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Across Lydekker's Line – first report of mite harvestmen (Opiliones:Cyphophthalmi:Stylocellidae) from New Guinea

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Abstract. Opiliones (harvestmen) in the suborder Cyphophthalmi are not known to disperse across oceans and each family in the suborder is restricted to a clear biogeographic region. While undertaking a revisionary study of the South-east Asian family Stylocellidae, two collections of stylocellids from New Guinea were noted. This was a surprising find, since the island appears never to have had a land connection with Eurasia, where the rest of the family members are found. Here, 21 New Guinean specimens collected from the westernmost end of the island (Manokwari Province, Indonesia) are described and their relationships to other cyphophthalmids are analysed using molecular sequence data. The specimens represent three species, *Stylocellus lydekkeri*, sp. nov., *S. novaguinea*, sp. nov. and undescribed females of a probable third species, which are described and illustrated using scanning electron microscope and stereomicroscope photographs. *Stylocellus novaguinea*, sp. nov. is described from a single male and it was collected with a juvenile and the three females of the apparent third species. Molecular phylogenetic analyses indicate that the new species are indeed in the family Stylocellidae and they therefore reached western New Guinea by dispersing through Lydekker's line – the easternmost limit of poor dispersers from Eurasia. The New Guinean species may indicate at least two episodes of oceanic dispersal by Cyphophthalmi, a phenomenon here described for the first time. Alternatively, the presence in New Guinea of poor dispersers from Eurasia may suggest novel hypotheses about the history of the island.

Additional keywords: Arachnida, biogeography, dispersal, molecular data, phylogeny.

Introduction

Members of the Cyphophthalmi, a suborder of the arachnid order Opiliones ('harvestmen'), are excellent subjects for biogeographical studies owing to their worldwide distribution, poor dispersal abilities and long history (Boyer and Giribet 2007; Boyer *et al*. 2007). Found in stable, humid leaf litter on all continents (except Antarctica) and most islands of continental origin (Juberthie and Massoud 1976; Giribet 2000; Giribet and Kury 2007), the worldwide distribution of Cyphophthalmi is best explained by an ancient distribution across Pangea, the megacontinent that formed and began rifting apart during the Permian (Rogers and Santosh 2004). Despite being able to disperse across Pangea while the continent attained its condition of maximum packing at *c*. 250 mya, members of the Cyphophthalmi have low vagility, with most species known only from their type localities (Shear 1980; Giribet 2000) and none from oceanic islands ('Darwinian islands' *sensu* Gillespie and Roderick 2002 – those islands that have never been in contact with a continental landmass). The suggested Pangean distribution indicates an ancient origin for Cyphophthalmi, a hypothesis supported by phylogenetic analyses and fossil discoveries (e.g. Shultz 1998; Dunlop 2004). Cyphophthalmi are considered the sister group to all other Opiliones (e.g. Shultz 1998; Giribet *et al*. 1999, 2002; *contra* Martens 1980; Martens *et al*. 1981), a group that includes the suborder Eupnoi (along with two other suborders), a fossil of which is now known from the Early Devonian Rhynie cherts of Scotland (Dunlop *et al*. 2003, 2004).

Among Cyphophthalmi, the South-east Asian family Stylocellidae Hansen & Sørensen, 1904 is exceptionally speciose (e.g. Shear 1993), but it has received little attention from a systematic point of view and a large proportion of its diversity remains unstudied. The first extensive phylogenetic analysis of the suborder recovered the family as a monophyletic group (Giribet and Boyer 2002), but with little internal resolution. A later analysis explored the family's monophyly and focused on the members of the genus *Fangensis* Rambla, 1994 (Schwendinger and Giribet 2005), but our understanding of the relationships of the members of this family and the delimitation of its genera remain obscure. Stylocellidae has received more attention from a biogeographic perspective (e.g. Boyer *et al*. in press) owing to its known distribution. The geologically complex area of South-east Asia and the Indomalayan Archipelago is a region that provides several opportunities to test and broaden our understanding of cyphophthalmid evolution. Members of Stylocellidae have previously been reported from the Thai–Malay Peninsula, the Greater Sunda Islands (Sumatra, Java, Borneo and Sulawesi) and Palawan (the Philippine island north-north-east of Borneo) (Hansen and Sørensen 1904; Shear 1993; Rambla 1994; Giribet 2002). These areas originated as terranes that rifted from Gondwana from the

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Late Devonian to the Late Permian (365–255 mya) and accreted to Eurasia from the Late Permian to the Triassic (255–220 mya) (Metcalfe 1998; Hall 2002; references to 'Eurasia' below include these accreted terranes, *sensu* Hall 2002). The area has served as a cradle for the study of biogeography, and the unique mixture of species on each island led to the early observation by Alfred Russell Wallace that although the Indomalayan Archipelago appears to be a unified collection of islands, it is composed of landmasses with distinctly different origins. Today most biologists are familiar with the famous boundary known as 'Wallace's Line,' which lies between Borneo and Sulawesi and marks where, heading east, certain faunal groups lose Eurasian members and become more Australian (Wallace 1890; George 1981).

The distribution of Stylocellidae in this region closely matches our understanding of its geological history. Noteworthy is the lack of stylocellid collections from the Philippine islands other than Palawan. As mentioned earlier, Palawan has a continental origin, whereas the other islands are volcanic and of an oceanic origin (Hall 2002). Also, the presence of Stylocellidae on Sulawesi poses no conflict with Wallace's Line, since western Sulawesi and eastern Borneo were part of a single landmass before the middle Eocene (42 mya) (Moss and Wilson 1998) – the Makassar Straits have only been a dispersal hindrance to biota that migrated southward from Eurasia during the Cenozoic (such as birds and mammals) (Wallace 1876; Lydekker 1903; Myers 1953), long after Cyphophthalmi were present in the area.

While studying the stylocellid fauna, we were presented with two collections of specimens from New Guinea. They constitute a significant departure from the family's normal distribution and a challenge to our understanding of biogeographic trends in its entire suborder, Cyphophthalmi. Unlike stylocellids on Sulawesi, stylocellids from New Guinea do pose a significant challenge to current geological models of the history of South-east Asia or our understanding of cyphophthalmid dispersal capabilities. Located at the eastern end of the Malay Archipelago, New Guinea is an amalgam of volcanic arcs and microcontinents pushed into high peaks, which, during times of low sea levels, was broadly connected to Australia (the entire area being called the Sahul) (Pieters 1982; Polhemus and Polhemus 1998; Hall 2002). New Guinea, however, has only recently been in close proximity to South-east Asia, having moved northward ahead of Australia, a continent with which it has had extensive terrestrial connections in the past (Hall 2002).

New Guinea is noted for its biodiversity, even among tropical areas, and significant portions of its forests are still unexamined scientifically. Recent announcements of numerous new species of orchids, birds, frogs and butterflies have highlighted how unknown much of New Guinea's biodiversity remains (Conservation International 2006; World Wildlife Fund 2006). These discoveries, while exciting, do not appear to diverge from normal biogeographic patterns in the region. However, the discovery of stylocellids on the island conflicts with what has become known as 'Lydekker's Line' (Fig. 1), a faunal break between the Moluccas and New Guinea that marks the eastern limit of poor oceanic dispersers from Eurasia, such as birds (Mayr 1953), mammals (George 1981; Lydekker 1915) and freshwater fishes (Smith 1943). Good dispersers from Eurasia, including most arthropods, have extensively colonised New Guinea (except for the extreme south and south-west) more so

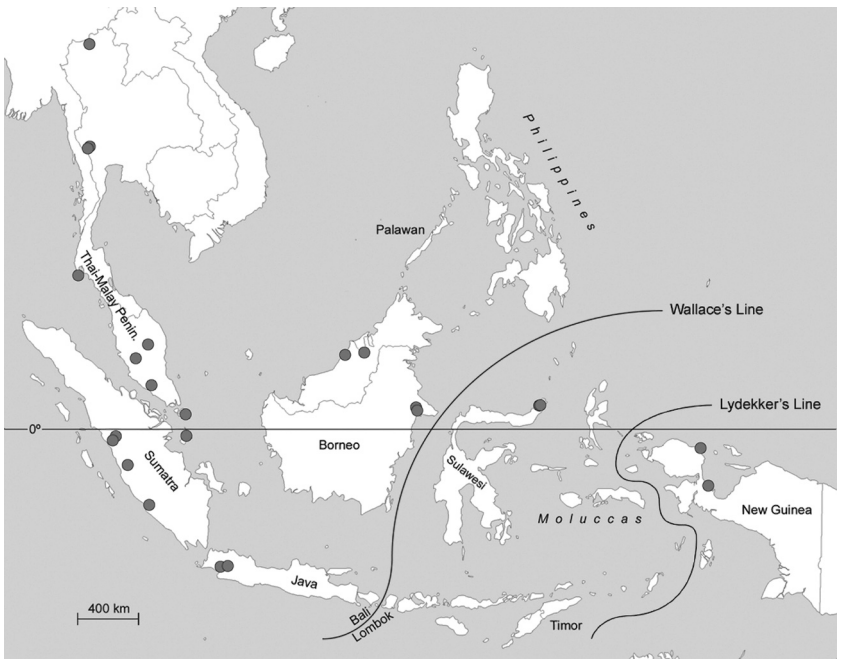

Fig. 1. The Malay Archipelago region, showing localities for Stylocellidae specimens used in the phylogenetic analysis. For the New Guinea collections, *Stylocellus lydekkeri*, sp. nov. is from the southern locality, and *S. novaguinea*, sp. nov. and females of a third species are from the other.

than Australian ones, probably because of the shared tropical habitat (Cheesman 1951; Gressitt 1956, 1982; Baker *et al*. 1998). Given their demonstration of low vagility elsewhere, members of the Cyphophthalmi in South-east Asia are expected to conform much more readily to the mammalian and avian halt at Lydekker's Line than to other arthropod distributions. As the only clear exception to Lydekker's Line of which we are aware, the systematics of these New Guinean stylocellids take on special importance. Thus we conducted a special study of these New Guinean specimens and here present descriptions of the species and a phylogenetic analysis of their relationships to other members of the Cyphophthalmi.

Materials and methods

Abbreviations

Specimens cited in this study are lodged in the following institutions:

MCZ	Department of Invertebrate Zoology, Museum of Comparative Zoology, Harvard University, Cambridge, MA (USA).
MHNG	Muséum d'histoire naturelle, Genève (Switzerland).

Descriptions of new species

Bodies and removed appendages were coated with an Au-Pd film using a Denton Desk II sputter coater (www.dentonvacuum.com) and then examined and photographed on an FEI Quanta 200 (www.fei.com) scanning electron microscope (SEM). Type specimens were photographed under a Leica MZ 12.5 stereomicroscope (www.leica-microsystems.com) using a mounted JVC KY-F70B digital camera (www.pro.jvc.com). Digital images captured at different focal planes were assembled using the application Auto-Montage Pro Version 5.00.0271 by Syncroscopy (www.syncroscopy.com). This application was also used to make measurements on stereomicroscope and SEM images. Genitalia were dissected out and examined and photographed on a Leica DMRB microscope equipped with a digital camera.

The length of the most basal article of the chelicera was measured from the dorsal crest on specimens that were examined whole. Cheliceral depths were measured vertically behind the dorsal crest to a point between the ventral processes. Leg widths were measured at the widest point and for leg IV of males, this was just proximal to the adenostyle. There are fewer trochanter measurements than for other leg articles, since they were often broken when appendages were removed for SEM mounts; for average total leg lengths in Table 4, those with and without trochanters are presented separately.

Phylogenetic analysis

We tested the placement of the New Guinea species within the family Stylocellidae by including them in a phylogenetic analysis of 19 stylocellid specimens, seven cyphophthalmid outgroups and a representative of the opilionid subfamily Eupnoi (Table 1). The family Stylocellidae currently contains the genera *Fangensis* Rambla, 1994, *Leptopsalis* Thorell, 1882, *Miopsalis* Thorell, 1890 and *Stylocellus* Westwood, 1874, and our phylogenetic analysis included representatives of each genus except *Leptopsalis* (as it is currently defined, but see our discussion below). We chose specimens for our analysis if they added taxonomic and geographic coverage and provided adequate sequence data. The molecular data analysed consisted of two nuclear ribosomal genes: the nearly complete 18S rRNA (~1.8 Kb) and ~2.2 Kb of 28S rRNA. Extraction, amplification and sequencing was done as described in previous studies of cyphophthalmid molecular systematics (Giribet *et al*. 2002; Boyer *et al*. 2005; Schwendinger and Giribet 2005), except that a wider variety of primers were used for amplification and sequencing and the 28S rRNA fragment was longer owing to the inclusion of an additional ~900 Kb upstream of the forward primer 28Sa. For 18S rRNA, in addition to the forward primers 1F, 3F, 4F, 7F and 18Sa2.0 and the reverse primers 3R, 4R, 5R, 7R, 8R, 18Sbi and 9R (all are described in Giribet *et al*. 1996, except 18Sa2.0 and 18Sbi, which are described in Whiting *et al*. 1997; Table 2), we also used the newly developed reverse primer 18SbiC (5′– GAG TCT CGT TCG TTA ACG GA – 3′). The 28S rRNA primers used were 28S D1f, 28S ZX1f, 28Sa, 28S rd1a and 28S rd4.8s (forward) and 28Sb, 28S rd5b and 28S rd7b1 (reverse) (28S D1f was described by Park and Ó Foighil (2000); 28S ZX1f was described by Van Der Auwera *et al*. (1994); 28Sa and 28Sb were described by Whiting *et al*. (1997); 28S rd4.8s, rd5b and rd7b1 were described by Schwendinger and Giribet (2005); 28S rd1a was described by Edgecombe and Giribet (2006)). Sequence data were submitted to GenBank (www.ncbi.nlm.nih.gov/Genbank/index.html) and accession numbers are provided in Table 1. Insufficient 28S rRNA was sequenced for *Stylocellus* sp. MCZ DNA101525 for that specimen to be included in the 28S partition.

Unaligned DNA sequence data were analysed using direct optimisation under the parsimony optimality criterion (Wheeler 1996) with the computer package POY version 3.0.11 (Wheeler *et al*. 2003). We analysed nodal stability with a sensitivity analysis, using ten parameter sets of indel-to-change and transition-to-transversion ratios (Wheeler 1995). We identified the optimal parameter set using a modified version of the incongruence length difference test (ILD), choosing the set that minimised overall incongruence. Nodal support was investigated primarily with 1000 replicates of jackknifing on unaligned data in POY; in addition, 100 bootstrap replicates in PAUP* version 4.0b10 (Swofford 2001) and 500 000 generations in MrBayes version 3.1.1 (Ronquist and Huelsenbeck 2003) were done on an implied alignment generated by POY using the optimal parameter set and its consensus tree (Wheeler 2003; Giribet 2005) for the combined 18S and 28S rRNA dataset. For the parsimony bootstrap analysis in PAUP*, we conducted a heuristic search with 100 Wagner replicates holding up to 1000 trees per replicate followed by tree bisection and reconnection (TBR) branch swapping, gaps counted as a fifth base and with a step matrix equivalent to that of the optimal parameter set (411). All characters were unordered, branches with a maximum length of zero collapsed. For MrBayes, the following settings were used: Nucmodel = 4by4, Nst = 6, Covarion = No, Number of States = 4 and Rates = Invgamma. The standard deviation of the split frequencies changed little from 0.015 after 350 000 generations, so the number of generations was stopped at 500 000.

Taxonomy

Order **OPILIONES** Sundevall, 1833

Suborder **CYPHOPHTHALMI** Simon, 1879

Family **STYLOCELLIDAE**, Hansen & Sørensen, 1904

Genus ***Stylocellus*** Westwood, 1874

Remarks

Stylocellus currently contains 25 named species distributed on the Thai–Malay Peninsula and through the Indomalayan Archipelago. Ten species have been described from Borneo, four each from Sulawesi and the Thai–Malay Peninsula, three each from Sumatra and Java and one from Palawan Island. However, we have examined a large assemblage of undetermined material and it is clear that the named species in this group are most likely less than a third of its total diversity (for species list, go to http://collections.oeb.harvard.edu/Invertebrate/Cyphophthalmi/species.cfm).

Stylocellus lydekkeri, sp. nov.

(Figs 2–9, 10*A*, *C*; Tables 3, 4)

Material examined

Holotype. Male (MHNG), Indonesia, Irian Jaya, Manokwari Province, Wandammen Bay, Wasior, Wondiwoi Mountains, 300–980 m alt.; leg. A. Riedel, 3.i.2001.

Paratypes. 6 males (2 articulated specimens (MHNG), 2 used for SEM examination (MCZ), 1 dissected for genitalia (MHNG) and 1 used for DNA analysis and SEM examination (MCZ DNA101064)) and 7 females (4 artic-

Table 1. List of specimens used in the phylogenetic analysis

With MCZ DNA accession numbers, locality description and coordinates and GenBank accession numbers for analysed markers.

Family	Species	MCZ accession number	Locality	Latitude	Longitude	18S rRNA	28S rRNA
Stylocellidae	*Fangensis cavernarus*	DNA101460	Thai–Malay Penin.	14°23′54″N	99°04′53″E	DQ133714	DQ133726
	Fangensis insulanus	DNA101063	Thai–Malay Penin.	7°53′07″N	98°26′14″E	DQ133711	DQ825552
	Fangensis insulanus	DNA100388	Thai–Malay Penin.	7°53′06″N	98°26′13″E	DQ133710	DQ825551
	Fangensis leclerci	DNA100913/100865[A]	Thai–Malay Penin.	19°34′33″N	99°3′40″E	DQ133713	DQ825553
	Fangensis spelaeus	DNA100669	Thai–Malay Penin.	14°17′59″N	98°58′59″E	DQ133712	DQ825554
	Miopsalis sp.	DNA101629	Sumatra	0°14′1″S	100°34′35″E[B]	EF025893	EF025875
	Miopsalis sp.	DNA101513	Borneo	4°00′00″N	114°49′00″E	EF025892	DQ133727
	Stylocellus sp.	DNA100870	Java	6°49′S	106°35′E[B]	EF025890	EF025874
	Stylocellus sp.	DNA101483	Thai–Malay Penin.	4°23′49″N	102°25′50″E	DQ825532	EF025865
	Stylocellus sp.	DNA101489	Thai–Malay Penin.	3°42′59″N	101°44′19″E	DQ518095	EF025867
	Stylocellus sp.	DNA101490	Thai–Malay Penin.	3°42′59″N	101°44′19″E	EF025885	EF025868
	Stylocellus sp.	DNA101474	Sumatra	1°41′S	101°16′E[B]	DQ518093	EF025863
	Stylocellus sp.	DNA101486	Thai–Malay Penin.	2°21′22″N	102°37′49″E	DQ825533	EF025866
	Stylocellus sp.	DNA101469	Sumatra	3°42′S	102°30′E[B]	EF025883	EF025862
	Stylocellus sp.	DNA101478	Sumatra	0°26′S	100°25′E[B]	DQ518094	EF025864
	Stylocellus sp.	DNA101446	Lingga	0°52′33″N	104°34′45″E	EF025880	EF025859
	Stylocellus sp.	DNA101507	Lingga	0°12′35″S	104°36′58″E	EF025878	EF025857
	Stylocellus sp.	DNA100611	Lingga	0°12′35″S	104°36′58″E	EF025879	EF025858
	Stylocellus sp.	DNA101523	Borneo	3°53′07″N	113°43′16″E[B]	EF025881	EF025860
	Stylocellus sp.	DNA101525	Borneo	4°0′0″N	114°49′0″E	EF025882	
	Stylocellus sp.	DNA101755	Java	6°47′S	107°01′00″E	EF025891	EF025877
	Stylocellus sp.	DNA101753	Java	6°47′S	107°01′00″E	EF025889	EF025873
	Stylocellus sp.	DNA101468	Borneo	1°14′N	117°46′E[B]	EF025884	EF025861
	Stylocellus sp.	DNA101517	Borneo	1°04′N	117°50′E[B]	DQ825527	DQ825564
	Stylocellus sp.	DNA101511	Sulawesi	1°19′N	124°49′E[B]	EF025887	EF025871
	Stylocellus sp.	DNA101756	Sulawesi	1°20′44″N	124°52′16″E	EF025888	EF025872
	S. lydekkeri, sp. nov.	DNA101064	New Guinea	2°43′S	134°30′E[B]	DQ133717	EF025869
	S. novaguinea, sp. nov.	DNA101510	New Guinea	0°50′S	134°02′E[B]	DQ825536	EF025870
	Stylocellus sp.	DNA101509	New Guinea	0°50′S	134°02′E[B]	EF025886	EF025876
Neogoveidae	*Huitaca* sp.	DNA101407	Colombia	5°46′46″N	73°27′13″W	DQ518090	DQ825596
	Metasiro americanus	DNA101532	Florida, USA	30°33′53″N	84°57′05″W	DQ825542	DQ825595
	Paragovia sironoides	DNA101059	Bioko, Eq. Guinea	3°43′32″N	8°50′17″E	DQ518092	DQ825606
Pettalidae	*Pettalus* sp.	DNA101282	Sri Lanka	7°23′05″N	80°49′01″E	DQ825537	DQ825576
Sironidae	*Siro rubens*	DNA100457	France	44°05′00″N	3°34′53″E	AY428818	DQ825584
	Suzukielus sauteri	DNA101543	Japan	35°38′03″N	139°14′28″E	DQ513138	DQ513116
Protolophidae (Suborder Eupnoi)	*Protolophus singularis*	DNA101033	California, USA	32°49′60″N	116°32′46″W	EF028095	EF028096

[A] DNA sequence data combined.

[B] Latitude and longitude estimated from locality description.

Table 2. List of primer sequences used for amplification and sequencing with original references

Primer name	Sequence	Reference
18S rRNA		
1F	5′ – TAC CTG GTT GAT CCT GCC AGT AG – 3′	Giribet *et al*. (1996)
3F	5′ – GTT CGA TTC CGG AGA GGG A – 3′	Giribet *et al*. (1996)
3R	5′ – AGG CTC CCT CTC CGG AAT CGA AC – 3′	Giribet *et al*. (1996)
4F	5′ – CCA GCA GCC GCG CTA ATT C – 3′	Giribet *et al*. (1996)
4R	5′ – GAA TTA CCG CGG CTG CTG G – 3′	Giribet *et al*. (1996)
5R	5′ – CTT GGC AAA TGC TTT CGC – 3′	Giribet *et al*. (1996)
7F	5′ – GCA ATA ACA GGT CTG TGA TGC CC – 3′	Giribet *et al*. (1996)
7R	5′ – GCA TCA CAG ACC TGT TAT TGC – 3′	Giribet *et al*. (1996)
8R	5′ – ACG GGC GGT GTG TAC – 3′	Giribet *et al*. (1996)
9R	5′ – GAT CCT TCC GCA GGT TCA CCT AC – 3′	Giribet *et al*. (1996)
18Sa2.0	5′ – ATG GTT GCA AAG CTG AAA C – 3′	Whiting *et al*. (1997)
18Sbi	5′ – GAG TCT CGT TCG TTA TCG GA – 3′	Whiting *et al*. (1997)
18SbiC	5′ – GAG TCT CGT TCG TTA ACG GA – 3′	
28S rRNA		
D1f	5′ – GGG ACT ACC CCC TGA ATT TAA GCA T – 3′	Park and ó Foighil (2000)
ZX1f	5′ – ACC CGC TGA ATT TAA GCA TAT – 3′	Van Der Auwera *et al*. (1994)
28Sa	5′ – GAC CCG TCT TGA AAC ACG GA – 3′	Whiting *et al*. (1997)
28Sb	5′ – TCG GAA GGA ACC AGC TAC – 3′	Whiting *et al*. (1997)
28S rd1a	5′ – CCC SCG TAA YTT AGG CAT AT – 3′	Edgecombe and Giribet (2006)
28S rd5b	5′ – CCA CAG CGC CAG TTC TGC TTA C – 3′	Schwendinger and Giribet (2005)
28S rd4.8a	5′ – ACC TAT TCT CAA ACT TTA AAT GG – 3′	Schwendinger and Giribet (2005)
28S rd7b1	5′ – GAC TTC CCT TAC CTA CAT – 3′	Schwendinger and Giribet (2005)

ulated specimens (MHNG), 1 used for DNA analysis and SEM examination (MCZ DNA101064), 1 dissected for genitalia and used for DNA analysis (MCZ DNA101064) and 1 used for DNA analysis (MCZ DNA101064)), same collection data as holotype.

Additional material examined. 2 juveniles (1 used for DNA analysis (MCZ DNA 101064)), same collection data as holotype.

Diagnosis

Stylocellus species relatively general in appearance, lacking several conspicuous features found in various combinations among other species, including anal gland pores, an anal plate ridge, troglomorphic characters (reduced eyes and elongate appendages) and pits on the posterior body; average in colour, size and proportions – not dark, as with species from northern Sulawesi and Borneo, nor excessively narrow, as with certain Javanese and Bornean species; opisthosomal–prosomal and opisthosomal transverse sulci prominent, but longitudinal sulcus not so; dorsum rising steeply at chelicers and then relatively flat; body and appendages not shining, except for the second cheliceral article, which is mostly smooth; first cheliceral article with second ventral anterior process and third article with relatively evenly sized teeth.

Description

Overall orange to brownish orange body with yellow to brownish yellow appendages, outline oval, body and most appendage surfaces tuberculate–microtuberculated, following the nomenclature of Murphree (1988).

Holotype male

Body length (3.3 mm) nearly twice its widest point (1.7 mm) between second and third opisthosomal segment, slightly wider than distance across ozophores (1.6 mm); length/width ratio 1.95 (Table 3).

Eyes present, lens clearly visible, in a lateral position anterior to the ozophores (Figs 2*B, C*, 3*A*), typical of *Stylocellus*. Ozophores of type 2 (in a lateral position but raised above the edge of the carapace (Juberthie 1970; Giribet 2003*a*)); with an infolded opening (*sensu* de Bivort and Giribet 2004). Extensive

Table 3. Length and length/width ratios for appendages

For the *Sylocellus lydekkeri*, sp. nov. holotype, given as 'length in mm, length/width ratio'. Abbreviations used: Tr, trochanter; Fe, femur; Pa, patella; Ti, tibia; Mt, metatarsus; Ta, tarsus; TL, total length.

Appendage	Segments						
Chelicer	I: 0.62, 1.55	II: 1.29, 6.45	III: 0.32, 5.33				
Palp	Tr: 0.31, 2.07	II: 0.62, 3.88	III: 0.37, 2.85	IV: 0.42, 3.82	Ta: 0.36, 3.60	TL: 2.08	
Legs							
I	Tr: 0.28, 1.07	Fe: 0.97, 3.59	Pa: 0.54, 2.16	Ti: 0.63, 2.52	Mt: 0.30, 1.30	Ta: 0.86, 3.19	TL: 3.59
II	Tr: 0.27, 1.08	Fe: 0.80, 3.20	Pa: 0.42, 1.62	Ti: 0.47, 1.81	Mt: 0.29, 1.45	Ta: 0.74, 3.52	TL: 2.99
III	Tr: 0.20, 0.87	Fe: 0.70, 2.69	Pa: 0.42, 1.56	Ti: 0.46, 1.77	Mt: 0.26, 1.37	Ta: 0.68, 3.24	TL: 2.72
IV	Tr: 0.31, 1.19	Fe: 0.92, 3.41	Pa: 0.47, 1.62	Ti: 0.56, 2.00	Mt: 0.30, 1.36	Ta: 0.90, 3.21	TL: 3.46

tuberculate–microtuberculate (*sensu* Murphree 1988) ornamentation on dorsal and ventral body surfaces (except for smooth medial area extending from the gonostome posteriorly to opisthosomal sternite 3), ozophores, legs, palps and proximal cheliceral segment (Figs 2, 3, 4, 5). Transverse prosomal–opisthosomal sulcus and transverse opisthosomal sulci conspicuous, free of ornamentation. Longitudinal dorsal opisthosomal sulcus inconspicuous. Ventrum flat and dorsum rising steeply from chelicers and then flattening before descending after opisthosomal tergite IV, the two surfaces parallel for most of the body length in lateral view (Fig. 2C). Sternal opisthosomal region lacking conspicuous modifications or sternal gland openings.

Ventral prosomal complex (Figs 2*A*, 3*B*, 6*A*)

Typical for stylocellids, with coxae IV meeting extensively in the midline for a distance shorter than the gonostome length; gonostome anterior and posterior edges straight, opening approximately twice as wide as long; lateral walls of gonostome formed by elevated posteroproximal processes of coxae IV.

Anal region

Anal plate and tergites VIII and IX unmodified (Fig. 6*C*), covered with tuberculate–microtuberculate sculpturing as remainder of body, lacking anal gland openings, ridges or midline smooth area.

Chelicerae

With distinct dorsal crest that articulates with the anterior carapace (Fig. 2*B*, *C*); two ventral processes, the anterior one being quite indistinct and protruding as much laterally as ventrally (Figs 2*B*, 3*A*, 5*A*); proximal article extensively granulated, ornamentation continuing on basal portion of second article just past the joint, becoming more widely spaced and fainter laterally, but second article nearly completely smooth. Dentition on fixed cheliceral finger with 10 teeth after the apex, the most distal two teeth small, the third larger than all others and then gradually decreasing in size towards the joint (Fig. 7*B*, *C*). Third article 26% of second article length (Table 3) with similar but smaller dentition.

Palp (Fig. 5*B*)

Without processes on trochanter or other segments; with even tuberculate–microtuberculate ornamentation from trochanter to segment IV. Article measurements and length/width ratios in Table 3.

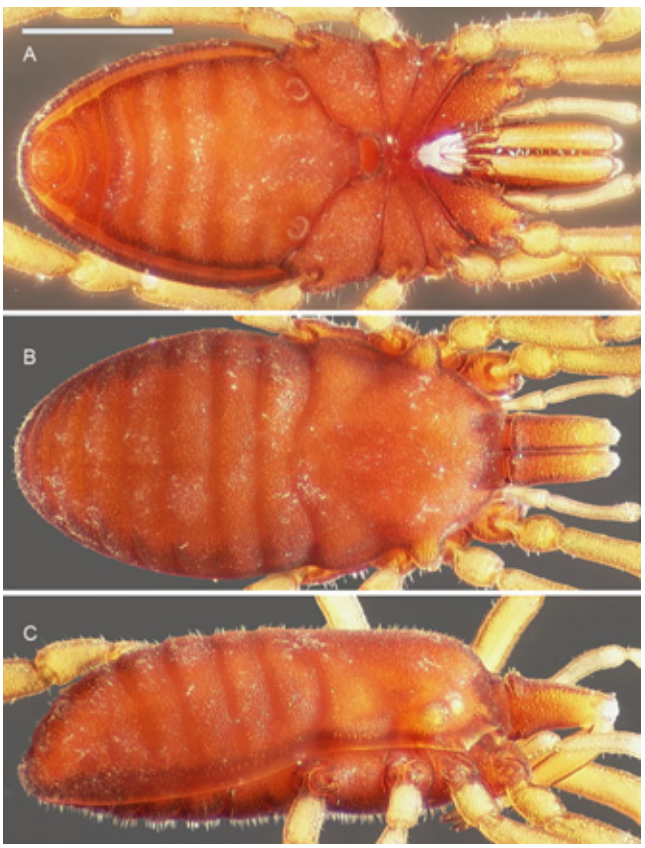

Fig. 2. *Stylocellus lydekkeri*, sp. nov. male holotype: *A,* ventral; *B,* dorsal; *C,* lateral views; scale bar = 1 mm.

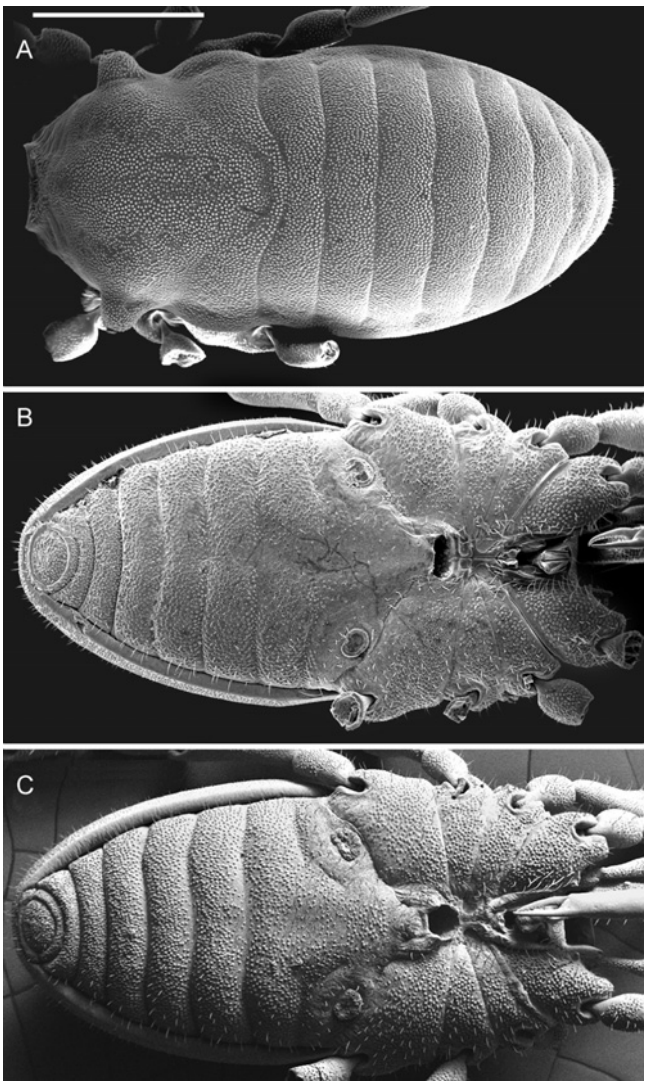

Fig. 3. *Stylocellus lydekkeri*, sp. nov. *A,* male paratype: dorsal and *B,* ventral; *C,* female paratype ventral views; scale bar = 1mm.

Legs (Fig. 4*A,D, F–I*)

With heavy tuberculate-microtuberculate ornamentation and numerous setae; ornamentation weakening on distal and ventral half of tarsus I and disto-ventral third of tarsus II. Leg I with a dense concentration of short ventral setae, but not forming a distinct solea. Conspicuous median dorsal groove on tarsi I and II; ~2/3 of distal tarsus I with distinct concentration of sensory setae on ventral surface; leg IV with adenostyle fringed at tip and located medially on dorsal side of tarsus; legs without processes or depressions, without Rambla's organ; claws without lateral projections. Leg article lengths and length/width ratios in Table 3.

Spermatopositor (Fig. 8)

Typical size and appearance for stylocellids (Shear 1980; Schwendinger and Giribet 2005) microtrichial formula (one examined): 3, 4, 6 + 6.

Variation

Male body lengths ranged from 2.98 mm to 3.38 mm ($n = 4$) and the length/width ratio ranged from 1.88 to 1.98. The average range for lengths and length/width ratios for appendage articles was 11% (Table 4). Gonopore complex not studied.

Females (Figs *3C,* 4*E, J,* 9, 10*A, C;* Table 4)

Similar to males in coloration and ornamentation. Females ~10% longer than males with a larger length/width ratio (2.05), length/width ratios for appendage articles comparable with those of males (Figs 4*A–E*). Gonostome larger than in males, posterior edge straight; lateral walls of gonostome formed by elevated posteroproximal processes of coxae IV; these processes slightly larger and situated more posteriorly in females than in males; anterior edge evenly rounded and separating fourth coxae, which do not meet in the midline (Figs 3*C*, 9*A*). Ornamentation posterior of gonostome not as sparse as in males (Fig. 3*C*). Ovipositor (Fig. 10*A*, *C*) with a shaft composed of 31

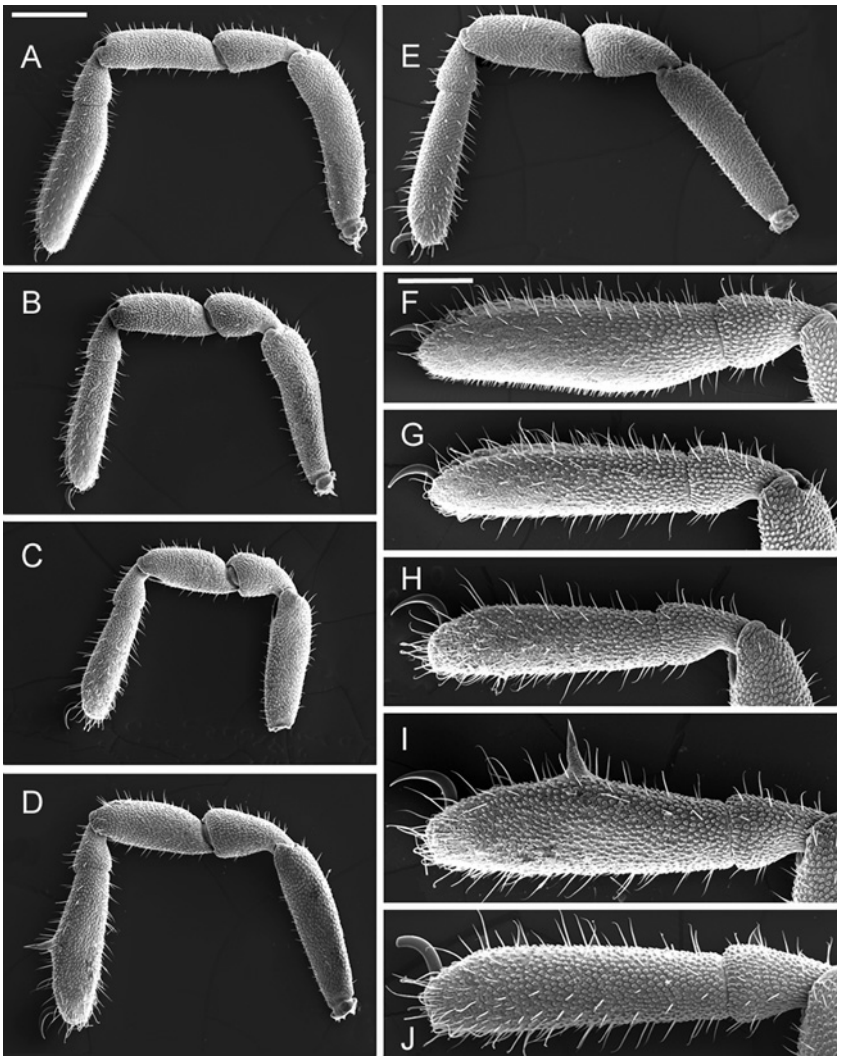

Fig. 4. *Stylocellus lydekkeri*, sp. nov.: *A–D*, male paratype legs I–IV; *E,* female paratype leg IV; scale bar = 0.4 mm; *F–I*, male tarsi I–IV; *J*, female tarsus IV; scale bar = 0.2 mm.

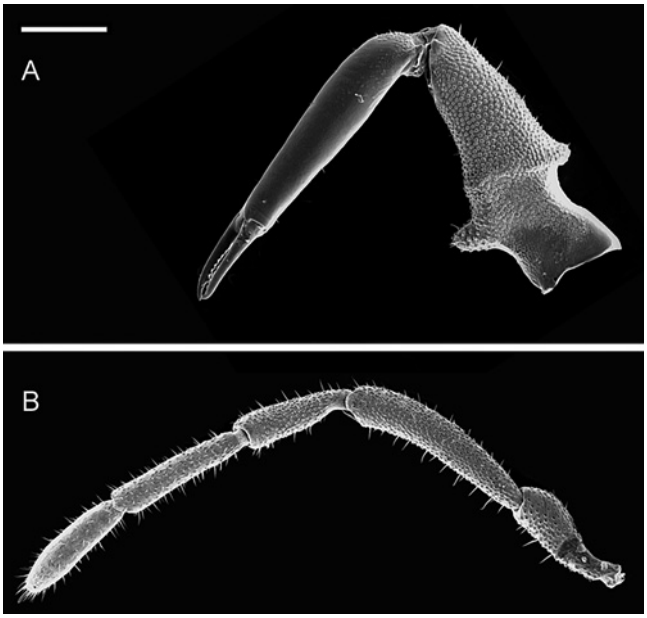

Fig. 5. *Stylocellus lydekkeri*, sp. nov. male paratype: *A,* chelicer; *B,* palp; scale bar = 0.3 mm.

segments and a terminus with two elongate lobes; each lobe with subapical, lateral clump of simple and branched processes ('sense organs' of Shear 1980) typical of Stylocellidae (Giribet 2002; Schwendinger and Giribet 2005); apex of each terminus lobe a with cluster of approximately three long projections.

Distribution

Known only from the Wondiwoi Mountains of the Vogelkop area of New Guinea (Indonesian, Irian Jaya). The sole collection was made in Manokwari Province at 300–980 m, along Wandammen Bay in Wasior District, which is on the eastern coast of the peninsula connecting the Vogelkop ('Bird's Head') area to mainland New Guinea.

Remarks

Compared with described species of *Stylocellus*, the body of *S. lydekkeri*, sp. nov. is distinctly longer than only *S. ramblae* Giribet, 2002 from Singapore and *S. kinabalu* Shear, 1993 from Borneo. Its length is most similar to *S. pangrango* Shear, 1993 from Java, *S. tambusisi* Shear, 1993 from Sulawesi and *S. mulu* Shear, 1993 from Borneo. The body is wider across the ozophores and the second cheliceral segment longer and narrower than *S. pangrango*; the body is narrower, the spermato-

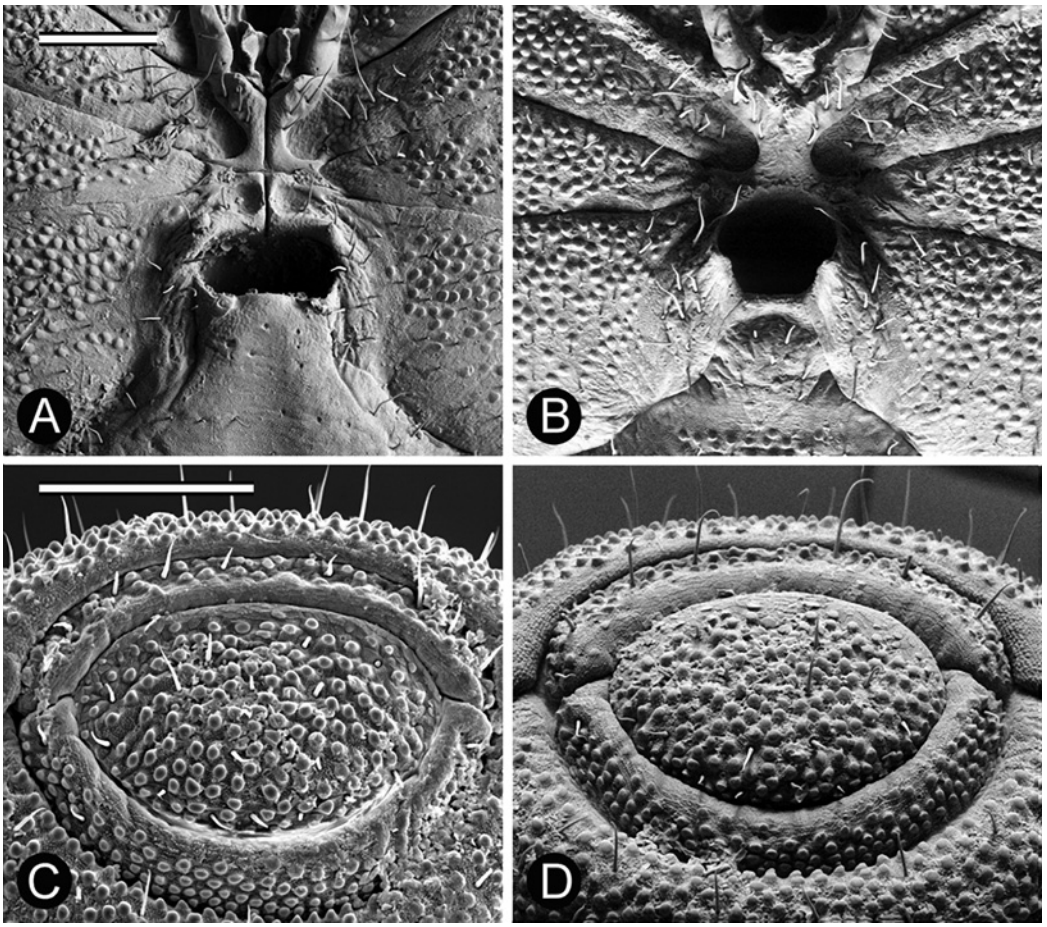

Fig. 6. *Stylocellus lydekkeri*, sp. nov.: *A,* male paratype gonopore; *B,* female paratype gonopore; *C,* male paratype anal plate; *D,* female paratype anal plate; scale bar = 0.2 mm.

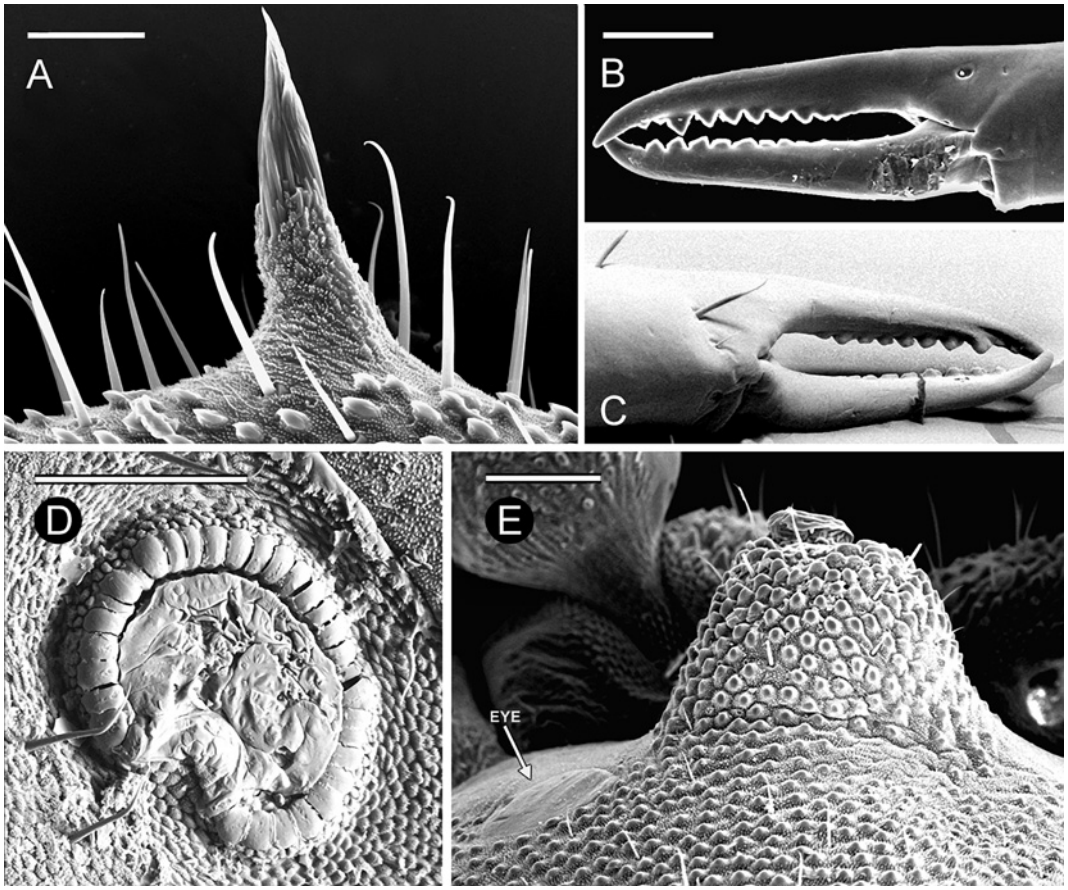

Fig. 7. *Stylocellus lydekkeri*, sp. nov. male paratype: *A,* adenostyle, scale bar = 50 μm; *B,* chelicer claw; *C,* claw inside; scale bar = 0.1 mm; *D,* spiracle; *E,* eye and *F,* ozophore dorsal view; scale bar = 0.1 mm.

positor wider and with a different dorsal setal arrangement, and the adenostyle is longer and more median on the tarsus than *S. tambusisi*; the second cheliceral segment is distinctly wider in proportion and the cheliceral teeth more evenly sized than *S. mulu*; the body is also granulated, not shining, as in *S. mulu*.

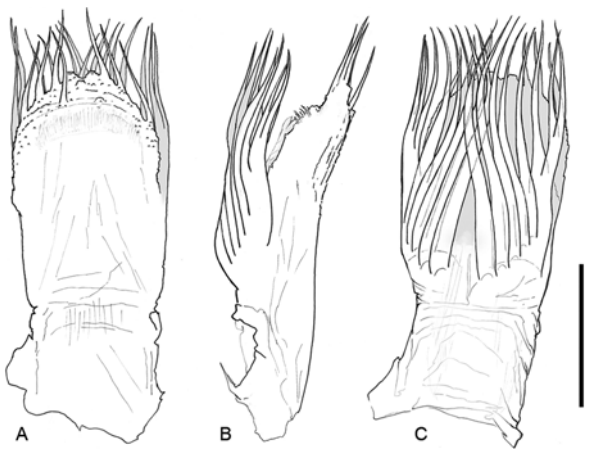

Fig. 8. *Stylocellus lydekkeri*, sp. nov. spermatopositor of male paratype: *A,* ventral; *B,* lateral; *C,* dorsal views; scale bar = 0.1 mm.

Etymology

This species is named in honour of Richard Lydekker (1849–1915), who made important contributions to vertebrate paleontology, mammalian systematics and biogeography while at The Natural History Museum (London). His interest in modern faunas and their distributions led him write about, among other puzzles, the strange combinations of animals on Timor, Sulawesi and other islands immediately west of New Guinea.

Stylocellus novaguinea, sp. nov.

(Figs 11–13; Table 5)

Material examined

Holotype. Male (MHNG), Indonesia, Irian Jaya, Manokwari Province, Gunung Meja, 200 m alt., leg. A. Riedel, 30.xii.2000–1.i.2001, two legs used for DNA extraction (MCZ DNA101510). Left third leg missing and left chelicera missing (from natural injury, not specimen damage).

Diagnosis

Stylocellus species with a dark, broadly oval body in dorsal view; anterior dosum rising gradually and dorsal and ventral surfaces convex in lateral view; transverse sulci conspicuous, longitudinal sulcus not so; tuberculate–microtuberculate sculp-

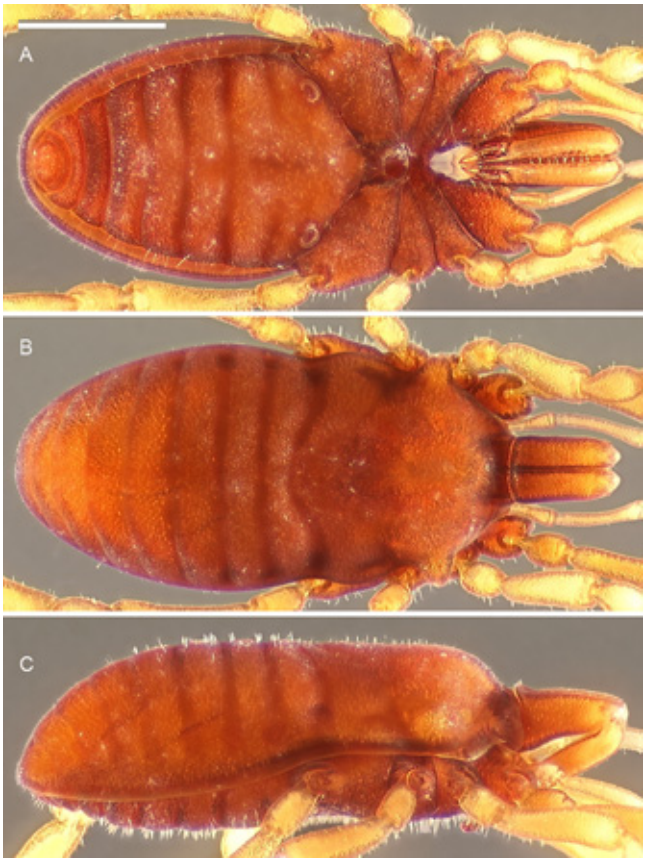

Fig. 9. *Stylocellus lydekkeri*, sp. nov. female paratype: (MHNG) *A,* ventral; *B,* dorsal; *C,* lateral views; scale bar = 1 mm.

turing prominent on body and appendages but missing on the lateral dorsum and opisthosomal sulci; first cheliceral article with second ventral anterior process, second article almost entirely smooth, third article with evenly sized teeth; without modifications of the anal region and, as with *S. lydekkeri*, sp. nov. (above), lacking body wall and appendage modifications found in many other species.

Description

Body dark reddish brown, legs becoming light orange distally; body and appendage surface ornamentation, when present, distinctly tuberculate–microtuberculated.

Holotype male

Body length (3.72 mm) 1.85 times longer than widest point (2.00 mm) located at second opisthosomal segment, which is distinctly wider than distance across ozophores (1.76 mm) (Table 5).

Eyes present, lens clearly visible, located in a lateral position and anterior to the ozophores (Figs 11*C*, 12*A*), typical of *Stylocellus*. Ozophores of type 2 (Juberthie 1970; Giribet 2003*a*) (Fig. 11*C*). Body and appendages mostly presenting a tuberculate–microtuberculate ornamentation. Dorsal scutum ornamented medially, ornamentation extending laterally towards ozophores; ozophores sculpted; smooth at tarsal sutures and laterally (Fig. 11*B*). Transverse prosomal–opisthosomal sulcus and transverse opisthosomal sulci conspicuous, free of ornamentation. Longitudinal dorsal opisthosomal sulcus inconspicuous. Ventral surface with ornamentation somewhat irregularly spaced, becoming sparser medially, smooth at sternal sutures and around spiracles (Fig. 10*A*). Dorsal surface rising gradually from chelicerae; ventrum convex, body oval in lateral view (Fig. 11*C*).

Ventral prosomal complex (Fig. 11*A*)

Typical for stylocellids, with coxae IV meeting extensively in the midline for a distance shorter than the gonostome length. Gonostome posterior edge convex, wider than anterior edge, which is straight (Fig. 12*C*); lateral walls of gonostome formed by elevated posteroproximal processes of coxae IV.

Anal region

Sternites 8 and 9 and tergite IX free, not forming a corona analis. Anal plate (tergite IX) unmodified, with ornamentation as in the remainder of the body, lacking a median ridge or medial smooth area (Fig. 12*D*). Tergites VIII and IX without anal gland pores.

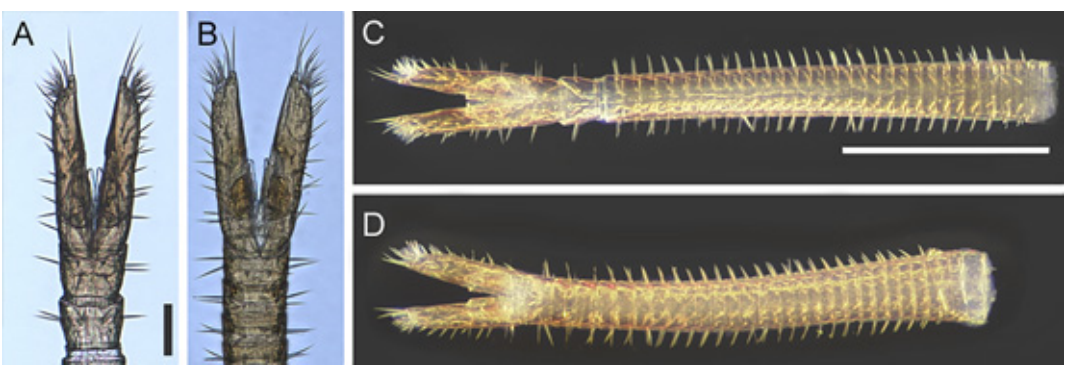

Fig. 10. *A, Stylocellus lydekkeri*, sp. nov. ovipositor terminus of female paratype; *B, Stylocellus* sp. MCZ DNA101509 ovipositor terminus; scale bar = 0.1 mm; *C, Stylocellus lydekkeri*, sp. nov. ovipositor of female paratype whole mount; *D, Stylocellus* sp. MCZ DNA101509 ovipositor whole; scale bar = 0.5 mm.

Table 4. Average length and length/width ratios for body and appendages

For *Sylocellus lydekkeri*, sp. nov. males and females and *Stylocellus* sp. females, given as 'length in mm (range), length/width ratio (range);' sample sizes are in parentheses after first mention of body part or segment; leg and palp average total lengths are given as 'average for appendages with trochanters (range), average for appendages missing trochanters (range)'. Abbreviations as for Table 3.

Body part	Segments						
Sylocellus lydekkeri, sp. nov. males							
Body	Length (4): 3.25 (0.4)	W-ozophore (3): 1.63 (0.13)	W-widest (4): 1.67 (0.12)	L/W ratio (4): 1.94 (0.1)			
Chelicer	I (4): 0.67 (0.15), 1.74 (0.33)	I (3): 1.1 (0.11), 2.91 (0.39)	II (4): 1.29 (0.11), 6.1 (0.72)	III (4): 0.33 (0.05), 6.16 (2.39)			
Palp	Tr (2): 0.26 (0.09), 1.76 (0.62)	II (3): 0.63 (0.11), 4.63 (1.17)	III (3): 0.36 (0.08), 3.1 (0.66)	IV (3): 0.44 (0.06), 4.47 (1.18)	Ta (3): 0.38 (0.06), 3.78 (0.3)	TL: 2.14 (0.12) / 1.68	
Legs							
I	Tr (I:2, II–IV:1): 0.28 (0.02), 1.1 (0.06)	Fe (4): 0.96 (0.08), 3.7 (0.44)	Pa (4): 0.49 (0.08), 2.07 (0.26)	Ti (4): 0.62 (0.07), 2.68 (0.24)	Mt (4): 0.28 (0.08), 1.28 (0.39)	Ta (4): 0.84 (0.05), 3.18 (0.25)	TL: 3.48 (0.21) / 3.23 (0.26)
II	Tr: 0.27, 1.08	Fe: 0.81 (0.03), 3.28 (0.46)	Pa: 0.44 (0.03), 1.76 (0.24)	Ti: 0.48 (0.07), 1.98 (0.35)	Mt: 0.28 (0.05), 1.47 (0.36)	Ta: 0.72 (0.04), 3.44 (0.9)	TL: 2.99 / 2.73 (0.11)
III	Tr: 0.20, 0.87	Fe: 0.71 (0.03), 2.88 (0.66)	Pa: 0.41 (0.05), 1.65 (0.18)	Ti: 0.44 (0.03), 1.82 (0.22)	Mt: 0.26 (0.03), 1.38 (0.2)	Ta: 0.65 (0.09), 3.1 (0.39)	TL: 2.72 / 2.45 (0.15)
IV	Tr: 0.31, 1.19	Fe: 0.9 (0.05), 3.44 (0.4)	Pa: 0.49 (0.03), 1.81 (0.28)	Ti: 0.59 (0.06), 2.18 (0.37)	Mt: 0.28 (0.04), 1.31 (0.11)	Ta: 0.86 (0.09), 3.09 (0.2)	TL: 3.46 / 3.11 (0.13)
Sylocellus lydekkeri, sp. nov. females							
Body	Length (2): 3.57 (0.28)	W-ozophore (2): 1.61 (0.06)	W-widest (2): 1.745 (0.11)	L/W ratio (2): 2.05 (0.03)			
Chelicer	I (2): 0.67 (0.01), 1.69 (0.26)	I (1): 1.06, 2.93	II (2): 1.29 (0.13), 6.03 (0.21)	III (2): 0.32 (0.02), 5.6 (0.2)			
Palp	Tr (1): 0.26, 1.86	II (2): 0.65 (0.11), 4.78 (0.58)	III (2): 0.37 (0.01), 2.98 (0.42)	IV (2): 0.43 (0.04), 4.25 (0.32)	Ta (2): 0.38 (0.02), 3.55 (0.02)	TL: 2.17 / 1.75	
Legs							
I	Tr (1): 0.36, 1.33	Fe (2): 0.96 (0.09), 3.67 (0.15)	Pa (2):0.5 (0.03), 1.96 (0.3)	Ti (2): 0.6 (0.02), 2.56 (0.03)	Mt (2): 0.28 (0.02), 1.28 (0.09)	Ta (2): 0.83 (0.07), 3.17 (0.1)	TL: 3.63 / 3.1
II	Tr: 0.26, 1.13	Fe: 0.75 (0.02), 3.05 (0.41)	Pa: 0.45 (0.01), 1.7 (0.02)	Ti: 0.47 (0), 1.94 (0.12)	Mt: 0.28 (0.01), 1.44 (0.18)	Ta: 0.7 (0.03), 3.34 (0.23)	TL: 2.91 / 2.64
III	Tr: 0.31, 1.19	Fe: 0.7 (0.05), 2.71 (0.01)	Pa: 0.43 (0.02), 1.65 (0.18)	Ti: 0.45 (0), 1.81 (0.15)	Mt: 0.27 (0), 1.52 (0.19)	Ta: 0.65 (0.04), 3.24 (0.21)	TL: 2.85 / 2.47
IV	Tr: 0.38, 1.52	Fe: 0.92 (0.03), 3.61 (0.07)	Pa: 0.5 (0.02), 1.79 (0.08)	Ti: 0.6 (0.02), 2.24 (0.11)	Mt: 0.29 (0.04), 1.34 (0.15)	Ta: 0.84 (0.07), 3.76 (0.39)	TL: 3.7 / 3.09
S. sp. females							
Body	Length (2): 2.74 (0.06)	W-ozophore (2): 1.29 (0.05)	W-widest (2): 1.35 (0.01)	L/W ratio (2): 2.03 (0.05)			
Chelicer	I (2): 0.45 (0.02), 1.41 (0.11)	I (0): –	II (2): 0.97 (0.08), 5.71 (0.47)	III (2): 0.28 (0.01), 5.5 (0.2)			
Palp	Tr (2): 0.25 (0.01), 1.96 (0.08)	II (2): 0.45 (0.03), 3.71 (0.25)	III (2): 0.29 (0.01), 2.72 (0.35)	IV (2): 0.3 (0), 3.54 (0.42)	Ta (2): 0.3 (0), 3.17 (0.33)	TL: 1.58 (0.05)	
Legs							
I	Tr (2): 0.26 (0.04), 1.24 (0.05)	Fe (2): 0.67 (0.1), 3.19 (0.48)	Pa (2): 0.34 (0.03), 1.52 (0)	Ti (2): 0.38 (0.04), 1.95 (0.1)	Mt (2): 0.2 (0.01), 1.03 (0.16)	Ta (2): 0.65 (0.13), 2.58 (0.11)	TL: 2.49 (0.33)
II	Tr: 0.2 (0.06), 1.11 (0.09)	Fe: 0.54 (0.09), 2.61 (0.31)	Pa: 0.33 (0.04), 1.61 (0.04)	Ti: 0.3 (0.03), 1.55 (0.01)	Mt: 0.19 (0), 1.23 (0.08)	Ta: 0.5 (0.06), 2.86 (0.15)	TL: 2.05 (0.28)
III	Tr: 0.19 (0.01), 1 (0.11)	Fe: 0.49 (0.01), 2.56 (0.32)	Pa: 0.28 (0), 1.52 (0.25)	Ti: 0.29 (0.03), 1.5 (0)	Mt: 0.16 (0.01), 1.12 (0.23)	Ta: 0.47 (0.01), 2.84 (0.46)	TL: 1.86 (0.03)
IV	Tr: 0.24 (0.1), 1.32 (0.41)	Fe: 0.62 (0.07), 2.93 (0.05)	Pa: 0.36 (0.02), 1.64 (0.06)	Ti: 0.37 (0.04), 1.74 (0.43)	Mt: 0.19 (0.01), 1.12 (0.01)	Ta: 0.54 (0.11), 2.67 (0.28)	TL: 2.31 (0.27)

Table 5. Length and length/width ratios for appendages

For the *Stylocellus novaguinea*, sp. nov. holotype, given as 'length in mm, length/width ratio'. Abbreviations as for Table 3.

Appendage	Segments						
Chelicer	I: 0.60, 1.42	II: 1.30, 5.64	III: 0.37, 5.29				
Palp	Tr: 0.13, 0.83	II: 0.56, 3.75	III: 0.41, 3.03	IV: 0.44, 3.75	Ta: 0.37, 3.17	TL: 2.07	
Legs							
I	Tr 0.32, 0.96	Fe 1.01, 2.66	Pa 0.58, 1.80	Ti 0.65, 2.18	Mt 0.28, 1.04	Ta 0.96, 3.02	TL: 3.81
II	0.31, 1.12	0.88, 2.36	0.50, 1.49	0.54, 1.62	0.30, 1.17	0.81, 3.18	TL: 3.33
III	0.30, 1.04	0.80, 2.40	0.48, 1.50	0.51, 1.39	0.26, 1.13	0.80, 2.90	TL: 3.16
IV	0.36, 1.38	0.76, 2.37	0.48, 1.66	0.48, 1.53	0.20, 0.98	0.73, 2.64	TL: 3.01

Chelicerae

Conspicuous dorsal crest that articulates with the front of the carapace; not of the protruding type; with two prominent ventral processes (anterior one shown in Fig. 12*B*); proximal article heavily ornamented, continuing on second article only through the joint; second article nearly completely smooth (Figs 12*B*, 13*E*). Pincer with ~11 evenly sized and spaced teeth on each article (Fig. 13*E*). Third article 28% of second article length (Table 5).

Palps (Fig. 13*F*)

Without processes on trochanter or other segments; with even tuberculate–microtuberculate ornamentation from trochanter to segment III; segment IV and tarsus smooth. Article measurements and length/width ratios in Table 5.

Legs (Figs 12*A*, 13*A–D*)

Ornamented with setae mostly on tarsi; granulation weakening towards ends of tarsi I and II but not disappearing, especially dorsally; median dorsal groove on tarsus I and II; ventral tarsus I with concentration of extremely short, fine setae for almost the length of the entire tarsus, but not forming a distinct solea; tarsus IV with dorsal adenostyle, fringed on the tip, located medially; legs without processes or depressions; claws smooth, without lateral projections, largest on leg IV. Leg article lengths and length/width ratios in Table 5.

Spermatopositor not studied.

Female

Unknown.

Distribution

Known only from Gunung (Mountain) Meja, at 200 m, on the eastern coast of the Vogelkop ('Bird's Head') area of New Guinea (Indonesia, Irian Jaya).

Remarks

Stylocellus novaguinea, sp. nov. is larger and wider than *S. lydekkeri*, sp. nov. (above) but is still one of the smaller species named in the family. The body is distinctly longer than *S. ramblae*, *S. kinabalu*, *S. pangrango* and *S. tambusisi*, slightly longer than *S. mulu* and distinctly smaller than the remaining described species. It is easily distinguished from *S. mulu* by the body outline, which is broader in *S. novaguinea*; the dorsum sculpturing, which is heavily granulated in *S. novaguinea* but smooth and shining in *S. mulu*, and the proportions of the second cheliceral segment, which are much narrower in *S. mulu*.

Etymology

As a member of the very first-known collection of Cyphophthalmi from New Guinea, we have named this species for the island. The species name stands as a noun in apposition to the genus, translated in its traditional fashion – with 'Guinea' treated as a non-Latinised place name and 'novum' declined to modify a feminine noun in the nominative case.

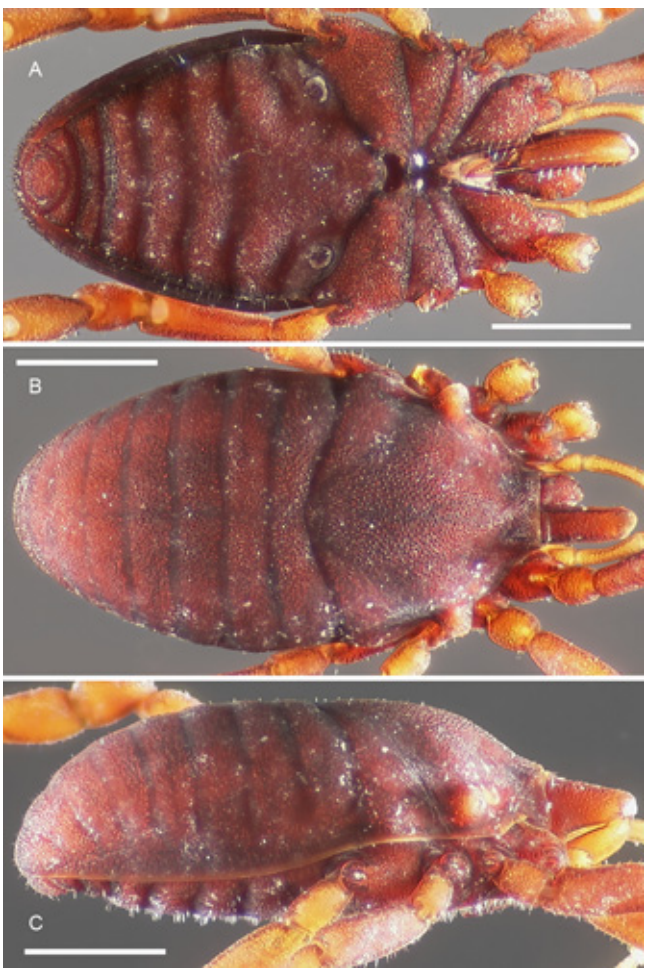

Fig. 11. *Stylocellus novaguinea*, sp. nov. male holotype: *A,* ventral; *B,* dorsal; *C,* lateral views; scale bar = 1 mm.

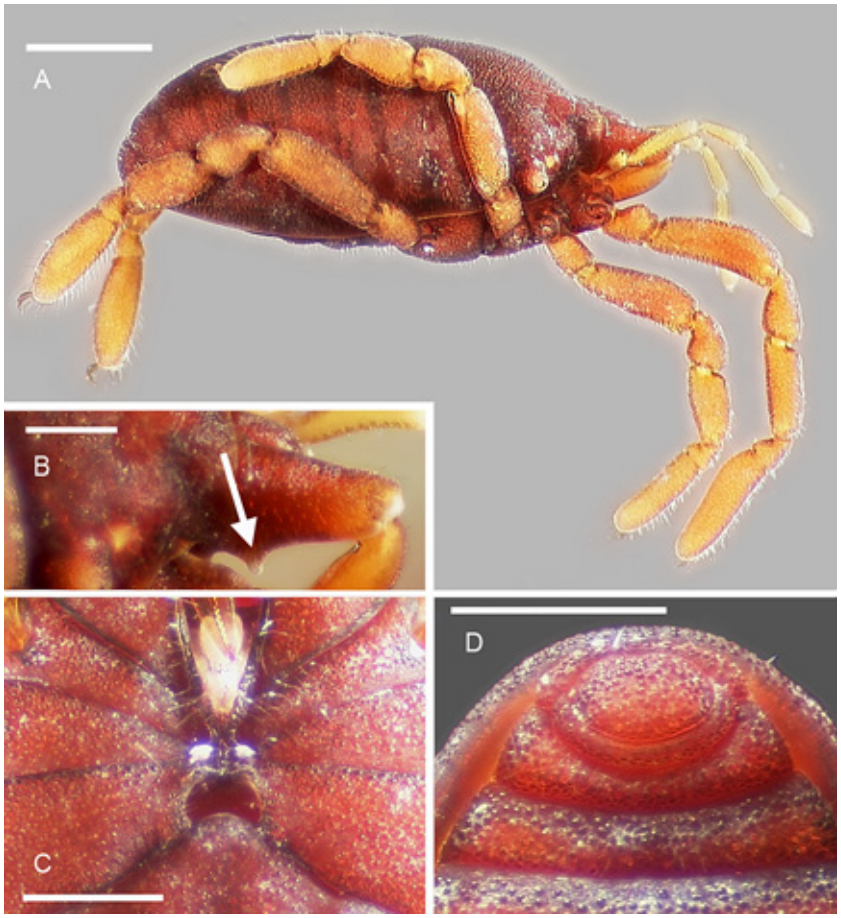

Fig. 12. *Stylocellus novaguinea*, sp. nov. male holotype: *A,* lateral view with legs; scale bar = 1 mm; *B,* chelicer article I, showing anterior ventral process (arrow); *C,* gonostome; *D,* anal region; scale bars = 0.5 mm.

Stylocellus sp.

(Figs 10*B*, *D*, 14; Table 4)

Remarks

The collection of *Stylocellus novaguinea*, sp. nov. also included three females and one juvenile very similar in overall appearance to *S. lydekkeri*, sp. nov. One of the three females appears illustrated in Fig. 14 and clearly differs in overall shape from the male of *S. novaguinea*, sp. nov. The females have nearly identical coloration, sculpturing and body proportions (L/W ratio = 2.03, *n* = 2) to *S. lydekkeri*, sp. nov. females, but they are, on average, about 23% smaller. The ovipositor is similar to that of *S. lydekkeri*, sp. nov. (Fig. 10*B*, *D*), but the shaft is composed of 28 segments instead of 31, and the terminal lobes are not as slender (although only a single ovipositor has been examined from each locality). In addition, length/width proportions of appendage articles for the unidentified females are smaller than *S. lydekkeri*, sp. nov. and are more similar to those of *S. novaguinea*, sp. nov. (Fig. 14); this is best seen in a lateral view of the chelicera (Fig. 14*C*). The chelicerae are also slightly constricted laterally at the base (Fig, 14*B*), unlike those of *S. lydekkeri*, sp. nov., which are more parallel-sided (Fig. 2*B*). Shear (1993) noted size and leg length/width ratios as good characters for distinguishing stylocellid species, but with no associated male of this species in this collection, we only report the apparent presence of a third species in this area and leave it undescribed for now.

Molecular phylogenetic analysis

The consensus tree obtained from an analysis of both genes under the optimal parameter set showed monophyly of Stylocellidae, including the New Guinean species, and it contained four clades of further interest within the family: the genus *Fangensis* (shown to be monophyletic), all specimens from Borneo + *Miopsalis*, *Stylocellus lydekkeri*, sp. nov. + *Stylocellus* sp. MCZ DNA101509 and a fourth clade containing *S. novaguinea*, sp. nov. and the two specimens from Sulawesi. Consensus trees obtained under the optimal parameter set for each gene and their combination are shown in Fig. 15*A–C*; monophyly of Stylocellidae was also found in consensus trees for both loci separately. The preferred parameter set for our phylogenetic analysis of the combined 18S and 28S rRNA dataset, as determined by the ILD analysis, was the one with a gap cost of 4 and a base-transformation cost of 1 (Table 6). Under this parameter set, 20 shortest trees were found each for

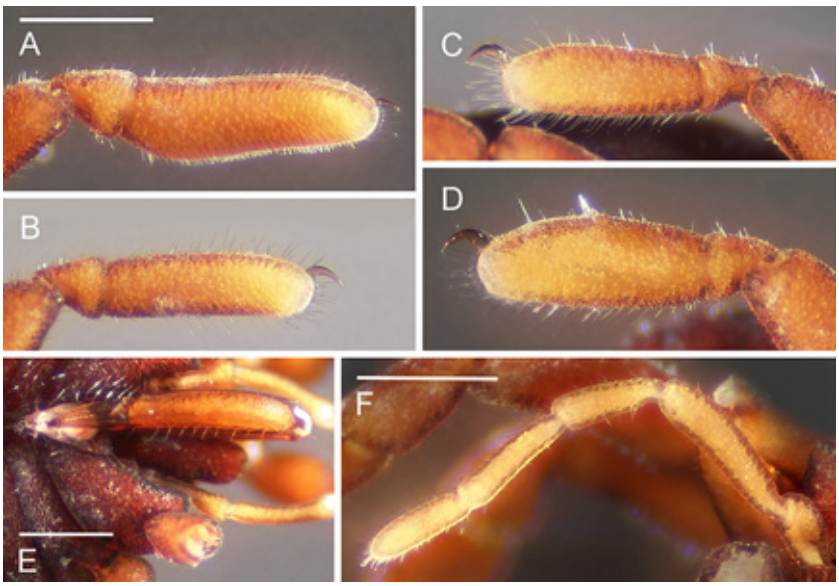

Fig. 13. *Stylocellus novaguinea*, sp. nov. male holotype: *A–D*, tarsi I–IV; *E,* chelicer articles II and III; *F,* palp; scale bars = 0.5 mm.

the 18S, 28S and combined datasets and they had 244, 1829 and 2077 weighted steps, respectively. Although the 20 trees are the result of limiting the maximum number of trees to search (–holdmaxtrees 20), the use of the command –fitchtrees guarantees finding a set of most diverse trees, avoiding storing only 20 neighbour trees. The use of tree fusing should also contribute towards reporting the most diverse set among the 20 chosen trees.

Monophyly of Stylocellidae and the two clades containing the New Guinea species (*S. lydekkeri* + *Stylocellus* sp. MCZ DNA101509 and *S. novaguinea* + Sulawesi species) received jackknife support of 86, 98 and 93, respectively, in the combined analysis (Fig. 15, upper numbers), but monophyly of *Fangensis* and the Borneo + *Miopsalis* clade did not receive jackknife support greater than 50%. Bootstrap analysis of the combined dataset did support the clades of interest (Fig. 15*C*, lower numbers), but this analysis was done using an implied alignment generated using the consensus topology and so was predisposed to support the same topology. Analysis of the combined dataset in MrBayes, also done on the implied alignment generated by POY, found 94% posterior probability for Stylocellidae and 100% posterior probability for *Fangensis*, the Borneo + *Miopsalis* clade, the clade containing non-Bornean *Stylocellus*, *S. novaguinea* + Sulawesi and *S. lydekkeri* + *Stylocellus* sp. MCZ DNA101509.

Under the optimal parameter set, the clades *Fangensis*, Borneo + *Miopsalis* and *S. novaguinea* + Sulawesi were found among the shortest trees in the analyses of both the separate loci and the combined datasets (Fig. 16*A*), but only *S. novaguinea* + Sulawesi was found in the consensus tree of a single locus (28S rRNA) (Fig. 15*B*). *Stylocellus lydekkeri* consistently appeared as sister to *Stylocellus* sp. MCZ DNA101509 from New Guinea and closely related to *Stylocellus* sp. MCZ DNA101755 from Java, but the different loci disagreed as to whether these three species were also closely related to *Stylocellus* sp. MCZ

Fig. 14. *Stylocellus* sp. MCZ DNA101509 female: *A,* ventral; *B,* dorsal; *C,* lateral views; scale bar = 1 mm.

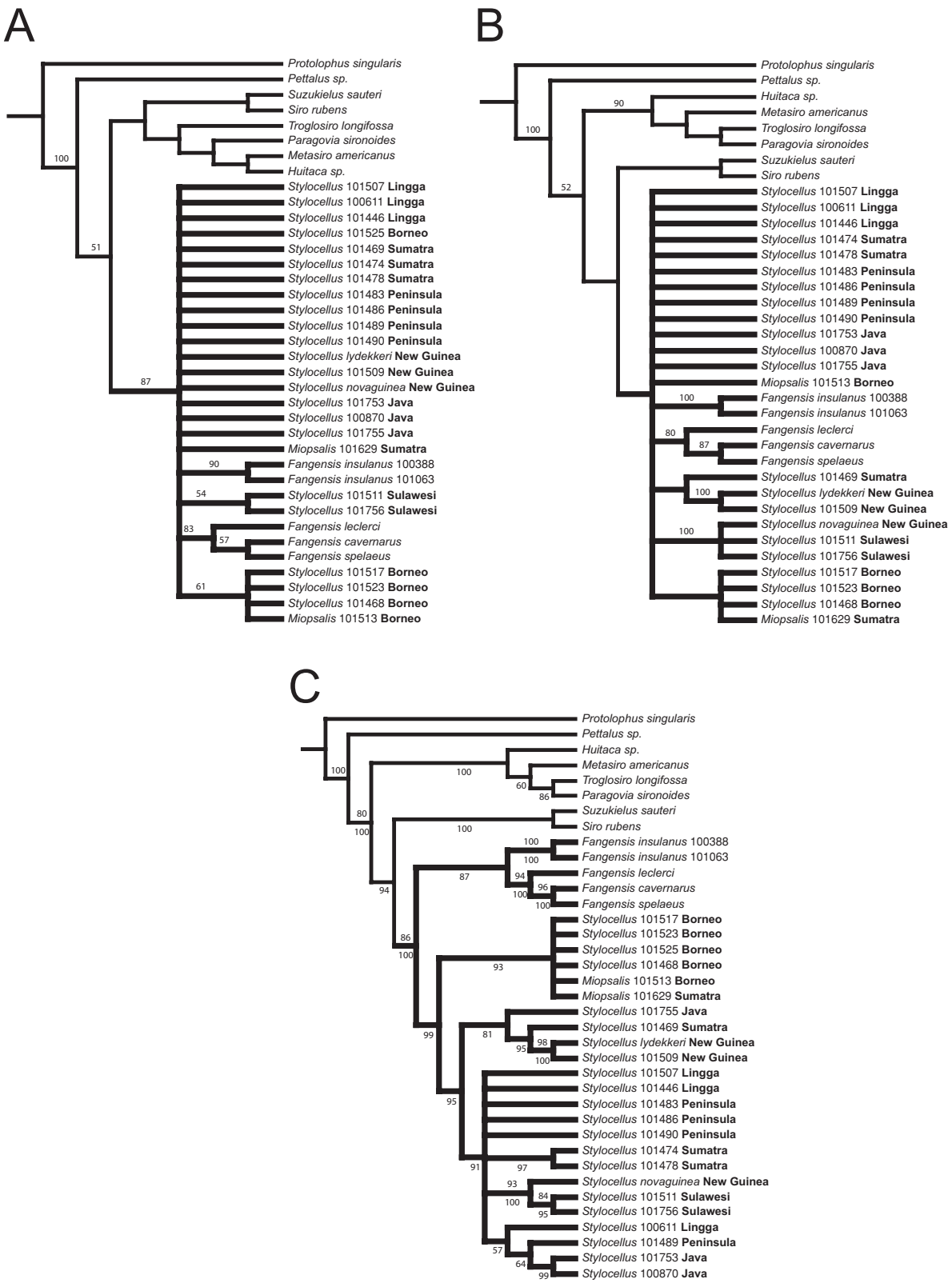

Fig. 15. *A*, Strict consensus of 20 shortest trees at 244 weighted steps for the 18S rRNA dataset analysis using parameter set 411; *B*, strict consensus of 20 shortest trees at 1829 weighted steps for the 28S rRNA dataset analysis using parameter set 411; *C*, strict consensus of 20 shortest trees at 2077 weighted steps for the analysis of the combined 18S and 28S rRNA datasets under parameter set 411; numbers above branches are jackknife support values; numbers below branches are bootstrap support values. Branches in bold indicate the family Stylocellidae.

DNA101469 from Sumatra (Fig. 16*A*). Although receiving low jackknife support, the Borneo + *Miopsalis* clade was not particularly unstable, appearing in the consensus trees of the combined data under eight of the ten parameter sets and appearing in some of the shortest trees from separate partition analyses for seven of the parameter sets (Fig. 16*B*).

Discussion

The two species described here are clear stylocellids owing to the presence of all the diagnostic characters of the family, including the C-shaped spiracles, the stylocellid anal and prosomal ventral regions, and chelicerae with a single type of dentition and an ornamented second article (Giribet 2002). Eyes located anteriorly to the ozophores and with a lens are typical of *Stylocellus* (and *Leptopsalis*) and they differ from the pettalid eyes, which are incorporated into the base of the ozophores (Sharma and Giribet 2006; Boyer and Giribet 2007). This fundamental difference in the eyes alone summarises the puzzle of the New Guinean species, since most of New Guinea has formed part of the Australian continent, where members of the family Pettalidae are found (Giribet 2000, 2003*a*). The fact that New Guinean Cyphophthalmi are members of Stylocellidae and not Pettalidae is remarkable in itself.

Our molecular phylogeny suggests several important relationships within Stylocellidae. It confirms proper placement of the New Guinean Cyphophthalmi within the family and it confirms the presence of three distinct species in the two collections. It is also the most comprehensive analysis to date for the family and it is the first to show a distinct clade of Bornean *Stylocellus* and Bornean and Sumatran *Miopsalis* (the Borneo + *Miopsalis* clade). The low support but high stability of this clade likely indicates a small number of unequivocal state changes distinguishing it, hence the chance that its support could strengthen by including more loci in future molecular analyses (Giribet 2003*b*). Morphologically, the clade is also distinguished by the following character combination in males: presence of anal glands opening on opisthosomal tergite IX and a smooth longitudinal strip on the anal plate but the absence of Rambla's organ (a distinct secretory area on the retrolateral portion of tarsus IV in males (Rambla 1994; Schwendinger and Giribet 2005)). (*Stylocellus* sp. MCZ DNA101525, a member of this clade, is only known from females.) Anal glands and Rambla's organ are found in males of *Fangensis* and the modified anal plate is found in *F. insulanus* Schwendinger & Giribet, 2005 and *F. leclerci* Rambla, 1994 (Table 7). But anal glands are also known from several other species of stylocellids not considered in this study, including the nominal species of the family, *Stylocellus sumatranus* Westwood, 1874, and at least one stylocellid from the Thai–Malay Peninsula, *Stylocellus globosus* Schwendinger & Giribet, 2004 (Schwendinger *et al*. 2004). In addition, anal glands are found in Sironidae (see Juberthie 1967; de Bivort and Giribet 2004), which was one reason why Rambla (1994) originally considered *Fangensis* to be a member of that family. Anal glands are now also known from Pettalidae, although their opening differs in some members of the three

Table 6. Tree lengths and calculated ILD (incongruence length differences)

For two individual ribosomal loci (18S and 28S rRNA), individually and combined (rib), for ten parameter sets, ranging from equal weights (111) to a ratio of indel opening to transversion to tansitions to indel extension of 3:2:2:1 (3221); the optimal parameter set is highlighted in boldface; whenever three integers are indicated, indel opening and indel extension were not differentiated.

Parameter set	18S	28S	rib	ILD-rib
111	225	1437	1668	0.00360
121	305	2090	2403	0.00333
141	461	3218	3695	0.00433
211	232	1608	1844	0.00217
221	318	2375	2699	0.00222
241	485	3798	4305	0.00511
411	**244**	**1829**	**2077**	**0.00193**
421	341	2783	3138	0.00446
441	528	4612	5162	0.00426
3221	457	2932	3404	0.00441

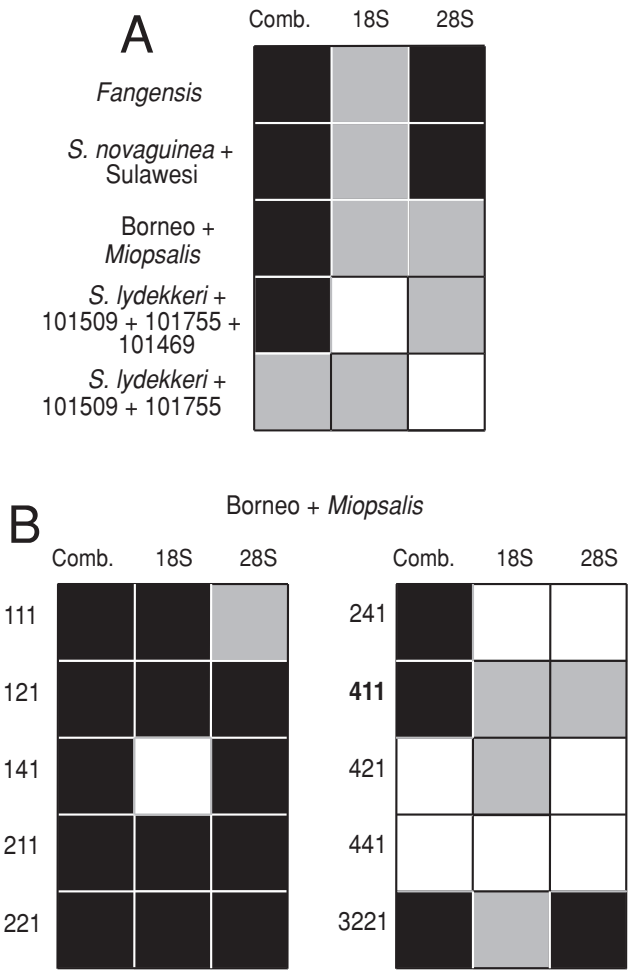

Fig. 16. Navajo rug summarising appearance of monophyly *A,* for several clades of interest under the parameter set 411 and *B*, the Borneo + *Miopsalis* clade under all parameter sets. Results are shown for each partition (18S and 28S), combined ('comb.') and separately. Black indicates that monophyly was found in the consensus tree, grey that it was found in some of the shortest trees, and white that it was never found. Specimen numbers are MCZ DNA accession numbers (e.g. '101509' = '*Stylocellus* sp. MCZ DNA101509').

families, which has led to the raising of doubts about their homology by some authors (Schwendinger *et al*. 2004; but see Sharma and Giribet 2005 for a broader interpretation of anal glands).

Still, our phylogeny suggests that the presence of anal glands is a plesiomorphic character in Stylocellidae, and considered with the geographic proximity of *Fangensis* and the Borneo + *Miopsalis* clade, we postulate that stylocellid diversification proceeded from the North over ancient Sundaland. Evidence of this process may be found in the distribution of various other plesiomorphic characters, such as the extensive sculpturing on the distal segment of the chelicer, a character found in *Fangensis* but also some *Stylocellus* from the Thai–Malay Peninsula, Sumatra, Borneo and the Lingga-Riau Archipelago, including four species included in our phylogeny here (Table 7). Even Rambla's organ seems to have a homologous counterpart among in at least one species of *Stylocellus*, again from Borneo, *S. silhavyi* Rambla, 1991; its presence across the whole family is pending a complete SEM image database, because the character is difficult to observe with a light microscope.

We do not yet understand the phylogenetic importance of the second ventral process on the basal segment of the chelicer or the sternum (characters *10* and *28*, respectively, in de Bivort and Giribet 2004) in Stylocellidae. The second ventral cheliceral process was hypothesised to be an autapomorphy that might indicate a derived clade of *Stylocellus* and require an expansion of the genus *Leptopsalis* (currently containing only one species, although its status is unresolved) (Giribet 2002), but it appears to exist in a wide variety of species not closely related (such as *Fangensis* and the New Guinean species described here). Moreover, it is quite variable in size and shape and in some species is difficult to see without removing the chelicer, so its prevalence across the family is not fully known. As for the presence of a sternum in the prosomal region (see Hansen and Sørensen 1904), it also appears to be widespread in the family. However, it is best seen in scanning electron micrographs of very clean specimens, so its analysis is also still pending for most of our undescribed material. Thus, entries for the presence of the second ventral cheliceral process and the sternum in Table 7 should be considered tentative, but we notice already that those species with small processes are also usually lacking a sternum.

Although the second cheliceral process does not alone appear to distinguish a major split in *Stylocellus*, the generic name *Leptopsalis* may still be needed for stylocellids that lack anal modifications and other putative plesiomorphic characters. *Stylocellus sumatranus* Westwood, 1874, the type species for its genus, also has an anal pore and smooth strip on the anal plate

Table 7. List of specimens and their states for morphological characters of interest

Characters are: anal gland pore ('Pore'), smooth strip on the anal plate ('Strip'), extensive sculpturing on the second cheliceral process ('Sculpt.'), second ventral process on the chelicer ('Process'), sternum present, miniaturised ('Mini.'), and eyes reduced or missing.

Species	Region	Pore	Strip	Sculpt.	Process	Sternum	Mini.	Eyes reduced
Fangensis cavernarus	Peninsula	Yes	No	Yes	Yes	Yes	No	Yes
Fangensis insulanus	Peninsula	Yes	Yes	Yes	Yes	Yes	No	Yes
Fangensis leclerci	Peninsula	Yes	Yes	Yes	Yes	Yes	No	Yes
Fangensis spelaeus	Peninsula	Yes	No	Yes	Yes	Yes	No	Yes
Stylocellus sp. MCZ DNA101483	Peninsula	No	No	No	Yes	No	No	No
Stylocellus sp. MCZ DNA101486[A]	Peninsula	?	?	No	Small	No	No	No
Stylocellus sp. MCZ DNA101489	Peninsula	No	No	No	Yes	Yes	No	No
Stylocellus sp. MCZ DNA101490	Peninsula	No	No	Yes	Small	No	No	No
Miopsalis sp. MCZ DNA101513	Borneo	Yes	Yes	No	Small	No	Yes	Yes
Stylocellus sp. MCZ DNA101468	Borneo	Yes	Yes	Yes	Yes	Yes	No	No
Stylocellus sp. MCZ DNA101517	Borneo	Yes	Yes	Yes	Yes	Yes	No	No
Stylocellus sp. MCZ DNA101523	Borneo	Yes	Yes	No	Yes	Yes	No	No
Stylocellus sp. MCZ DNA101525[A]	Borneo	?	?	No	Yes	Yes	No	No
Stylocellus sp. MCZ DNA100611	Lingga	No	No	No	Yes	Yes	No	No
Stylocellus sp. MCZ DNA101446	Lingga	No	No	No	Yes	No	No	No
Stylocellus sp. MCZ DNA101507	Lingga	No	No	Yes	?	No	Yes	Yes
Miopsalis sp. MCZ DNA101629	Sumatra	Yes	Yes	No	Yes	Yes	Yes	Yes
Stylocellus sp. MCZ DNA101469	Sumatra	No	No	No	Small	No	No	No
Stylocellus sp. MCZ DNA101474	Sumatra	No	No	No	Yes	Yes	No	No
Stylocellus sp. MCZ DNA101478	Sumatra	No	No	No	Yes	Yes	No	No
Stylocellus sp. MCZ DNA100870[B]	Java	?	?	?	?	?	No	No
Stylocellus sp. MCZ DNA101753[A]	Java	?	?	No	Small	No	No	No
Stylocellus sp. MCZ DNA101755	Java	No	No	No	Yes	Yes	No	No
Stylocellus sp. MCZ DNA101511[B]	Sulawesi	?	?	?	?	?	No	No
Stylocellus sp. MCZ DNA101756	Sulawesi	No	No	No	Yes	No	No	No
Stylocellus lydekkeri, sp. nov.	New Guinea	No	No	No	Small	No	No	No
Stylocellus novaguinea, sp. nov.	New Guinea	No	No	No	Yes	Yes	No	No
Stylocellus sp. MCZ DNA101509[A]	New Guinea	?	?	No	Small	No	No	No

[A]Known only from females.
[B]Known only from juveniles.

(Schwendinger *et al*. 2004) and thus may be closely related to the Borneo + *Miopsalis* clade. If so, the genus *Leptopsalis*, retired when *L. beccarii* Thorell, 1882 was synonomised with *Stylocellus sumatranus* by Thorell (1890/91) (since resurrected as a valid species by Giribet [2002]), may actually contain the bulk of stylocellid species.

The existence of a clade containing *Miopsalis* and the Bornean *Stylocellus* leads us to postulate that *Miopsalis* comprises miniaturised descendants of early stylocellids. Moreover, the loss of eyes in Stylocellidae appears to be a common phenomenon associated with cave distributions (as in *Fangensis*, *S. globosus* and an undescribed Bornean species not included in our analysis) and small size. The exact delimination of *Miopsalis* is unclear anyway, as we have not been able to examine the type material of its only named species, *Miopsalis pulicaria* Thorell, 1890, supposedly deposited at the Museo Civico di Storia Naturale 'Giacomo Doria', Genoa (Italy). Its description highlights few distinguishing features of their morphology other than a lack of eyes and extremely small size; the description, in fact, may be of a female (Thorell 1890/91; Giribet 2002). We have provisionally determined extremely small stylocellids with reduced eyes as members of this genus, but only '*Miopsalis* sp.' MCZ DNA101513 from Borneo seems to completely lack eyes. There also exist species, such as *Stylocellus* sp. MCZ DNA101507 from the Lingga-Riau Archipelago, which are small and have reduced eyes but are not as small as those we originally determined as *Miopsalis*. It appears highly likely that the various *Miopsalis*-like species will not form a clade and eventually be placed within *Stylocellus* or *Leptopsalis*.

Our phylogenetic analysis places the New Guinean species into widely separated clades, with the females collected alongside *Stylocellus novaguinea*, sp. nov. being more closely related to *S. lydekkeri*, sp. nov. The presence of two distinct New Guinean clades suggests at least two dispersal events, further defying a simple explanation for the presence of stylocellids on New Guinea. The presence of Cyphophthalmi on New Guinea could be explained by terrestrial dispersal were they closely related to Australian members of the temperate Gondwanan family Pettalidae. However, they are not, and reconstructions of sea level changes since the mid Oligocene (30 mya) do not present a continuous land bridge at any one time between Eurasia and New Guinea (Hall 1998), even during the glaciation events of the past 250 000 years (Voris 2000). The shallow sea in Wallacea (the area between Wallace's and Lydekker's Lines) over the past 20 million years has at best only provided island-hopping routes and if there had been a continuous or sequential land bridge available, we would expect Eurasian birds and mammals to use it also, which they apparently have not done. A very early land bridge – before birds and mammals were around to use it – is not possible simply because New Guinea had not yet approached Sundaland at that time.

Hypotheses of oceanic dispersal from the Greater Sunda Islands present problems too. Such a route to New Guinea makes it difficult to explain why these or closely related species are not found in the Philippine archipelago or have become widespread throughout Indonesia and South-east Asia. It is worth mentioning here that P. Schwendinger recently reported the finding of alleged cyphophthalmid remains near Banaue (North Luzon, Philippines) in the 1980s (P. Schwendinger, pers. comm.), but we have not been able to locate this material. The Philippine islands have been postulated as part of a commonly used island-hopping route to New Guinea in other organisms (Moss and Wilson 1998) and they have clearly been a destination for rafting and windblown arthropods; thus the absence of any confirmed stylocellid or even cyphophthalmid records from there (except Palawan Island, discussed above), the islands of Melanesia, or eastern New Guinea highlights the oddity of their presence in western New Guinea.

The area of New Guinea where these species were collected is known as the Vogelkop or 'Bird's Head,' and certain disjunct distributions, especially among plants and birds, suggest it has a peculiar relationship to both South-east Asia and the remainder of New Guinea (Heads 2003). For example, the dipterocard *Hopea inexpecta* and the genus *Myrmephytum* (Rubiaceae) cross Lydekker's Line but only to the Vogelkop, a distribution similar to that of *Stylocellus*; also, the fern *Christensenia aesculifolia* is distributed from South-east Asia to the Solomons but is not found in New Guinea, with the sole exception of the Vogelkop (Baker *et al*. 1998). However, such distributions among good dispersers could indicate unique patterns of recent ocean or air currents around the Vogelkop or ecological factors affecting colonisation; other than the Stylocellidae discussed here, we know of no other examples of extremely poor dispersers from Eurasia in the Vogelkop or the rest of New Guinea.

New Guinea has other arachnids that could also be considered poor dispersers, such as non-cyphophthalmid Opiliones and mygalomorph spiders, but these cases are not as difficult to explain as stylocellids. The nearly two dozen Opiliones described from New Guinea (probably only a trivial fraction of the island's true opilionid fauna) are, inasmuch as their closest relatives can be reasonably hypothesised at this point, allied with species found in the Philippines, the Moluccas and/or the islands of Melanesia and the Western Pacific, a pattern that holds even for those from the Vogelkop (*Ibalonius simoni* Roewer 1915 from Dorey, *Ibalonianus impudens* (Loman 1906) from Manikion-Gebiet and Monokwari and *Dibunus pseudobiantes* Loman 1906 also from Manikion-Gebiet). The mygalomorph spiders in New Guinea are represented mostly by the suborder's oddly vagile, invasive species (York 1982), or, in the case of the pan-tropical, extremely cryptic Barychelidae, apparent local endemics in eastern New Guinea that have congeners in Melanesia (Raven 1994). In general, even if the ancestors of these opilionid and mygalomorph species could be identified as having a Eurasian origin, they can already be characterised as being more vagile than Stylocellidae.

Given their old age, it is likely that Cyphophthalmi were present on the terranes that rifted from temperate Gondwana and formed South-east Asia, and until those terranes completely migrated to Eurasia, those comprising present-day New Guinea and the Thai–Malay Peninsula were apparently in close proximity (Metcalfe 1998; Archbold *et al*. 1982). However, the subsequent submersion of New Guinea (including the Vogelkop) from 120 mya (Metcalfe 1998) through the Mesozoic (Pieters 1982) hampers a pre-rifting origin hypothesis for New Guinean stylocellids. Moreover, the results of our phylogenic analysis weaken such a hypothesis, since it finds all three species as some of the more derived members of the family. Most notable are the Sulawesi species (sisters to *S. novaguinea*, sp. nov.), which are

from the northern peninsula of the island. That area originated as a volcanic arc that accreted on to western Sulawesi around 50–40 mya (Moss and Wilson 1998) and would have likely been populated by species derived from western Sulawesi, itself composed mostly of volcanic arc populated by species from Borneo. Thus, the highly derived placement of the Sulawesi species in our phylogeny agrees with the history of northern Sulawesi, but it also necessitates a recent migration of *S. novaguinea*, sp. nov. from there to New Guinea.

Unless a radical departure from current geologic models is proposed, the only explanation for New Guinean stylocellids is transoceanic dispersal, the only known case of such in Cyphophthalmi. With more a comprehensive phylogeny of Stylocellidae, a more refined hypothesis for when and where the New Guinea Stylocellidae originated should emerge. Interest in the biogeography of South-east Asia, the Indomalaysian Archipelago and New Guinea has waned little over the past 150 years, for it has persisted in presenting interesting biogeographic problems. The faunal break first observed by Wallace was difficult to explain without knowledge of plate tectonics (Wallace, 1890; Mayr 1953), but with this theory, the lack of a break in certain groups is equally puzzling if one is not inclined to invoke oceanic dispersal (Cheesman 1951).

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