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# A new species of Tithaeidae (Arachnida: Opiliones: Laniatores) from Mindanao reveals contemporaneous colonisation of the Philippines by Sunda Shelf opiliofauna

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**Abstract.** The Philippine archipelago harbours a remarkable diversity of harvestmen, with respect to both taxonomy and complexity of biogeographic origins. Among the armoured harvestmen (suborder Laniatores), six families of distantly related groups occur in this archipelago. Here, we describe a new species of the family Tithaeidae, *Tithaeus odysseus* sp. nov., discovered during a collecting campaign on the island of Mindanao. The description of this species expands the known distribution of the family and demonstrates another exception to the zoogeographic boundary known as Huxley's Line which putatively separates the biota of the Philippines (excluding the Palawan island group) from the Sunda Shelf biota. Given the coincident distributions of Tithaeidae and the mite harvestman family Stylocellidae (Cyphophthalmi), a group renowned for its poor dispersal ability, we inferred phylogenetic relationships and divergence times of the Philippines lineages of both families by using a comprehensive molecular dating analysis of all Opiliones. The internal phylogeny of Tithaeidae mirrored the biogeography of Philippine Stylocellidae, showing a close affinity between the Philippine and Bornean species. Molecular dating showed contemporaneous colonisation of Mindanao by both families in the Cretaceous. We infer these patterns to reflect faunal connections between the southern Philippines and Borneo via the Zamboanga Peninsula. To render the genus *Tithaeus* monophyletic, we synonymise *Metatithaeus* with *Tithaeus* (new synonymy).

**Additional keywords:** comparative biogeography, Cyphophthalmi, Epedanoidea, Grassatores, Southeast Asia.

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## Introduction

The arachnid order Opiliones (harvestmen) is renowned for its suitability for historical biogeographic study, owing to high fidelity to landmasses of continental origin, ancient age of diversification, and a propitiously well characterised fossil record (Giribet and Kury 2007; Giribet and Sharma 2015). Exemplifying this phenomenon best are the families of the suborder Cyphophthalmi (mite harvestmen), the distributions, phylogenetic patterns and ages of diversification of which have been established to mirror closely the history of the geological landmasses they inhabit (Boyer and Giribet 2007; Boyer *et al*. 2007; Murienne and Giribet 2009; Clouse and Giribet 2010; Giribet *et al*. 2012; Oberski *et al*. 2018), with only a few exceptional cases of ambiguous biogeographic history (Shear 1993*a*; Sharma and Giribet 2005; Clouse and Giribet 2007; Sharma and Giribet 2009*a*, 2009*b*). Within the other suborders of Opiliones, numerous lineages exhibit strong provincialism, with entire superfamilies or families restricted to specific

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biogeographic terranes (Giribet and Kury 2007; Sharma and Giribet 2011; Sharma *et al*. 2011*a*; Groh and Giribet 2014; Schönhofer *et al*. 2015). Although cases of transoceanic dispersal are known, only a handful of lineages of Opiliones are capable of this feat. Notable among these are the Laniatores families Zalmoxidae (Sharma and Giribet 2012), Samoidae (Pérez González and Kury 2007) and Podoctidae (Sharma *et al*. 2017).

Because of its complex geological history, the Philippine archipelago comprises a fascinating test case for the diagnostic power of Opiliones in comparative historical biogeography. Geologically, parts of the Philippine archipelago are hypothesised to constitute ancient continental crust. Specifically, the islands of Palawan and Mindoro include continental crust of South China origin and were connected to the Indo-Chinese plate (Hall 2002). In addition, metamorphic rocks of putatively continental origin are known from the Zamboanga Peninsula (western Mindanao) and the Daguma Range (south Mindanao; Pubellier *et al*. 2000, 2003, 2004; Hall 2002), which may reflect some contribution of northern Borneo to form part of Mindanao by the mid-Oligocene (fig. 19 of Hall 2002). Large parts of the remainder of the archipelago are inferred to be volcanic in origin (Yumul *et al*. 2009).

Reflecting these complex origins, the Philippines are inhabited by a rich assemblage of Opiliones families. Endemics of no less than eight families of harvestmen were known to inhabit the Philippine archipelago heretofore, with clearly independent biogeographic origins. The family Stylocellidae (Cyphophthalmi), a renowned model system for continental biogeography of Southeast Asia and one of the oldest lineages to inhabit this terrane (Poinar 2009; Clouse and Giribet 2010; Stelbrink *et al*. 2012), was described from Palawan on the basis of a single specimen collected in 1980 (Shear 1993*b*). A second putative species was discovered more recently from a collection of just two juveniles from Mindanao. Although sequence data exist for the Mindanao collection, the adults have not been observed (Clouse *et al*. 2011). Within Eupnoi, several species of Gagrellinae (Sclerosomatidae) have been described from the Philippines, but little is understood about the biogeography of this largest family of harvestmen, with preliminary molecular phylogenetic efforts having focused on the diversity of the New World (Hedin *et al*. 2012).

Laniatores are decidedly more abundant, more diverse and better understood in the Philippines. Families with endemics in this archipelago include Epedanidae (particularly the subfamily Dibuninae), Podoctidae (several distantly related genera, corresponding to three erstwhile subfamilies; Sharma *et al*. 2017), Sandokanidae (including the Philippine endemic genus *Biantoncopus*, as well as many species of *Gnomulus*) and Petrobunidae (whose type genus, *Petrobunus*, is endemic to the Philippine islands of Palawan and Panay). These four families are clearly of south-eastern Asian origin, as inferred from distributions and molecular phylogenies (Sharma and Giribet 2009*b*; Sharma and Giribet 2011; Sharma *et al*. 2017). Another Laniatores family with Philippine endemics is the vagile family Zalmoxidae, which has been described from Luzon, Panay, Mindoro, Mindanao and Palawan (Sharma *et al*. 2011*b*, 2012). The Philippine *Zalmoxis* constitutes at least two independent groups (species from Luzon and Panay form a clade; the Palawan endemic *Zalmoxis sabazios* is nested within a Bornean clade), but sequence data are not available for *Zalmoxis* from Mindanao or Mindoro; the family, more generally, has a clear Neotropical origin (Sharma 2012; Sharma and Giribet 2012). Last, the largely Afrotropical and poorly understood family Assamiidae is represented in the Philippines by a handful of species (Giribet and Kury 2007).

In the course of two collecting campaigns in 2010 (Luzon and Palawan) and 2014 (Luzon, Panay and Mindanao) aimed towards rediscovering populations of Stylocellidae, we encountered a new species of Tithaeidae from four collecting localities on the island of Mindanao. Tithaeidae was previously considered to be a member of Epedanidae, but was established as a separate family on the basis of morphology and molecular sequence data some years ago (Sharma and Giribet 2011). This family was previously known to inhabit only the Sunda Shelf (Lian *et al*. 2008; Zhang and Zhang 2010; Fig. 1), a distribution closely reflecting that of Stylocellidae before 2011 (Clouse and Giribet 2010; Clouse *et al*. 2011). During the 2014 campaign, we also discovered adult Cyphophthalmi putatively belonging to the stylocellid juveniles described in 2011 (Clouse *et al*. 2011).

The discovery of both Stylocellidae and Tithaeidae in Mindanao, taken together with the overall similarity of their distributions, substantiates the possibility that these groups colonised the southern Philippines via a common mechanism. To test this hypothesis, we investigated the phylogenetic relationships of Tithaeidae, in tandem with taxonomic description of the new species. We sequenced both the specimens of the Mindanao Tithaeidae and Stylocellidae, and placed them in a dated molecular phylogeny including all major groups of Opiliones. Here, we show that the phylogeny and divergence time estimates of both groups indicate a close affinity of Mindanao species with Bornean counterparts, as well as an approximately contemporaneous colonisation of Mindanao in the Cretaceous.

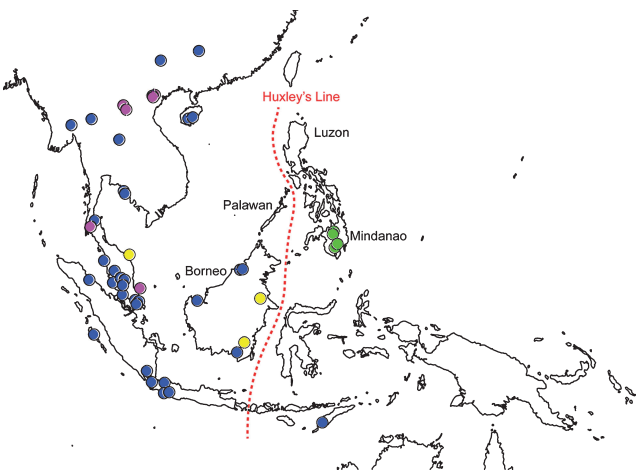


**Fig. 1.** Distribution of described species of Tithaeidae in Southeast Asia. Blue icons denote previously described species. Yellow icons indicate localities of specimens previously sequenced by Sharma and Giribet (2011). Pink icons denote additional localities of Sunda Shelf Tithaeidae sequenced in the present study. Green icons denote collecting localities for *Tithaeus odysseus* sp. nov.

## Materials and methods

### *Taxonomy*

Examined specimens have been deposited in the following institutions: National Museum of Natural History of the Philippines, Manila, Luzon, Philippines (PNM) and Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA (MCZ).

The holotype and a female paratype of the new species were photographed using a Leica MC120 digital camera mounted on a Leica M60 stereomicroscope, driven by LAS X software (Leica Microsystems, Wetzlar, Germany). A series of images (from 5 to 15) was taken at different focal planes and assembled with the dedicated software Helicon Focus ver. 6.7.2 (Helicon Soft, Kharkiv, Ukraine). Multiple specimens were examined with a Quanta FEI 200 scanning electron microscope (SEM; FEI, Hillsboro, OR, USA). The genitalia of male and female paratypes were also examined by SEM. Specimens previously used for DNA extraction are indicated as such among the type material. Methods concerning molecular-sequence data obtained from these specimens are described below. All measurements are given in millimetres, unless otherwise indicated. Nomenclature on cuticular ornamentation follows Murphree (1988).

Material used for comparison encompassed specimens of *Tithaeus kokutnus* Suzuki, 1985, *Metatithaeus rubidus* Suzuki, 1969, and three morphospecies of *Tithaeus* from Laos and Vietnam that are not described here. All of these were included in the molecular phylogeny.

### *Species sampling*

Specimens of Philippine harvestmen were collected during an expedition to the islands of Luzon, Panay and Mindanao in 2014 by RMC and PPS. Collected specimens were preserved in 96% ethanol and stored at −20°C. Other new morphospecies of *Tithaeus* were discovered in the collections of the Musee d'Histoire Naturelle Genève (MHNG) during collecting campaigns of Peter J. Schwendinger in Southeast Asia. Data collected in a previous study (Sharma and Giribet 2011) were accessed from GenBank for sampling of Tithaeidae and outgroup taxa. The list of new specimens, including voucher numbers, GenBank accession codes and collection details, is found in Tables 1 and 2.

### *Molecular methods*

Methods for DNA extraction, amplification and Sanger sequencing follow our published procedures (Sharma and Giribet 2009*b*, 2011; Clouse and Giribet 2010). Molecular markers consisted of two nuclear ribosomal genes (18S rRNA and 28S rRNA), two nuclear protein-encoding genes (histone H3 and histone H4), and one mitochondrial protein-encoding gene (cytochrome *c* oxidase subunit I; henceforth, COI). Primer sequences are indicated in Table 3. Chromatograms were read and sequences assembled using the sequence-editing software Geneious R9 (Geneious, Auckland, New Zealand). Sequence data were edited in Seaview ver. 4.7 (Gouy *et al*. 2010).

### *Phylogenetic analysis*

Sequences were aligned using MUSCLE ver. 3.6 (Edgar 2004) with default parameters, and, subsequently, treated with GBlocks ver. 0.91b (Castresana 2000) to cull positions of ambiguous homology. Sequences of protein-encoding genes were aligned as translated peptides using MUSCLE ver. 3.6 (as embedded within Seaview ver. 4.7) with default parameters as well, and, thereafter, alignments were reverted to nucleotide format, with subsequent treatment with GBlocks ver. 0.91b. The size of data matrices for each gene prior and subsequent to treatment with GBlocks ver. 0.91b is provided in Table 4.

Two datasets were created for the analysis. A compact 34-taxon dataset was generated, comprising 22 specimens of *Tithaeus* (encompassing localities in Mindanao, the Thai–Malay Peninsula, the Indo-Chinese plate and Borneo), two Podoctidae, two Petrobunidae, two Assamiidae, two Epedanidae, two Zalmoxidae and two Sandokanidae. The sandokanid outgroups were used to root the tree, following the phylogenomic tree topology of Fernández *et al*. (2017). This dataset is referred to, henceforth, as Dataset 1. The alignment is provided as Supplementary Material S1 to this paper.

For the purpose of comparative biogeography and comprehensive molecular dating, a 357-taxon dataset was created by fusing datasets targeting the phylogeny of Opiliones broadly (Giribet *et al*. 2010; Groh and Giribet 2014), Cyphophthalmi (Giribet *et al*. 2012, 2016) and Laniatores (Sharma and Giribet 2011) for the following loci: 16S rRNA, COI, 18S rRNA, 28S rRNA, and histone H3 (histone H4 was excluded because of its small size and limited phylogenetic informativeness). New data incorporated into this matrix consisted of the new *Tithaeus* sequences generated herein, as well as new *Miopsalis* sequences from adults of two morphospecies of Stylocellidae, collected contemporaneously with the *Tithaeus* of Mindanao (refer to Table 1). The tree was rooted by using sequence data from two species of Solifugae, following the results of Sharma *et al*. (2014). This dataset is referred to, henceforth, as Dataset 2. The alignment is provided as Supplementary Material S2 to this paper.

Maximum-likelihood analyses for both datasets were conducted using RAxML ver. 8.2 (Stamatakis 2014). A unique GTR model of sequence evolution with corrections for a discrete gamma distribution was specified for each data partition and 500 independent searches were conducted. Nodal support was estimated via the rapid bootstrap algorithm with 500 replicates (Stamatakis *et al*. 2008).

Estimation of divergence times was conducted using BEAST ver. 1.8 (Drummond *et al*. 2006; Drummond and Rambaut 2007). We specified a unique GTR model of sequence evolution, with corrections for a discrete gamma distribution and a proportion of invariant sites (GTR + Γ + I) for each partition; COI was further partitioned with two separate site models, for first and second positions versus the third codon position. Model selection followed the results of model testing as implemented by Sharma and Giribet (2011) and Giribet *et al*. (2012).

Fossil taxa were used to calibrate divergence times, as in previous studies (Garwood *et al*. 2014; Sharma and Giribet 2014). We constrained the age of Eupnoi and Dyspnoi by using truncated normal distribution priors with a mean of 360 million years and a standard deviation of 30 million years, with the truncation set to 305 million years ago. These priors reflect the ages of the oldest crown group Eupnoi

**Table 1. Voucher numbers and locality data for sequenced terminals**

| Taxon | UW accession # | Locality | Coordinates | Elevation (m) | Date | Collector |
|---|---|---|---|---|---|---|
| Tithaeidae | | | | | | |
| *Tithaeus odysseus*, sp. nov. | Ti01 | Philippines, Mindanao Island, Bukidnon, Center for Environmental Development and Recreation | 8.254894 N, 125.035732 E | 767 | 3.vii.2014 | D. Mohagan, D.-J. Mohagan, V. Yamba, D.E. General, R.M. Clouse |
| *Tithaeus odysseus*, sp. nov. | Ti02 | Philippines, Mindanao Island, western slope of Mt Kitanglad, Bukidnon, Lantapan, Kaatoan | 8.072258 N, 125.008909 E | 1300 | 1.vii.2014 | A. Mohagan, D. Mohagan, D.-J. Mohagan, V. Yamba, R.M. Clouse |
| *Tithaeus odysseus*, sp. nov. | Ti03 | Philippines, Mindanao Island, Mt Apo, Davao City, Toril, Sibulan, Mama-on | 6.99708 N, 125.358061 E | 1341 | 20.vi.2014 | D.E. General, R.M. Clouse |
| *Tithaeus odysseus*, sp. nov. | Ti04 | Philippines, Mindanao Island, Bukidnon, Impasug-ong, Impalutao, Center for Environmental Development and Recreation | 8.254933 N, 125.035749 E | 774 | 30.vi.2014 | D. Mohagan, V. Yamba, R.M. Clouse |
| *Tithaeus odysseus*, sp. nov. | Ti05 | Philippines, Mindanao Island, Bukidnon, Impasug-ong, Impalutao, Center for Environmental Development and Recreation | 8.254933 N, 125.035749 E | 774 | 30.vi.2014 | D. Mohagan, V. Yamba, R.M. Clouse |
| *Tithaeus odysseus*, sp. nov. | Ti06 | Philippines, Mindanao Island, Bukidnon, Impasug-ong, Impalutao, Center for Environmental Development and Recreation | 8.254933 N, 125.035749 E | 774 | 30.vi.2014 | D. Mohagan, V. Yamba, R.M. Clouse |
| *Tithaeus odysseus*, sp. nov. | Ti07 | Philippines, Mindanao Island, Bukidnon, Impasug-ong, Impalutao, Center for Environmental Development and Recreation | 8.254933 N, 125.035749 E | 774 | 30.vi.2014 | D. Mohagan, V. Yamba, R.M. Clouse |
| *Tithaeus odysseus*, sp. nov. | Ti08 | Philippines, Mindanao Island, Bukidnon, Impasug-ong, Impalutao, Center for Environmental Development and Recreation | 8.254933 N, 125.035749 E | 774 | 30.vi.2014 | D. Mohagan, V. Yamba, R.M. Clouse |
| *Tithaeus odysseus*, sp. nov. | Ti09 | Philippines, Mindanao Island, Bukidnon, Impasug-ong, Impalutao, Center for Environmental Development and Recreation | 8.254933 N, 125.035749 E | 774 | 30.vi.2014 | D. Mohagan, V. Yamba, R.M. Clouse |
| *Tithaeus odysseus*, sp. nov. | Ti10 | Philippines, Mindanao Island, Davao City, Malagos Watershed | 7.183092 N, 125.414422 E | 371 | 4.vii.2014 | D.E. General, R.M. Clouse |
| *Tithaeus* sp. | As118 | Thailand, Phang Nga Province, Phang Nga District, hillside above Chao Nu Cave | 8.4486111 N, 98.5477778 E | 200 | 14.vii.2011 | P.J. Schwendinger (MHNG-TH-11/09) |
| *Tithaeus* sp. | As122 | Laos, Oudomxai Province, ~3 km east of Tad Lak 11, south-east of Oudomxai (= Muang Xai) city, primary forest | 20.6055556 N, 102.021111 E | 1020 | 18.xi.2010 | P.J. Schwendinger (MHNG-LT-10/12) |
| *Tithaeus* sp. | As123 | Vietnam, Quang Ninh Province, Yen Tu Mountain, pilgrim trail, evergreen forest | 21.1416667 N, 106.721389 E | 200–500 | 27–29.v.2012 | P.J. Schwendinger (MHNG VN-12/09) |
| *Tithaeus* sp. | As129 | Laos, Luang Prabang Province, ~2 km north-east of Phou Khoun, near Tham Süa | 19.4455556 N, 102.440833 E | 1180 | 10-XI-2010 | P.J. Schwendinger (MHNG LT-10/06) |

(*continued next page*)

**Table 1.** (*continued*)

| Taxon | UW accession # | Locality | Coordinates | Elevation (m) | Date | Collector |
|---|---|---|---|---|---|---|
| *Tithaeus* sp. | As131 | W-Malaysia, Tioman Island, above Japanese Resort, rainforest | 2.7451944 N, 104.124361 E | 117 | 23–27-I-2012 | Lionel Monod (MHNG VMI-12/16) |
| *Tithaeus* sp. | As136 | Vietnam, Hanoi Prov., Ba Vi District, Mt Ba Vi, evergreen forest | 21.0597222 N, 105.367222 E | 1000–1070 | 16–18.v.2012 | P.J. Schwendinger, A. Schulz (MHNG VN-12/05c) |
| Stylocellidae | | | | | | |
| *Miopsalis* sp. Mindanao | NGS45 | Philippines, Mindanao Island, Bukidnon, Impasug-ong, Impalutao, Center for Environmental Development and Recreation | 8.254933 N, 125.035749 E | 774 | 30.vi.2014 | D. Mohagan, V. Yamba, R.M. Clouse |
| *Miopsalis* sp. Mindanao | NGS47 | Philippines, Mindanao Island, western slope of Mt Kitanglad, Bukidnon, Lantapan, Kaatoan | 8.072258 N, 125.008909 E | 1300 | 1.vii.2014 | A. Mohagan, D. Mohagan, D.-J. Mohagan, V. Yamba, R.M. Clouse |

**Table 2. GenBank accession numbers for new sequence data of Tithaeidae and Stylocellidae**

| Taxon | Accession # | 18S rRNA | 28S rRNA | COI | H3 | H4 |
|---|---|---|---|---|---|---|
| Tithaeidae | | | | | | |
| *Tithaeus odysseus*, sp. nov. | Ti01 | | MH925032 | MH925048 | MH925063 | LC425362 |
| *Tithaeus odysseus*, sp. nov. | Ti02 | | MH925033 | MH925049 | MH925064 | LC425363 |
| *Tithaeus odysseus*, sp. nov. | Ti03 | | MH925034 | MH925050 | MH925065 | LC425364 |
| *Tithaeus odysseus*, sp. nov. | Ti04 | MH925019 | MH925035 | MH925051 | MH925066 | LC425365 |
| *Tithaeus odysseus*, sp. nov. | Ti05 | | | | MH925067 | LC425366 |
| *Tithaeus odysseus*, sp. nov. | Ti06 | | | | MH925068 | LC425367 |
| *Tithaeus odysseus*, sp. nov. | Ti07 | MH925020 | MH925036 | MH925052 | MH925069 | LC425368 |
| *Tithaeus odysseus*, sp. nov. | Ti08 | MH925021 | MH925037 | MH925053 | MH925070 | LC425369 |
| *Tithaeus odysseus*, sp. nov. | Ti09 | MH925022 | MH925038 | MH925054 | MH925071 | LC425370 |
| *Tithaeus odysseus*, sp. nov. | Ti10 | | MH925039 | MH925055 | MH925072 | LC425371 |
| *Tithaeus* sp. | As118 | MH925023 | | MH925056 | MH925073 | LC425372 |
| *Tithaeus* sp. | As122 | MH925024 | MH925040 | | MH925074 | LC425373 |
| *Tithaeus* sp. | As123 | MH925025 | MH925041 | | MH925075 | LC425374 |
| | As129 | MH925027 | MH925043 | MH925058 | MH925077 | |
| *Tithaeus* sp. | As131 | MH925028 | MH925044 | MH925060 | MH925078 | LC425376 |
| *Tithaeus* sp. | As136 | MH925029 | MH925045 | MH925059 | MH925079 | LC425377 |
| Stylocellidae | | | | | | |
| *Miopsalis* sp. Mindanao | NGS45 | MH925030 | MH925046 | MH925061 | MH925080 | |
| *Miopsalis* sp. Mindanao | NGS47 | MH925031 | MH925047 | MH925062 | MH925081 | |

(*Macrogyion cronus* Garwood *et al.* 2011) and Dyspnoi (*Ameticos scolos* Garwood *et al.* 2011); the use of the truncated normal prior reflects a compromise between ages obtained using node versus tip-dating strategies (Sharma and Giribet 2014). The age of Opiliones was constrained on the basis of the recently reinterpreted placement of the Devonian harvestman *Eophalangium sheari* Dunlop *et al*. 2004 (see Dunlop *et al*. 2003, 2004; Garwood *et al*. 2014). A truncated normal distribution prior with a mean of 430 and a standard deviation of 10, with the truncation set to 410 million years ago, was used to calibrate this node. Although we explored using the oldest stylocellid fossil (*Palaeosiro burmanicum* Poinar, 2008; refer to Giribet *et al*. 2012) and the oldest known Laniatores fossil (the epedanid *Petrobunoides sharmai*; refer to Selden *et al*. 2016) as calibration points by using uniform distribution priors, the comparatively young (i.e. Cretaceous) ages of these fossils relative to the Mesozoic diversification of Laniatores families (Sharma and Giribet 2011) resulted in their having no effect on the analysis.

An uncorrelated log-normal clock model was applied to each partition, and a birth–death speciation process with incomplete sampling was assumed for the tree prior. We selected the uncorrelated lognormal model because its accuracy is comparable to an uncorrelated exponential model, but it has narrower 95% highest posterior density intervals. Additionally, the variance of the uncorrelated log-normal model can better accommodate data that are already clock-like (Drummond *et al*. 2006). Priors were sequentially optimised in a series of iterative test runs (data not shown). Two Markov chains were run for 200 million generations, sampling every 20 000 generations. Convergence

**Table 3. List of primer sequences used for amplification and sequencing**
Original references are provided in Sharma and Giribet (2011)

| Primer | Sequence |
|---|---|
| 16S rRNA | |
| 16Sa | 5′-CGC CTG TTT ATC AAA AAC AT-3′ |
| 16Sb | 5′-CTC CGG TTT GAA CTC AGA TCA-3′ |
| 18S rRNA | |
| 3F | 5′-GTT CGA TTC CGG AGA GGG A-3′ |
| 5R | 5′-CTT GGC AAA TGC TTT CGC-3′ |
| 28S rRNA | |
| 28Sa | 5′-GAC CCG TCT TGA AAC ACG GA-3′ |
| 28Srd5b | 5′-CCA CAG CGC CAG TTC TGC TTA C-3′ |
| COI | |
| LCO1490 | 5′-GGT CAA CAA ATC ATA AAG ATA TTG G-3′ |
| HCOoutout | 5′-GTA AAT ATA TGR TGD GCT C-3′ |
| Histone H3 | |
| H3aF | 5′-ATG GCT CGT ACC AAG CAG ACV. GC-3′ |
| H3aR | 5′-ATA TCC TTR GGC ATR ATR GTG AC-3′ |
| Histone H4 | |
| H4F2S | 5′-TSC GIG AYA ACA TYC AGG GIA TCA C-3′ |
| H4F2er | 5′-CKY TTI AGI GCR TAI ACC ACR TCC AT-3′ |

**Table 4. Length of gene-partition alignments prior and subsequent to treatment with GBlocks ver. 0.91b (Dataset 1)**

| Partition | Original length of alignment (bp) | Fraction retained by GBlocks (%) | Final length of alignment (bp) |
|---|---|---|---|
| *18S rRNA* | 858 | 99 | 849 |
| *28S rRNA* | 540 | 97 | 522 |
| *COI* | 665 | 100 | 665 |
| *H3* | 327 | 100 | 327 |
| *H4* | 160 | 100 | 160 |

diagnostics were assessed using Tracer ver. 1.7 (Rambaut and Drummond 2009).

## Taxonomy

### Order **OPILIONES** Sundevall, 1833

### Suborder **LANIATORES** Thorell, 1876

### Family **TITHAEIDAE** Sharma and Giribet, 2011

*Type genus*: *Tithaeus* Thorell, 1891, by monotypy.
*Type species*: *Tithaeus laevigatus* Thorell, 1891, by original designation.
*Genera included*: *Tithaeus* Thorell, 1891; *Metatithaeus* Suzuki, 1969 **new synonymy**.

### ***Tithaeus odysseus*** Schmidt and Sharma, sp. nov.

(Figs 2–5, Tables 5, 6)

#### *Material examined*

*Holotype.* ♂ (PNM 13650 [ex UW Ti08]), Philippines, Mindanao I., Bukidnon, Impasug-ong, Impalutao, Center for Environmental Development and Recreation, 774 m alt. (8.254933 N, 125.035749 E), leg. D. Mohagan, V. Yamba, R.M. Clouse, 30.vi.2014; one leg III extracted for DNA.

*Paratypes.* Two ♂ (ex UW Ti06, Ti07]), same collecting data as holotype; one leg III extracted from each for DNA; dissected for genitalia and mounted on SEM stubs (MCZ IZ 149805–149810). One ♂ (MCZ IZ 149797; ex UW Ti02), Mindanao I., Bukidnon, Lantapan, Kaatoan, western slope of Mt Kitanglad, 1300 m alt. (8.072258 N, 125.008909 E), leg. A. Mohagan, D. Mohagan, D.J.B. Mohagan, V. Yamba, R.M. Clouse, 1.vii.2014; one leg III extracted for DNA and one leg IV mounted on SEM stub (MCZ IZ 149798). One ♀ (PNM 13651 [ex UW Ti09]), same collecting data as holotype; in alcohol, one leg III extracted for DNA. One ♀ (MCZ IZ 149803; ex UW Ti04), same collecting data as holotype; in alcohol, one leg III extracted for DNA and one palp mounted on SEM stub (MCZ IZ 149804). One ♀ (MCZ IZ 149795; ex UW Ti01), Philippines, Mindanao I., Impalutao, Impasug-ong, Bukidnon Province, Center for Environmental Development and Recreation (CEDAR), 767 m alt. (8.254894 N, 125.035732 E), leg. D. Mohagan, D.J.B. Mohagan, V. Yamba, D.E.M. General, R.M. Clouse, 3.vii.2014; in alcohol, one leg III extracted for DNA and one leg IV mounted on SEM stub (MCZ IZ 149796). One ♀ (ex UW Ti03), Philippines, Mindanao I., Mt Apo, Davao City, Toril, Sibulan, Mama-on, Mt. Apo, 1341 m alt. (6.99708 N, 125.358061 E), leg. D.E.M. General, R.M. Clouse, 20.vi.2014; one leg III extracted for DNA and remainder mounted on SEM stubs (MCZ IZ 149799–149802). One ♀(UW Ti10) in alcohol, Philippines, Mindanao I., Davao City, Malagos Watershed, 371 m alt. (7.183092 N, 125.414422 E), leg. D.E. M. General, R.M. Clouse, 4.vii.2014; in alcohol, one leg III extracted for DNA.

*Additional material studied.* One subadult male (UW Ti05), same collecting data as holotype.

#### *Diagnosis*

Distinguished from congeners by (1) absence of pigmentation and reticulate patterning, (2) legs being smooth and unarmed, (3) ventral plate of the penis lacking the deep cleft (typical of the genus) and bearing instead a shallow depression at the ventral plate apex, (4) arrangement of setae on ventral plate, with a single pair of setae set proximally to widest region of the ventral plate, and (5) elongate setae of the ovipositor.

#### *Description*

Total length of male holotype (female paratype (UW Ti09) in parentheses) 4.14 mm (4.72 mm), greatest width of prosoma 2.04 mm (1.87 mm), greatest width of opisthosoma 3.06 mm (3.39 mm); length-to-width ratio 2.03 (2.52) (Fig. 2). Body either trapezoidal (holotype) or campaniform (female) in shape, yellow in colour (in alcohol, depending on the incidence of light), almost entirely with a dense microgranulate surface microstructure. Eyes present on low, well developed ocularium, without median ocularial tubercle. Ocularium 0.44 mm (0.40 mm) long, 0.70 mm (0.67 mm) wide, removed from anterior margin of carapace. Anterior margin of carapace smooth. Scutal grooves of mesotergum distinct, free of transverse bands of pigmentation. Free tergites granulated, unarmed (Fig. 3).

Ventral prosomal complex of male with coxae II and III meeting in midline, coxae I and IV not so. Anterior and posterior margins of coxae III without tubercular bridges to adjacent coxae. Genital operculum subtriangular. Spiracles not concealed, unardorned. Opisthosomal sternites smooth, unarmed. Anal plate granulated, without spines or tubercles (Fig. 3).

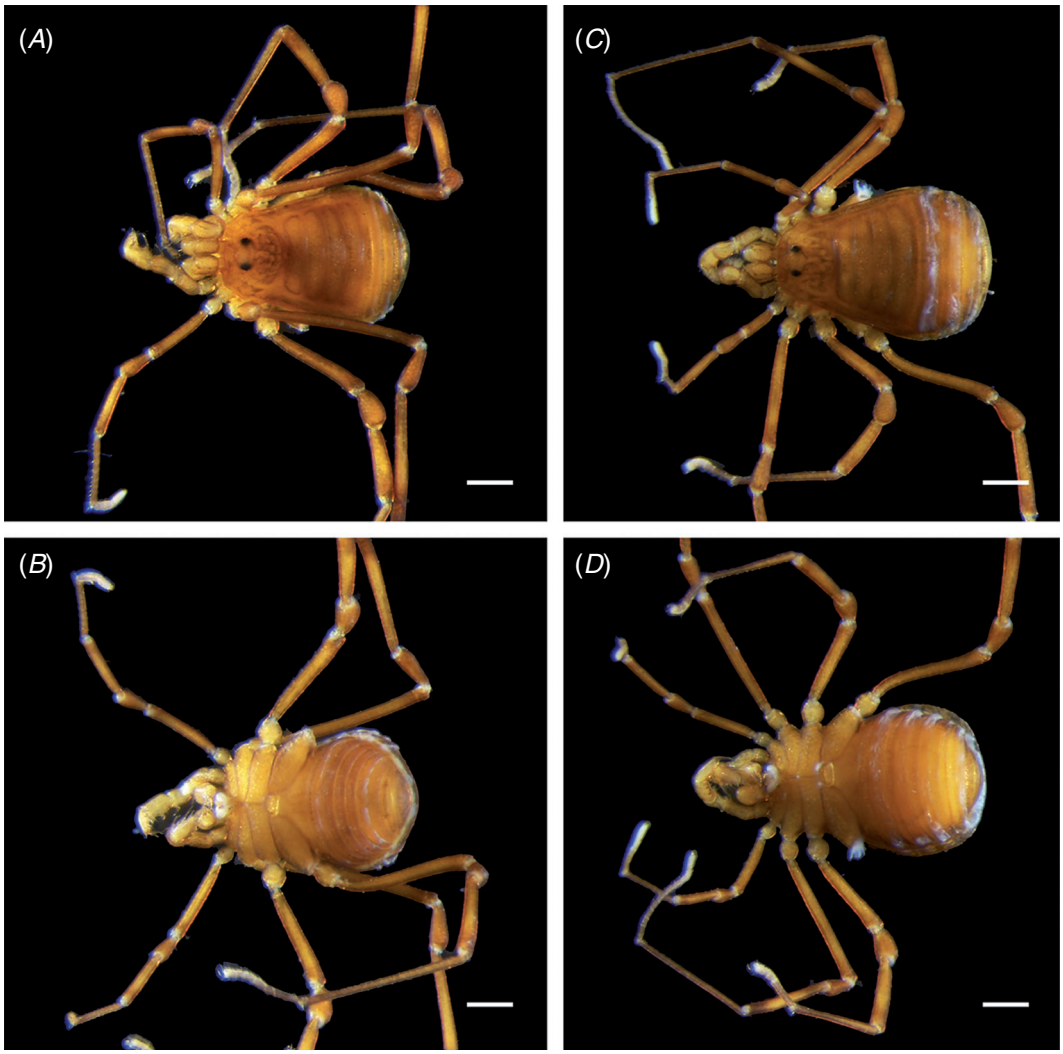


**Fig. 2.** *Tithaeus odysseus* sp. nov. (*A*) Male holotype, dorsal view. (*B*) Male holotype, ventral view. (*C*) Female paratype (UW Ti09), dorsal view. (*D*) Female paratype, ventral view. All scale bars = 1.00 mm.

Chelicerae (Fig. 4*A*) sexually monomorphic, with prominent bulla on proximal article. Proximal article with denticulate granulation basally and ventrally. Second article not incrassate, free of ornamentation, with dorsal margin bearing several setae. Distal article with delicate dentition, free of ornamentation. Proximal article 0.52 mm (0.52 mm), second article 0.78 mm (0.78 mm), movable digit 0.24 mm (0.24 mm).

Palpi (Fig. 4*B*) robust and spined ventrally or ventrolaterally. Palpal trochanter with one ventral spine. Palpal femur with two proximal ventral spines in a row, and two smaller distal spines (one ventral, one mesoventral), as well as one small seta between proximal ventral spines; four setae present on dorsal surface. Palpal patella without spines. Palpal tibia with three pairs of spines, and a few setae on distal and dorsal margin. Palpal tarsus with two pairs of spines, several setae. Palpal claw nearly as long as palpal tarsus.

Legs I–IV (Fig. 4*C–G*) slender, elongate, finely granulated, with small and irregularly distributed setiferous tubercles on femora and tibiae. No sexually dimorphic armaments or ornamentation present. Tarsal claws I–IV smooth, unmodified, double claws on legs III and IV (typicaly of Grassatores). Distitarsi of first and second tarsi each with two tarsalia. Tarsal formula 5: 10–11: 5: 6.

Penis (Fig. 5*A*, *B*) elongate, narrow and slender, in the shape of a spear blade. Ventral plate with very shallow apical cleft (Fig. 5*C*). Ventral surface with one pair of setae, lateral margins with two pairs of setae (Fig. 5*B*). Basal sac immovable and partly sunken into truncus, lacking complex introverting structures.

Ovipositor (Fig. 5*D*, *E*) composed of two apical lobes, each bearing two dorsal setae and two ventral setae. Distal surfaces of apical lobes smooth. Bases of setae not in contact. All setae longer than apical lobes. Two irregular rows of smaller setae proximal to apical setae (Fig. 5*E*).

### *Sexual dimorphism*

Males smaller than females, with shorter leg IV, trapezoidal body shape and subtriangular genital operculum. Female body

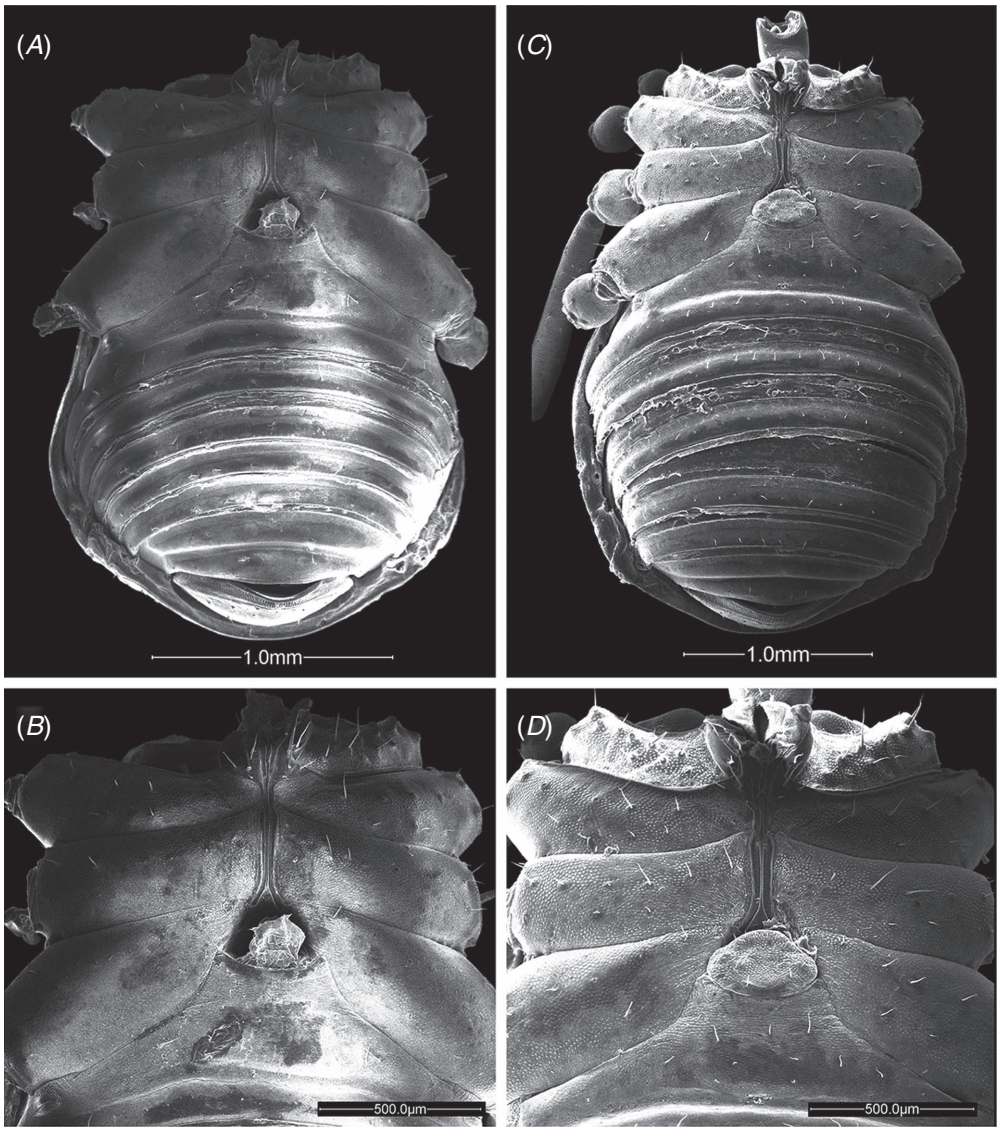


**Fig. 3.** *Tithaeus odysseus* sp. nov. (*A*) Ventral view of male paratype (MCZ IZ 149809). (*B*) Prosomal complex of male paratype. (*C*) Ventral view of female paratype (MCZ IZ 149799). (*D*) Prosomal complex of female paratype.

rounder than that of males and genital operculum semicircular in shape.

### *Distribution*

Known from the five localities in Mindanao indicated in Table 1.

### *Etymology*

The specific epithet, a noun in apposition, is derived from the titular character of Homer's *Odyssey* and recognises the traversing of Huxley's Line by this lineage of Tithaeidae.

## Results

### *Phylogenetic analysis*

The ML analysis of Dataset 1 recovered the monophyly of Tithaeidae with 100% bootstrap (BS) resampling frequency (Fig. 6). As in previous datasets, the sister group of Tithaeidae was ambiguous (Sharma *et al*. 2017); Podoctidae was recovered as the sister family of Tithaeidae, but without support (BS = 30%). Within Tithaeidae, the following three clades were recovered: (1) a clade composed of species from the Thai–Malay Peninsula and the Indo-Chinese plate (BS = 87%); (2) a clade composed of species from Borneo, including *Metatithaeus rubidus* (BS = 64%); and (3) a clade composed of all 10 specimens from Mindanao (BS = 100%). Notably, maximal nodal support was obtained for the sister-group relationship of the Philippine and Bornean Tithaeidae.

Maximum likelihood analysis of Dataset 2 recovered the same relationships within Tithaeidae, with comparable support for the sister-group relationship of the Philippine and Bornean tithaeids (BS = 95%) and the monophyly of Tithaeidae (BS = 100%; see Supplementary Material S3). Relationships among the families of Grassatores were variably supported, with particularly low support for the cohesion of epedanoid families.

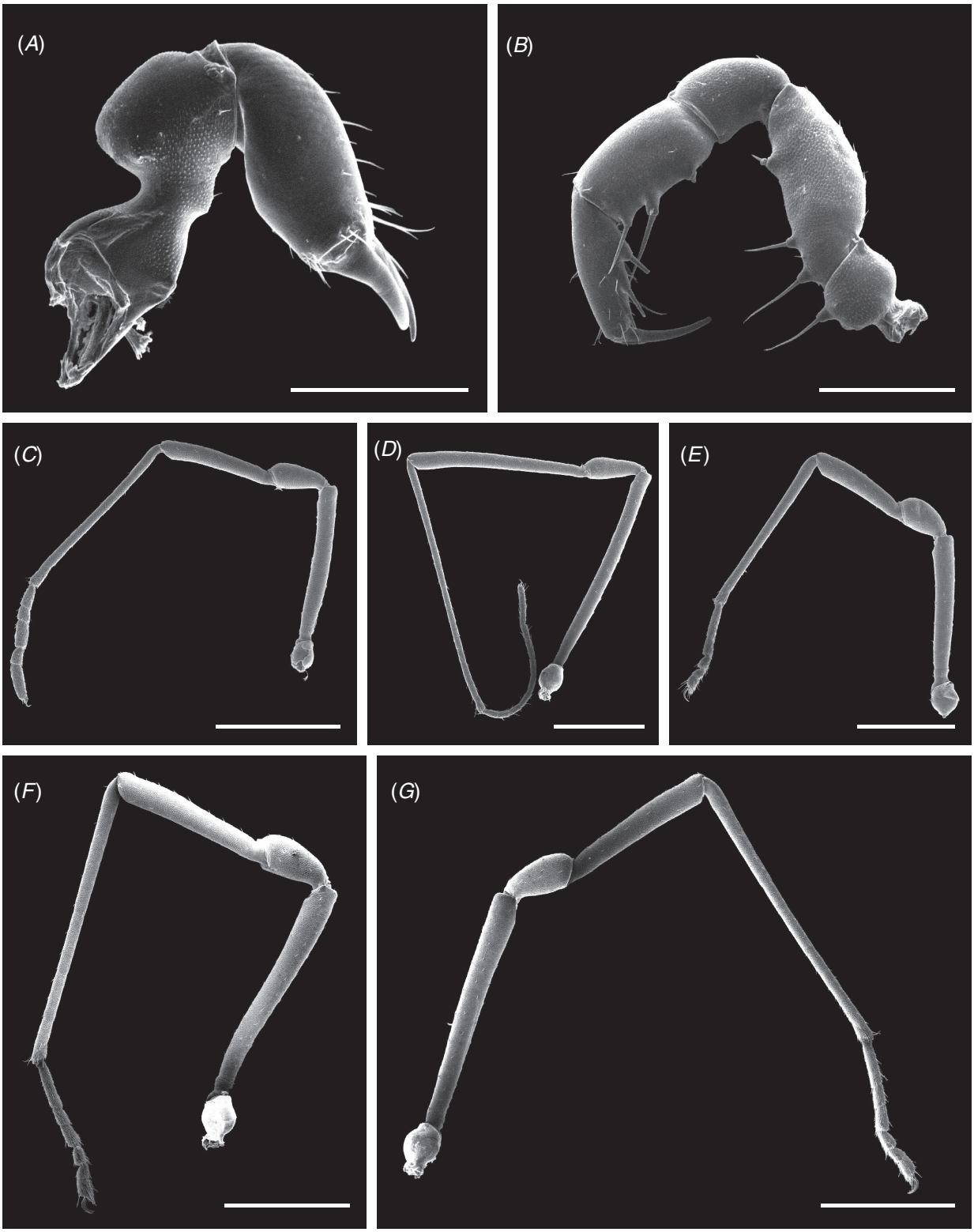


**Fig. 4.** *Tithaeus odysseus* sp. nov. (*A*) Right chelicera of male paratype (MCZ IZ 149810). (*B*) Left palp of male paratype (MCZ IZ 149810). (*C*) Male left leg I (MCZ IZ 149798). (*D*) Male left leg II (MCZ IZ 149806). (*E*) Male left leg III (MCZ IZ 149806). (*F*) Male left leg IV (MCZ IZ 149798). (*G*) Female right leg IV (MCZ IZ 149796).

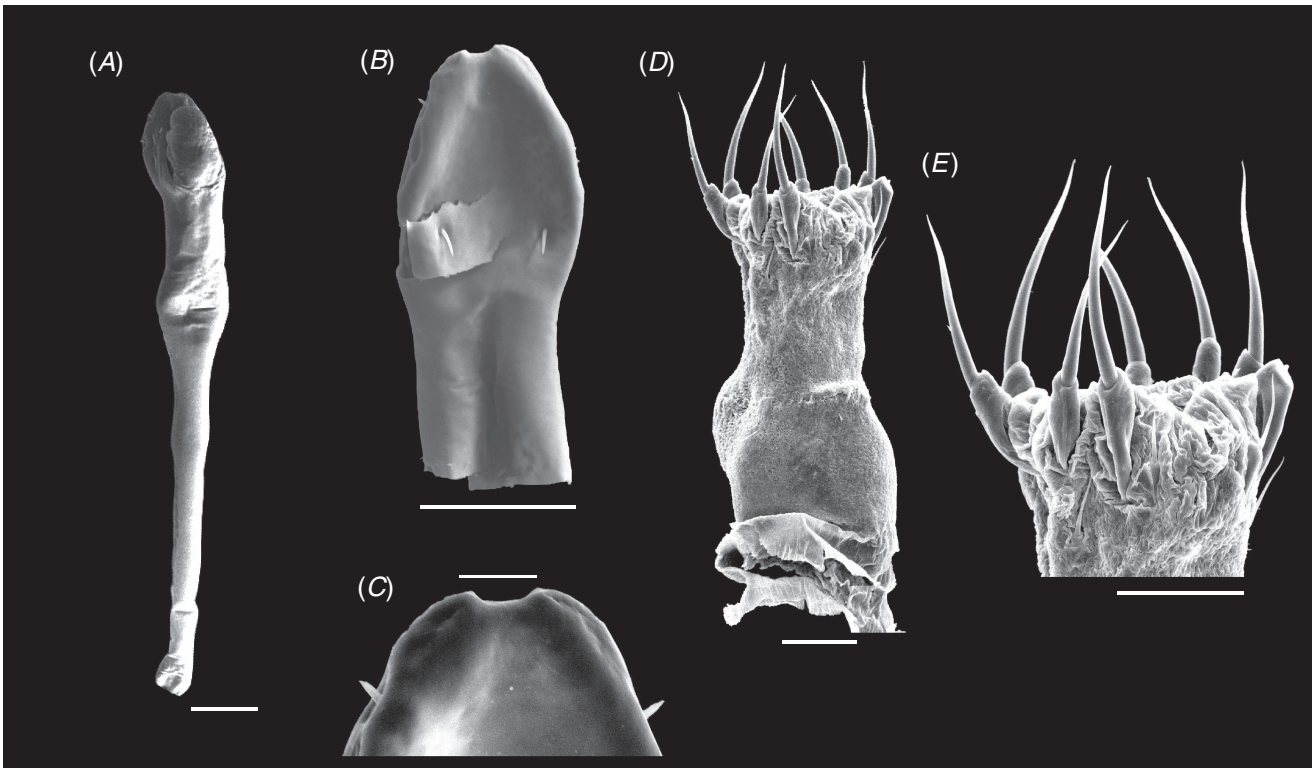


**Fig. 5.** *Tithaeus odysseus* sp. nov. (*A*) Male genitalia, dorsal view (MCZ IZ 149805). (*B*) Pars distalis of male genitalia, ventral view. Note that the specimen has undergone damage on the ventral size during preparation. (*C*) Detail of apical cleft, ventral view. (*D*) Ovipositor of female paratype (MCZ IZ 149800). (*D*) Detail of apical and subapical setae of ovipositor.

**Table 5. Appendage measurements of holotype**
All measurements in mm

| Appendage | Tr | Fe | Pa | Ti | Me | Ta | Total |
|---|---|---|---|---|---|---|---|
| Leg I | 0.20 | 1.17 | 0.39 | 0.85 | 1.38 | 0.89 | 4.88 |
| Leg II | 0.30 | 2.20 | 0.57 | 1.87 | 2.70 | 1.64 | 9.28 |
| Leg III | 0.30 | 1.39 | 0.47 | 0.91 | 1.67 | 0.84 | 5.58 |
| Leg IV | 0.34 | 1.78 | 0.50 | 1.19 | 2.21 | 1.04 | 7.06 |
| Palp | 0.19 | 0.53 | 0.25 | 0.39 | | 0.39 | 1.75 |

**Table 6. Appendage measurements of female paratype UW Ti-09**
All measurements in mm

| Appendage | Tr | Fe | Pa | Ti | Me | Ta | Total |
|---|---|---|---|---|---|---|---|
| Leg I | 0.25 | 1.01 | 0.42 | 0.77 | 1.17 | 0.78 | 4.39 |
| Leg II | 0.34 | 1.82 | 0.53 | 1.53 | 2.13 | 1.59 | 7.95 |
| Leg III | 0.36 | 1.22 | 0.51 | 0.86 | 1.47 | 0.88 | 5.31 |
| Leg IV | 0.35 | 1.72 | 0.48 | 1.09 | 2.21 | 1.04 | 6.89 |
| Palp | 0.19 | 0.54 | 0.30 | 0.39 | | 0.39 | 1.81 |

Within Cyphophthalmi, relationships recovered were comparable to those in our previous studies (Giribet *et al*. 2012, 2016; Oberski *et al*. 2018), albeit with the paraphyly of Sironidae. The stylocellid terminals from Mindanao, including the juveniles sequenced previously (Clouse *et al*. 2011), were recovered as a clade with high support (BS = 98%) and, in turn, were nested deeply within the largely Bornean genus *Miopsalis* (BS = 66%; Clouse and Giribet 2010), which is consistent with previous results (Clouse *et al*. 2011; Fig. 7*B*; Supplementary Material S3). The taxonomy and internal relationships of the Philippine stylocellids are addressed elsewhere (S. M. Schmidt and P. P. Sharma, pers. comm.).

### *Estimation of divergence times*

Runs of BEAST reached stationarity after 12 million generations; 20 million generations (10%) were discarded as burn-in (Fig. 7*A*). Diversification of key Laniatores lineages is estimated as follows: Laniatores, 357 million years ago (95% highest posterior density (HPD) interval: 336–395 million years ago); Grassatores, 315 million years ago (95% HPD interval: 286–342 million years ago); Tithaeidae, 162 million years ago (95% HPD interval: 133–194 million years ago); Bornean + Philippine tithaeids, 129 million years ago (95% HPD interval: 93–167 million years ago); *Tithaeus odysseus* sp. nov., 18 million years ago (95% HPD interval: 12–24 million years ago). Diversification of key Cyphophthalmi lineages is estimated as follows: Cyphophthalmi, 377 million years ago (95% HPD interval: 343–410 million years ago); Stylocellidae, 190 million years ago (95% HPD interval: 161–217 million years ago); *Miopsalis*, 136 million years ago (95% HPD interval: 112–156 million years ago); Bornean + Philippine *Miopsalis*, 115 million years ago (95% HPD interval: 93–136 million years ago); Philippine *Miopsalis*, 52 million years ago (95% HPD interval: 32–74 million years ago). The annotated

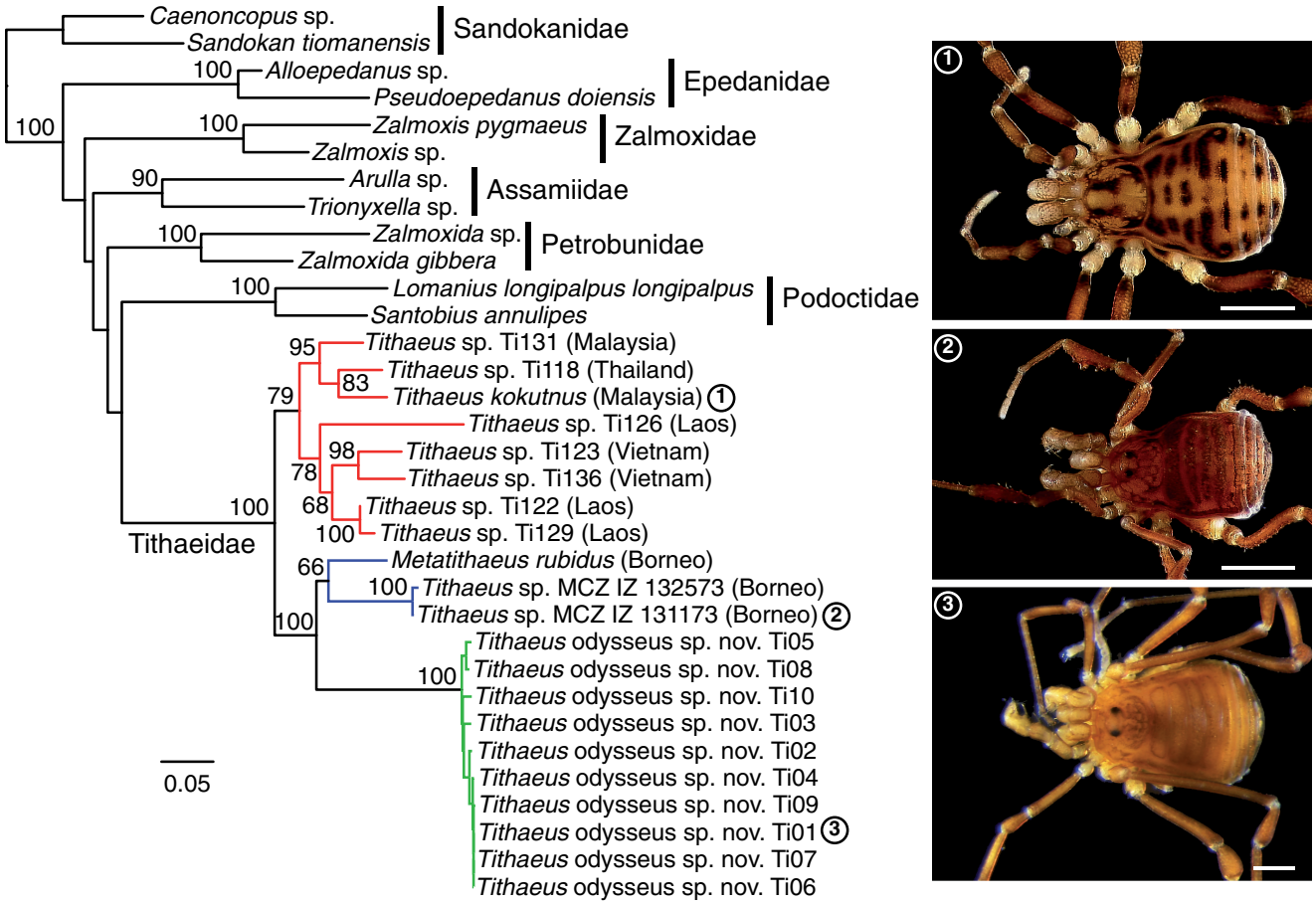


**Fig. 6.** Phylogenetic relationships of Tithaeidae inferred from maximum-likelihood analysis of five molecular loci (ln*L* = –16572.49; Dataset 1). Numbers on nodes indicate bootstrap resampling frequencies. Coloured branches correspond to geological terranes (mainland Southeast Asia, red; Borneo, blue; Philippines, green). Photographs of exemplars from each clade are shown to the right.

timetree of Opiliones is provided as Supplementary Material S4 to this paper.

## Discussion

### *Systematics of Tithaeidae*

Long held to be a member of the wastebasket taxon Phalangodinae, *Tithaeus* was subsequently interpreted to be related to epedanids (Kury 1993, 2003, 2006). The genus was later elevated to family level on the basis of molecular phylogenetics and re-examination of genitalic structures (Sharma and Giribet 2011; Sharma *et al*. 2011*a*), both of which suggested a closer relationship to Podoctidae (Sharma *et al*. 2017). Although the sister group of Tithaeidae is not clearly established by molecular phylogenetic studies, in part owing to its absence from phylogenomic datasets (Fernández *et al*. 2017), the increased taxonomic sampling of this lineage and re-analysis of phylogenetic placement corroborated a placement distant from Epedanidae.

One outstanding matter not addressed during the establishment of Tithaeidae, owing to previous limitations in taxonomic sampling, was the status of the Bornean species *Metatithaeus rubidus*. The monotypic genus *Metatithaeus* was established by Suzuki (Suzuki 1969) and distinguished from *Tithaeus* on the basis of (1) a dorsal hump anterior of its ocularium, giving the ocularium a bilobed appearance in lateral view, and (2) the absence of a medial-apical spine on the pedipalpal femur. Although not part of the diagnosis, the genitalia of this species was also markedly different from that of typical *Tithaeus* in lacking the apical cleft of the ventral plate (Suzuki 1969). However, the *Metatithaeus* specimen sequenced previously (Sharma and Giribet 2011) was recovered as derived within a paraphyletic *Tithaeus* in all our phylogenetic analyses, with support. This result supports the inference that the characters used to diagnose *Metatithaeus* are autapomorphies. To resolve the paraphyly of the larger genus, we synonymise *Metatithaeus* as a junior synonym of *Tithaeus* **new synonymy.**

It is highly likely that three other monotypic Roewerian genera matching the general description of tithaeids (*Istithaeus atroluteus* (holotype collected in Borneo), *Kondosus borneoensis* (Borneo), and *Tithaeomma tenuissimum* (Malaysia)) belong to Tithaeidae as well. A fourth species, *Sterrhosoma brevipalpe* (Sumatra), has also been considered to belong to this group (Lian *et al*. 2008). Because we have not examined specimens of these four genera, we leave the matter for future treatment. However, their inclusion would not expand significantly the

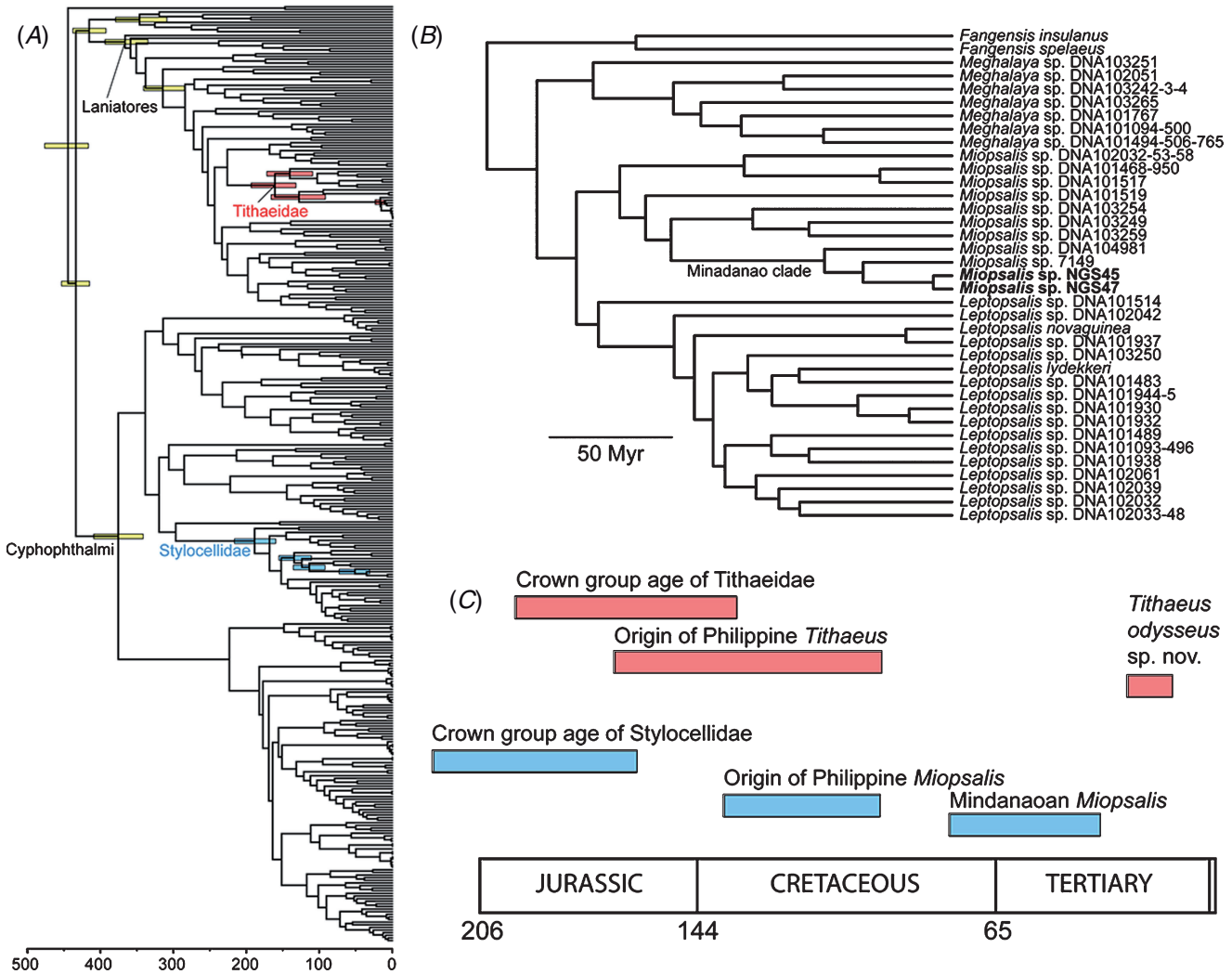


**Fig. 7.** (*A*) BEAST tree topology inferred from analysis of Dataset 2, showing key events in the diversification of Tithaeidae and Stylocellidae. (*B*) Magnification of relationships within Stylocellidae from the BEAST analysis. Boldfaced terminals were sequenced in the present study. (*C*) Detail of age intervals for nodes of interest show significant temporal overlap in the diversification of both families and the origins of their respective Philippine lineages.

known distribution of Tithaeidae, because all these taxa are Sunda Shelf endemics.

### *The multifaceted history of the Philippine opiliofauna*

For its comparatively small landmass relative to neighbouring terranes, the Philippines represents one of the most complex assemblages of opiliofauna, comprising several distantly related families. The application of molecular phylogenetics to many of these understudied families in Southeast Asia is beginning to shed light on the complexity of harvestman origins in this biogeographic theatre. The harvestman lineages that have given rise to Philippine endemics mostly originated in continental Southeast Asia, with particularly strong biogeographic links to the Sunda Shelf (Clouse and Giribet 2007, 2010; Clouse *et al*. 2011; Sharma and Giribet 2009*c*, 2011; Sharma *et al*. 2017). This is especially the case for lineages endemic to the islands of Palawan and Mindanao, which have been transiently connected to Borneo and/or the Indo-Chinese Plate during the Cenozoic (Clouse *et al*. 2011; Sharma and Giribet 2012).

The discovery of Tithaeidae in the Philippines and its phylogenetic proximity to Bornean counterparts reinforces the biogeographic link between the southern Philippine archipelago and the northeastern part of Borneo, previously reported in Stylocellidae (Clouse *et al*. 2011). The accruing understanding of tithaeid distribution parallels that of the mite harvestman family Stylocellidae, with recent discoveries greatly expanding the known distribution of Tithaeidae in southern China (Lian *et al*. 2008; Zhang and Zhang 2010) and of stylocellids in eastern India (Giribet *et al*. 2007), Irian Jaya (Clouse and Giribet 2007), and, most recently, Mindanao (Clouse *et al*. 2011). Although we were not able to sample Chinese specimens of tithaeids in our phylogeny because of

the age of available collections, we surveyed, as a proxy, new morphospecies from Laos and Vietnam, so as to represent a geological terrane contiguous with the Chinese localities.

The tree topology we recovered supports the phylogenetic proximity of Philippine and Bornean tithaeids, to the exclusion of the mainland lineage. This topology accords with the backbone of Stylocellidae (Clouse and Giribet 2010) and is suggestive of a comparable biogeographic history in these two families. Although tithaeid distribution and records are not as extensive as those of Stylocellidae, we infer that these discrepancies may be partly attributable to a paucity of leaf-litter surveys in such regions as Palawan and Irian Jaya. In addition, during our collecting campaigns, we observed that Stylocellidae and Tithaeidae were relatively scarce in comparison to the far greater abundance of Epedanidae, Podoctidae and Zalmoxidae in the same collecting localities. As a case in point, we did not rediscover specimens of *Stylocellus tarumpitao* (Shear 1993*b*) in Palawan during either the 2010 or the 2014 collecting campaigns.

### *Contemporaneous colonisation of Mindanao by Tithaeidae and Stylocellidae*

The remarkable degree of overlap of tithaeids and stylocellids that we observed prompted us to investigate the hypothesis of a common biogeographic mechanism for their distribution in Mindanao. Consistent with this hypothesis, our estimation of divergence times recovered contemporaneous ages of both the families, being consistent with their candidacy for a shared biogeographic process. Moreover, the split between the Bornean and the Mindanao species was inferred to be contemporaneous for each family as well and dated to the Late Cretaceous. The span of the 95% HPD intervals for these splits coincides with the timing of a contiguous connection between Borneo and Mindanao, whose remnant today is the Zamboanga Peninsula. This biogeographic umbilicus (*sensu* Diamond and Gilpin 1983; Jones and Kennedy 2008) persisted through the end of the Oligocene and is consistent with the availability of land connections for facilitating colonisation via Borneo during the origin of the Mindanao tithaeids and stylocellids (Hall 2002).

Taken together, our data support the signal of ancient vicariance between Mindanao and Borneo, and underscore the diagnostic power of Opiliones as model systems for study of comparative biogeography. Although we did not explore additional families here, other families of Opiliones that we encountered in the same collecting locality included Epedanidae, Zalmoxidae and Podoctidae. Whereas the latter two families are capable of transoceanic dispersal (Sharma and Giribet 2012; Sharma *et al.* 2017), Epedanidae is restricted to Southeast Asia and its internal phylogeny is largely unexplored. Future investigations of Philippine opiliofauna should emphasise the origins of the epedanids in Mindanao and test whether a biogeographic link between Borneo and Mindanao is a generalisable model framework across non-vagile Opiliones in this archipelago.

## Conclusions

Southeast Asian landmasses, and the Philippine archipelago in particular, represent understudied frontiers for biodiversity discovery of leaf-litter invertebrates. Here, we discovered a new species of Tithaeidae, a family whose distribution is comparable to that of the distantly related mite harvestman family Stylocellidae. These families are of comparable age and diversified across the Sunda Shelf contemporaneously. The timing of colonisation of Mindanao by both lineages supports the inference of a shared vicariant event across the Zamboanga Peninsula. Our results reinforce the importance of biodiversity discovery on islands for studies of comparative biogeography.

## Conflicts of interest

The authors declare that they have no conflicts of interest.

## Declaration of funding

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