



# Phylogenetic evidence for an independent origin of extreme sexual size dimorphism in a genus of araneid spiders (Araneae: Araneidae)

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## ABSTRACT

*Cyphalonotus* is a poorly studied Old World araneid spider genus of which the phylogenetic proximity remains unknown due to the paucity of morphological and molecular data. We test the phylogenetic placement and the taxonomic composition of *Cyphalonotus* and place the male and female size variation of *Cyphalonotus* and related genera in an evolutionary context. Our collection and field observations from Taiwan and China facilitate description of a new and a known species, and original sequence data enable species delimitation and phylogenetic analyses. The phylogenetic results reject all four classification hypotheses from the literature and instead recover a well-supported clade comprising *Cyphalonotus* + *Polys*. We review the male and female size variation in *Cyphalonotus*, *Polys* and related genera. These data reveal that all known species of *Polys* are extremely sexually size dimorphic (eSSD = females over twice the size of males) reaching values exceeding 10-fold differences, whereas *Cyphalonotus* and other genera in phylogenetic proximity are relatively sexually monomorphic (SSD < 2.0). This confirms an independent origin of eSSD in *Polys*, one of multiple convergent evolutionary outcomes in orbweb spiders.

**Keywords:** *Cyphalonotus*, eSSD, extreme phenotype, female gigantism, orbweb spider, male dwarfism, *Polys*, sexual size monomorphism, size evolution.

## Introduction

With seven known species distributed in tropical and subtropical Africa and Asia (World Spider Catalog, ver. 22.0, Natural History Museum, Bern, Switzerland, see <http://wsc.nmbe.ch>), the spider genus *Cyphalonotus* Simon, 1895 has been poorly studied due to the rarity and cryptic behaviour (Dzulhelmi *et al.* 2015). Although authors agree that *Cyphalonotus* is an araneid, the more precise phylogenetic placement is unresolved due to the paucity of morphological data and the lack of molecular data (Simon 1895; Archer 1951, 1965; Smith 2005).

Based on a female specimen from Africa, *Polys larvatus* Simon, 1881 represents the first description of any *Cyphalonotus* species. The genus itself was treated subsequently with *C. larvatus* as the type species, when Simon (1895) established the diagnostic differences between *Polys* C. L. Koch, 1843 and *Cyphalonotus* in the eye position, the shape of the eye tubercle and the depressed metatarsus in the latter. Following these genus assignments, three African and four Asian *Cyphalonotus* species have been described to date. However, over half of these species are dubious, given a lack of subsequent reports on these since the original, often insufficient descriptions. Moreover, only one species, *C. larvatus*, has been described from both sexes, whereas the males of any other described species remain unknown.

More recent studies define *Cyphalonotus* as a genus that resembles *Polys*, but differs in eye arrangement, legs, genital details and size ratio between the sexes (Archer 1951, 1965; Smith 2005, 2006a). As pointed out above, these studies mostly fail to describe the male morphology in detail, with the exception of *C. larvatus* (see Archer 1951, 1965), and one unnamed species (see Smith 2005).

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**Table 1.** Phylogenetic hypotheses tested in the present study with their authors and taxa or species included.

Phylogenetic hypothesis	Author	Presumed relatives of <i>Cyphalonotus</i>
Poltyeae	Simon 1895	<i>Polty</i> , <i>Pycnacantha</i> , <i>Kaira</i> , <i>Homalopolty</i> (= <i>Dolichognatha</i> ; now in Tetragnathidae)
Cyphalonotini	Archer 1951	<i>Simonarachne</i> (= <i>Eriovixia</i> )
Dolophonini	Archer 1965	<i>Dolophones</i>
Proximity with <i>Araneus</i>	Smith 2005	<i>A. diadematus</i> , <i>A. marmoreus</i> , <i>A. angulatus</i>

The first objective of our study was to test the phylogenetic placement of *Cyphalonotus*. Based exclusively on morphological data, prior literature has put forth four mutually exclusive hypotheses about the phylogenetic proximity of *Cyphalonotus* (Table 1). To test the validity of these hypotheses, these are listed in accordance with authors as ‘Poltyeae’, ‘Cyphalonotini’, ‘Dolophonini’ and the ‘proximity with *Araneus* Clerck, 1757’. Based on female carapace and abdominal similarities, Simon (1895) proposed ‘Poltyeae’ to group *Cyphalonotus*, *Polty*, *Kaira* O. Pickard-Cambridge, 1889, *Pycnacantha* Blackwall, 1865 and *Homalopolty* Simon, 1895 (= *Dolichognatha* O. Pickard-Cambridge, 1869; now in Tetragnathidae Menge, 1866). Within the ‘Cyphalonotini’ hypothesis, Archer (1951) removed *Cyphalonotus* from Poltyeae, and instead grouped this with *Simonarachne* Archer, 1951 (= *Eriovixia* Archer, 1951; Araneidae). Archer (1951) based this grouping on observations on male palpal complexity and lesser sexual size dimorphism in *Cyphalonotus* compared with *Polty*. After having examined an additional *Cyphalonotus* species, Archer (1965) posed the ‘Dolophonini’ hypothesis as a grouping of *Cyphalonotus* and the Australasian *Dolophones* Walckenaer, 1837. Smith (2005) hypothesised a clade uniting *Cyphalonotus* with *Araneus*. This work used the cladistic araneid matrix of Scharff and Coddington (1997) with 82 morphological and a few web characters, and included three European species of *Araneus*: *A. diadematus* Clerck, 1757, *A. marmoreus* Clerck, 1757 and *A. angulatus* Clerck, 1757.

Scharff *et al.* (2020) recently generated a molecular phylogeny of Araneidae. Although this study did not include *Cyphalonotus*, molecular data for the other taxa relevant to the four hypotheses mentioned above were included. Therefore we added sequence data for *Cyphalonotus* to the matrix of Scharff *et al.* (2020) to test the phylogenetic position of *Cyphalonotus* within Araneidae and the validity of the four hypotheses (Table 1).

The second objective of our study was to place the male and female size variation of *Cyphalonotus* and related genera in an evolutionary context. Female-biased sexual size dimorphism (SSD) is a phenomenon typical of orbweb spiders where female size dwarfs that of the male (Kuntner and Coddington 2020). Preliminary data suggested, and our reports confirm, that *Cyphalonotus* is not particularly biased in sexual size dimorphism. Understanding the phylogenetic proximity of the sexually size monomorphic *Cyphalonotus* to the extremely sexually size dimorphic (eSSD) *Polty*

would inform the patterns of SSD evolution in orbweb spiders.

The third objective of our study was to test the taxonomic composition of *Cyphalonotus*. Prior work emphasised diagnostics based on species from Africa, therefore we tested taxonomic composition using newly studied Asian specimens and provided the formal description of only the second *Cyphalonotus* species known for male morphology. Our original collection and field observations from Taiwan and China facilitated description of a new and a known species, and newly provided sequence data enabled species delimitation.

## Materials and methods

### Sequencing methods

Following the manufacturer’s instructions, genomic DNA of all *Cyphalonotus* specimens was extracted using a FavourPrep Tissue Genomic DNA Extraction Mini Kit (Favourgen Biotech, Ping-Tung, Taiwan). We amplified cytochrome *c* oxidase I (*COI*) from each *Cyphalonotus* specimen to help delimit the number of species. For species level phylogenetic analysis, four additional molecular markers were amplified from one specimen per species, including one mitochondrial gene fragment, 16S rRNA (16S) and three nuclear gene fragments, 28S rDNA (28S), 18S rDNA (18S) and histone 3 (*H3*). Sequences of other araneid taxa were obtained from the dataset of Scharff *et al.* (2020).

The PCR reaction mixture (25 µL) contained 12.5 µL of EmeraldAmp MAX HS PCR Master Mix (Takara Bio Inc., USA), 0.5 µL of each primer, 8–9 µL of distilled water and 2.5–3.5 µL of genomic DNA. Sequence amplification protocols included at least 35 cycles with 44–46°C annealing temperatures and 72–96°C polymerising temperatures. PCR products were sent to the Sequencing Center, National Yang-Ming University, Taipei, Taiwan for purification and sequencing. All sequences were edited in Geneious Prime (ver. 2019.2.3, see <https://www.geneious.com>) and uploaded to GenBank. The GenBank accession numbers, the primers used in this study and the aligned sequence matrix are included in the Supplementary material.

### Species delimitation

We performed two species delimitation analyses based on *COI* data. We ran the Automatic Barcode Gap Discovery

(ABGD) (Puillandre *et al.* 2012). To obtain a *COI* gene tree, we ran a maximum likelihood (ML) analysis in RAXML (ver. 8.2.12, see <https://cme.h-its.org/exelixis/web/software/raxml/>; Stamatakis 2014) on CIPRES Science Gateway portal (Miller *et al.* 2010) with 100 bootstrap replicates using the program's rapid bootstrapping algorithm, with sequences partitioned by codon. Based on this gene tree, we ran a multi-rate Poisson tree analysis under ML and Markov chain Monte Carlo, or mPTP (Kapli *et al.* 2017). Both species delimitation methods followed the Kimura 2 parameter genetic distance substitution model (Kimura 1980).

## Alignment and phylogenetic analysis

We used Mesquite (ver. 3.61, W. P. Maddison and D. R. Maddison, <http://www.mesquiteproject.org/>, accessed April 2020) for concatenating matrices. For the alignment of each molecular marker, we followed the procedures from

Scharff *et al.* (2020). We ran ML phylogenetic analyses in RAXML (Stamatakis 2014) on the CIPRES Science Gateway portal (Miller *et al.* 2010) with 1000 bootstrap replicates using the program's rapid bootstrapping algorithm. We applied the default GTR + Gamma model of nucleotide substitution to each partition of the sequence matrix as follows: protein coding genes (*COI*, *H3*) were partitioned by codon, *28S* followed the partition method in Scharff *et al.* (2020), and *16S* and *18S* were partitioned by gene.

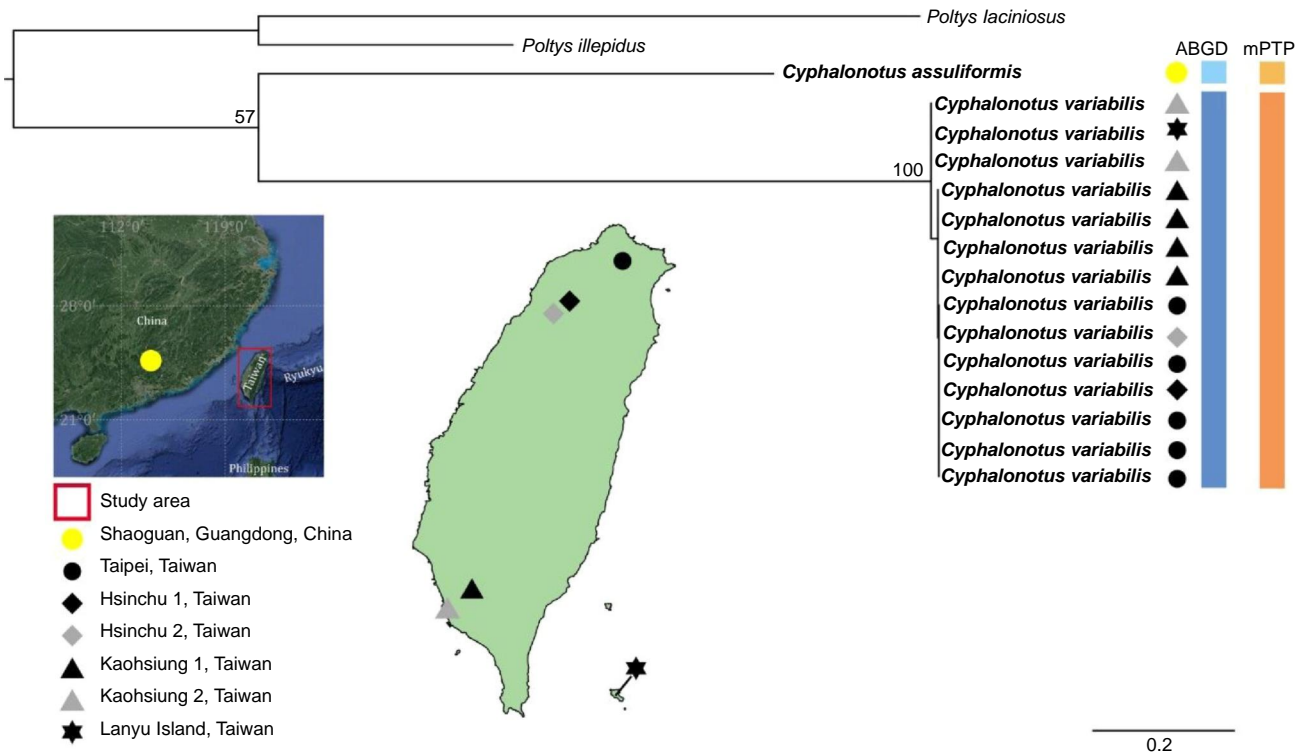
## SSD comparison

An intuitive value of SSD was easily obtained as the ratio of female and male body (part) lengths (Kuntner and Coddington 2020). For this SSD quantification, we used mean adult body and carapace length measurements obtained either from our original collection or the literature (Table 2). As an arbitrary threshold between sexually size

**Table 2.** Comparison on the degrees of sexual size dimorphism between *Polys* C. L. Koch, 1843, *Cyphalonotus* Simon, 1895, and four araneid species that belong to the nearby clade and known to both sexes (*Araneus mitificus* (Simon, 1886), *Araneus rotundicornis* Yaginuma, 1972, *Eriovixia laglaizei* (Simon, 1877), and *Perilla teres* Thorell, 1895).

Genus	Species	Carapace length SSD (female/male ratio)	Body total length SSD (female/male ratio)	Data source
<i>Cyphalonotus</i>	<i>larvatus</i>		1.45	Pavesi 1897; De Lessert 1930
	<i>variabilis</i>	1.05	1.16	This paper
<i>Polys</i>	<i>columnaris</i>		5	Tanikawa 2007
	<i>frenchi</i>	5.1		Hogg 1899; Chrysanthus 1961; Smith 2006a
	<i>grayi</i>	3.36		Smith 2006a
	<i>illegidus</i>	5.46	5.74	Thorell 1878, pp. 28–29; Keyserling 1886; Rainbow 1898; Pocock 1900; Rainbow 1920; Barrion and Litsinger 1995; Smith 2006a; Tanikawa 2007; Hawes 2020
	<i>jujorum</i>	3.22		Smith 2006a
	<i>laciniosus</i>	3.46		Keyserling 1886; Rainbow 1904; Smith 2006a
	<i>milledgei</i>	3.81		Smith 2006a
	<i>noblei</i>	3.45		Smith 2006a
	<i>stygius</i>	5.13		Thorell 1898, pp. 344–345; Rainbow 1916; Smith 2006a
	<i>timmei</i>	2.68		Smith 2006a
	cf. <i>nigrinus</i>	5.34	5.21	Original collection
	cf. <i>mouhoti</i>	10.94	10.43	Original collection
	sp. 1	4	3.71	Original collection
	sp. 2	3.75	3.91	Original collection
<i>Araneus</i>	<i>mitificus</i>	1.39	1.64	Barrion and Litsinger 1995; Namkung 2003; Tanikawa 2007; Yin <i>et al.</i> 2012
	<i>rotundicornis</i>	0.98	1.14	Yaginuma 1972; Tanikawa 2007; Kim and Lee 2012, pp. 28–29
<i>Eriovixia</i>	<i>laglaizei</i>	0.85	1.11	Tikader 1982; Yaginuma and Wen 1983; Yin <i>et al.</i> 1997; Han and Zhu 2010; Sen <i>et al.</i> 2015, p. 120
<i>Perilla</i>	<i>teres</i>	1	1.5	Kuntner 2002

SSD, sexual size dimorphism.



**Fig. 1.** ABGD and mPTP species delimitation analyses based on *COI* indicate that all *Cyphalonotus* specimens from Taiwan are conspecific.

dimorphic and monomorphic taxa, we used the index value of 2.0 following Kuntner and Coddington (2020). Species with average SSD values higher than 2.0 are considered to be eSSD, whereas those with SSD values between 1.0 and 2.0 are sexually monomorphic to moderately sexually size dimorphic.

## Taxonomic methods

Specimens examined in this study were collected by hand and preserved in 70% ethanol. Measurements and photography were undertaken using Nikon SMZ800N and SAGE Vision SL/730T cameras. The measurements of palps consist of femur, patella, tibia and tarsus whereas those of legs consist of femur, patella, tibia, metatarsus and tarsus. All measurements are given in millimetres. Variation values are given as mean  $\pm$  s.d. Four legs of each specimen were removed and preserved in 95% ethanol for DNA extraction and sequencing. The specimens are held at the Department of Life Sciences, National Chung Hsing University (NCHU) (vouchers coded ABARA) but the type specimens are deposited at the Biodiversity Research Museum, Academia Sinica, Taipei, Taiwan (BRMAS) (vouchers coded ASIZCH) and Senckenberg Museum Frankfurt, Frankfurt, Germany (SMF).

Abbreviations used include the following: AER, anterior eye row; ALE, anterior lateral eyes; AME, anterior median eyes; C, conductor; CY, cymbium; E, embolus; eSSD, extreme sexual size dimorphism, MA, median apophysis;

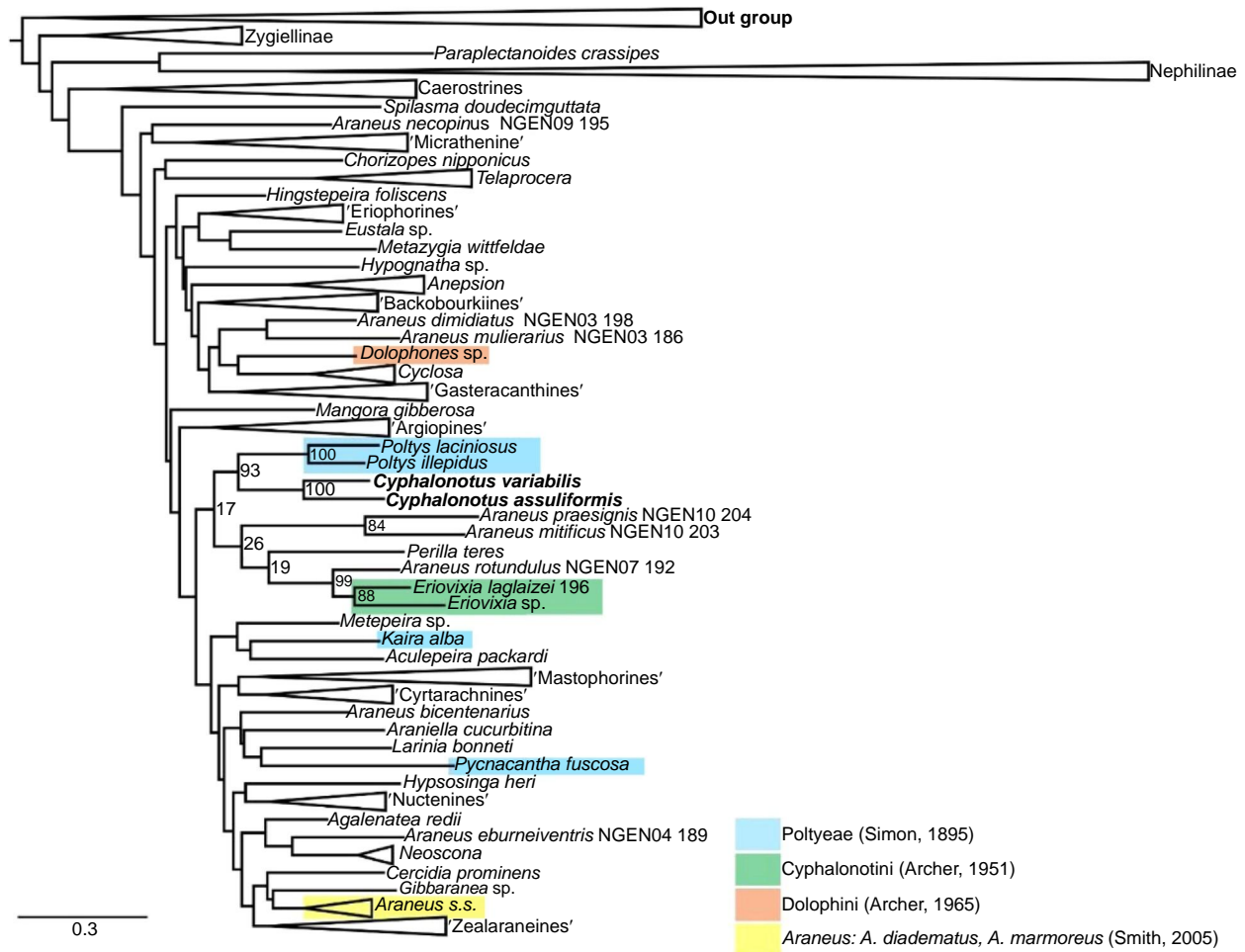
MOA, median ocular area; PC, paracymbium; PER, posterior eye row; PLE, posterior lateral eyes; PME, posterior median eyes; STA, sub-terminal apophysis; SSD, sexual size dimorphism; T, tegulum; TA, terminal apophysis; TL, tegular lobe.

## Results

### Phylogeny and SSD comparison

A total of 15 *Cyphalonotus* specimens were used in this study, including 1 *C. assuliformis* from Southern China and 14 specimens of *C. variabilis* sp. nov. from Taiwan. All specimens of *C. variabilis* sp. nov. from different localities were grouped together in a well-supported clade with no distinct population structure on the *COI* gene tree (Fig. 1). The results of ABGD and mPTP species delimitation analyses both agree that all individuals from Taiwan are conspecific, including that from the isolated Lanyu Island, whereas *C. assuliformis* is a distinct species (Fig. 1).

The ML analyses of the concatenated matrix from Scharff *et al.* (2020) with the addition of the two *Cyphalonotus* species revealed the genus to be monophyletic and sister to *Poltys*. The reciprocal monophyly of *Cyphalonotus* and *Poltys*, and the monophyly of *Cyphalonotus* + *Poltys* were all well supported (Fig. 2). However, the sister relationship of the latter clade was relatively weak (Fig. 2). This sister clade united *Eriovixia*, *Araneus rotundulus* Yaginuma, 1972



**Fig. 2.** Results of the maximum likelihood analysis recover *Cyphalonotus* as sister to *Polty*s. The genera on which previous phylogenetic or classification hypotheses were based are colour-coded (Table 1).

and *Perilla teres* Thorell, 1895 with a clade of two *Araneus* species, *A. praesignis* (C. L. Koch, 1872) and *A. mitificus* (Simon, 1886) (Fig. 2).

Our data revealed that all known *Polty*s species were eSSD (SSD > 2.5) considering both body length and carapace length (Fig. 3). *Polty*s cf. *mouhoti* from our original collection reached record values exceeding 10-fold differences (Table 2). However, *Cyphalonotus* and other taxa within phylogenetic proximity (*Eriovixia laglaizei* (Simon 1877), *Araneus rotundulus*, *A. praesignis*, *A. mitificus* and *Perilla teres*) were all sexually size monomorphic, with SSD index values being or approximating 1.5 (Table 2, Fig. 3).

The following novel natural history data on *Polty*s may be worth reporting to be placed within the evolutionary context of SSD. Our observations suggest that mature females of several *Polty*s species (*P. cf. nigrinus*, *P. cf. stygius*, *P. cf. muhoti* and *P. aff. columnaris*) can occupy higher and more open forest compared with *Cyphalonotus variabilis* sp. nov. that occurs in the same habitat. This species builds large, dense webs above trails, in the canopy or in large gaps between trees. The diet of *Polty*s is also unique, with

moths as the most common prey (Smith 2006b). We observed *Polty*s spiderlings gathering en masse to make individual small orbs on a branch or stick. Sub-adult males, whose body size is no larger than that of hatched spiderlings, are sometimes found intermixed within such aggregations along with immature spiderlings.

## Taxonomy

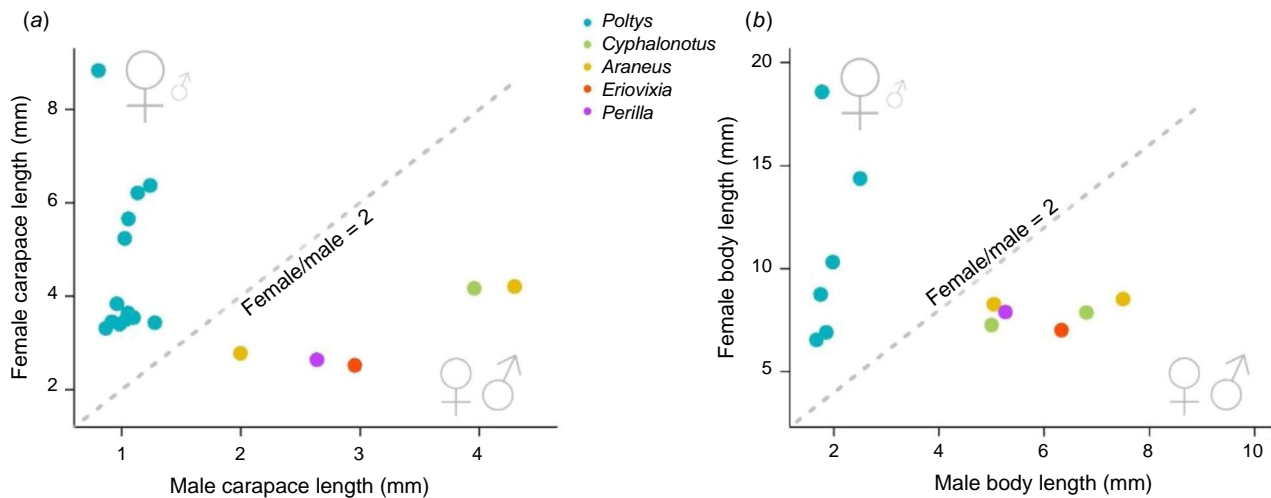
Family **ARANEIDAE** Clerck, 1757

Genus ***Cyphalonotus*** Simon, 1895

## Type species

*Polty larvatus* Simon, 1881. Simon described the type species from Zanzibar and the species is currently believed to inhabit a wide area from Congo through east Africa and to Socotra (Yemen) (World Spider Catalog, ver. 22.0, see <http://wsc.nmbe.ch>).





**Fig. 3.** Female to male size ratios in *Cyphalonotus* and related genera measured by: (a) carapace length; (b) total body length. All known *Poltys* species are extremely sexually size dimorphic (SSD ratio > 2), whereas *Cyphalonotus* and other close relatives are sexually size monomorphic (SSD < 2).

## Diagnosis

*Cyphalonotus* differs from all other araneid genera except for *Poltys* in the following combination of characters: pear-shaped carapace without any spines or protrusions (Fig. 4b–f); both AER and PER strongly recurved, four anterior eyes located anteriorly on the eye tubercle, PME and PLE separated; abdomen extending anteriorly, shield-shaped or cone-shaped, possessing numerous protrusions (Fig. 4b, e, 5c, 6d–f, 7c, 8b); tibia of each leg slightly bent in ‘S’ shape (Fig. 4d, 8a; *Poltys*: Fig. 4a).

*Cyphalonotus* differs from *Poltys* in the following combination of characters: carapace smooth rather than strongly depressed at the fovea (Fig. 4d, e, 5b, 8a; *Poltys*: Fig. 4b, arrow); eye tubercle wider, rather than thin and extending anteriorly (Simon 1895); lateral eyes located closer to each other, anterior eyes at the base of tubercle or sometimes on the lateral side of tubercle (Fig. 4e, f, 5a, b, h, i, 7a, b, 8a; *Poltys*: Fig. 4b, c) (Smith 2006a); leg tibiae and metatarsi thinner and depressed anteriorly (Fig. 4d, 8a; *Poltys*: Fig. 4a) (Simon 1895); epigynum with an extended and wrinkled scape (Fig. 4d–f, 6a–c, 7d–f, 8c–e) (Smith 2005); male palpal femur with a distinct ventral tubercle (Fig. 4i, arrow on the right), endite with a hook (Fig. 4h, arrow), tibia II modified with several strong spines (Fig. 4g, arrow), coxa I with a hook (Fig. 4i, arrow on the left), femur II with a groove (Fig. 4j, arrow). The male palp lacks a paramedian apophysis but has a STA, the conductor is lobed (Smith 2005), the TA is distinct with an enlarged base and the MA is heavily sclerotised (Fig. 5k–m, 6g–i).

Our newly acquired measurements reveal that *Cyphalonotus* is sexually size monomorphic to moderately dimorphic (SSD ranges from 1.05 to 1.5), whereas species of *Poltys* are extremely dimorphic (SSD > 2.5) (Table 2).

The web of *Cyphalonotus* shows spirals of a lower density compared with the known webs of *Poltys* (Fig. 9).

## Distribution

Tropical to subtropical Africa and Asia, Madagascar and Socotra Island.

## Composition

*Cyphalonotus assuliformis* Simon, 1909, *C. benoiti* Archer, 1965, *C. columnifer* Simon, 1903, *C. elongatus* Yin, Peng & Wang, 1994, *C. larvatus* (Simon, 1881), *C. selangor* Dzulhelmi, Suriyanti & Norma, 2015, *C. sumatranus* Simon, 1899, *C. variabilis* sp. nov.

## *Cyphalonotus variabilis* Yu, Kuntner & Cheng, sp. nov.

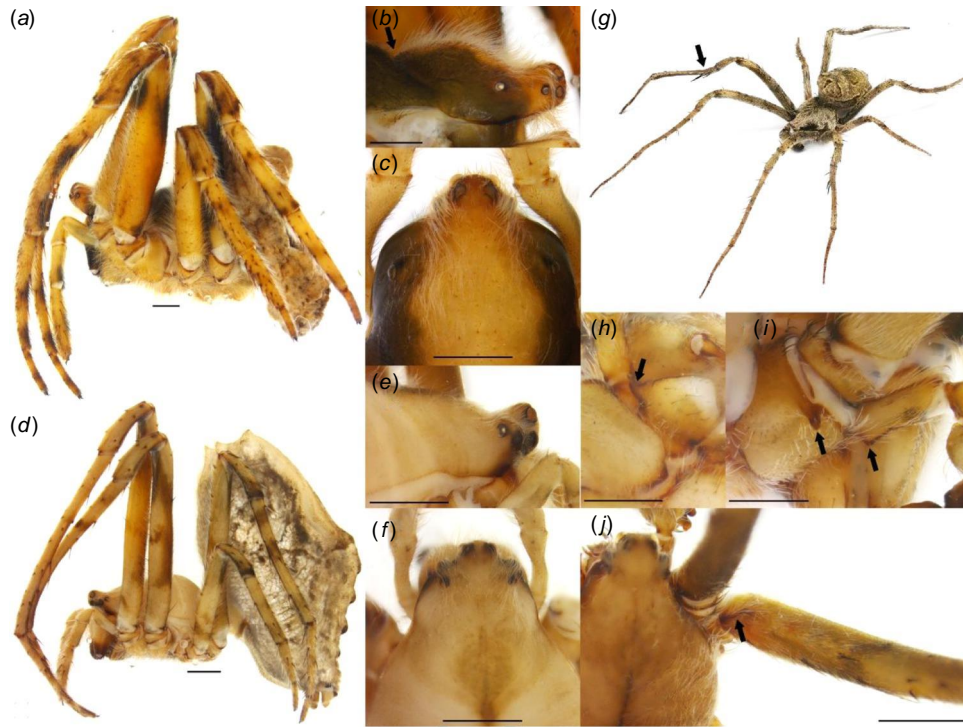
(Fig. 4d–j, 5, 6, 9b, 10a–e)

<http://zoobank.org/NomenclaturalActs/3e8cc36b-cc1a-4d70-bc02-1c8a3f0c22d0>

## Material examined

**Holotype.** Taiwan: 1♂, Kaohsiung City, Southern part of Shoushan (22°38′31.2″N, 120°15′28.8″E), 23 February 2018 (Jing-Han Liu leg.), ASIZCH000103 (BRMAS).

**Paratypes series.** Taiwan: 1♀, same data as holotype, ASIZCH000104 (BRMAS); 1♂, Taipei City, Xianjiyan Trail (24°59′32.2″N, 121°32′48.2″E), 6 July 2019 (Kuang-Ping Yu (KPY) leg.), ABARA00521 (SMF); 1♀, Taipei City, Xianjiyan Trail, 1 August 2019 (KPY leg.), ABARA01336 (SMF).



**Fig. 4.** Somatic characters diagnosing the sister genera *Cyphalonotus* Simon, 1895 and *Poltys* C. L. Koch, 1843. (a–c) Female *Poltys* cf. *nigrinus* Saitō, 1933: (a) lateral; (b) carapace, lateral view, showing a depressed fovea (arrow); (c) frontal carapace, dorsal view showing the eye tubercle. (d–f) Female *Cyphalonotus variabilis* sp. nov.: (d) lateral view; (e) carapace, lateral view, without a depressed fovea; (f) frontal carapace, dorsal view showing the eye tubercle. (g–j) Male *Cyphalonotus variabilis* sp. nov.: (g) male body showing a modified second tibia (arrow); (h) right endite, ventral view, showing a hook (arrow); (i) first coxa and palpal femur, lateral view, showing coxal hook (left arrow) and palpal femoral ventral tubercle (right arrow); (j) second femur, prolateral view, showing a basal femoral groove (arrow). Scale bars: (a–f) 1 mm; (h–j) 0.5 mm.

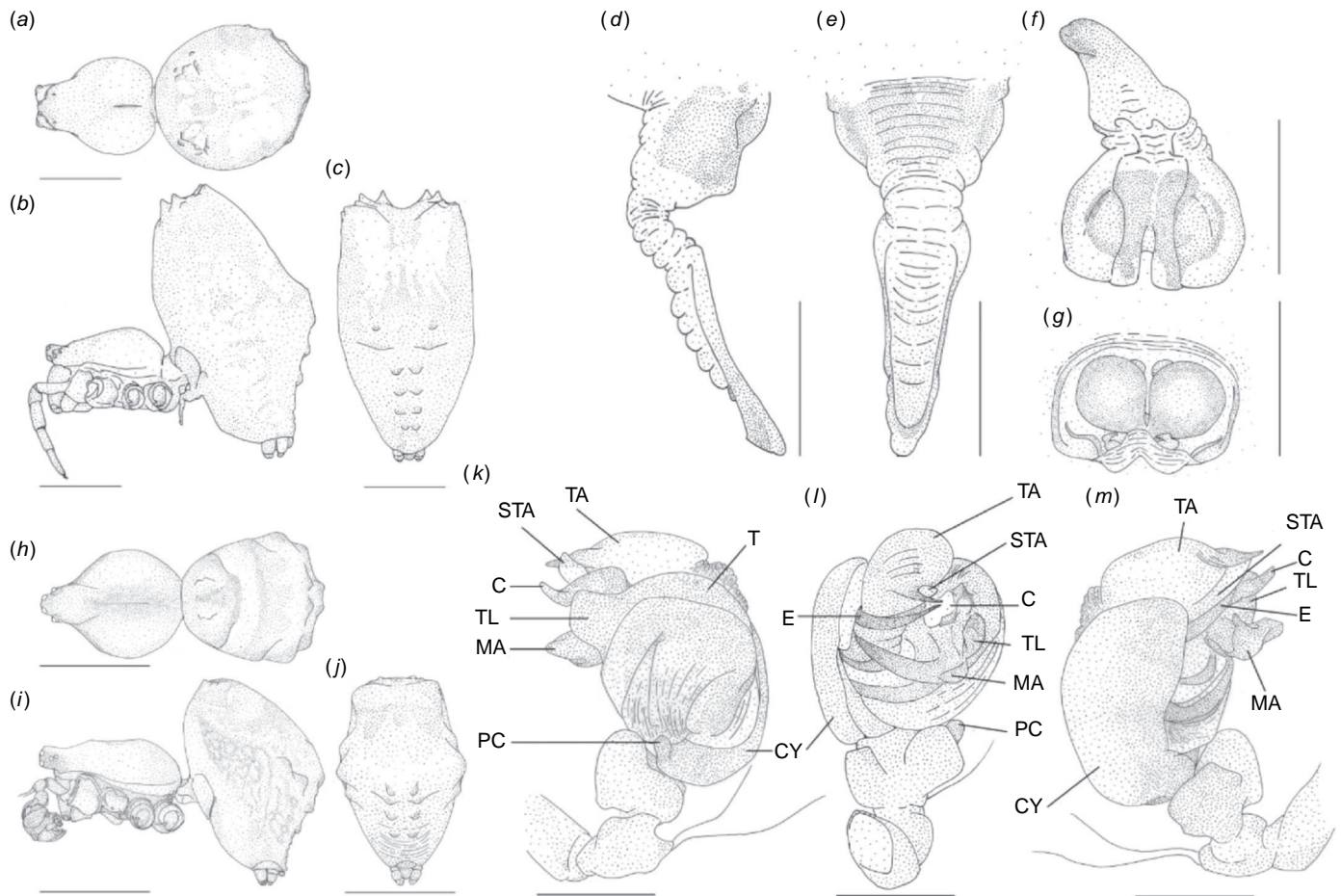
*Non-type specimens. Taiwan:* 1♂, 2 juveniles, Taipei City, Xianjiyan Trail, 6 July 2019 (KPY leg.), ARA00679–81 (NCHU); 1♀, Hsinchu County, Matai trail (24°41'45.6"N, 121°11'24.0"E), 7 March 2020 (Taiwan, Anansi Brigade leg.), ABARA01303 (NCHU); 1♂, Hsinchu County, Shuiliandong trail (24°39'20.3"N, 121°1'30.2"E), 8 May 2018 (Chi-Wen Hsu leg.), ABARA01331 (NCHU); 1♂, 3♀, Kaohsiung City, Heshan road (22°42'25.4"N, 120°24'55.6"E), 23 July 2019 (KPY leg.), ABARA01332–35 (NCHU); 1♀, Taitung County, Lanyu Island, Tianchi trail (22°0'55.3"N, 121°34'17.4"E), 31 March 2020 (Ting-Kuan Lin leg.), ABARA01316 (NCHU).

## Diagnosis

Females of *Cyphalonotus variabilis* sp. nov. can be separated from *C. assuliformis* by abdominal shape that is oval to conical (Fig. 4d, 5b, c, 6d–f) rather than long, cylindrical and anteriorly elongated (Fig. 7b, c, 8a, b) (Simon 1909; Dzulhelmi et al. 2015). *Cyphalonotus variabilis* sp. nov. can be distinguished from *C. larvatus*, *C. elongatus*, *C. sumatranus*, *C. benoiti* and *C. sp.* in Smith, 2005 (figure only) by the shape of the epigynal scape: spindle-shaped with broadened part at one-fourth from the top in *C. variabilis* sp. nov. (Fig. 5d–f, 6a–c), whereas *C. larvatus*,

*C. elongatus*, *C. sumatranus* and *C. sp.* have a narrower scape without a distinctly broad part (Simon 1899; Archer 1965; Yin et al. 1994; Smith 2005; Dzulhelmi et al. 2015); whereas *C. benoiti* also has a spindle-shaped scape with the broadest part at the middle of the scape (Archer 1965; Dzulhelmi et al. 2015). *Cyphalonotus variabilis* sp. nov. can be separated from *C. columnifer* by the light-yellowish sternum and brown femora (Fig. 4d) that are both black in the latter (Simon 1903; Dzulhelmi et al. 2015). *Cyphalonotus variabilis* sp. nov. is most similar to *C. selangor* in both appearance and shape of the scape but can be distinguished from the latter by the strongly sclerotised edge that forms a distinct pocket at the tip of the scape (Fig. 5d–f, 6a–c).

The males of *C. variabilis* sp. nov. differ from *C. larvatus*, the other *Cyphalonotus* species with known male and *C. sp.* in Smith (2005, figure only) by the larger and longer median apophysis, a thinner and longer conductor, a smaller stipes, a longer embolus and a terminal apophysis with blunter basal part and sharper tip (Fig. 5k–m, 6g–i) (Archer 1965; Smith 2005).



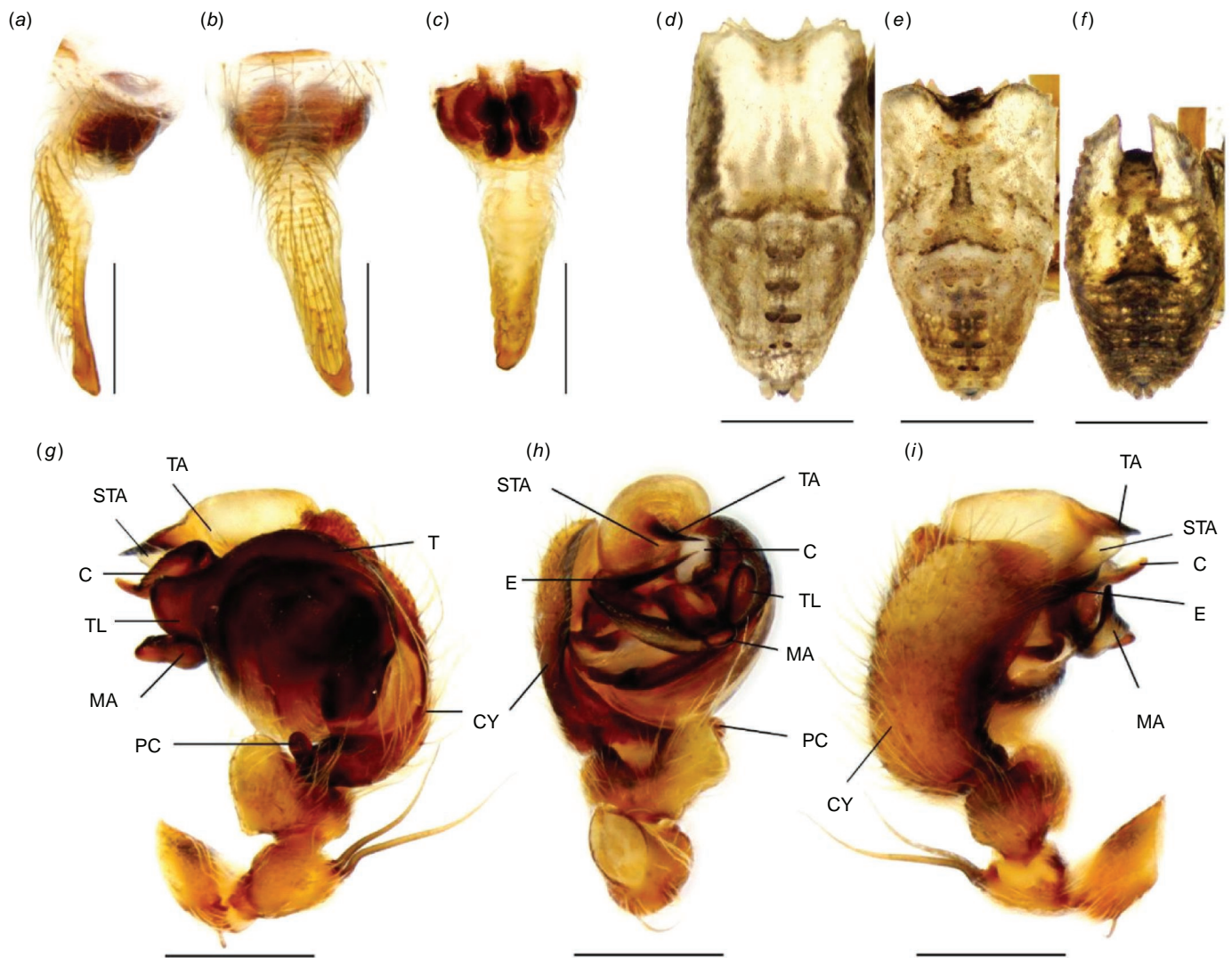
**Fig. 5.** *Cyphalonotus variabilis* sp. nov. from Kaohsiung, Taiwan. (a–g) Female paratype (voucher code ASIZCH000104): (a) dorsal view; (b) lateral view; (c) posterior view of abdomen; (d) epigynum, lateral view; (e) epigynum, ventral view; (f) epigynum, posterior view; (g) vulva, dorsal view. (h–m) Male holotype (voucher code ASIZCH000103): (h) dorsal view; (i) lateral view; (j) abdomen, posterior view; (k) left palp, retrolateral view; (l) left palp, ventral view; (m) left palp, prolateral view. Scale bars: (a–c, h–j) 3 mm; (d–g, k–m) 0.5 mm.

## Description

**Female** (ASIZCH000104, *Paratype*). Total length 9.91; cephalothorax length 4.70, width 3.42; abdomen length 9.54, width 5.10. Length of palps and legs: palp 4.57 (1.18, 0.53, 0.92, 1.94); leg I 22.81 (8.38, 2.31, 7.22, 3.52, 1.38); leg II 20.57 (7.46, 2.21, 6.52, 3.11, 1.27); leg III 10.75 (3.99, 1.63, 2.67, 1.51, 0.95); leg IV 17.52 (6.69, 2.05, 4.94, 2.81, 1.03). Leg formula 1243. Carapace yellowish-brown, pear shaped with low, weakly and anteriorly extended post caput. Whole carapace bearded with sparse yellowish-brown short setae, with darker colouration at post caput, thoracic groove and fovea (Fig. 4d–f, 5a, b). Eight eyes ringed with black. Eyes arranged in two rows. Both AER and PER are strongly recurved. MOA light brown and covered by yellowish-brown setae. Diameters of AME 0.21, ALE 0.16, PME 0.18, PLE 0.17; MOA length 0.48, anterior width of MOA 0.53, posterior width of MOA 0.43; interval of AMEs 0.27, interval of PMEs 0.25, interval of ALEs 0.29, interval of PLEs 0.46. Clypeus 0.20. Clypeus dark

brown with black margin and covered by yellowish-brown setae. Chelicerae yellowish-brown and blackish-brown at the tips. Chelicerae with four promarginal and three retro-marginal teeth, both fang and marginal teeth chestnut brown. Endites and labium yellowish-brown. Width of the labium is approximately two-thirds the length. Sternum is also yellowish-brown with light brown margin, nearly round and shrunk at the posterior part. Palps yellowish-brown, without markings. Legs brown, with dark blackish markings on ventral side of each leg section, tarsus and metatarsus of each leg depressed anteriorly. Both legs and palps covered by yellowish-brown setae and several long spines. Abdomen long oval with wider upper part and tapering gradually to spinnerets, dorsum yellowish-brown while ventral, lateral, and lower part dark brown, covered by short yellowish-brown setae and with irregular dark brown flakes located laterally. Top of the abdomen with 12 protrusions arranged circularly, and 12 blackish paired humps arranged in six rows along lower part of the abdomen (Fig. 4d, 5a–c, 6d).



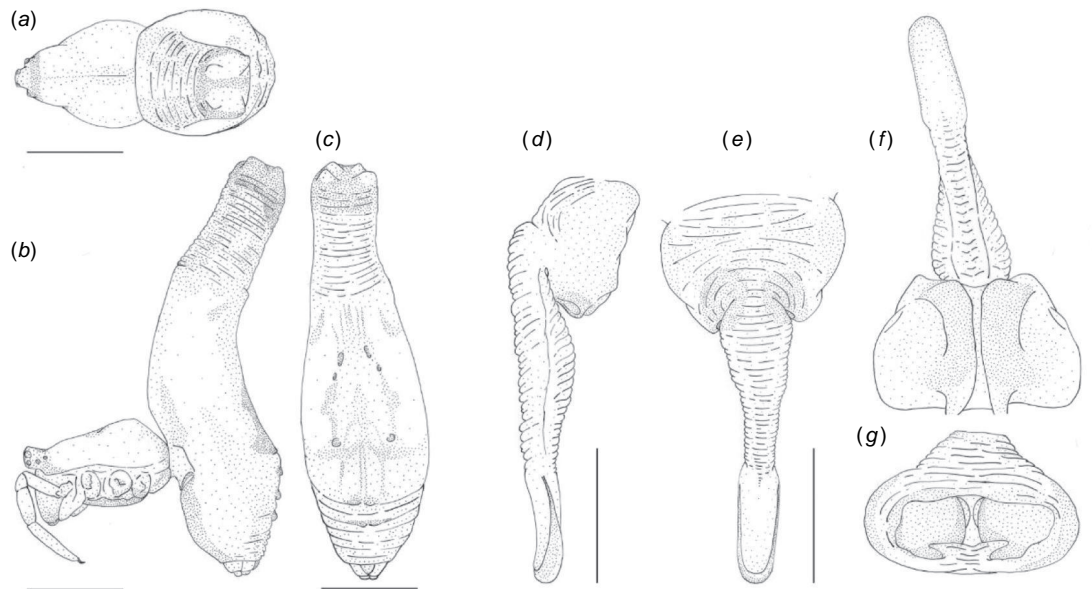


**Fig. 6.** *Cyphalonotus variabilis* sp. nov. from Kaohsiung, Taiwan. (a–d) Female paratype (voucher code ASIZCH000104): (a) epigynum, lateral view; (b) epigynum, ventral view; (c) epigynum, posterior view; (d–f) variation of posterior view of abdomen. (g–i) Left palp of male holotype (voucher code ASIZCH000103): (g) retrolateral view; (h) ventral view; (i) prolateral view. Scale bars: (d–f) 3 mm; (a–c, g–i) 0.5 mm.

Epigynum with distinct scape, light yellow and gradually turning light brown at the tip. Scape flattened and spindle-shaped, top one-fourth of the scape broadest and gradually tapering to the tip. Length of the scape is nearly 3.5 times the width at the basal part. The scape with brownish, strongly sclerotised and recurved edge, forming a thick and distinct pocket at the tip. Conjunction part between scape and epigynum narrow and curved (Fig. 5d–g, 6a–c).

**Male** (ASIZCH000103, *Holotype*). Total length 7.53: cephalothorax length 3.97, width 3.02; abdomen length 5.61, width 3.52. Length of palps and legs: palp 2.44 (0.69, 0.37, 0.41, 0.97); leg I 18.34 (6.52, 1.75, 5.85, 3.01, 1.21); leg II 16.34 (5.77, 1.73, 4.97, 2.77, 1.10); leg III 8.02 (2.96, 1.14, 1.96, 1.27, 0.69); leg IV 12.57 (4.90, 1.50, 3.03, 2.34, 0.80). Leg form 1243. Diameters

of AME 0.20, ALE 0.15, PME 0.20, PLE 0.12; MOA length 0.42, anterior width of MOA 0.52, posterior width of MOA 0.41, interval of AMEs 0.26; interval of PMEs 0.21, interval of ALEs 0.13, interval of PLEs 0.32. Clypeus 0.06. Male is similar to female, but darker in the colouration and the post caput of cephalothorax extends longer than in female (Fig. 5h–i). Depression of tarsus and metatarsus of each leg stronger than female, and the beginning of prolateral tarsus of leg II modified with four additional strong spines (Fig. 4g, arrow). Palpal cymbium kidney-shaped, terminal apophysis distinct, enlarged at the base and shrunk at the tip. Subterminal apophysis membranous, attached with terminal apophysis. Embolus thin and long. Conductor consists of two parts, the light-coloured membranous part that is in close contact to the embolus; and the long, thin,



**Fig. 7.** Female *Cyphalonotus assuliformis* Simon, 1909 from Guangdong, China (voucher code ABARA01337): (a) dorsal view; (b) lateral view; (c) abdomen, posterior view; (d) epigynum, lateral view; (e) epigynum, ventral view; (f) epigynum, posterior view; (g) dorsal view of vulva. Scale bars: (a–c) 3 mm; (d–g) 0.5 mm.

sclerotised part with a distinct extended lobe at the base. Median apophysis slightly bent, long, thin and highly sclerotised, with a spoon-shaped extension at the basal part (Fig. 5k–m, 6g–i).

### Variation

Given as female variation followed by male variation in parentheses. Total length  $7.87 \pm 1.50$  ( $6.80 \pm 0.56$ ); cephalothorax length  $4.16 \pm 0.38$  ( $3.96 \pm 0.16$ ), width  $3.19 \pm 0.25$  ( $3.07 \pm 0.14$ ); abdomen length  $7.45 \pm 1.62$  ( $4.68 \pm 0.66$ ), width  $4.19 \pm 0.60$  ( $2.85 \pm 0.40$ ); palp  $4.42 \pm 0.30$  ( $2.55 \pm 0.13$ ); leg I  $20.95 \pm 1.74$  ( $19.16 \pm 0.99$ ); leg II  $18.80 \pm 1.66$  ( $16.76 \pm 1.07$ ); leg III  $10.00 \pm 0.69$  ( $8.80 \pm 1.14$ ); leg IV  $16.33 \pm 1.23$  ( $14.32 \pm 1.66$ ). Diameters of AME  $0.20 \pm 0.02$  ( $0.22 \pm 0.02$ ), ALE  $0.17 \pm 0.01$  ( $0.13 \pm 0.01$ ), PME  $0.19 \pm 0.02$  ( $0.19 \pm 0.02$ ), PLE  $0.15 \pm 0.02$  ( $0.13 \pm 0.01$ ); clypeus  $0.14 \pm 0.04$  ( $0.06 \pm 0.01$ ). The shape of the abdomen, especially protrusions, varies (see Etymology). Some female individuals sport two large, horn-like protrusions on the anterior edge of the abdomen (Fig. 6d–f, 10a, b).

### Natural history

Cryptic, medium-sized nocturnal orb-weaver. Females and juveniles build vertical or near vertical orb webs in low vegetation of forest edges or bushes. The orb web has a sparser spiral pattern compared with those of the known *Poltys* (Fig. 9). Mature males do not build webs and are

found traveling or hanging on silks (Fig. 10e). During foraging, spiders sit at the hub of the web (Fig. 10b). The legs are skewed (Fig. 10c) and spiders self-camouflage as a piece of debris or small twig when facing disturbances or in daylight (Fig. 10d). Adults can be found throughout the year, with the main breeding season between July and September, when these can be locally abundant.

### Remarks

This is the second *Cyphalonotus* species known from both sexes and the first male description of any Asian *Cyphalonotus*.

### Etymology

The specific name is a Latinised adjective, referring to the large variation in the shape of protrusions on the female abdomen.

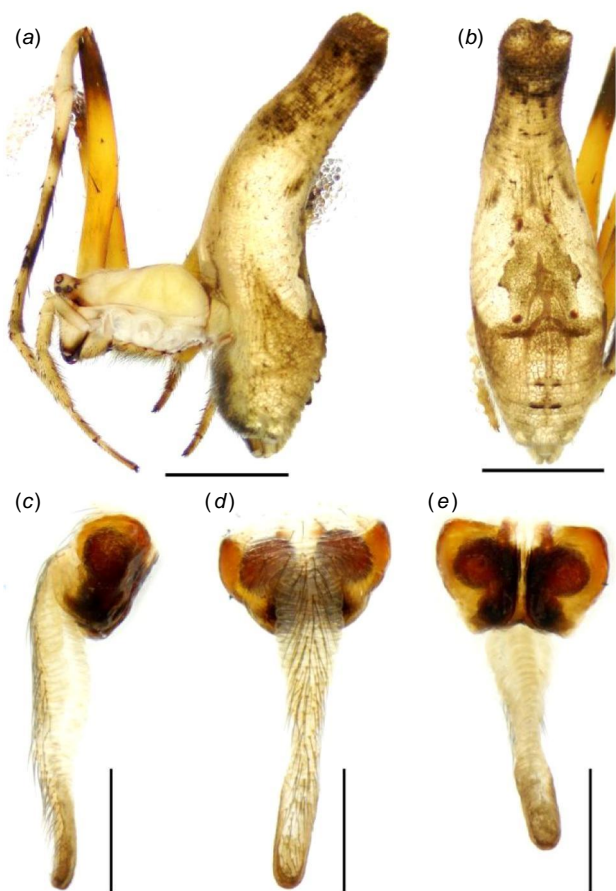
### Distribution

Low altitude primary and secondary forests of Taiwan (main island, Lanyu Island) (Fig. 1). Also found on Green Island.

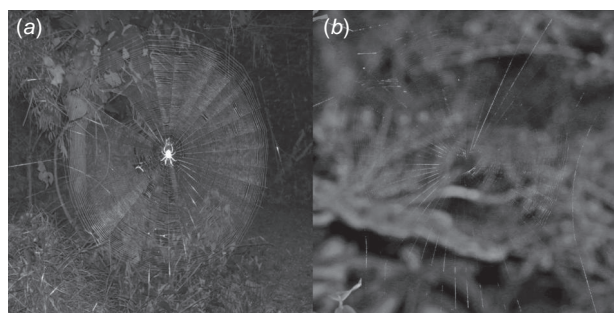
## *Cyphalonotus assuliformis* Simon, 1909

(Fig. 7, 8, 10f)

*Cyphalonotus assuliformis* E. Simon, 1909: 69–147.



**Fig. 8.** Female *Cyphalonotus assuliformis* Simon, 1909 from Guangdong, China (voucher code ABARA01337): (a) lateral view; (b) abdomen, posterior view; (c) epigynum, lateral view; (d) epigynum, ventral view; (e) epigynum, posterior view. Scale bars: (a, b) 3 mm; (d, e) 0.5 mm.



**Fig. 9.** Webs of (a) female *Poltys* cf. *nigrinus* (credit: Ting-Kuan Lin) and (b) female *Cyphalonotus variabilis* sp. nov. reveal architectural differences. In *Poltys*, the number of spirals along the radii ranges from 89 to 115, and in *Cyphalonotus*, from 67 to 73.

## Material examined

*Non-type specimens.* **China:** 1♀, Guangdong province, Shaoguan City (24°57'15.4"N, 113°06'53.1"E), 7 June 2019 (KPY leg.), ABARA01337 (NCHU).

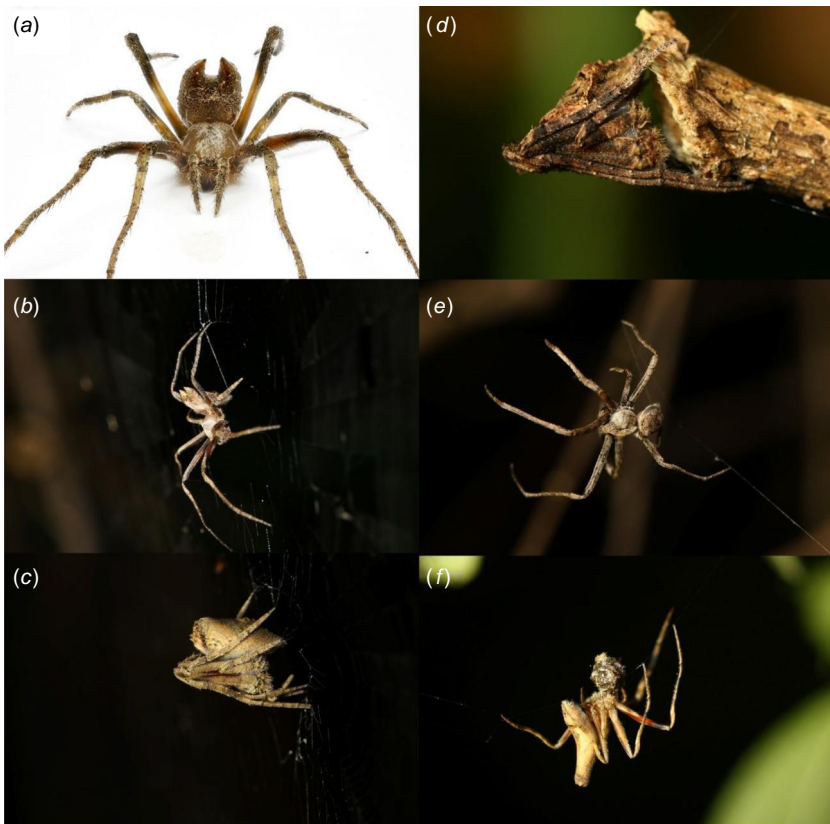
## Diagnosis

Females of *C. assuliformis* differ from all other known *Cyphalonotus* species by the cylindrical and anteriorly elongated abdomen (Fig. 7b, c, 8a, b) (Simon 1909; Dzulhelmi et al. 2015). The species also has the longest epigynal scape among known *Cyphalonotus*, that is nearly five times longer than the width (Fig. 7d–f, 8c–e).

## Description

*Female* (ABARA01337). Total length 8.01: cephalothorax length 4.49, width 3.41; abdomen length 11.34, width 3.93. Length of palps and legs: palp 4.49 (1.26, 0.48, 0.99, 1.76); leg I 22.48 (8.06, 1.94, 7.32, 3.79, 1.37); leg II 20.45 (7.26, 1.90, 6.58, 3.44, 1.27); leg III 10.57 (3.90, 1.49, 2.68, 1.54, 0.96); leg IV 17.78 (7.07, 1.76, 5.28, 2.85, 0.82). Leg formula 1243. Carapace yellowish-brown, pear-shaped with lower and weakly anteriorly extended post caput, whole carapace bearded with sparse yellowish-brown short setae, with darker colouration between lateral eyes and MOA (Fig. 7a, b, 8a). Eight eyes ringed with black. Eyes arranged in two rows. Both AER and PER are strongly recurved. MOA light brown and covered by yellowish-brown setae. Diameters of AME 0.19, ALE 0.16, PME 0.19, PLE 0.13; MOA length 0.48, anterior width of MOA 0.56, posterior width of MOA 0.52; interval of AMEs 0.29, interval of PMEs 0.28, interval of ALEs 0.24, interval of PLEs 0.46. Clypeus 0.11. Clypeus dark brown and covered by yellowish-brown setae. Chelicera yellowish-brown and blackish-brown at the tip. Chelicera with four promarginal and three retromarginal teeth, both fang and marginal teeth chestnut brown. Endites and labium yellowish-brown. Width of the labium is approximately two-thirds the length. Sternum is also light brown with brown margin, nearly round and shrunk at the end, covered by brown setae. Palps yellowish-brown, without marking. Legs femur brown, dark blackish at one-fourth from the end, then yellowish-brown, tarsus ringed with blackish markings, tarsus and metatarsus of each leg slightly depressed anteriorly. Both legs and palps covered by brown setae and several long spines. Abdomen cylindrical, elongated anteriorly, with six paired sigilla; dorsum lower part brown, upper part yellowish-brown with greyish-brown triangular marking around cardiac mark; the elongated part greyish-brown, turning blackish-brown at the tip; venter dark brown, covered by black setae. Tip of the abdomen with four humps, and four blackish paired humps arranged in two rows along the lower abdomen (Fig. 7a–c, 8a, b). Epigynum with distinct long, straight scape, light yellow and gradually turning light brown at the tip. Scape long and wrinkled, spindle-shaped with strong ridge on the dorsal side. The length of the scape is approximately five times longer than the width. One-third from the tip flattened, with brownish sclerotised and recurved edge. The conjunction between scape and epigynum short and curved (Fig. 7d–g, 8c–e). Male unknown.





**Fig. 10.** Photographs of two described *Cyphalonotus* species. (a, b) Female *Cyphalonotus variabilis* sp. nov. with two horn-like protrusions on the apex of the abdomen. (c) Lateral view of a female *C. variabilis* sp. nov., without horn-like protrusions. (d) A female *C. variabilis* sp. nov. in a cryptic posture at a twig tip. (e) Male *C. variabilis* sp. nov. wandering around on silken threads. (f) Female *C. assuliformis* feeding.

## Remarks

The abdominal shape of the specimen from southern China matches the juvenile morphology of a specimen from north-east Vietnam (Simon 1909) that formed the original description of *C. assuliformis*. According to Dzulhelmi *et al.* (2015), among *Cyphalonotus* species only *C. assuliformis* possesses such a narrow, long, cylindrical abdomen. The simplest explanation based on the available taxonomic data and to avoid unnecessary synonymy, is that the specimen from China is the mature form of *C. assuliformis*.

## Distribution

Low altitude forest (North-east Vietnam to Southern China).

## Discussion

Our study of newly acquired specimens of *Cyphalonotus* confirmed the previous genus level status and revealed an undescribed species from Taiwan. We base the formal descriptions of *Cyphalonotus variabilis* sp. nov. from Taiwan and of *Cyphalonotus assuliformis* from Southern China (a species originally described from a juvenile specimen) on the comparative morphology of both sexes and results of a molecular species delimitation analysis. The newly provided sequence data also enabled phylogenetic re-analyses of the araneid matrix with the addition of

*C. variabilis* sp. nov. and *C. assuliformis*. Our phylogenetic results reject all four previous classification hypotheses and recover a well supported clade comprising *Cyphalonotus* + *Poltys* instead. The new data on male and female size variation confirm that all species of *Poltys* show eSSD (even reaching a 10-fold size difference) and reveal that *Cyphalonotus* and other related genera are relatively sexually monomorphic (SSD < 2.0). We conclude that *Poltys* represents a clade with an independent origin of eSSD.

## Phylogeny

Our phylogenetic results reject the four phylogenetic hypotheses as originally proposed in the literature (Table 1). Contrary to the hypotheses of Archer (1951, 1965), *Cyphalonotus* does not group with *Simonarachne* (synonym of *Eriovixia*), nor does the genus group with *Dolophones*. Also, rejecting the hypothesis of Smith (2005), *Araneus* is not the sister clade of *Cyphalonotus*. Finally, although our analyses do not confirm Poltyeae precisely as proposed by Simon (1895), these do recover a sister relationship between *Cyphalonotus* and *Poltys*, confirming a hypothesis from the hand-patched phylogeny of Pekár (2014). Future classification efforts should likely classify this clade as Poltynae. However, at this point, classification of Araneidae is too far from a consensus on the subfamilies and families (Kallal *et al.* 2018; Kuntner *et al.* 2019; Scharff *et al.* 2020), therefore we refrain from proposing this subfamily here.



## Evolutionary implications

We report here on novel natural history observations that sub-adult males of *Poltys*, the body size of which is no larger than that of newly hatched spiderlings, can be found intermixed within colonies of immature spiderlings. The implication of this finding agrees with the rearing experiment of Smith (2006b) in which male *Poltys* reached maturation after only 2–4 moults whereas females needed 11–18 moults. Such a maturation mismatch suggests that males must mate with females from previous generations. This interpretation suggests that the natural history and development that leads to eSSD in *Poltys* is unique, perhaps following an ultra-fast maturation strategy in males that results in a true case of male dwarfism or a combination of male dwarfism and female gigantism (Kuntner and Coddington 2020).

The modified abdomen and camouflaging behaviour of female *Poltys* may be involved in the evolution of eSSD (Cheng and Kuntner 2015). As large females need more moults to reach maturation, the time spent on foraging on the web is longer and therefore the risks imposed by predators are also higher for females than males. The modified abdomen and twig or leaf camouflaging, as a type of passive defence, presumably to increase survival rates (Pekár 2014), likely better protects large females. Alternatively, although small-sized males are considered to have higher climbing and rappelling ability when searching for mates (Moya-Laraño et al. 2002; Grossi and Canals 2015; but, see Quiñones-Lebrón et al. 2019), this may not be relevant to male *Poltys* dwarfs. Studies mentioned above hypothesise that agility only affects males of body sizes above a threshold (7.6 mm, 42.5 mg). However, males of most of the known eSSD Araneidae, including *Poltys*, are significantly below this threshold (Quiñones-Lebrón et al. 2019).

Our data reveal that *Cyphalonotus*, unlike the sister genus *Poltys*, are not close to the threshold of eSSD. Rather, *Cyphalonotus* species known from both sexes are sexually size monomorphic to moderately dimorphic (SSD from 1.05 to 1.5). According to our phylogeny, *Cyphalonotus* and other related genera are all relatively sexually monomorphic, implying that only *Poltys* is an eSSD lineage. This suggests an independent origin of eSSD in *Poltys*, one of multiple convergent evolutionary outcomes in orbweb spiders.

Previous studies hypothesise at least four (Hormiga et al. 2000) or nine (Kuntner et al. 2015) independent origins of eSSD across araneoid spiders. These eSSDs are usually relatively apical in phylogenies (Kuntner and Coddington 2020), usually found at the genus (Scharff et al. 2020) or even species levels (Framenau et al. 2010; Magalhães and Santos 2012). The four to nine origins of eSSD in orbweb spiders may be severely underestimated, as a study on *Micrathena*, for example, found six origins in this one genus (Magalhães and Santos 2012). Araneid taxa have apparently repeatedly evolved, lost and regained eSSD, and documented cases of independent origins of eSSD, such

as in *Poltys*, will shed important new light on this evolutionary phenomenon that has perplexed researchers for decades (Darwin 1871; Hormiga et al. 2000; Foellmer and Moya-Laraño 2007; Kuntner and Elgar 2014; Kuntner and Coddington 2020). Furthermore, independent cases of eSSD may reveal predictable evolutionary correlates of extreme phenotypic traits (Kuntner and Coddington 2020), such as developmental pathways, web architectures, mating rituals and other aspects of natural history, and the costs of eSSD.

## Taxonomy

Our examination of the Asian *Cyphalonotus* species and the second male description in this genus confirm the validity of the diagnostic features for the genus that were previously based solely on African exemplars (Simon 1895; Archer 1951; Smith 2005). Smith's (2005) morphological trait matrix of *Cyphalonotus* categorised the epigynal scape as a 'normal scape', as the length did not exceed five times the width (Scharff and Coddington 1997). *C. assuliformis* possesses the longest epigynal scape of known *Cyphalonotus* species that reaches the limits of a 'normal scape', questioning the taxonomic validity of this characteristic.

## Conclusions

Studying poorly known taxonomic diversity is important not only to understand global biodiversity patterns, but also to potentially shed light on evolutionary phenomena. We demonstrated this for *Cyphalonotus*, the species diversity, taxonomic composition and phylogenetic placement of which were previously virtually unknown. By demonstrating a sister relationship to *Poltys*, and collecting information on the natural history and phenotypic variation, we pinpointed an independent origin of extreme SSD in this clade of orbweb spiders.

## Supplementary material

Supplementary material is available [online](#).

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