


A new *Miopsalis* from Mindanao supports a biogeographic umbilicus between Borneo and the southern Philippines (Arachnida: Opiliones: Cyphophthalmi: Stylocellidae)

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Abstract

A new species of Cyphophthalmi belonging to the Southeast Asian genus *Miopsalis* Thorell, 1890 is described and illustrated using SEM and confocal microscopy. The species is known from two localities in the northern part of Mindanao and constitutes only the second described Cyphophthalmi species endemic to the Philippines. Sequence data obtained from this species show that it is phylogenetically distinct from two juvenile specimens previously collected from Bangaray Kimlawis (southern Mindanao) in 2009. The new *Miopsalis* is clearly distinguishable from other *Miopsalis* by characters pertaining to spermatopositor morphology.

Key words: mite harvestmen, vicariance, Zamboanga Peninsula

Introduction

Stylocellidae Hansen & Sørensen, 1904 is one of the oldest animal lineages endemic to Southeast Asia and a mainstay of evolutionary studies in this biogeographic theater (Boyer *et al.* 2007; Clouse & Giribet 2010; Giribet *et al.* 2012; Stelbrink *et al.* 2012). The origin of this lineage was estimated to span the Permo-Triassic boundary, with diversification of crown group lineages in the Jurassic (Giribet *et al.* 2012; Oberski *et al.* 2018). The attendant scenario of this group's biogeographic history would place the ancestral stylocellid on the Sibumasu terrane, which rifted away from Gondwanaland in the Triassic and subsequently formed the eastern part of the Cimmerian paleo-continent (Metcalf 2002). In the present day, the equivalent of this terrane extends from northeastern India to the Thai-Malay Peninsula and constitutes the reconstructed ancestral area of Stylocellidae (Clouse & Giribet 2010). Like most of the remaining Cyphophthalmi, stylocellid species typically exhibit short-range endemism and the group as a whole is characterized by poor dispersal ability (Giribet & Sharma 2015; Clouse *et al.* 2016). Apropos, the ranges and inferred diversification ages of stylocellid genera closely accord with the geological history of the Thai-Malay Peninsula and the formation of the Sunda Shelf islands (Clouse & Giribet 2010; Giribet *et al.* 2012).

Following the revision of generic limits by Clouse (2012) and Clouse & Giribet (2012), there are presently 34 valid described stylocellid species divided into six genera and three subfamilies. The largest of these subfamilies, Leptopsalidinae Clouse, 2012 (spelling following Kury 2018), contains the two most species-rich stylocellid genera, *Leptopsalis* Thorell, 1882 and *Miopsalis* Thorell, 1890. These two genera exhibit overlapping distributions in the Sunda Shelf, with *Miopsalis* diversity concentrated in Borneo and *Leptopsalis* diversity in Sumatra, Java, and Sulawesi. These genera are also unusual in that they include species on landmasses whose geological connections to the Sunda Shelf are ambiguous. *Leptopsalis* contains two species in Irian Jaya (western Papua New Guinea), which is not reconstructed to have been connected to the Sunda Shelf as a contiguous landmass (Clouse & Giribet 2007). Similarly, a single species of *Miopsalis* was previously described from Palawan in the Philippines (Shear 1993), an

island that is hypothesized to have originated from the south China plate and close enough to Borneo for a possible land connection only in the past 10 million years (Hall 2002; Yumul *et al.* 2009). The faunas of these islands have historically been held to reflect this geological connection, with Palawan's fauna exhibiting a distinctly Bornean character, in contrast to the oceanic eastern islands of the Philippine Archipelago (Gressitt 1956; Schuh & Stonedahl 1986). A previous collecting campaign by us in 2010 did not yield any specimens of *M. tarumpitao*, though many key groups of the suborder Laniatores were obtained from that expedition (Sharma & Giribet 2011; 2012; Sharma *et al.* 2012).

An even more intriguing addition to the range of Stylocellidae was the discovery of two juvenile specimens in southern Mindanao, which were recovered in a Bornean clade in a molecular phylogeny using five loci (Clouse *et al.* 2011). Mindanao is comprised mostly of an oceanic island that originated to the east and moved west to collide with Zamboanga Island, which had arisen off the coast of Borneo much earlier. Discoveries of possible continental rock on the Zamboanga Peninsula and in western Mindanao suggest that these regions were once connected to Borneo (Pubellier *et al.* 2000, 2003, 2004; Hall 2002). This is a novel view of the island's history, but one strongly supported by the presence of biotic elements with poor capabilities of dispersal and of Bornean origin there. Our second collecting campaign in the Philippines therefore focused sampling efforts in Mindanao, successfully obtaining 18 Cyphophthalmi from two localities. These samples included 15 adult specimens. We previously treated this collection as constituting two morphospecies and sequenced an exemplar of each locality for four loci (Schmidt *et al.* 2019). We subsequently dated the diversification of *Miopsalis*, together with the Laniatores family Tithaeidae (encountered for the first time in Mindanao during the 2014 collecting campaign). *Miopsalis* and *Tithaeus* of Mindanao were shown to be closely related to Bornean counterparts, with molecular dating inferring contemporaneous independent colonizations of Mindanao by these genera (Schmidt *et al.* 2019).

In that previous work we focused on the taxonomy, phylogeny, and biogeography of Tithaeidae; the taxonomy of Cyphophthalmi was not included. Here, we present the description of the Mindanao *Miopsalis* collected in 2014.

Materials and methods

Abbreviations. Examined specimens are lodged in the following repository institutions:

AMNH	American Museum of Natural History, New York, NY, USA
BMNH	The Natural History Museum, London, UK
MCSN	Museo Civico di Storia Naturale “Giacomo Doria”, Genoa, Italy
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA
MHNG	Muséum d'histoire naturelle, Geneva, Switzerland
NMP	National Museum of the Philippines, Manila, Luzon, Philippines

Taxonomy. 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). 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. Paratypes were examined with a Quanta FEI 200 scanning electron microscope (SEM; FEI, Hillsboro, OR, USA).

Spermatopositors of three male paratypes were extracted and mounted on glass slides in a 75% glycerol/25% phosphate buffered saline solution, and imaged using a Zeiss LSM 710 confocal microscope driven by ZEN v. 2.3 (Carl Zeiss, Jena, Germany). One of the three spermatopositors was further dissected with fine forceps to reveal details of the gonopore complex. Specimens were illuminated with 405, 526, and 555 nm wavelengths to detect chitin autofluorescence. A Z-series spanning 19–26 slices at 4 µm intervals was captured and focus stacking with maximum intensity projection was performed using inbuilt tools of ZEN.

Specimens previously used for DNA extraction are indicated as such among the type material. Methods concerning molecular sequence data, multiple sequence alignment and trimming, and phylogenetic inference are described in our previous work (Schmidt *et al.* 2019). GenBank accession numbers of the specimens treated here can also be found in that publication. All measurements are given in millimetres unless otherwise indicated. Nomenclature on cuticular ornamentation follows Murphree (1988).

Type material for all 36 named species of Stylocellidae (which includes 12 *Miopsalis*) was examined for comparison (see Clouse 2012).

Molecular phylogenetics. Methods for DNA extraction, PCR amplification, Sanger sequencing, and data matrix assembly are described in our previous works (Clouse & Giribet 2010; Clouset *et al.* 2011; Schmidt *et al.* 2019). We incorporated sequence data for three Mindanao Cyphophthalmi (the more complete juvenile specimen from Clouse *et al.* 2011 [specimen 7150] and one exemplar of the new species from each of the two localities) into molecular data matrices previously generated for Stylocellidae (Clouse & Giribet 2010; Clouse *et al.* 2009, 2011). The data matrix analyzed consisted of four molecular loci: 18S rRNA, 28S rRNA, cytochrome *c* oxidase subunit I, and histone H3. The resulting alignment and tree topology are provided as Supplementary Files 1 and 2, respectively. We performed maximum likelihood analysis of the 148-terminal dataset using IQ-TREE (Nguyen *et al.* 2015) with automated fitting of edge-proportional partition models and 1500 independent searches (Kalyaanamoorthy *et al.* 2017). Nodal support was estimated via the ultrafast bootstrap algorithm (1000 replicates; Hoang *et al.* 2018).

Taxonomy

Order Opiliones Sundevall, 1833

Suborder Cyphophthalmi Simon, 1879

Infraorder Boreophthalmi Giribet, Sharma, Benavides, Boyer, Clouse, de Bivort, Dimitrov, Kawauchi, Murienne & Schwendinger, 2012

Family Stylocellidae Hansen & Sørensen, 1904

Subfamily Leptopsalinae Clouse, 2012

Genus *Miopsalis* Thorell, 1890

Miopsalis Thorell, 1890: 381.—Hansen & Sørensen 1904: 99; Roewer 1923: 47–48, fig. 50; Roewer 1926: 263; Shear 1979: 356–357; Giribet 2000: 72 (as *nomen dubium*); Clouse & Giribet 2012: 247–249 (validated); Clouse 2012: 28–32.

Type species. *Miopsalis pulicaria* Thorell, 1890, by monotypy.

Miopsalis dillyi sp. nov.

(Figs. 1–4, Tables 1–2)

Types. Male holotype (NMP) from Center for Environmental Development and Recreation (CEDAR), Impalutao, Impasug-ong, Bukidnon Province, Mindanao I., Philippines, 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 July 2014, from sifted leaf litter. Two male (both dissected for genitalia) and one female paratypes in 96% EtOH (MCZ 154598), same collecting data as for holotype; 1 male mounted on SEM stubs (MCZ 154599), same collecting data as for holotype. One male and 2 female paratypes in 96% EtOH (MCZ 154600) from Center for Environmental Development and Recreation (CEDAR), Impalutao, Impasug-ong, Bukidnon Province, Mindanao I., Philippines, 775 m alt. (8.254933°N, 125.035749°E), leg. D. Mohagan, V. Yamba, R.M. Clouse, 30 June 2014, from sifted leaf litter. One male and 2 female paratypes in 96% EtOH (MHNG) from Center for Environmental Development and Recreation (CEDAR), Impalutao, Impasug-ong, Bukidnon Province, Mindanao I., Philippines, 775 m alt. (8.254933°N, 125.035749°E), leg. D. Mohagan, V. Yamba, R.M. Clouse, 30 June 2014, from sifted leaf litter. One male paratype (1 dissected for genitalia) in 96% EtOH (MCZ 154601) from western slope of Mt. Kitanglad, Lantapan, Kaatoan, Bukidnon Province, Mindanao I., Philippines, 1300 m alt. (8.072258°N, 125.008909°E), leg. A. Mohagan, D. Mohagan, D.J.B. Mohagan, V. Yamba, R.M. Clouse, 1 July 2014, from sifted leaf litter. Two female paratypes (extracted for DNA) in 96% EtOH (MCZ 154602) and 1 female paratype on SEM stubs (MCZ 154603), from western slope of Mt. Kitanglad, Lantapan, Kaa-

toan, Bukidnon Province, Mindanao I., Philippines, 1300 m alt. (8.072258°N, 125.008909°E), leg. A. Mohagan, D. Mohagan, D.J.B. Mohagan, V. Yamba, R.M. Clouse, 1 July 2014, from sifted leaf litter.

Additional material studied. Three juveniles (1 extracted for DNA; MCZ) in 96% EtOH from Center for Environmental Development and Recreation (CEDAR), Impalutao, Impasug-ong, Bukidnon Province, Mindanao I., Philippines, 775 m alt. (8.254933° N, 125.035749° E), leg. D. Mohagan, V. Yamba, R.M. Clouse, 30 June 2014, from sifted leaf litter.

Etymology. The specific epithet honors the invertebrate physiologist Geoffrey Fowler Dilly.

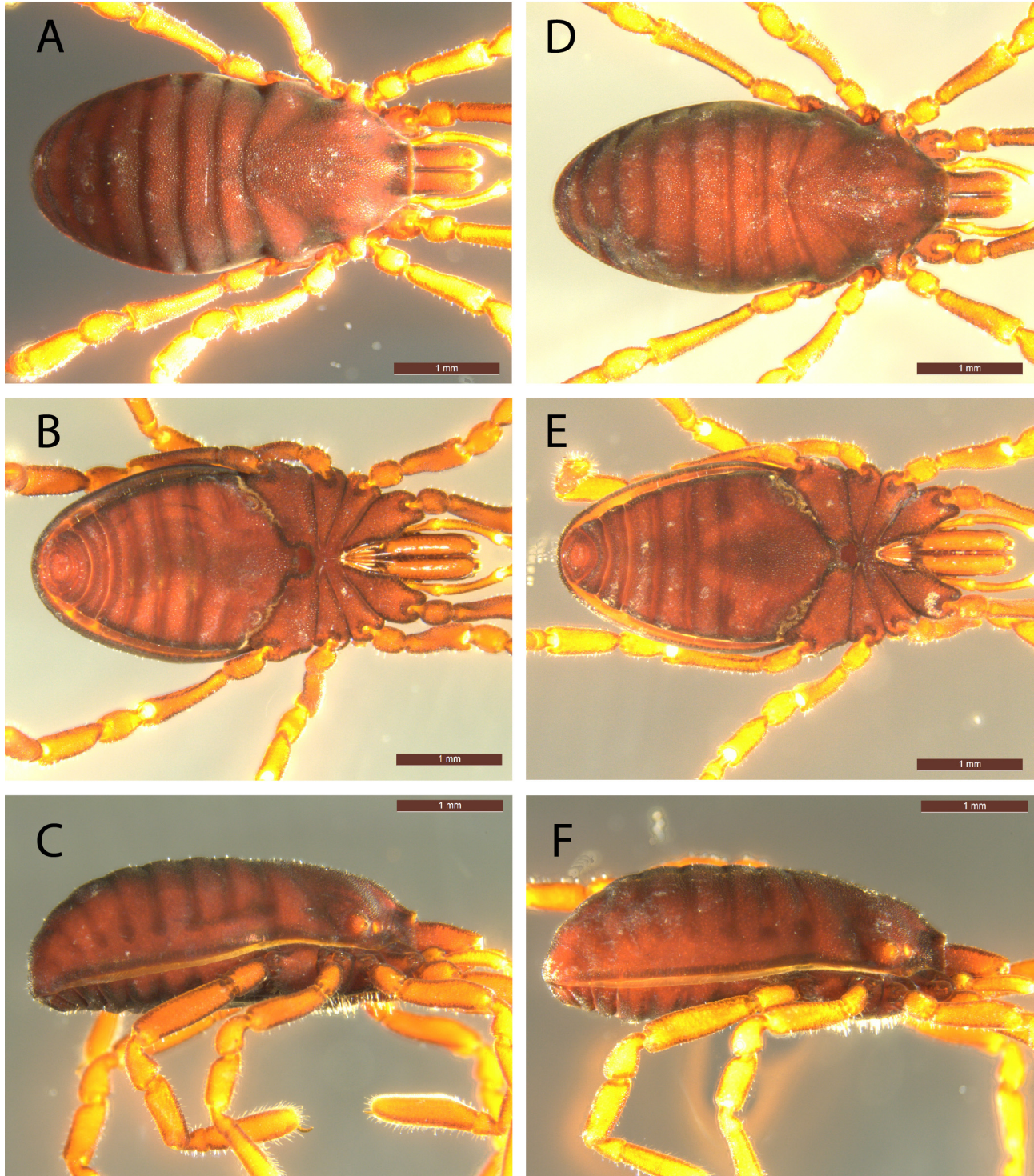


FIGURE 1. *Miopsalis dillyi* sp. nov. (A) Habitus of male holotype, dorsal view. (B) Same, ventral view. (C) Same, lateral view. (D) Habitus of female paratype, dorsal view. (E) Same, ventral view. (F) Same, lateral view. Scale bars as indicated.

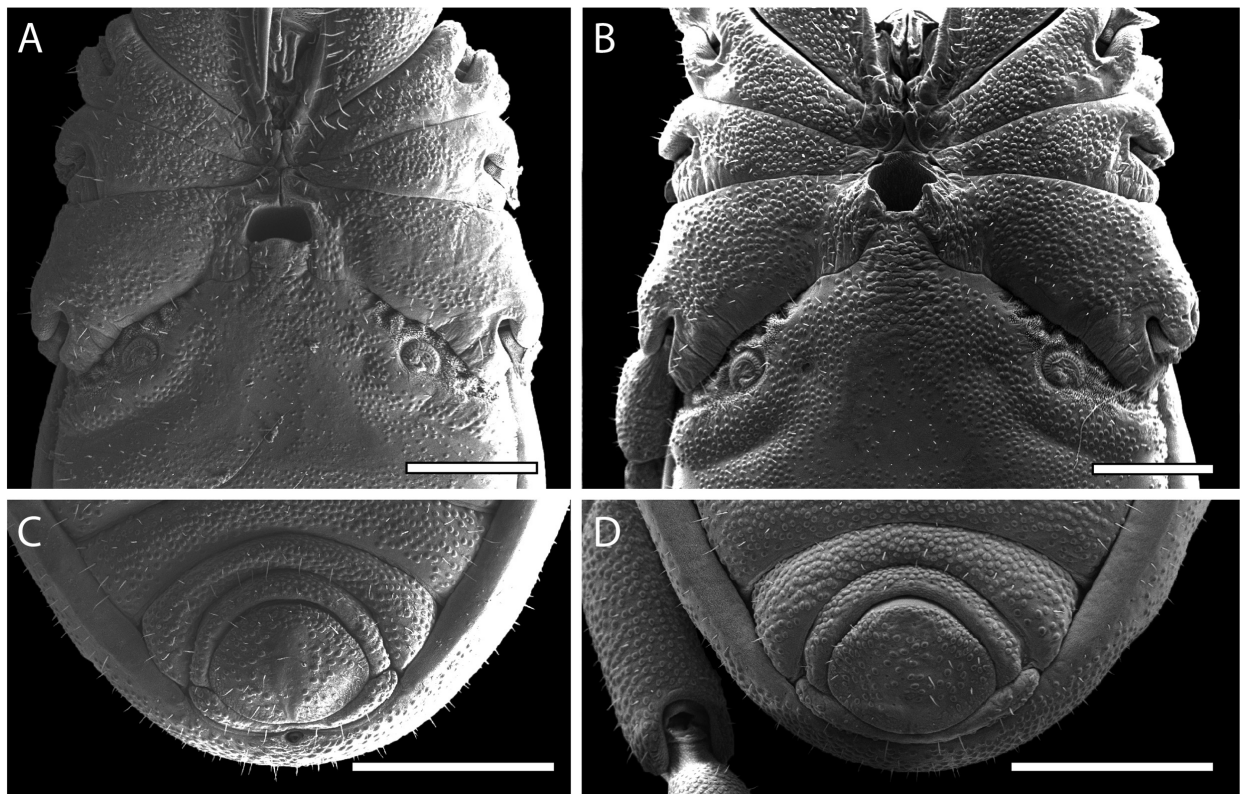


FIGURE 2. *Miopsalis dilly* **sp. nov.** (A) Male paratype, ventral view of prosomal complex. (B) Female paratype, same. (C) Male paratype, ventral view of posterior part of opisthosoma. (D) Female paratype, same. Scale bars: 500 µm.

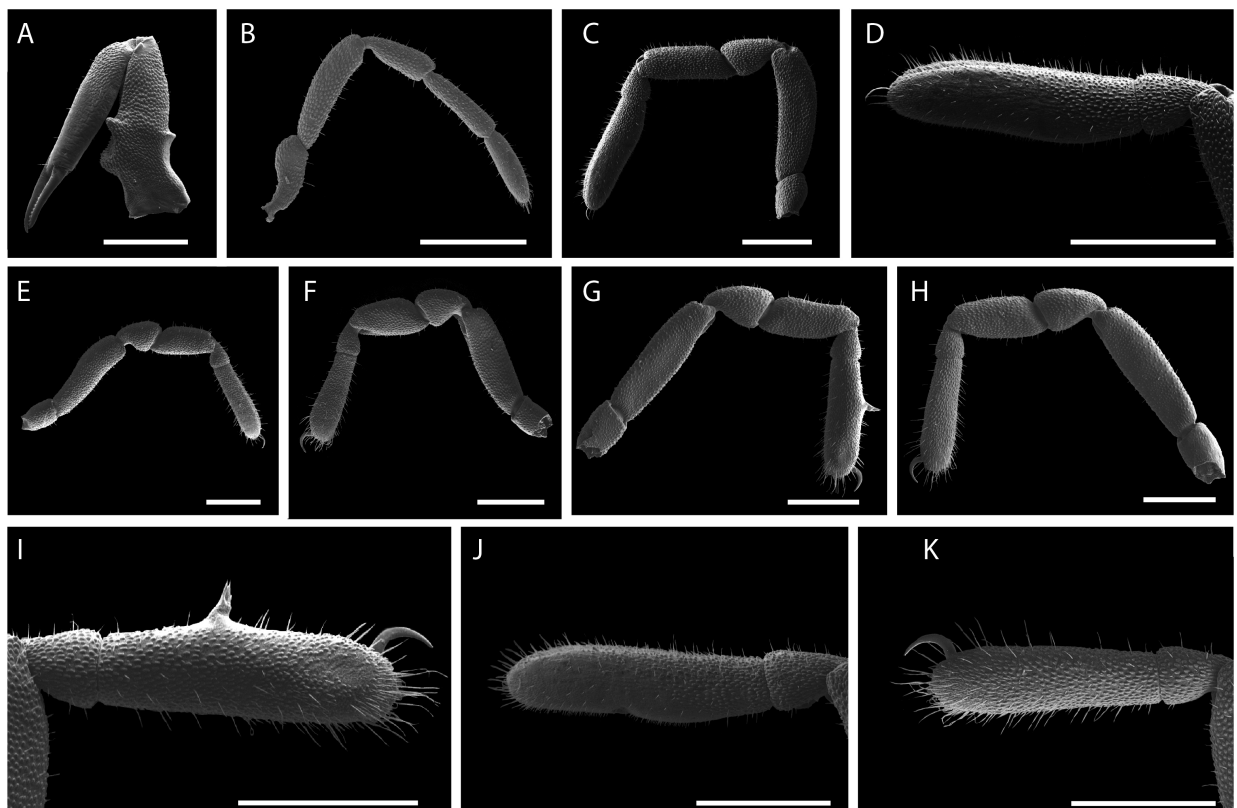


FIGURE 3. *Miopsalis dilly* **sp. nov.**, details of limbs in retrolateral view. (A) Left chelicera of male paratype. (B) Right palp of male paratype. (C) Left leg I of male paratype. (D) Tarsus I of male paratype. (E) Right leg II of male paratype. (F) Left leg III of male paratype. (G) Right leg IV of male paratype. (H) Left leg IV of female paratype. (I) Tarsus IV of male paratype. (J) Tarsus I of female paratype (tarsal claw damaged during preparation). (K) Tarsus IV of female paratype. Scale bars: 500 µm.

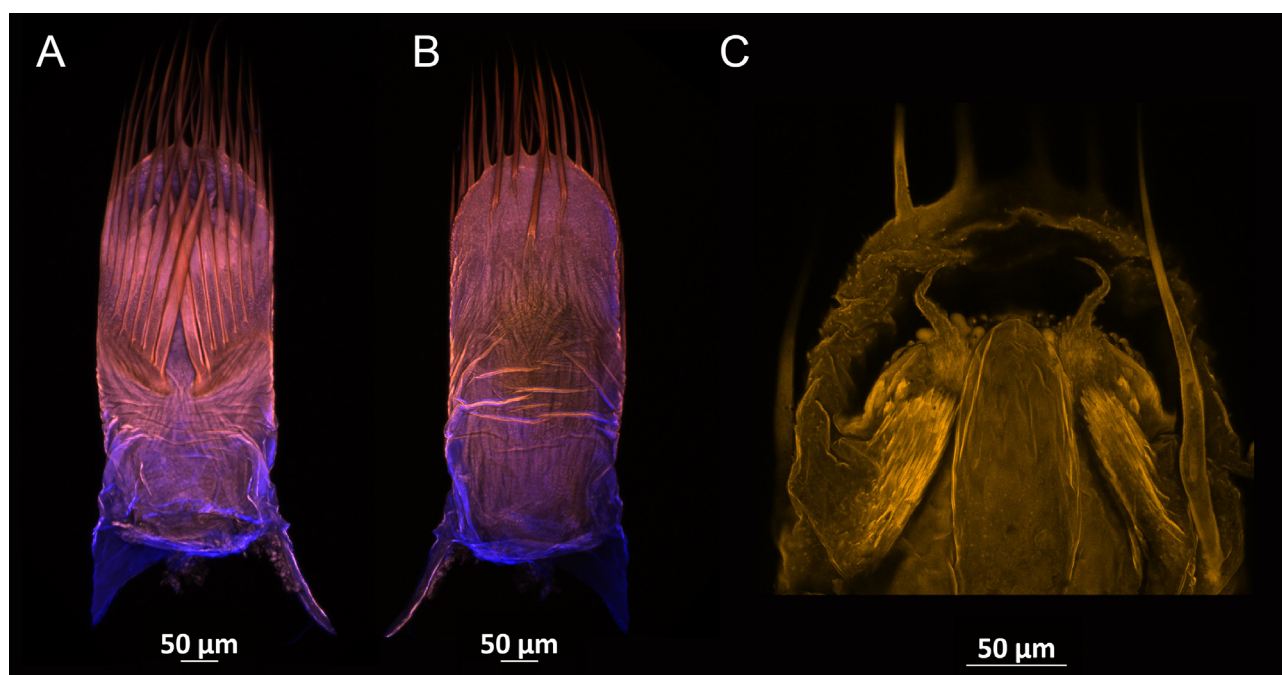


FIGURE 4. *Miopsalis dilly* sp. nov. (A) Spermatopositor, dorsal view. (B) Same, ventral view. (C) Detail of the gonopore complex. Scale bars as indicated.

Diagnosis. Medium-sized (ca. 3.6 mm) Cyphophthalmi presenting a character combination diagnostic for *Miopsalis*: distinct eyes, anal gland pore and Rambla's organ present, distinct sternum, extensive sculpturing on second cheliceral article, nearly parallel ventral opisthosomal sulci, nearly straight posterior margin of gonostome, and coxae II and IV each with distinct meeting points in males. Male also with distinct solea on tarsus I; presence of digiti of the gonopore complex; and arrangement of five ventral microtrichia of spermatopositor, with one proximal microtrichium on ventral midline and four subdistal microtrichia arranged in an arc. Distinguished from congeners by unique combination of medium size, and presence of anal gland pore, eyes, Rambla's organ, prominent second ventral cheliceral process, and claw-like chelicerae. For example, *M. mulu* (Shear, 1993) and *M. sabah* (Shear, 1993) are also medium-sized and have anal gland pores, but they have attenuate chelicerae and no Rambla's organ; *M. gryllospeca* (Shear, 1993) has a small Rambla's organ, claw-like chelicerae, and a large second ventral cheliceral process, but lacks an anal gland pore and is considerably larger (>5 mm) (see table 1 and figure 19 in Clouse 2012 for further comparison).

Description. Length of holotype (female paratype in parentheses) 3.64 (3.59); maximum body width 1.93 (1.84) at third opisthosomal segment; length/width ratio 1.88 (1.95). Distance between ozopores, 1.67 (1.61) (Fig. 1)

Body oval, dark orange-coloured to reddish brown (in alcohol) depending on incidence of light (Fig. 1). Body almost entirely with a dense tuberculate-microgranulate surface microstructure. Distinct eye lenses anterior to Type I ozophores (Juberthie 1970; see also Giribet 2003) (Fig. 1C, F). Mid-dorsal, longitudinal opisthosomal sulcus absent (male; Fig. 1A) or poorly defined (female; Fig. 1D). Posterior end of body evenly rounded. Coxae of leg II fused to coxae of legs III and IV (Fig. 2A, 2B). Sternum present (Fig. 2A, 2B). Proximal end of coxae I or III of males not meeting along the midline (in females, only coxae II meeting in midline; Fig. 2A, B). Male gonostome semicircular to trapezoidal, with weakly concave posterior edge, without cuticular projections (Fig. 2A). Spiracles C-shaped (Fig. 2A, B). Sternal opisthosomal glands absent. Sternites 8 and 9 and tergite IX free. Tergite IX of male distinctly bilobed. Anal plate of male with indistinct, raised, medial, longitudinal area lacking granulation, with shallow medial groove posteriorly (Fig. 2C, D). Anal gland pore present in male (Fig. 2C).

Chelicerae (Fig. 3A) not of the protruding type (Giribet 2003) and claw-like (Clouse 2012), distal article/median article ratio 0.32 (0.31); widest part of median cheliceral article near the base and with ornamentation concentrated proximally; proximal article with dorsal crest and two distinct ventral processes. Palpal trochanter without ventral process (Fig. 3B). Legs with all metatarsi and tarsi ornamented; claws of all legs smooth (Fig. 3C–K). Tarsus I with

a distinct solea (Fig. 3D, J). Rambla's organ of male small, oval in shape, in distal portion of tarsus IV adjacent to tarsal claw (Fig. 3I). Adenostyle conspicuous, subtriangular, robust, fringing at the tip; located in proximal half of tarsus (Fig. 3I). Appendage measurements provided in Tables 1–2.

TABLE 1. Limb measurements of male holotype. All measurements in mm.

Appendage	Tr	Fe	Pa	Ti	Me	Ta	Total
Leg I	0.31	0.95	0.49	0.69	0.21	0.94	3.59
Leg II	0.32	0.85	0.41	0.47	0.25	0.76	3.06
Leg III	0.25	0.85	0.42	0.48	0.20	0.66	2.86
Leg IV	0.38	0.98	0.49	0.59	0.24	0.85	3.53
Palp	0.35	0.62	0.35	0.43		0.39	2.14
	Proximal	Median	Distal				Total
Chelicera	0.62	1.24	0.40				2.26

TABLE 2. Limb measurements of female paratype. All measurements in mm.

Appendage	Tr	Fe	Pa	Ti	Me	Ta	Total
Leg I	0.29	0.94	0.45	0.64	0.29	0.87	3.48
Leg II	0.28	0.86	0.42	0.45	0.23	0.70	2.94
Leg III	0.29	0.83	0.38	0.53	0.24	0.65	2.92
Leg IV	0.40	1.08	0.44	0.60	0.30	0.79	3.61
Palp	0.36	0.63	0.36	0.44		0.37	2.16
	Proximal	Median	Distal				Total
Chelicera	0.65	1.21	0.38				2.24

Spermatopositor (Fig. 4), examined in three male paratypes, in dorsal view with eight long microtrichia on each side, their bases separated at midline. Dorsal microtrichia without serration (Fig. 4A). Ventral side with small denticles and five microtrichia, i.e. one proximal microtrichium on the ventral midline and four subdistal microtrichia arranged in an arc (Fig. 4B). Gonopore complex with a pair of long and gracile digiti (Fig. 4C).

Variation. Range of measurements of males (n=4) and females (n=6, in parentheses): Body length 3.48–3.79 (3.59–3.85), maximum width 1.82–1.96 (1.84–1.94).

Distribution. Known only from the two localities provided.

Results of molecular analysis

Maximum likelihood analysis of the four-gene dataset resulted in a tree topology with $\ln L = -41566.92$ (Fig. 5). Seven Phalangida and 21 non-stylocellid Cyphophthalmi were used to root the tree, following previous phylogenetic analyses of Stylocellidae (Clouse & Giribet 2010). The tree topology accorded closely with results from previous analyses, with respect to the monophyly of Fangensinae (*Fangensis* + *Giribetia*; bootstrap support [BS] = 90%), *Meghalaya* (BS = 84%), and *Miopsalis* (BS = 59%). Monophyly of *Leptopsalis* was not recovered, due to the inclusion of a few data-poor terminals from Borneo. As previously shown, *Leptopsalis* monophyly is better supported in a six-locus phylogeny that includes 16S rRNA and histone H4 (Clouse & Giribet 2010). All Mindanao *Miopsalis* terminals clustered together with high nodal support (BS = 99%), and were in turn nested within a clade of Bornean *Miopsalis* (BS = 80%), following our previous analyses of these taxa using Bayesian inference of molecular dating (Schmidt *et al.* 2019). Other relationships were as previously recovered in phylogenies of Cyphophthalmi (Clouse & Giribet 2010; Clouse *et al.* 2011; Giribet *et al.* 2012).

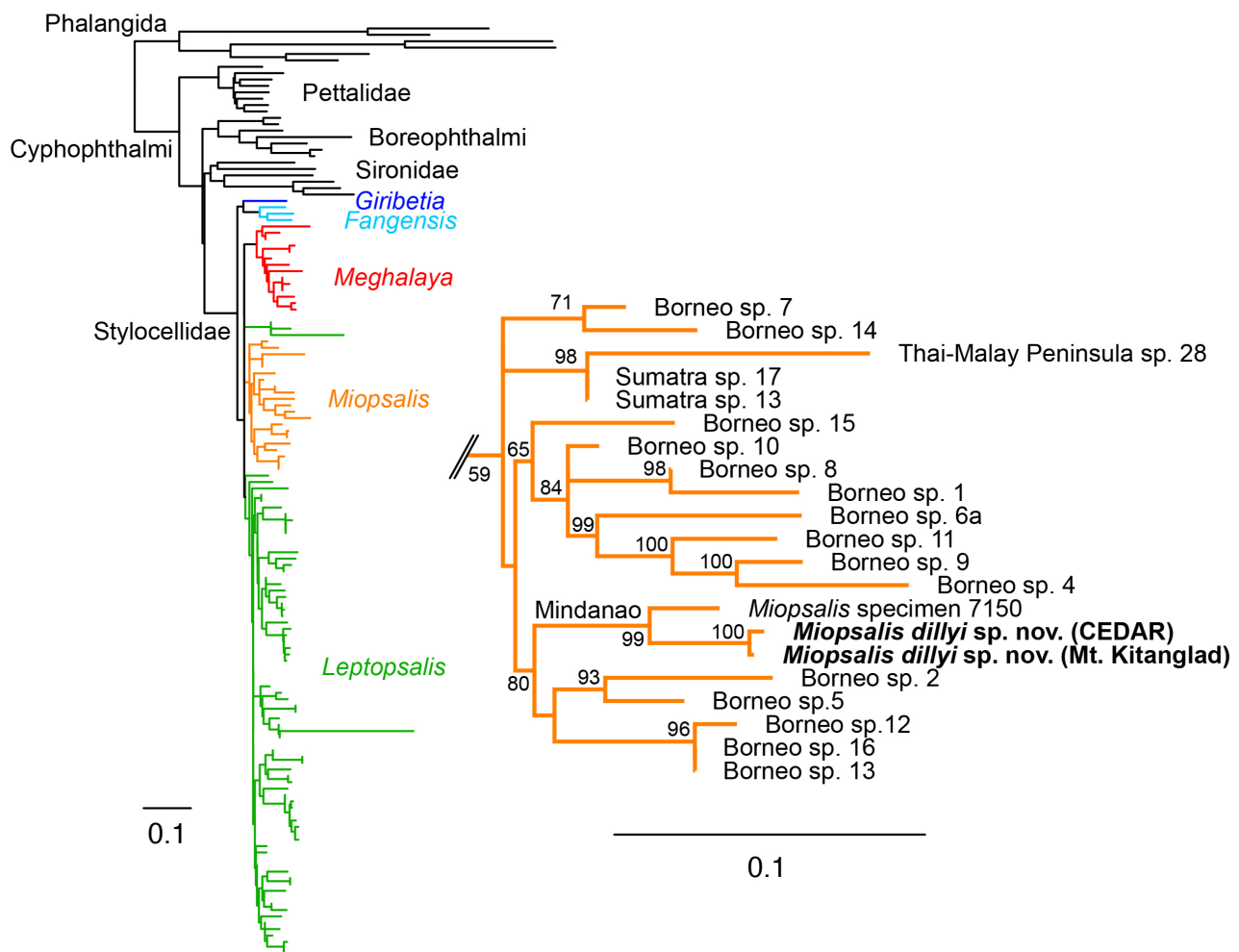


FIGURE 5. Left: Schematic of complete phylogeny inferred from maximum likelihood analysis of four molecular loci ($\ln L = -41177.18$), showing major groups of Opiliones. Right: Detail of phylogenetic relationships and geographical origins of *Miopsalis* specimens. Numbers on nodes indicate ultrafast bootstrap resampling frequencies.

Discussion

Could the Zamboanga Peninsula and the Sulu Archipelago constitute the remnant of the biogeographic umbilicus connecting Mindanao and Borneo? The occurrences of *Miopsalis* species on Mindanao and Palawan are biogeographically compelling because there is evidence that these parts of the Philippines have been connected to Borneo at different points in the Cenozoic (Pubellier *et al.* 2000, 2003, 2004; Hall 2002), but the issue is not settled nor understood in detail. Outstanding biogeographic questions include the timing of such connections and the degree to which they consisted of contiguous dry land. Although geological and biotic connections of Palawan and Borneo have long been discussed, any contiguity of the Mindanao biota with that of Borneo is less clear. Ancient groups like Cyphophthalmi are promising study taxa for testing these connections, as they are renowned for poor vagility and high fidelity to continental landmasses (Boyer *et al.* 2007; Giribet *et al.* 2012). Stylocellidae in particular is a formidable model taxon for the study of historical biogeography of Southeast Asia, given its distribution across the various islands of this region, a fossil record that includes a crown group stylocellid in Burmese amber from the early Cretaceous, and a well-established molecular phylogeny (Clouse & Giribet 2010; Clouse *et al.* 2009; Poinar 2009).

The previous discovery of two juvenile Cyphophthalmi in Mindanao, together with their strongly supported placement with the largely Bornean genus *Miopsalis* in a multilocus phylogeny, supported the inference of a biotic connection between Borneo and Mindanao (Clouse *et al.* 2011). In our recent work, we described a species

of Tithaeidae that is sympatric with *Miopsalis dillyi* **sp. nov.** and we performed molecular dating on a five-locus dataset broadly sampling Opiliones diversity (358 taxa). We were thus able to show that the Mindanao *Tithaeus* and *Miopsalis* exhibit overlapping inferred ages of Philippine colonization, with the Mindanao *Miopsalis* splitting from Borneo at 115 ± 21.5 (95% HPD) Mya (Schmidt *et al.* 2019). These patterns suggest that certain elements of the Philippine opiliofauna have retained the signature of biotic connections to Borneo via a corridor that is represented today by the Zamboanga/Sulu umbilicus. Regrettably, we have not yet been able to sample *M. tarumpitao* from Palawan during two previous collecting campaigns in 2010 and 2014. The rediscovery of this species would greatly facilitate testing the hypothesis of independent colonizations of Mindanao and Palawan via separate land bridges from Borneo.

While we previously treated the northern Mindanao Cyphophthalmi from two localities as specimens of two different morphospecies (Schmidt *et al.* 2019), further morphological examination and molecular sequence data support their treatment as belonging to populations of a single species. The single known male from Mt. Kitanglad is smaller (3.48 mm) than specimens collected from the type locality (average length of male 3.61 mm in CEDAR population), but we did not detect any differences in male genitalia or in the morphology of females from the two localities. Furthermore, exemplars of the two localities are separated by only six synonymous changes across a 658-bp fragment of COI. By contrast, *Miopsalis dillyi* **sp. nov.** is separated from the *Miopsalis* juvenile from southern Mindanao previously sequenced in 2011 (Clouse *et al.* 2011) by 51 changes across a 361-bp overlapping region of COI. These phylogenetic distances support the inference that another *Miopsalis* species occurs in southern Mindanao, whose adults remain unknown (Figs. 5, 6).

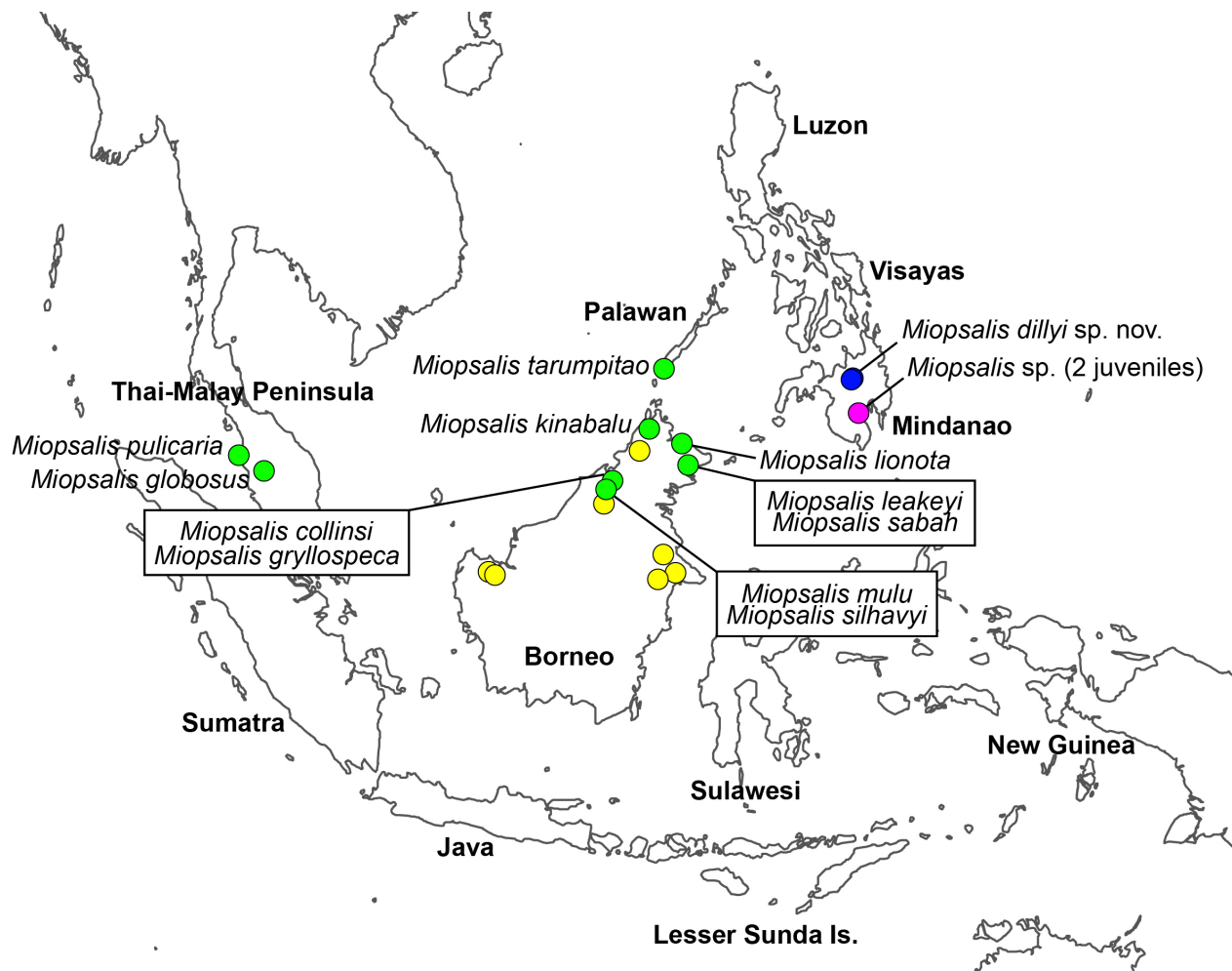


FIGURE 6. Map of collecting localities for *Miopsalis*. Green: Previously described species. Blue: *Miopsalis dillyi* **sp. nov.** Pink: Two juvenile *Miopsalis* sp. previously sequenced for DNA and distinct from *Miopsalis dillyi* **sp. nov.** Yellow: Undescribed morphospecies of *Miopsalis* included in previous molecular phylogenetic analyses.

The occurrence of many *Miopsalis* species in sympatry or geographic proximity throughout the range of the genus suggests that the true diversity of this group remains largely unknown. As an example, a subset of these undescribed morphospecies have been collected from Borneo and are known to be phylogenetically distinct lineages. Future efforts to elucidate the historical biogeography of the Philippine opiliofauna must sample intensively the leaf litter of poorly explored islands such as Palawan and Mindanao. Molecular systematic efforts aiming to test the importance of Zamboanga and the Sulu Islands and biogeographic umbilici should target groups that are represented in the Philippines, and whose ancestral areas are likely to be on the Thai-Malay Peninsula or the Indo-Chinese plate, such as Assamiidae, Epedanidae (especially the subfamily Dibuninae), and Petrobunidae.

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SUPPLEMENTARY FILE 1. Multiple sequence alignment of four loci in nexus format.

SUPPLEMENTARY FILE 2. Maximum likelihood tree topology inferred by IQ-TREE in newick format.