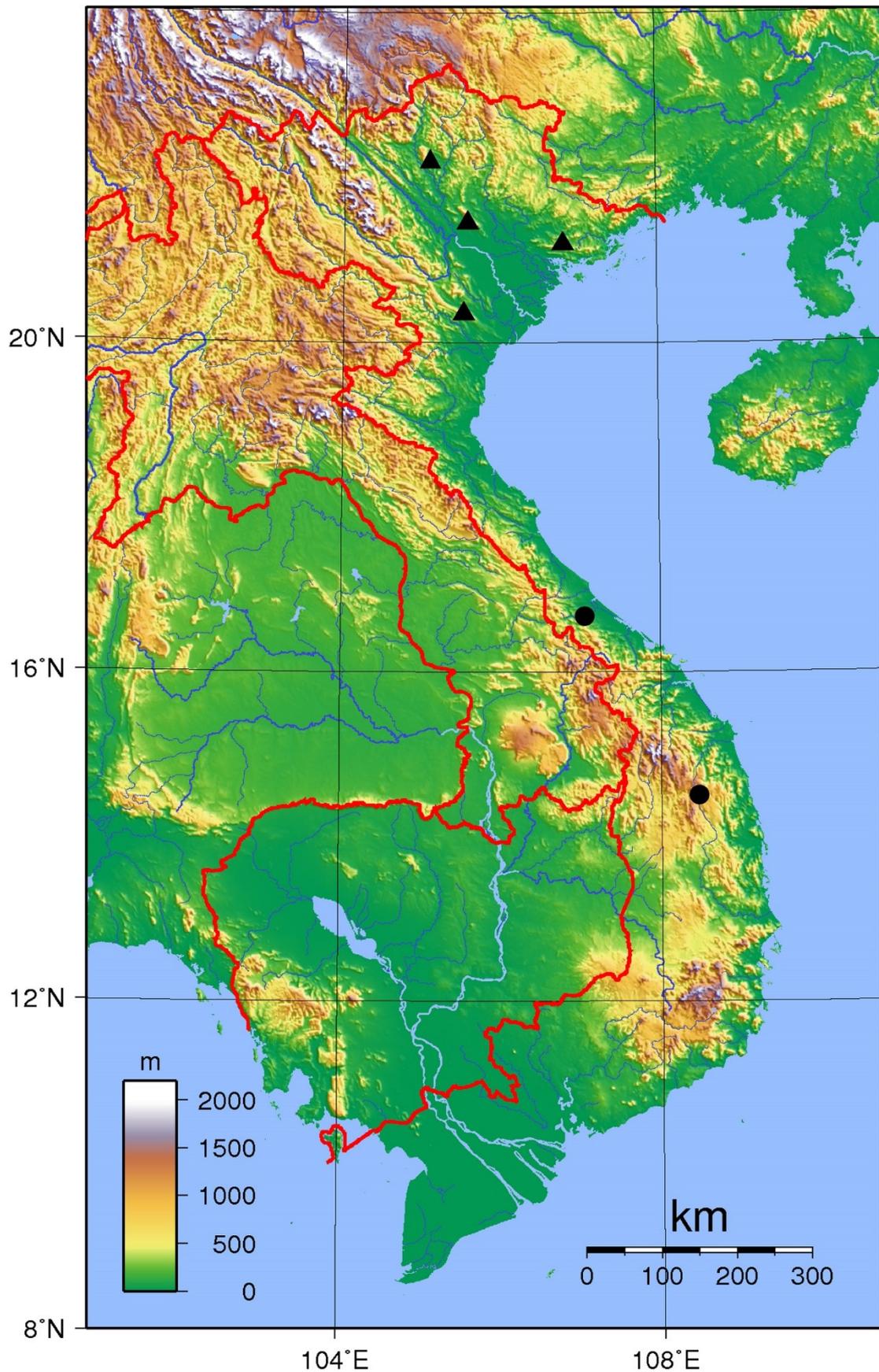


Fig. 6. Distribution map of *Titanodula fruhstorferi* comb. nov. (▲) and *Titanodula attenboroughi* sp. nov. (●) in Vietnam. From top to bottom: *T. fruhstorferi*; Cham Chu N.R., Tam Dao N.P., Tay Yen Tu N.R., Cuc Phuong N.P. *T. attenboroughi*; Da Krong N.R., Kon Chu Rang N.R.

deforestation and suitable habitats are strongly fragmented with large gaps between them. More distribution data is needed to assess its conservation status.



Fig. 7. *Titanodula grandis* comb. nov. syntype male, Natural History Museum of Geneva, Switzerland, images used with permission from [SVENSON, G.J. 2020. The Mantodea Image Database. <https://specimens.mantodearesearch.com/>]. A, dorsal view. B, ventral view. C, labels. *Titanodula grandis* comb. nov. additional male specimen from MNHN, Paris, France. D, genitalia preparation N° 4648 by R. Roy & T. Schubnell on microscope slide. © MNHN, Paris.

Discussion

TAXONOMIC CONSIDERATIONS

Additional to the description of *T. attenboroughi* sp. nov. and a reassessment of *T. fruhstorferi* comb. nov. with for the first time a description and illustration of the male and its genitalia, the two new combinations *T. grandis* comb. nov. (Fig. 7) and *T. formosana* comb. nov. (Fig. 8) are proposed. The similarity of these four species in terms of external morphology is remarkable, particularly since they can be easily separated from each other based on the morphology of the male genitalia. In Vietnam *T. attenboroughi* sp. nov. is separated from *T. fruhstorferi* comb. nov. by a physical biogeographical barrier, namely the elevated plateaus of the Annamite mountain range which are characterised by their high degree of endemism (STERLING & HURLEY, 2005). *T. formosana* comb. nov. was described by GIGLIO-TOS (1912) from a single male specimen from Taiwan (Fig. 8). BEIER (1935) added Malacca and the Sunda Islands to the

species distribution, although this is likely erroneous and requires confirmation. WANG *et al.* (2020) illustrated the habitus of *Hierodula formosana* along with the dissected male genitalia based on specimens from Southern China. In the same paper the authors also illustrated *Hierodula grandis* and its genitalia, showing a species that doesn't match with *Titanodula* gen. nov. Our current knowledge on the actual distribution of both species within the Oriental region remains incomplete. Given the similarity in male genitalia morphology between them, with merely a difference in length of pafa, there is a chance that these two species could be subspecies of each other, or even the same species showing clinal variation across its distribution range. More research is needed to fully elucidate this matter and a complete reassessment of all specimens appointed to these species is in order. In the meanwhile, the genus *Hierodula* remains a very problematic and poorly studied group. An in-depth revisional work including related Hierodulinae genera is absolutely needed to solve long-standing taxonomic issues and to facilitate the work of taxonomists to attribute a correct taxonomic placement to newly described species.



Fig. 8. *Titanodula formosana* comb. nov. holotype male, Museum für Naturkunde, Berlin, Germany. A, dorsal view. B, ventral view. C, labels. © Kai Schütte. *Titanodula formosana* comb. nov., non-type male. D, genitalia (preparation and photograph by Chih-Ting Hsu, specimen collected by Yuan-Teng Wang at Hengshan, Hsinchu, Taiwan, 21.VI.2020. © Chih-Ting Hsu.

NATURAL HISTORY

Despite their impressive size, very little is still known about *Titanodula* gen. nov., their natural history and distribution. Males were captured at light traps, suggesting excellent flight capabilities. Other specimens were found in various kinds of bushes and low trees both inside the closed canopy forest and at forest edges, and even occasionally in semi-open and open areas with abundant vegetation near the forest. Adult females are very heavy and are typically hanging upside down under large leaves or twigs. The ootheca is currently unknown.

ADDITIONAL OBSERVATIONS

About a quarter of the specimens of *T. attenboroughi* sp. nov. that were found in the Annamite Mountains of Vietnam were parasitized with fly larvae of unidentified Tachinidae. The larvae insertion sites were clearly visible as a blackish coloured wound in the lateral intersegmental membrane of the abdomen. Infected mantises could host multiple fly larvae, one adult female

was observed to have three distinct insertion sites on the abdomen. Larvae would emerge from the abdomen upon maturation to pupate outside of the host. In some cases, this emergence of larvae did not kill the host right away, even allowing the host to successfully moult afterwards. Some specimens were infected with horsehair worms. (personal observations XV, Kon Chu Rang N.R., VII. 2018).

Dried specimens of *Titanodula* gen. nov. tend to lose their natural colouration and turn brown or yellowish with some remaining hints of green. Old museum specimens at MNHN of *T. grandis* are coloured dark beige to brown, making it uncertain what live colouration could be and if the colour of the collection specimens is resulting from long-term conservation or not.

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