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Weygoldtia, a new genus of Charinidae Quintero, 1986 (Arachnida, Amblypygi) with a reappraisal of the genera in the family☆

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ABSTRACT

The modestly diverse order Amblypygi Thorell, 1883 includes five families, of which Charinidae Quintero, 1986 is the most diverse and with the widest geographical distribution. The family currently comprises three genera, *Catageus* Thorell, 1889, *Charinus* Simon, 1892 and *Sarax* Simon, 1892, the first known by one species from a single locality in Myanmar, the second with currently 74 species globally distributed, and the last with 17 species present in Southeast Asia and India. In this paper we describe and illustrate a new genus to accommodate the species *Sarax davidovi* Fage, 1946 based on unique characters. *Weygoldtia* gen. nov. (Laos, Vietnam and Cambodia) is supported by two synapomorphies: the presence of a straight crest anterior to the lateral eyes and the longitudinal orientation of the rod sensilla on tarsus of leg I. The new genus can be distinguished from *Charinus* and *Sarax* by the number of trichobothria on distitibia IV and the presence of one or two setae on the base of the cleaning organ on pedipalp tarsus. The enigmatic species *Catageus pusillus* Thorell, 1889 (the single species in the genus) is here synonymized with *Stygophrynus cavernicola* (Thorell, 1889) (family Charontidae Simon, 1892) and a neotype is designated. As *Stygophrynus cavernicola* is the type species of the genus, the synonymization of the two species results in the synonymy of the genera. Following the principle of priority, *Catageus* is maintained and all nine species of *Stygophrynus* Kraepelin, 1895 now have the following new combination: *Catageus berkeleyi* (Gravely, 1915), comb. nov., *C. brevispina* (Weygoldt, 2002), comb. nov., *C. cavernicola*, comb.nov., *C. cerberus* (Simon, 1901), comb. nov., *C. dammermani* (Roewer, 1928), comb. nov., *C. longispina* (Gravely, 1915), comb. nov., *C. moultoni* (Gravely, 1915), comb. nov., *C. orientalis* (Seiter and Wolf, 2017), comb. nov. and *C. sunda* (Rahmadi and Harvey, 2008), comb. nov.

1. Introduction

Whip spiders are conspicuous animals with large and spiny pedipalps and long sensorial first pair of legs. The order currently includes 17 genera in five families (Charinidae Quintero, 1986, Charontidae Simon, 1892, Phrynidae Blanchard, 1852, Phrynichidae Simon, 1900 and Paracharontidae Weygoldt, 1996) and is therefore the second most diverse order in Pedipalpi (after Schizomida) (Harvey, 2013; Weygoldt, 1996). The 220 whip spider species currently known have a pantropical distribution, inhabiting a diversity of climates, such as dry areas in Africa and humid rainforests in South America and Asia (Weygoldt, 2000; Zhang, 2013).

The first phylogenetic assessment of Amblypygi families and genera was done by Weygoldt (1996), and his hypothesis of relationship is considered the scaffold of the current classification of the order (Garwood et al., 2017). In the current phylogenetic tree of the living families, Paracharontidae is the sister group to all other families (Euamblypygi), followed by Charinidae as the sister to Neoamblypygi, which includes Phrynidae, Phrynichidae and Charontidae, with the first two more closely related to each other than to the latter (see figure 52 of Weygoldt (1996)). Within

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Charinidae, Weygoldt (1996) could not resolve the relationship of the genera known at that time (*Sarax* Simon, 1892, *Phrynichosarax* Gravely, 1915, *Tricharinus* Quintero, 1986, *Charinus* Simon, 1892, *Charinides* Gravely, 1911 and *Catageus* Thorell, 1889) and, despite several taxonomical rearrangements (Delle Cave, 1986; Harvey, 2003; Weygoldt, 2000), there was no other attempt to understand the relationship of the genera.

Charinidae is the most diverse family of whip spiders, with 92 described species. The family has a circumtropical distribution (Fig. 1) and the highest diversity in the Neotropics. Currently, Charinidae includes three genera: *Catageus*, *Charinus* and *Sarax*. The first genus has only one described species from a cave in Myanmar; *Charinus* has 74 species found in caves, in leaf litter, bromeliads and synanthropic areas in Africa, Asia, Europe, Oceania, and the Americas (except North America); and *Sarax* includes 17 species that are restricted to Southeast Asia and India, inhabiting the same type of habitats as *Charinus* species (which might explain the rare finding of sympatric species of the two genera).

Charinidae went through various taxonomical changes in recent years (summarized by Rahmadi et al. (2010)) and currently includes only the three above cited genera (*Catageus Charinus* and *Sarax*). Several papers described and redescribed species within these genera (Armas, 2006; Delle Cave et al., 2009; Giupponi and Miranda, 2012; Miranda et al., 2016a; Miranda and Giupponi, 2011; Miranda et al., 2016b; Miranda et al., 2016c; Rahmadi et al., 2010; Rahmadi and Kojima, 2010; Seiter and Wolff, 2014; Seiter et al., 2015; Torres-Contreras et al., 2015; Vasconcelos et al., 2016; Vasconcelos and Ferreira, 2016; Vasconcelos and Ferreira, 2017; Vasconcelos et al., 2013, 2014; Weygoldt, 2006), but none presented a thorough revision of species and genera or phylogenetic evidence for its monophyly.

Based on distinguishing morphological characters supported by the results of a morphological and molecular phylogenetic analysis of the family (Miranda et al., unpublished) we here describe a new genus of Charinidae to accommodate the species *Sarax davidovi* Fage, 1946. We also investigate the validity of the genus *Catageus* after analyses of new material from the type locality.

2. Material and methods

Specimens were studied under a Leica M205AC stereo microscope, provided with a camera lucida for drawing. Measurements of pedipalp segments were taken between the external condyles of each segment in order to establish fixed points and proper length measurements (Baptista and Giupponi, 2002).

Spines on the pedipalp patella and teeth of the chelicerae are counted from base to apex. Sensilla terms on the first leg follow Foelix et al. (1975) and Igelmund (1987). Terminology of the male gonopod parts follows Giupponi and Kury (2013). The taxonomical discussion in the description of *Weygoldtia* already considers *Catageus* as the senior synonym of *Stygophrynus* in Charontidae.

Photographs were taken with a BK plus Imaging System from Visionary Digital (Palmyra, PA, USA; http://www.visionarydigital.com/) equipped with a Canon 7D digital camera at the Zoological Museum, University of Copenhagen (ZMUC). Stacks of images from multiple focal planes were combined using Zerene Stacker (Zerene Systems LLC, http://zerenesystems.com/cms/stacker) and processed in Photoshop CS6 (Adobe, San Jose, CA, USA) to adjust for color, brightness, and contrast. Plates were mounted in Adobe InDesign.

Scanning electron micrographs were taken with a JEOL JSM-6335F scanning electron microscope. SEM images were generated at the Zoological Museum, University of Copenhagen. Specimens were first dehydrated in a series of ethanol concentrations from 75% to 100% ethanol with 10% differences between consecutive concentrations and for 20–30 min in each concentration and finally stored overnight in 100% ethanol. Specimens were subsequently cleaned ultrasonically for 30 s using a Branson 200 sonicator of 40 kHz frequency (Danbury, CT, USA). Parts of the specimens to be mounted were then critical point dried using a Baltec CPD-030 dryer (Balzers, Liechtenstein). Dried parts were attached to round-headed rivets using aluminum tape with conductive adhesive and coated with platinum-palladium in a JEOL (Tokyo, Japan) JFC-2300HR high resolution coater.

Additional material examined

Charinus australianus (Koch, 1867): Samoa, Upolu Island (holotype, unknown sex due to lost opisthosoma, ZMUH 2281);

Charinus dominicanus Armas and González, 2002: Dominican Republic, Barahona Province, La Ciénaga Municipality, 3.4 Km N of Paraiso on DR 44, small farm with coffee plantation [18º0'56.46N̈ 71º8'40.62Ẅ, **new record**], S. of Barahona, Sierra de Bahoruco, 7–8.vii.2010, 115m, J. Huff and S. Schoenbrun leg., J. Huff det., (1 male, AMNH GSM 94);

Charinus neocaledonicus Simon, in Kraepelin, 1895: New Caledonia, Grande Terre Island, (male holotype, MNHN);

Charinus papuanus Weygoldt, 2006: Papua New Guinea, 6 km W of University of Papua New Guinea (U.P.N.G.), Port Moresby, National Capital District, under rocks, vi.1980, D. Black *leg.* (holotype male, WAM T68999);

Paracharon caecus Hansen, 1921: Guinea, Rio Cassine (12°N), 1900, L. Fea *leg.* (1 syntype female, ZMUC 245556);

Sarax brachydactylus Simon, 1892: Philippines, Luzon, Grotto de Antipolo (1 female, 1 male, NHM 1894.12.16.1-2);

Sarax huberi Seiter et al., 2015: Philippines, Cebu, surrounding of the Busay cave, Moalboal, iii.2008, S. Huber *leg.* (1 paratype female, SMNS);

Sarax javensis (Gravely, 1915): Indonesia, E. Java, Pacitan, Gua Kamidordo, Juguono *leg.* (2 females, 2 juveniles, WAM T80541);

Sarax rimosus (Simon, 1901): Malaysia, Kuala Aring, Kelantan, ix.1899, Skeat Expedition *leg.* (holotype female [with egg sac], CUMZ I.48100);

Stygophrynus cavernicola (Thorell, 1889): Myanmar, Mon, Mawlamyine, Kayan Gu, day time, 16.53324° 097.71501°, 27 m, 30.vii.2016, A. Giupponi & A. Kury leg. (3 females, 1 male, MNRJ 9352); Kayin State, Hpa-An, Saddan Cave, day time, 16.739735° 097.718175°, 250 m, 31.vii.2016, A. Giupponi & A. Kury leg. (11 females, 4 males, 2 juveniles, MNRJ 9353; 2 females, 2 males, 2 juveniles, CAVAISC ARA no number; 1 female, 4 juvenile, CAVAISC ARA no number).

Material was examined from the following collections:

AMNH	American Museum of Natural History, New York (Lorenzo Prendini);
CAVAISC	Coleção de Artrópodes Vetores Ápteros de Importância em Saúde das Comunidades, Rio de Janeiro (Marinete Amorim);
CUMZ	Cambridge University Museum of Zoology, UK (Matt Lowe);
MNHN	Muséum National d'Histoire Naturelle, Paris (Mark Judson);
MNRJ	Museu Nacional, Rio de Janeiro (Adriano Kury);
NHM	The Natural History Museum, London (Janet Beccaloni);
SMNS	Staatliches Museum für Naturkunde Stuttgart, Stuttgart (Joachim Holstein);
WAM	Western Australian Museum, Perth (Mark Harvey);
ZMUC	Zoological Museum of Copenhagen, Copenhagen (Nikolaj Scharff);

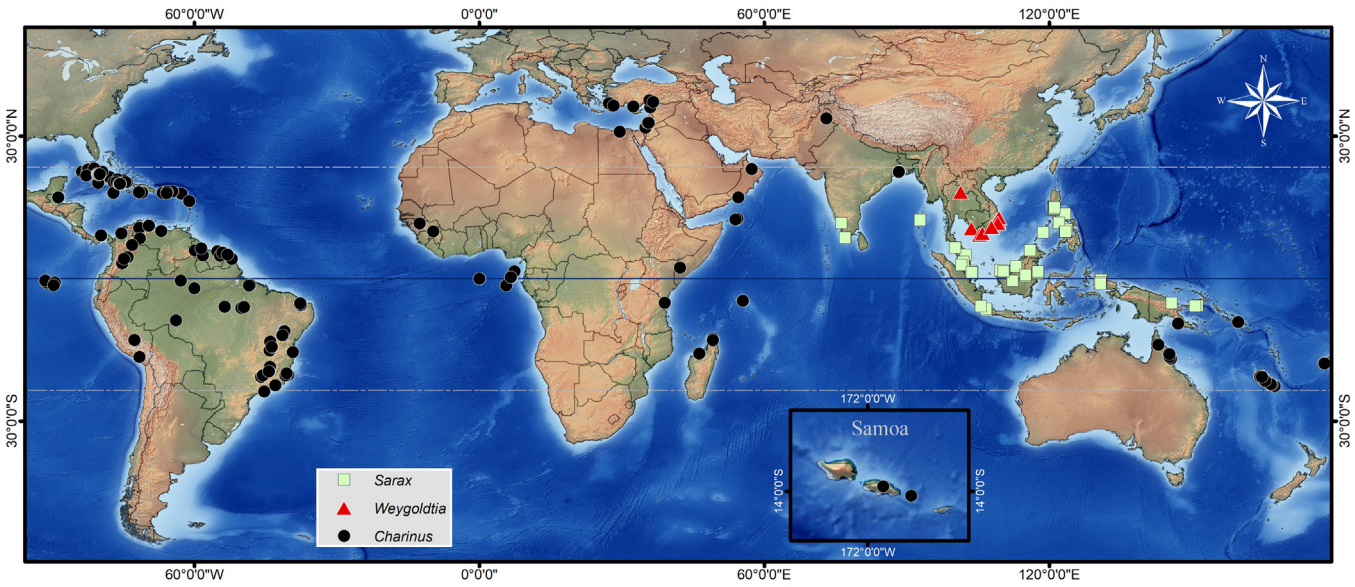

Fig. 1. Distribution map of the new accepted genera of Charinidae Quintero, 1986: *Charinus* Simon, 1892, *Sarax* Simon, 1892 and *Weygoldtia* gen. nov.

ZMUH Zoologisches Museum für Hamburg, Hamburg (Matthias Glaubrecht).

3. Results

Key to the genera of Charinidae

1. Distitibia IV with 6–9 and 7–8 trichobothria in caudal and frontal series, respectively (Fig. 4A); carapace with straight crest anterior to lateral eyes (Fig. 2A); 1 or 2 setae at base of cleaning organ..... ***Weygoldtia***

1'. Distitibia IV with 5–6 trichobothria in frontal and caudal series (Fig. 4B, C); carapace without straight crest anterior to lateral eyes; no setae at base of cleaning organ..... **2**

2 Abdomen without ventral sac cover; lateral eyes with seta behind the triad..... ***Charinus***

2'. Abdomen with ventral sac cover; lateral eyes with setae lateral to triad..... ***Sarax***

3.1. Taxonomy

Family Charinidae Quintero, 1986

Genus *Weygoldtia* gen. n

Type species: *Weygoldtia davidovi* (Fage, 1946), by monotypy.

Etymology: The new genus is named in honor of the arachnologist Peter Weygoldt, one of the greatest contributors to the study of Amblypygi. Peter Weygoldt's first published on whip spiders in 1969 (Weygoldt, 1969); since then, he published almost 60 works (papers, book chapters and entire books) on whip spider systematics, behavior and anatomy, pushing forward the research in the field like no other scientist before him. Among the more than 50 works published as single or first author, Weygoldt produced the much acclaimed book "Whip Spiders: Their Biology, Morphology and Systematics" (Weygoldt, 2000), which summarizes all knowledge on Amblypygi and continues to be the main reference to the order.

Diagnosis: Carapace frontal setae more distant from each other than in *Sarax* and *Charinus*; straight crest present anterior to lateral eyes (Fig. 2A); leg I, tibia with 25 articles and tarsus with 44 or 45; leg I, rod sensilla in a longitudinal groove; 1 or 2 setae present at base of ventral row of cleaning organ; distitibia IV with 6–9 trichobothria on *sc* and 7–8 on *sf* (Fig. 4A). Some of this character states are also found in *Catageus* (Charontidae), however, *Weygoldtia* can be distinguished from species of Charontidae, by the number of spines on dorsal and ventral pedipalp tibia (two dorsal spines and one ventral spine in the charinid genera and more than two spines in *Catageus* and *Charon*), the shape of the carina on the pedipalp trochanter (rounded in *Weygoldtia* and triangular in Charontidae), and the number of trichobothria on the frontal and caudal series of the distitibia of leg IV. Moreover, the frontal and caudal series of trichobothria in *Catageus* extends to close to the proximal end of the article, whereas in *Weygoldtia*, the series is restricted to the distal third of the distitibia, as in other charinids.

Distribution: Cambodia, Laos, Vietnam.

Weygoldtia davidovi (Fage, 1946)**, comb. nov.**

Sarax davidovi Fage (1946): 76–77, figs 2, 3a, 4; Harvey (2003): 8; Rahmadi et al. (2010): 10, 11, 19; Seiter et al. (2015): 547–550.

Material examined: ***Syntypes***: *Vietnam* (as Annam): Phan Rang, iii–iv.1939, Mission Dawydoff, 1938–39, (3 males, MNHN); Ba Ngoi [11°54′27.23″N 109°7′21.37″E], x.1938, Mission Dawydoff, 1938–39, Indochine (2 females, plus 1 specimen MNHN); Gia Rai (as Giaray) [09°15′36.51″N 105°22′31.11″E], Bac Liêu, xii.1938–iii.1939, Mission Dawydoff, 1938–39, Indochine (2 males and 3 juveniles, MNHN); Sóc Traeng [09°36′9.01"N 105°58′25.95"E], Sóc Traeng, xi.1938, Mission Dawydoff, 1938–39, Indochine (1 male, MNHN). *Laos*: Pak Lay [18°13′50.03″N 101°24′30.12″E], Xiangnabouli, i.1939, Mission Dawydoff, 1938–39, Indochine (1 juvenile, MNHN). *Cambodia*: Ream [10°35′2.75″N 103°38′35.34″E], iii.1939, Mission Dawydoff, 1938–39, Indochine (1 female, 2 juveniles, MNHN).

Non-type: *Vietnam*: Ninh Hòa (as Ninhoa) [12°30′38.89N̈ 109°9′52.35″E], Khan Hoa Province, iii.1939, Mission Dawydoff, 1938–39, Indochine (1 female, MNHN); NHA Trang (as Nhatrang) [12°14′20.28″N 109°11′12.49″E], Khanh Hoa Province, vi.1939, Mission Dawydoff, 1938–39, Indochine (3 juveniles, MNHN); same data as previous, iv.1939, Collection Dawydoff, Indochine, 1938–39 (1 female, MNHN); Vung Ro Bay (at the foot of [Cape] Varella) [12°52′48.29″N 109°26′39.29″E], vi.1939, Mission Dawydoff, 1938–39, Indochine (2 males, 2 females, MNHN); Nui Chua National Park [11°42′31.90″N 109°11′12.70″E, **new record**], Ninh Hai District, Ninh Thuan Province, 24.vi.2012, 98 m asl., L. Prendini and S.F. Loria *leg.*, dry deciduous forest on rocky

Fig. 2. General view of *Weygoldtia davidovi* (Fage, 1946). **A**. Dorsal view. **B**. Ventral view of sternum. **C**. Frontal view of frontal process. **D**. Dorsal view of pedipalp tarsus; arrows indicate the pair of setae at the base of the cleaning organ. **E**. Dorsal view of pedipalp. **F**. Ventral view of pedipalp. Scale bars: A, B, E, F: 1 mm; C: 0.1 mm; D: 0.5 mm.

granite/sandstone hills near coast, dry, coarse granitic sandy-loam soil, specimen collected under stone (1 male, AMNH [LP 1377]); Bin Thuan Province, Ham Thuan Nam Distr., Ta Kou Mountain Nature Reserve, Ta Kou Mountain (Nui Ta Kou) [10°49′01.9″N 107°53′49.3″E, **new record**], 23.vi.2012, 592 m asl., L. Prendini and S.F. Loria *leg*., trail above pagoda, rocky ravine on opposite side of summit, primary rainforest with dense stands of bamboo in rocky ravine below summit of inselberg surrounded by farmland, moderate to dense canopy with sparse to moderate understorey, brownish-grey sandy/clayey-loam soil with sandstone outcrops and scattered boulders, moderate leaf litter layer, moist soil, specimen taken from under stone (1 female, AMNH [LP 11375])

Diagnosis: prominent carina below the lateral eyes (Fig. 2A); straight crest projecting from lateral carina to frontal region (Fig. 2A); pedipalp trochanter with few setae; pedipalp femur with 2 or 3 large setiferous tubercles anterior to spine 1; one spine between tibia spine I and distal border (Fig. 2E); ventral sac cover present; tibia I with 25 and tarsus I with 45 articles; *sc* with 6 or 7 and *sf* with 7 or 8 trichobothria (Fig. 4A).

Description: **Carapace** (Fig. 2A) with small granules densely scattered between the lateral eyes and among the sulci. Median eyes and tubercle well developed; one pair of setae on median ocular tubercle; lateral eyes well developed, with one setae posterior to triad; lateral ocular triad close to border of carapace; corners of anterior margin extending ventrally in a wide, roundish boss; curved crest present between lateral eyes and border of carapace; straight crest anterior to the lateral eyes, extending near to median ocular tubercle; six thin and short frontal setae on frontal border of carapace; frontal process triangular.

Tritosternum (Fig. 2B) projecting anteriorly, with a pair of large setae close to apical pair of setae; tritosternum long, surpassing base of pedipalp coxae; other sternal platelets narrow and concave, each with pair of setae on the top and smaller ones on the base; pentasternum without setae close to membranous region and four setae distally.

Chelicera with short projection on ectal surface, opposite bifid tooth; ectal surface of cheliceral claw with row of setae extending to dorsal surface of the claw; cheliceral claw with 7–9 teeth; basal segment of chelicerae with more than 15 setae arranged in more than two rows on mesal surface; row of teeth on basal segment with bifid tooth and upper cusp larger than lower.

Abdomen (Fig. 2A) with short ventral sac cover. Male genitalia (Fig. 4E) with strongly sclerotized distal border of fistula and base of lateral lobe; lateral lobe 2 (LoL2) fimbriated with short projections. Dorsal lobe (LoD) extending upwards, enfolding LoL1. Posterior margin of female genital operculum (GO) slightly concave, with several setae along margin and on its surface (Fig. 3A). Pair of glandular openings on opposite sides close to lateral border of GO (Fig. 3B). Gonopods cushion-like, rounded, concave, wrinkled at base (Fig. 3C, E). Atrium of gonopod covered by flap-like projection with two protuberances: one on distal apex (forming small finger-like projection) and one mediolaterally. Glandular openings present in genital atrium (Fig. 3D). Inner distal border of genital operculum with smooth (opposed to denticulate) surface (Fig. 3F).

Pedipalp coxal carina with two setae at frontal border and no setae inside the round carina. Pedipalp **trochanter** with long, swollen setae close to apex of ventral apophysis; trochanter with several long and thin setae between two ventral spines. Pedipalp **femur** (Fig. 2E, F) with five dorsal and four ventral spines; ventral spine 1 apical third covered with several long, thin setae similar to those on trochanter; males with one small dorsal spine between spines 1–2, 2–3 and 3–4; femur dorsal with 2–3 spines and one prominent setiferous tubercle between first spine and proximal margin of segment; femur ventral with one short spine between spines 1–2 and 2–3; femur ventral with one long spine between spine 1 and proximal margin of the segment. Pedipalp **patella** (Fig. 2E, F) with six dorsal spines; one prominent spine distal to spine I, 1/3 its size; patella ventral with four spines; one small spine between each ventral spine of main series; one long, curved spine between spine I and distal border. Pedipalp **tibia** (Fig. 2E, F) with two dorsal spines, proximal spine one third the distal; ventrally with one distal spine and one seta between spine and distal margin. Pedipalp **tarsus** (Fig. 2D) with two or three short, equally sized dorsal spines; one or two short setae close to base of cleaning organ; ventral row of cleaning organ with 26 setae in ventral row.

Tibia I with 25 articles; tarsus I with 44 or 45 articles; first tarsal article same size as next article. Tip of leg I with small modified claw, emerging from common base. Lateral claws longer than middle claw. Segments covered with at least two sensilla types, bristle sensilla (long) and club sensilla (short). Bristle sensilla present on all segments of tarsus and tibia I; club sensilla only on first 3 or 4 segments (counting from distal to proximal) of tarsus I. Ventrally, tip segment of tarsus I has shallow longitudinal groove with several olfactory setae (rod sensilla). **Basitibia IV** divided into four pseudo-articles, with sclerotized, denticulated projected border at apex of each article; *bt* situated in distal third of pseudo-article (Fig. 4A); **distitibia IV** (Fig. 4A) with trichobothria *bc* closer to *bf* than to *sbf*, and *sc* with 6 or 7 and *sf* with 7 or 8 trichobothria.

Color pattern (alcohol preserved material). Chelicerae, pedipalps, carapace, and abdomen yellowish-brown; tibia and tarsus of legs lighter colored.

Measurements (3 males, in mm). Carapace: length 4.39 (4.16–4.80), width 6.61 (6.08–7.36). Pedipalp: Femur 6.39 (4.81–9.60), Patella 6.59 (4.88–10.00), Tibia 2.12 (2.00–2.50), Tarsus 1.59 (1.48–1.50), Claw 1.04 (0.93–1.18). Leg I: Femur 11.07 (9.87–13.46). Leg IV: Femur 6.37 (5.84–7.28), Basitibia I 3.71 (3.50–4.38), Basitibia II 1.14 (1.00–1.38), Basitibia III 1.14 (1.08–1.25), Basitibia IV 1.18 (1.16–1.38), Distitibia 2.56 (2.40–2.88), Basitarsus 0.98 (0.90–1.04), Other tarsal articles 1.07 (1.0–1.20).

3.2. Stygophrynus *Kraepelin, 1895 (Charontidae) is a junior synonym of* Catageus *Thorell, 1889*

The genus *Stygophrynus* (Charontidae) is among the most poorly studied genera of Amblypygi (Rahmadi and Harvey, 2008). Despite the large size of the animals in this genus (body length up to 2.5 cm; Weygoldt (2000)), there is no study exploring thoroughly its taxonomy.

The type species of *Stygophrynus* is *S. cavernicola* (Thorell, 1889), which occur in Myanmar and Thailand and was first placed in *Charon* (Thorell, 1889). In the same paper, Thorell (1889) described *Catageus pusillus*, a smaller animal found in the same cave as *S. cavernicola*. Kraepelin (1895) had access to the type material of *S. cavernicola* and *C. pusillus* and provided figures of the pedipalp patella, tibia and tarsus. Börner (1904) also examined the type specimens and mentioned that they are a male and a female. Gravely (1915a) claimed to have new material from the type locality and provided a simple illustration, similar to that of Kraepelin (1895). Delle Cave (1986) reported that the type specimens of both species are lost, information that was recently confirmed (M. Tavano, pers. com.).

According to depictions in the literature, the size and number of spines on the pedipalp of *Catageus pusillus* indicate that the type specimens are juveniles. Thorell (1889) described *C. pusillus* as having pedipalp femur with three dorsal and three ventral spines, pedipalp patella with five dorsal and two ventral spines, and pedipalp tibia with two dorsal and one ventral spine. Quintero (1986) placed *Catageus* within Charinidae based on the combination of these characters. The description of *C. pusillus* and the illustration available do not mention the presence of extra smaller spines on the pedipalp tibia between the main spine and the distal margin (as is common among *Stygophrynus* species) and this could be either due to absence of those spines in early stages of development or that the authors overlooked them, as it seems so, as the ventral spines were not shown by Kraepelin (1895) and Gravely (1915a).

In an effort to find new specimens of both species (*S. cavernicola* and *C. pusillus*), one of the authors (APLG) visited the type locality in Myanmar in 2016. After several days of exploration of the cave in different depths, no species similar to *C. pusillus* was found. Only the large and abundant *S. cavernicola* was present.

It is known that the number and size of spines on the pedipalp change during the ontogeny of large amblypygids (Weygoldt, 1995,

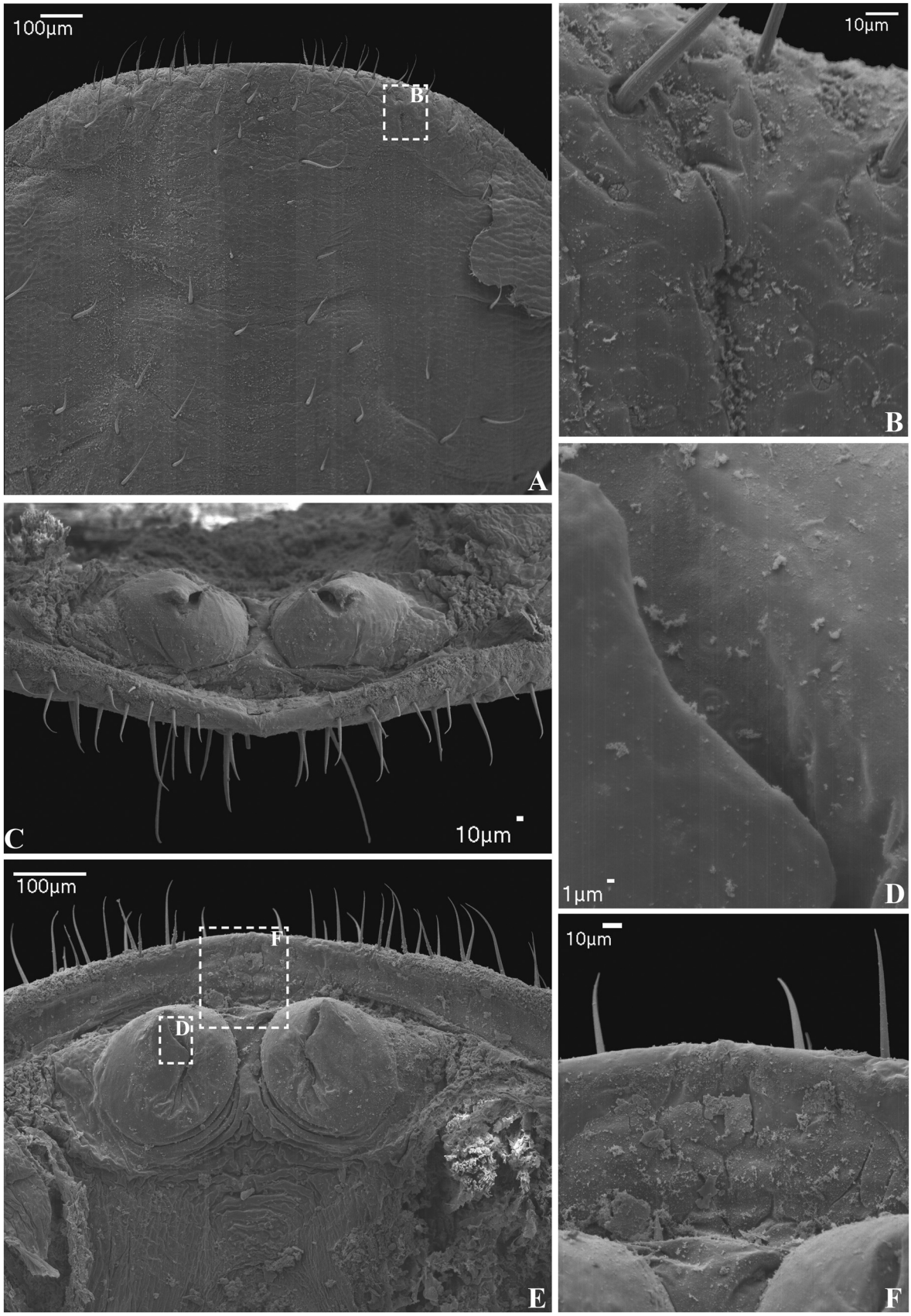

Fig. 3. Details of female gonopod of *Weygoldtia davidovi* (Fage, 1946). **A**. Ventral view of genital operculum. **B**. Detail of genital operculum showing glandular opening (ventral view). **C**. Posterior view of gonopod. **D**. Detail of the left genital atrium showing glandular opening. **E**. Dorsal view of female gonopod. **F**. Detail of posterior end of genital operculum (dorsal view). Values of scale bars in the figures.

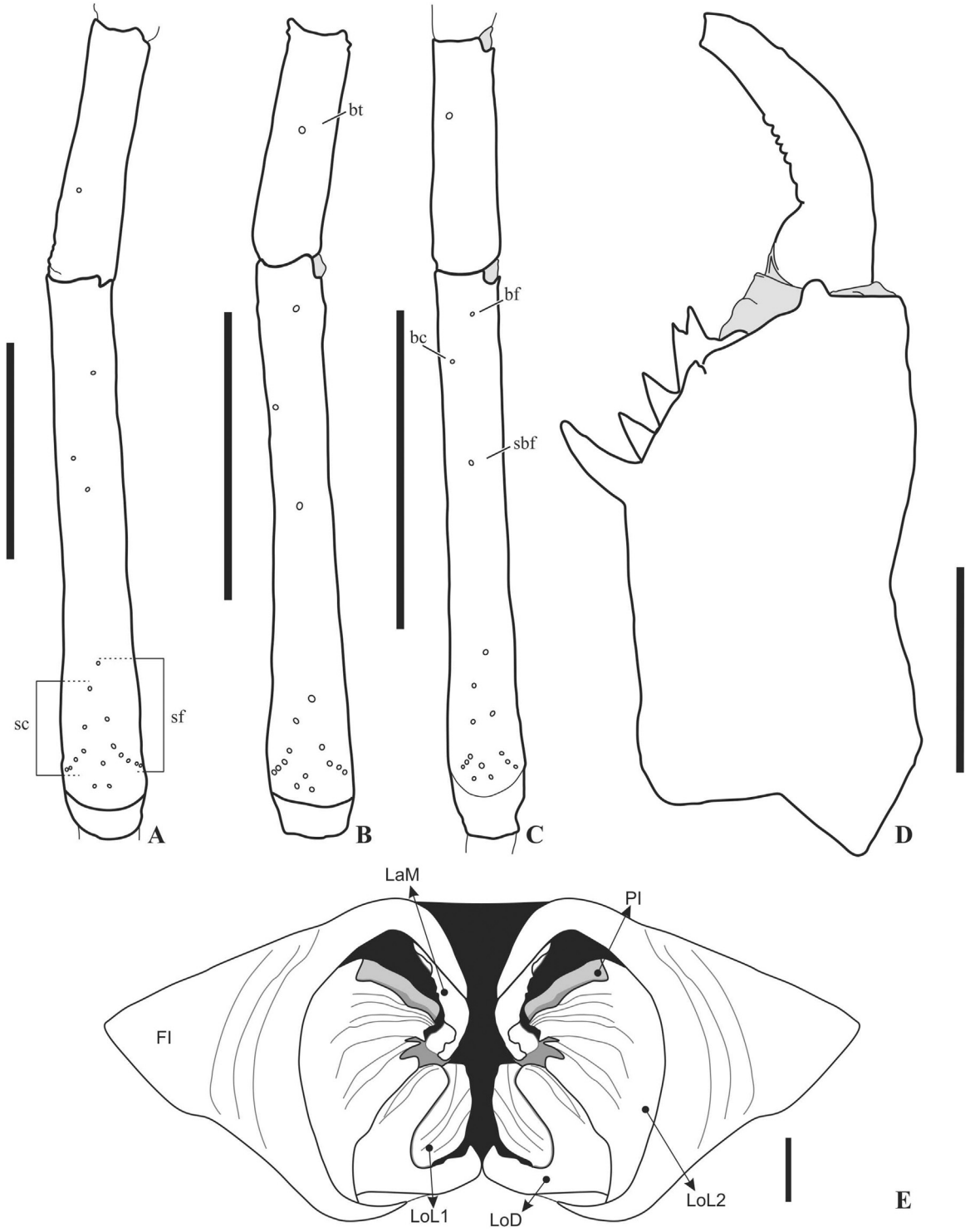

Fig. 4. Trichobothria of distitibia of right leg IV, chelicera and male genitalia. **A**. Basitibia and distitibia of leg IV of *Weygoldia davidovi* (Fage, 1946). **B**. Basitibia and distitibia of leg IV of *Charinus neocaledonicus* Simon, in Kraepelin, 1895. **C**. Basitibia and distitibia of leg IV of *Sarax brachydactylus* Simon, 1892. **D**. Ectal view of left chelicera of *Weygoldia davidovi*. **E**. Posterior view of male genitalia of *Weygoldia davidovi*. Scale bars: A-D, 1 mm; E, 0.1 mm.

2000). In most species of whip spiders small juveniles have a completely different arrangement of spines than adult individuals (Weygoldt, 1977, 1998). In phrynichids, some of the spines on the tibia get smaller, while spines on the patella get larger (Weygoldt, 1995, 2000). It is still not known what is the fate of the pedipalp spines in *Stygophrynus*, but in face of the evidences gathered, we conclude that *C. pusillus* was mistakenly described based on juveniles of *Stygophrynus cavernicola* collected in the same cave by L. Fea and described by Thorell (1889) as two different species. Thorell was one of the most prolific arachnologists in history (Platnick and Raven, 2013), but he repeatedly described juveniles as new species (Framenau, 2008; Kovblyuk et al., 2013; World Spider Catalog, 2017), and this is very likely one more of such case.

Therefore, *C. pusillus* is synonymized with *S. cavernicola*, being, accordingly, transferred to Charontidae. Both species were described in the same paper, so one has no priority over the

other; the name (epithet) *cavernicola* is maintained. The species *Stygophrynus cavernicola* is the type of the genus, so the synonymy of *Stygophrynus* with *Catageus* results in new combinations for all *Stygophrynus* species, as *Catageus* is the oldest available name (Article 23 of the ICZN (1999)). The change in name does not change the diagnosis of the family Charontidae and its genera, it affects only the nomenclature of the groups. A neotype to *Catageus* is designated.

Catageus Thorell (1889)

Catageus Thorell (1889): 530; Simon (1892): 48; Kraepelin (1895): 47; Kraepelin (1899): 251 (as *Catagius* [sic]); Pocock (1900): 130; Gravely (1915a): 437; Mello-Leitão (1931): 54; Werner (1935): 470; Weygoldt (2000): 25; Harvey (2002a): 470, 473; Harvey (2002b): 364; Harvey (2003): 3; Rahmadi and Kojima (2010): 476; Rahmadi et al. (2010): 2, 3; Giupponi and Miranda (2012): 165; Engel and Grimaldi (2014): 3; Pyron et al. (2014): 250.

Stygophrynus Kraepelin (1895): 44; Kraepelin (1899): 248; Pocock (1900): 129; Gravely (1915b): 443; Mello-Leitão (1931): 53; Werner (1935): 471; Weygoldt (2000): 25; Weygoldt (2002): 133; Harvey (2003): 10; Rahmadi and Harvey (2008): 281, 282; Rahmadi et al. (2010): 19; Rahmadi et al. (2011): 225. [**NEW SYNONYM**]

Stygophrynus (*Stygophrynus*) Kraepelin: Harvey (2003): 10. [**NEW SYNONYM**]

Type species:

of *Catageus*: *Catageus pusillus* Thorell, 1889, by original designation.

of *Stygophrynus*: *Charon cavernicola* Thorell, 1889, by original designation.

Neotype: Myanmar, Mon, Mawlamyine, Kayan Gu, Kha Yone cave (Kha Yon or Farm cave), day time, 16.53324° 097.71501°, 27 m, 30.vii.2016, A. Giupponi & A. Kury leg. (male, MNRJ 9354).

Records: Southeast Asia.

Catageus berkeleyi (Gravely, 1915)**, comb. nov.**

Stygophrynus berkeleyi Gravely (1915a): 445, 446, fig. 11 ; Speijer (1937): 173, figs 1–3; Mello-Leitão (1931): 53; Harvey (2003): 10; Seiter and Wolff (2017): 399, 406.

Type locality: Lenggong, *Perak*, Malaysia.

Distribution: Malaysia.

Catageus brevispina (Weygoldt, 2002)**, comb. nov.**

Stygophrynus brevispina Weygoldt (2002): 133–135, 142, 143, figs 1–8, 23–25; Seiter and Wolff (2017): 399, 406, 407.

Type Locality: Ko Siray, Phuket Island, Phuket, Thailand.

Distribution: Thailand

Catageus cavernicola (Thorell, 1889)**, comb. nov.**

Charon cavernicola Thorell (1889): 538–542.

Stygophrynus cavernicola (Thorell, 1889): Kraepelin (1895): 44, figs 32, 37; Kraepelin (1899): 248, fig. 9 2 ; Pocock (1900): 130, figs 44a, b; Kraepelin (1901): 265; Börner (1904): 5; Annandale and Gravely (1914): 407, 418, 419; Gravely (1915a): 444, 445; Gravely (1915b): 526; Mello-Leitão (1931): 53–54; Werner (1935): 471; Wolf (1938): 537; Vandel (1965): 93; Delle Cave (1986): 161–162; Deharveng and Leclerc (1989): 94; Harvey (2003): 10.

Catageus pusillus Thorell (1889): 531–538; Kraepelin (1895): 47, figs 34, 39; Kraepelin (1899): 251, fig. 94 (as *Catagius* [sic] *pusillus*); Pocock (1900): 130, figs 44c, d; Annandale and Gravely (1914): 407, 419 (as *Catagius* [sic] *pusillus*); Gravely (1915a): 437, fig. 1; Gravely (1915b): 526 (as *Catagius* [sic] *pusillus*); Mello-Leitão (1931): 54; Werner (1935): 470, fig. 174 (as *Catagaeus* [sic] *pusillus*); Wolf (1938): 537; Vandel (1965): 93 (as *Catagaeus* [sic] *pusillus*); Delle Cave (1986): 150; Weygoldt (1996): fig. 23 ; Weygoldt (2000): 25, fig. 16 ; Harvey (2003): 3; Rahmadi et al. (2010): 3. [**NEW SYNONYM**]

Type locality: Farm Caves, near Moulmein, Tenasserim, Mon, Myanmar.

Records: Myanmar, Thailand.

Catageus cerberus (Simon, 1901)**, comb. nov.**

Stygophrynus cerberus Simon (1901): 76, 77; Annandale and Gravely (1914): 407, 419; Gravely (1915a): 446, fig. 12 ; Gravely (1915b): 526; Mello-Leitão (1931): 54; Werner (1935): fig. 177b ; Wolf (1938): 537; Vandel (1965): 93; Harvey (2003): 10; Seiter and Wolff (2017): 399.

Type locality: Gua G'lap, near Biserat, *Pattani*, Thailand.

Distribution: Thailand.

Catageus dammermani (Roewer, 1928)**, comb. nov.**

Stygophrynus dammermani Roewer (1928): 16–19, figs 1–6; Giltay (1931): 24, 25; Mello-Leitão (1931): 54; Roewer (1933): fig. 3; Werner (1935): fig. 1; Dammerman (1948): 495, fig. 38 ; Janetschek (1957): fig. 7 ; Dubinin (1962): fig. 1270 ; Savory (1964): fig. 74 ; Somadikarta et al. (1964): 182; Savory (1977): fig. 45 ; Brusca and Brusca (1990): fig. 4e (as *Stegophrynus* [sic] *dammermani*); Harvey (2003): 10, 11; Rahmadi and Harvey (2008): 284–287, figs 2, 13–20; Seiter and Wolff (2017): 397, 399, 406.

Type locality: Guha Kuda (as Hóhle Goeha Koeda), near Lulut (as Loeloet), Buitenzorg (now Bogor), Java, *Jawa Barat*, Indonesia.

Distribution: Indonesia (Java, Verlaten Island).

Catageus longispina (Gravely, 1915)**, comb. nov.**

*Stygophrynus longispina*Gravely (1915a): 445, fig. 10 (as *Stygophrynus longispinus* [sic]): Mello-Leitão (1931): 54; Weygoldt (1994): 242; Weygoldt (1996): figs 4, 10, 24, 36, 41, 46, 48; Weygoldt (1999): 107, figs 6, 7; Weygoldt (2000): figs 12, 17, 105, 140, 206–207; Harvey (2003): 11; Seiter and Wolff (2017): 399, 406, 407.

Stygophrynus cf. *longispina* Gravely: Weygoldt (1990): fig. 4.

Type locality: Pulau Langkawi, *Kedah*, Malaysia.

Distribution: Malaysia.

Catageus moultoni (Gravely, 1915)**, comb. nov.**

Stygophrynus moultoni Gravely (1915a): 443, 444, fig. 9; Giltay (1931): 24, 25; Mello-Leitão (1931): 54; Werner (1935): fig. 177a; Quintero (1986): figs 2, 8; Seiter and Wolff (2017): 397, 399.

Stygophrynus (Neocharon) moultoni Gravely: Dunn (1949): 11.

Type locality: Klingkang Range, *Kalimantan Barat*, Indonesia.

Distribution: Indonesia (Kalimantan, Sumatra).

Catageus orientalis (Seiter and Wolf, 2017)**, comb. nov.**

Stygophrynus orientalis Seiter and Wolff (2017): 399–404, figs. 1–4, 5D–F.

Type locality: Indonesia, Central Sulawesi province, Island Banggai (Pulau Banggai),

Distribution: Indonesia.

Catageus sunda (Rahmadi and Harvey, 2008)**, comb. nov.**

Stygophrynus sunda Rahmadi and Harvey (2008): 282–284, figs 1, 3–12.

Type locality: Air Panas Cibiuk (=Hot Water spring), Desa Taman Jaya, Kecamatan Sumur, Kabupaten Lebak, Banten, Indonesia.

Distribution: Indonesia.

3.3. *Natural history of* Catageus cavernicola

The caves where specimens were collected (Kha Yone [also "Kha Yon" or "Farm cave", in the state of Mon] and Saddan cave [state of Kayin]) are in two independent limestone outcrops surrounded

by rice plantations. The mountain where Saddan cave is placed is densely covered with forest; the outcrop of Kha Yone cave has less vegetation coverage. Inside, the caves is intensely modified by humans and the cavities are used as religious temples.

Kha Yone and Saddan cave are 25 km apart from each other with a river in between. Both cavities have large aphotic areas, with high humidity and water running through its extension. Adult specimens were collected on the walls of the caves, and were seen hiding in cracks, and rarely found under stones on the ground. Juveniles, on the other hand, were encountered in large number under fallen stones, but also on the cave wall. Other arachnid species in common between the two caves are *Schizomus cavernicola* Gravely, 1912 (Schizomida) and *Heteropoda opo* Jäger, 2014 (Araneae). The scorpion *Plethoscorpiops profusus* Lourenço, 2017 (Scorpiones), was found in the same cave as the neotypes of *Catageus cavernicola*.

No specimen was found outside the caves visited, which indicate that *Catageus cavernicola* is dependent on the cave environment for survival. This also indicates that the record of this species from Thailand might be a misidentification (as was the case for the specimens from Vietnam; Rahmadi et al. (2011)).

4. Discussion

Charinidae as defined by Quintero (1986) went through several taxonomical rearrangements (summarized in Rahmadi et al. (2010)) and included the genera *Catageus*, *Charinus* and *Sarax*. The taxonomy of individual species or species groups has been reviewed in different papers, but an overall investigation of the variation of the morphology has never been carried out. This hampered a better definition of the various genera within the family. The study of most *Charinus* and *Sarax* species (Miranda et al. unpublished) allowed us to better define and circumscribe the genera, and reach the conclusion that it was necessary to create *Weygoldtia* gen. nov. to accommodate the species *Sarax davidovi*.

The presence of a curved crest ventral to the lateral eyes is shared by *W. davidovi* and several species of *Sarax* and *Charinus*. This character was first noted by Kraepelin (1899), but was rarely used to diagnose species (Gravely, 1915a). The new genus, however, is the only whip spider group with a straight crest anterior to the lateral eyes (which might be a homoplastic ophthalmic ridge) (Garwood et al., 2017; Shultz, 2007).

Weygoldtia davidovi was formerly placed in *Sarax* due to the presence of ventral sac covers. This character, however, is not synapomorphic for *Sarax* as it is also present in Charontidae and Phrynichidae species (Weygoldt, 1996). The ventral sac cover of *Weygoldtia* is reduced to small projections at the distal border of the third abdominal tergite and in some specimens is barely seen.

Charinus, *Sarax* and *Weygoldtia* exhibit equal numbers of trichobothria in the frontal and caudal series on distitibia IV, which can be five or six in *Charinus* and *Sarax* and six or nine in *Weygoldtia*. On leg I, *Weygoldtia*'s rod sensilla are arranged in a longitudinally long line; in *Sarax* it is rounded and in *Charinus* it is elliptical in a shallow groove. Contrary to the species of *Charinus* and *Sarax*, *Weygoldtia* has a rather restrict distribution; *W. davidovi* is an epigean species restricted to Indochina (Vietnam, Laos and Cambodia).

With the taxonomical reclassification presented here, the family Charinidae now includes three genera: *Charinus*, *Sarax* and *Weygoldtia*. The identity of the enigmatic genus *Catageus* was finally revealed, being transferred to Charontidae and synonymized with *Stygophrynus*. *Catageus* is the senior synonym, so all species of *Stygophrynus* were transferred to *Catageus* resulting in nine new combinations. Future works will address the relationships of the charinid genera and species, their biogeography and taxonomy.

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