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Zoosystematics and Evolution

A Bulletin of Zoology since 1898

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See paper of **de Souza LS, Pimenta AD** *Eulimacrostoma* gen. nov., a new genus of Eulimidae (Gastropoda, Caenogastropoda) with description of a new species and reevaluation of other western Atlantic species

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Taxonomy of the genus *Longipeditermes* Holmgren (Termitidae, Nasutitermitinae) from the Greater Sundas, Southeast Asia

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<http://zoobank.org/D123A73F-B056-46D3-AE9C-74EAFD34F792>

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Abstract

More than 200 colonies of the genus *Longipeditermes* were collected in our field surveys across the Sundaland region of Southeast Asia from 1998 to 2014. Two species, *L. kistneri* Akhtar & Ahmad and *L. logipes* Holmgren, are recognized and redescribed with color photographs of the workers and major soldiers. We use variation in characters of soldier caste (head capsules, antennae, and pronotum) and worker caste (antennae and mandibles) to distinguish these two species. *Longipeditermes kistneri* seems to prefer high-altitude forests (above 1,000 m) and has so far been found exclusively in Java and Sumatra, while *L. logipes* seems to prefer lowland and swamp forests and is widespread in the Greater Sundas.

Key Words

Morphological characters, Nasutitermitinae, Open-air processional columns termites, species description

Introduction

A termite colony typically consists of a large number of workers and defensive soldiers together with a single king and a queen. This arrangement can, however, vary with seasonal cohorts of reproductive nymphs and dispersive alates (Watson and Gay 1991; Pearce 1997). The castes within termite societies are morphologically and behaviorally specialized to perform particular tasks (Lee and Wood 1971; Grimaldi and Engel 2005) to the point where workers and soldiers are so specialized for non-reproductive helping and defensive tasks that they are considered to be functionally sterile (Roisin 2000). The sexuals, by contrast, are highly specialized for reproduction.

As the largest subfamily among the higher termites (Termitidae), Nasutitermitinae consists of more than 550 species (Emerson 1955), which belong to more than 63 genera (Collins 1989). This subfamily probably originated in the Neotropical region during the Cretaceous period (Emerson 1955) and is characterized by a highly specialized defensive caste (Collins 1989) that has a modified rostrum or “nasus” (Deligne et al. 1981; Prestwich 1984). This subfamily was erected by Hare (1937), who emphasized the conspicuous prolongation on the front of the head, which is often accompanied by degeneration of mandibles and the concomitant development of a frontal gland. The development of the nasus is continuously variable among species within the Na-

sutitermitinae from mild prolongation, as in *Syntermes*, to pronounced prolongation as in *Subulitermes*, *Convexitermes*, and *Nasutitermes*.

Longipeditermes, in the Nasutitermitinae, is a small genus with only two species so far recorded. These are *L. longipes* and *L. kistneri* from the Sundaland area (Gathorne: Hardy 2001; Hoare and Jones 1998). *Longipeditermes* is, however, well known for its remarkable foraging habit. Workers and soldiers form open-air processional columns on the ground, shrubs, and tree trunks typically inside forests (Gray and Dhanarajan 1974; Hoare and Jones 1998; Miura and Matsumoto 1998; Takematsu et al. 2013; Syaukani et al. 2016). The foraging activities of both species seem to be greatest during the day (Hoare and Jones 1998), as evidenced by workers carrying packed balls of organic matter between their mandibles and returning to the nest.

In the course of our long-term inventory and taxonomic research on termites in Southeast Asia, more than 200 colonies of *Longipeditermes* have been sampled from different habitats and altitudes across the Greater Sunda. In this paper, the two species of the genus are redescribed and illustrated using newly obtained nest series. Information on their life history is provided.

Materials and methods

We examined 216 colonies of *Longipeditermes* from various habitats and altitudes across the Greater Sunda (Table 1; Fig. 1). The specimens examined are deposited at the Museum Zoologicum Bogoriense (MZB), Cibinong, Indonesia; the Natural History Museum, London (UK);

and the Universitas Syiah Kuala (Biology Department), Darussalam, Banda Aceh (Indonesia).

The head, body (in profile), pronotum, and antenna of the soldier caste (preserved in 70% ethanol) were photographed using a digital microscope (KEYENCE HFVH-8000, Osaka). From these images, multifocused montages were produced using Helicon Focus v. 6.2.2 (Helicon Soft Ltd, Kharkov, Ukraine). Morphological terms and measurement characters follow those of Roonwal and Chhotani (1989), Sands (1998), Tho (1992), and Syaukani et al. (2011). We measured the characters (in millimeters): head capsule length including nasus (HLN), head capsule length excluding nasus (HL), nasus length (NL), nasus index = NL/HL, maximum head width at anterior part (HWA), maximum head width at posterior part (HWP), maximum height of head capsule excluding postmentum (HH), pronotum length (PL), and pronotum width (PW).

Results

Taxonomic accounts

Genus *Longipeditermes* Holmgren, 1913

Soldier. Bimodal in its size distribution. Head capsule pale brown to blackish; antenna much paler than head capsule in coloration, with the basal segments (first and second) generally darker than the remaining segments; pronotum paler than or as pale as head capsule; abdominal tergites pale brown to dark sepia brown; coxae yellow.

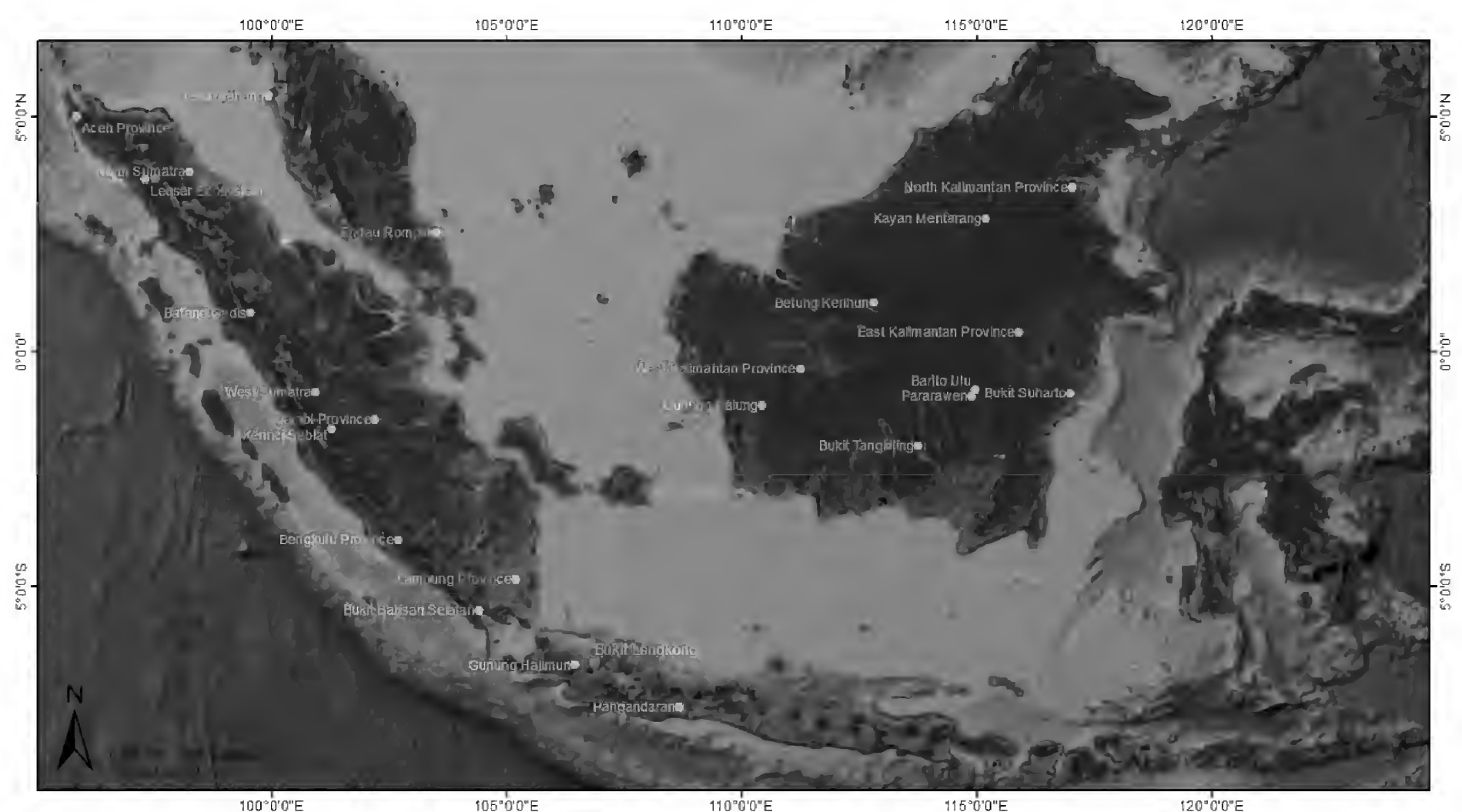


Figure 1. Distribution of *Longipeditermes longipes* (yellow dot) and *L. kistneri* (red dot) on the Greater Sundas, Southeast Asia.

lowish to pale brown; femora yellow to brown; tibiae pale yellow to yellow. In dorsal view head capsule excluding rostrum pear-shaped to somewhat triangular, weakly constricted behind antennal sockets; its posterior margin weakly to strongly convex; dorsal outline in profile weakly to strongly concave; rostrum excluding the apex somewhat cylindrical rather than conical. Antenna long, with 14 segments; 3rd segment at least twice as long as 4th. Mandible relatively long, with sharp apical processes. Legs very long.

Worker. Monomorphic but showing size variation. Pale brown to blackish. Antenna with 15 segments, with the basal segments darker than the following ones. Left mandible with 3rd marginal tooth weakly to moderately protruding from cutting edge, and 4th partially hidden behind molar prominence.

Remarks. In *Longipeditermes*, the soldier caste is dimorphic. The caste is subdivided into major and minor soldiers that differ markedly in size (Thapa 1981; Tho 1992; Gathorne-Hardy 2001; Miura and Matsumoto 1998) and slightly in coloration; the former being darker than the latter. The major soldier has more characters useful for species recognition and identification. Two varied

species, *L. longipes* and *L. kistneri*, were recognized in our collection (Table 1), while no additional species were found by our morphology-based examination. The two species are relatively easily distinguished from each other by a combination of characters given in Table 2. These characters are re-described below in detail.

***Longipeditermes longipes* (Haviland, 1898)**

Termes longipes Haviland 1898: 439–440. Type locality: Perak, Malay Peninsula. Syntypes examined.

Eutermes longipes Wasmann 1902: 131.

Eutermes (Longipeditermes) longipes: Holmgren 1902: 215–217; John 1925: 406.

Longipeditermes longipes: Snyder 1949: 317; Ahmad 1958: 126; Tho 1992: 180–181; Miura and Matsumoto 1998: 179–189 (ecology); Hoare and Jones 1998: 1357–1366.

Longipeditermes mandibulatus Thapa 1981: 349–352. Sabah, Borneo. Synonymized by Hoare and Jones 1998: 1357–1366.

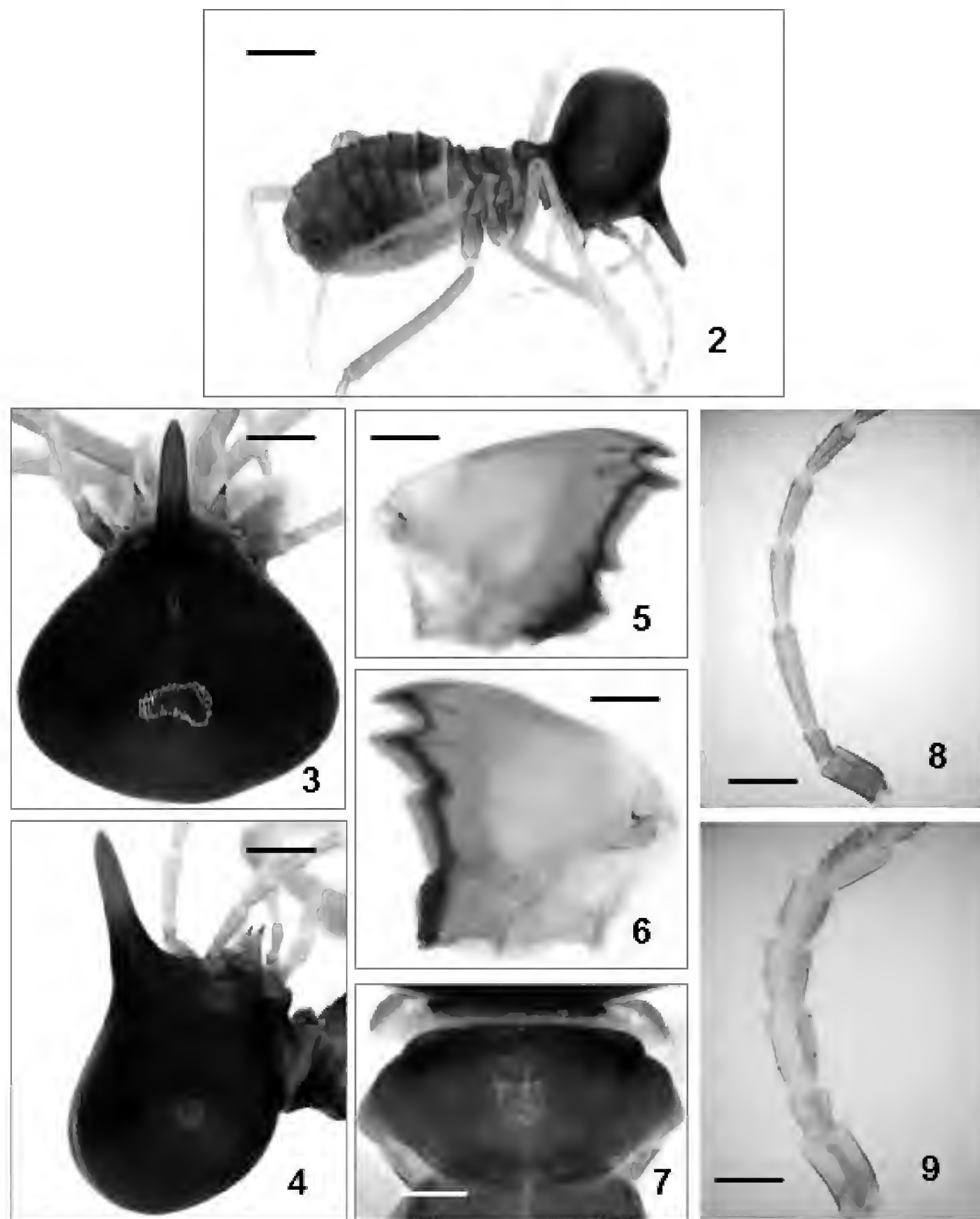
Materials examined. *Sumatra*. SYK1998 & 1999-L-1115, 1117, 1120, 1121, 1124, 1130, 1133, 1136, 1138, 1139, 1141, 1143, 1147, 3025: soldiers and workers from

Table 1. Summary of collection sites.

Site	Vegetation type	Altitude (m)
The Leuser Ecosystem, Sumatra	Lowland & subalpine forests Protected & unprotected	50–1400
Aceh Province (outside the Leuser Ecosystem), Sumatra	Lowland forest	20–600
Batang Gadis National Park, Sumatra	Lowland forest	800–1200
North Sumatra Province (except the Leuser Ecosystem)	Lowland & subalpine forests	20–1100
Kerinci Seblat National Park, Sumatra	Lowland & subalpine forests	300–1350
West Sumatra Province (outside Kerinci Seblat N. P.), Sumatra	Lowland forest	50–400
Jambi Province (outside Kerinci Seblat N.P.), Sumatra	Lowland forest	50–600
Bukit Barisan Selatan National Park, Sumatra	Lowland forest	50–600
Bengkulu Province (outside Bukit Barisan Selatan National Park), Sumatra	Lowland forest	100–700
Lampung Province (outside Bukit Barisan Selatan National Park), Sumatra	Lowland forest	10–300
Endau Ronpin National Park, Malay Peninsula	Lowland forest	150–600
Teluk Bahang National Park, Malay Peninsula	Lowland forest	5–200
Bukit Tangkiling Nature Preserve, Borneo	Lowland forest	25–170
Pararawen Nature Preserve, Borneo	Lowland forest	50–350
Barito Ulu, Borneo	Lowland & subalpine forests	900–1200
Gunung Palung National Park, Borneo	Lowland forest	50–300
Betung Kerihun National Park, Borneo	Lowland forest	400–850
West Kalimantan Province (outside Betung Kerihun NP) Borneo	Lowland forest	50–650
East Kalimantan Province (outside Gunung Palung NP) Borneo	Lowland forest	150–500
Bukit Suharto, Borneo	Lowland forest	40–300
North Kalimantan Province (outside Kayan Mentarang NP), Borneo	Lowland & subalpine forests	500–1200
Gunung Halimun National Park. West Java	Lowland & subalpine forest	800–1350
Pangandaran Natural Reserve, West Java	Lowland	10–40
Bukit Lengkong, West Java	Lowland & subalpine forest	800–1250

Table 2. Summary of morphological characters for the *Longipeditermes* based on major soldiers and workers.

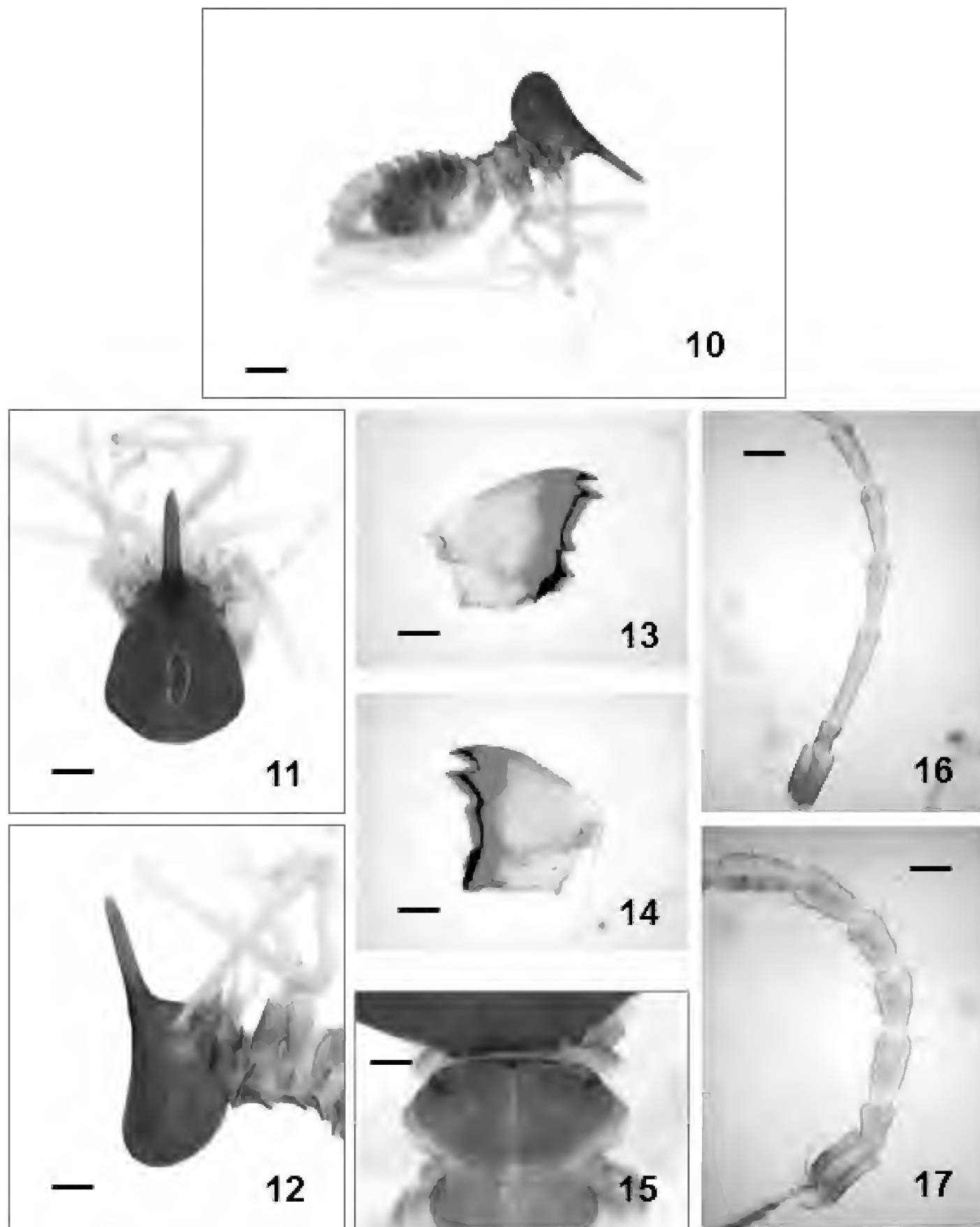
Species	Soldier			Worker	
	Coloration of head capsule	Rostrum	Anterior margin of pronotum	Antennae	Left mandible
<i>L. longipes</i>	Sepia brown to blackish	Apical 2/3 lighter & basal 1/3 darker	Nearly straight	4 th segment longer than 5 th	3 rd marginal tooth moderately protruding from cutting edge
<i>L. kistneri</i>	Pale brown to dark brown	Apical 2/3 darker and basal 1/3 lighter	Strongly indented in the middle	4 th to 6 th segments almost equal in length	3 rd marginal tooth weakly protruding from cutting edge



Figures 2–9. (SYK2006-KSNP-0011). *Longipeditermes longipes* (major soldier & major worker). Soldier (2–4, 7, 8) and worker (5, 6, 9). Habitus in profile (2), head in dorsal view (3), head in profile (4), left (5) and right (6) mandibles, pronotum (7), antennae (8, 9). Scale bars: 0.6 mm (2), 0.3 mm (3, 4), 0.1 mm (5–9), 1.7 mm (6).

undisturbed forest, 300–500 m altitude, Ketambe, Southeast Aceh. SYK1998-L-3005, 3010: soldiers and workers from disturbed forest, 450 m altitude, Lokop, East Aceh, Aceh. SYK-L-1148, 3006: soldiers and workers from disturbed forest, 80 m altitude, Soraya, Singkil, Aceh. SYK1998 & 2000-L-1126, 1127, 1131, 1199, 1145, 3007, 3008: soldiers and workers from undisturbed forest, 150–350 m altitude, Bukit Lawang, Langkat, North Sumatra. SYK1998-L-3009, 3022, 3024: soldiers and workers from disturbed forest, 200 m altitude, MRT Logging Concession, South Aceh. SYK1999 & 2001-L-1116, 1123, 1125, 1128, 1134, 1135, 1137, 1144, 1146: soldiers and workers from disturbed forest, 50 m altitude, Sekundur, Langkat, North Sumatra. SYK1999-L-1112, 1118, 1129, 1132, 1140, 1142: soldiers and workers from undisturbed forest, 200–400 m

altitude, Bengkung, Southeast Aceh. SYK2006-AL-0104: Soldiers and workers from disturbed forest, 50 m altitude, Maestong, Batang Hari, Jambi. SYK2006-KSNP-0011, 0019, 0080, 0091, 0093, 0095, 0096, 0097, 0104, 0206: soldiers and workers from the undisturbed forest, 300 m in altitude, Sungai Manau, Merangin, Jambi. SYK2006-AL-0100, 0101, 0102, 0103: soldiers and workers from disturbed forest, 50 m altitude, Maestong, Batang Hari, Jambi. SYK2007-LP-0019: soldiers and workers from undisturbed forest, 1350 m altitude, Sumber Jaya, Kota Bumi, Lampung. **Java.** SYK2001-HL-067, 072: soldiers and workers from protected forest, 1,450 m altitude, Halimun NP, West Java. SYK2006-PD-0011, 048: soldiers and workers from protected forest, 10 m altitude, Pangandaran Nature Reserve. West Java. **Malay Peninsula.**



Figures 10–17. (SYK2006-KSNP-0011). *L. longipes* (minor soldier & minor worker). Soldier (10–12, 15) and worker (13, 14, 17). Habitus in profile (10), head in dorsal view (11), head in profile (12), left (13) and right (14) mandibles, pronotum (15), antennae (16, 17). Scale bars: 0.6 mm (10), 0.3 mm (11, 12), 0.1 mm (13–17), 1.7 mm (15).

SYK2009-ER-084, 085, 086, 087, 088: soldiers and workers from protected forest, 50 m altitude, Endau Rompin NP. SYK2011-TB-011, 012, 013, 014: soldiers and workers from protected forest, 10 m altitude, Teluk Bahang NP. **Borneo.** SYK2014-BT-0054: soldiers and workers from protected secondary forest, 35 m altitude, Palangkaraya, Central Kalimantan. SYK-2014-P-0012: soldiers and workers from undisturbed forest, 220 m altitude, North Barito, Central Kalimantan. SYK-2014-P-0024: soldiers and workers from undisturbed forest, 270 m altitude, North Barito, Central Kalimantan.

Soldier (Figs 2–4, 7, 8, 10–12, 15, 16). Bimodal continuum in size. **Major soldier** (Figs 2–4, 7, 8). Head capsule sepia brown to blackish, in dorsal view somewhat triangular, very weakly constricted behind antennal sock-

ets, with posterior margin roundly convex; dorsal outline (including nasus) in lateral view moderately concave; rostrum feebly bicolored, with apical 2/3 lighter and basal 1/3 darker. Mandible with short to long apical processes in dorsal view. Antenna with 14 segments, much paler than head capsule; 1st antennal segment darker than the following segments, which are uniformly colored; 3rd segment approximately 1.5 times as long as 4th; 5th slightly shorter than 4th; 6th–14th gradually shortening toward the apex. Pronotum in dorsal view paler than head capsule; anterior margin nearly straight; posterior margin weakly indented in the middle. Coxae pale brown to brown; femora pale brown to yellow; tibiae pale yellow. Abdominal tergites pale brown to dark sepia brown. Measurements and index (20 major soldiers from 10 colonies): HLN 2.30–2.71 mm;

HL 1.57–1.62 mm; NL 0.72–0.77 mm; NL/HL 0.47–0.51; HWA 0.81–0.98 mm; HWP 1.87–1.92 mm; HH 1.22–1.32 mm; PL 0.37–0.40 mm; PW 0.75–0.78 mm.

Worker (Figs 5, 6, 9, 13, 14, 17). Monomorphic but showing size variation. **Worker (large-sized)** (Figs 5, 6, 9). Blackish brown to blackish. Left mandible with apical tooth shorter than 1st marginal tooth; 3rd marginal moderately protruding from cutting edge; 4th completely hidden, scarcely visible behind molar prominence. Right mandible with posterior edge of 2nd marginal tooth nearly straight or weakly concave; the inner layer of molar plate very moderately convex; notch moderately developed. Antenna with 15 segments, whitish yellow; 1st and 2nd segments darker than the following segments; 3rd clearly

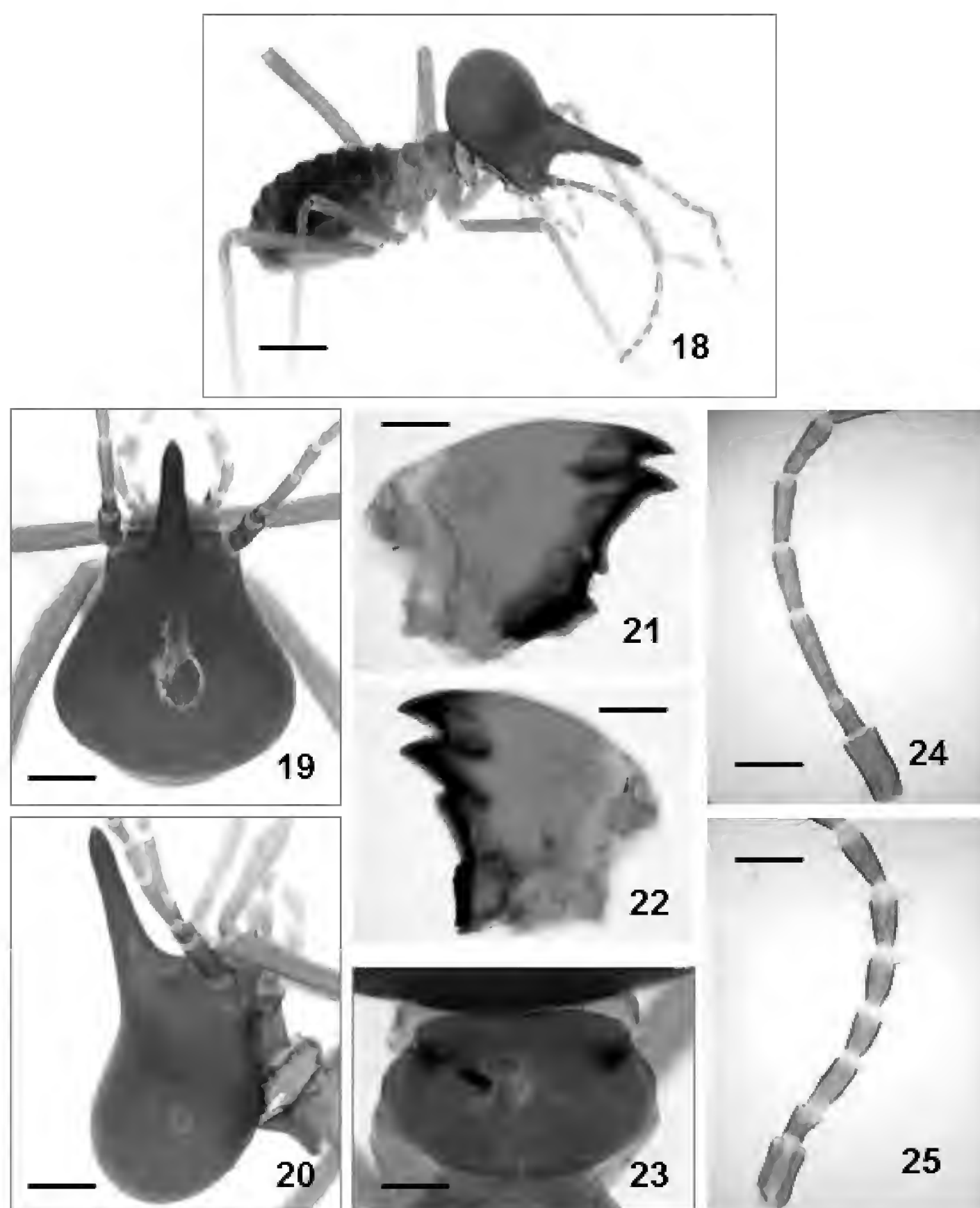
longer than 4th; 4th longer than 5th, 6th–15th gradually shortening toward the apex.

Distribution. Sumatra, Peninsular Malaysia, Java (**new record**), and Borneo.

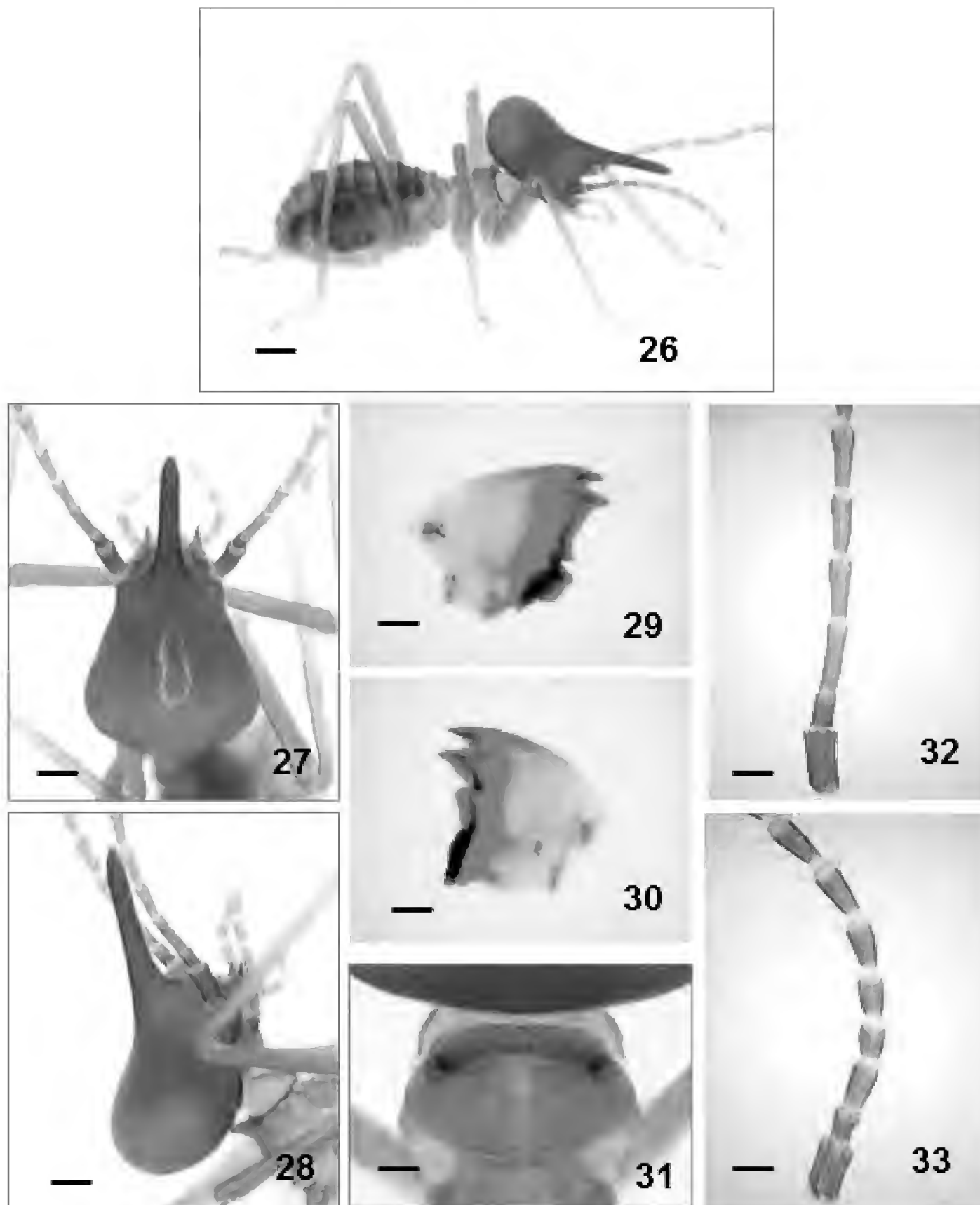
Longipeditermes kistneri Akhtar & Ahmad, 1985

Longipeditermes kistneri Akhtar and Ahmad 1985: 215–217. Bogor, West Java.

Material examined. SYK1998 & 1999-L-1098, 2001, 3011: soldiers and workers from the undisturbed forest, 1100–1400 m altitude, Kemiri Mountain, Southeast Aceh, Aceh, Sumatra.



Figures 18–25. (SYK1999-L-3011). *L. kistneri* (major soldier and major worker). Soldier (18–20, 23, 25) and worker (21, 22, 25). Habitus in profile (18), head in dorsal view (19), head in profile (20), left (21) and right (22) mandibles, pronotum (23), antennae (24, 25). Scale bars: 0.6 mm (18), 0.3 mm (19, 20), 0.1 mm (21, 22, 24, 25), 1.7 mm (23).



Figures 26–33. (SYK1999-L-3011). *L. kistneri* (minor soldier and minor worker). Soldier (26– 28, 32) and worker (29, 30, 33). Habitus in profile (26), head in dorsal view (27), head in profile (28), left (29) and right (30) mandibles, pronotum (31), antennae (32, 33). Scale bars: 0.6 mm (26), 0.3 mm (27, 28), 0.1 mm (29, 30, 32, 33), 1.7 mm (31).

Soldier (Figs 18–20, 23, 24, 26–28, 31, 32). Bimodal continuum in size. **Major soldier** (Figs 18–20, 23, 24). Head capsule pale to dark brown, in dorsal view somewhat triangular, very weakly constricted behind antennal sockets, with posterior margin roundly convex; dorsal outline (including nasus) in profile moderately concave; rostrum feebly bicolored, with apical 2/3 darker and basal 1/3 paler. Mandible with short to long apical processes. Antenna with 14 segments, much paler than head capsule; 1st and 2nd antennal segments darker than the following segments, which are uniformly colored; 3rd approximately 1.5 times as long as 4th; 5th slightly shorter than 4th; 6th–14th gradually shortening toward the apex. Pronotum in dorsal view as pale as or paler than head capsule; anterior margin indented in the middle; posterior margin weakly indented

in the middle. Coxae and femora yellowish to pale brown; tibiae pale yellow to yellow. Abdominal tergites brown to dark sepia brown. Measurements and index (20 major soldiers from 10 colonies): HLN 2.22–2.43 mm; HL 1.62–1.68 mm; NL 1.02–1.12 mm; NL/HL 0.66–0.73; HWA 0.86–0.90 mm; HWP 1.63–1.71 mm; HH 0.98–1.04 mm; PL 0.40–0.44 mm; PW 0.77–0.82 mm.

Worker (Figs 21, 22, 25, 29, 30, 33). Monomorphic but showing size variation. **Worker (large-sized)** (Figs 21, 22, 25). Body pale brown to brown. Left mandible with apical tooth shorter than 1st marginal tooth; 3rd marginal weakly protruding from cutting edge; 4th not completely hidden behind molar prominence. Right mandible with posterior edge of 2nd marginal tooth nearly straight; the inner layer of the molar plate very weakly concave; notch moderately

to strongly developed. Antenna with 15 segments, with 1st and 2nd segments slightly darker than the following segments; 3rd clearly longer than 4th; 4th–6th nearly equal in length; 7th–15th gradually shortening toward the apex.

Distribution. Sumatra and Java.

Discussion

Longipeditermes species are distinguished from those of the other groups of Southeast Asian nasutitermitine termites by forming open-air processional foraging columns (e.g., *Hospitalitermes* and *Lacessititermes*) and by having major and minor soldiers that both have long legs and a long rostrum. No information is available for the ratio of the largest and smallest soldiers in typical colonies, but minor soldiers appear to be more numerous (Figs 34, 35). The soldier does not exhibit a clear dimorphism, but a bimodal continuum in size.

Longipeditermes kistneri was only collected from Sumatra during our intensive surveys in the Greater Sundas, although the type locality is Java. Nine colonies were found in protected forests above 1,000 m in altitude. Four nests were located among buttresses and roots of big trees (under the ground covered with decayed leaf litter and small decayed branches). This nesting habit makes it difficult to estimate the sizes of their colonies. Both soldiers and workers forage on the surface of the ground. The size of foraging columns is smaller in *L. kistneri* than in *L. longipes*. Their pale- to dark-brown body color and smaller columns make it difficult to find colonies of *L. kistneri*.

Longipeditermes longipes seems to prefer lowland and swamp forests and is widespread in the Greater Sundas. Nests of *L. longipes* are usually constructed among buttresses of trees (Fig. 36) and in dead or decayed stumps, with decayed wood debris and leaves (Fig. 37). Several subterranean nests of this species were found in Lambir Hills National Park (Sarawak, Borneo) by Miura and Mat-



Figures 34, 35. Foraging column of *Longipeditermes longipes* on the forest floor in Southeast Asia. Workers collecting and transporting food source from a decayed branch (34) and leaf litter (35), soldiers protecting the worker from predators such as *Componotus gigas* (Latreille).



Figure 36. Nest entrances (red arrows) of subterranean nest of *Longipeditermes longipes* found in SE Asia tropical forests.

sumoto (1998). Underground nests are sometimes made from consisting of soil and litter. This species forages on the ground during the day. However, Hoare and Jones (1998) reported foraging activity at night, during which no food balls were being carried. We also found foraging columns at night; the columns consisted of limited numbers of workers carrying food balls to the nests. In typical processional foraging columns, numerous soldiers guard workers. Foraging ecology and diet of *L. longipes* have been poorly studied, but we know that this species feeds on leaf litter (Miura and Matsumoto 1998) and in the Pasoh Forest Reserve on the Malay Peninsula it prefers to consume older leaf litter rather than newly fallen leaves (Matsumoto and Abe 1979). We observed foraging columns consuming a mixture of bark, twigs, and decayed wood in forests of Sumatra and the Malay Peninsula.



Figure 37. Above-ground nest of *L. longipes* constructed in and around a dead tree stump (*Shorea* sp.). The cavity was fulfilled with a mixture of soil, debris and litter.

Conclusion

In general, from the current study, we conclude that only two species of *Longipeditermes* (*L. longipes* Holmgren and *L. kistneri* Akhtar & Ahmad) have so far been collected in the Greater Sundas. Long legs and size dimorphism of soldier caste can help to separate this genus from other nasute termites in Southeast Asia. The condition of rostrum, head capsule, pronotum, and antennae determine the soldier caste, while the condition of antennae and left mandibles of worker caste serve to distinguish these two species. *Longipeditermes kistneri* seems to prefer high-altitude forests and has been found exclusively from Java and Sumatra, while *L. longipes* seems to prefer lowland and swamp forests and is widespread in the Greater Sundas.

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A taxonomic review of the crab spider genus *Sidymella* (Araneae, Thomisidae) in the Neotropics

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Abstract

Four Neotropical species of *Sidymella* Strand, 1942, *S. furcillata* Keyserling, 1880, *S. longispina* (Mello-Leitão, 1943), *S. lucida* (Keyserling, 1880), and *S. kolpogaster* (Lise, 1973) are redescribed from both sexes. The holotype of *S. nigripes* (Mello-Leitão, 1947) is lost and this taxon is considered a *species inquierenda*. *Sidymella obscura* (Mello-Leitão, 1929), *S. parallela* (Mello-Leitão, 1929), and *S. spinifera* (Mello-Leitão, 1929) are all *nomina dubia*. Two new species are described: *Sidymella excavata* **sp. nov.** (males and females) and *S. marmorata* **sp. nov.** (female).

Key Words

crab spiders, morphology, new records, Stephanopinae, *Stephanopis*

Introduction

Crab spiders (Araneae, Thomisidae) are distributed worldwide but the highest diversity is found in tropical regions (WSC 2019). The group has been studied in many recent phylogenetic works, but its relationships are still being discussed (Benjamin et al. 2008; Benjamin 2011; Ramírez 2014; Wheeler et al. 2017) and broader relationships among basal thomisids such as the subfamily Stephanopinae remain weakly supported and unstable (Ramírez 2014). The presence of cheliceral teeth, which was previously considered as a synapomorphy for this group (Ono 1988), was recovered as a plesiomorphy by Benjamin (2011), and this subfamily remains as the most controversial and the least studied group in Thomisidae; it has many genera in need of revision and a considerable number of species yet to be described (Benjamin 2011). Based on the work of Mello-Leitão (1929), subsequent efforts were made to update the taxonomy of some Neotropical stephanopines (Lise 1973, 1981; Bonaldo and

Lise 2001; Machado et al. 2015, 2017; Silva-Moreira and Machado 2016; Prado et al. 2018). However, many genera are still known only from the original descriptions and poor diagnoses, and the accurate identification of many species is practically impossible.

The genus *Sidymella* Strand, 1942 is a prime example of such difficulties. The genus has a disjunct Gondwanan distribution, with 11 described species occurring in Australia and New Zealand whilst 10 are found in the Neotropics (WSC 2019). *Sidymella* is currently defined by a convex prosoma, both anterior and posterior eye rows recurved, anterior tibiae and metatarsi (I and II) with stout and spiniform macrosetae, and opisthosoma posteriorly bifurcated (Strand 1942; Mello-Leitão 1929; Lise 1973). Although the Neotropical *Sidymella* have been revised by Lise (1973), this author focused on somatic characters to describe and diagnose the species, neglecting both external and internal structures of female genitalia and the position, shape, and size of palpal apophyses of males. Therefore, the present paper provides a taxonomic review of the Neo-

tropical *Sidymella*, where the males of *S. furcillata* and *S. longispina* are described for the first time, two new species added to the genus, and new synonyms established.

Methods

The examined specimens belong to the Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires (MACN, Martín Ramírez), Museu de Ciências e Tecnologia da Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre (MCTP, A. A. Lise), Museu de Ciências Naturais da Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre (MCN, R. Ott), and the Museum of Comparative Zoology of Harvard, Cambridge (MCZ, G. Giribet and L. Liebensperger).

The terminology for somatic and copulatory structures follows Machado et al. (2018). Photos of copulatory structures were taken with a Multipurpose Zoom Microscope Leica M205A with a digital camera, and scanning electron microscopy were made with a Philips XL 30 Field Emission ESEM from the Centro de Microscopia e Microanálises (CEMM) of the Pontifícia Universidade Católica do Rio Grande do Sul (PUCRS). All measurements were taken in millimeters. Morphology abbreviations: ALE—anterior lateral eyes, AME—anterior median eyes, MOQ—median ocular quadrangle, PLE—posterior lateral eyes, PME—posterior median eyes, RTA—retrolateral tibial apophysis.

Results

Sidymella Strand, 1942

Sidyma Simon, 1895: 1056. Type species: *Stephanopsis lucida* Keyserling, 1880; by original designation and monotypy; Berland 1913: 95, pl. 9, figs 51–56. Preoccupied by Walker (1856) in Lepidoptera. *Sidymella* Strand, 1942: 399 (generic replacement name).

Diagnosis. *Sidymella* is similar to *Coenypha* Simon, 1895 and some species of *Stephanopsis* (e.g. *S. antennata*, *S. ditissima*, and *S. nodosa*) and these species share a male palp with a long, thin and curled embolus, well-developed pars pendula, and a retrolateral tibial apophysis with a short basal branch (Figs 1A, B, 11C–F, 13D); the epigynes have a septum formed by the posterior folds of the epigynal plate and long and coiled copulatory ducts (Figs 1C, D, 10C–F). However, *Sidymella* species can be recognized and distinguished from these genera by having a bifid opisthosoma (Fig. 1E, F), presence of spini-form macrosetae on the mesial surface of femora I and above the ALE (Fig. 10A, B), the epigyne have a single pair of walnut-shaped spermathecae compartmentalized in several smaller chambers, with accessory glandular heads (Figs 4D, F, 6D, F, 8D, F, 10D, F, 12D, F, 13D, F) while the male palp has a tibial trichobothrium and the RTA have a nodose surface (Fig. 1A, B) unlike other Stephanopinae which present a grooved RTA (with parallel creases on its surface).

Description. Small spiders (total length 3.00–3.96 in males, 4.68–7.93 in females) with slight sexual size dimorphism, presenting evidence of predominant green colouration *in vivo* (Fig. 1E, F). Prosoma longer than wide, covered with short and conical setae. Both anterior and posterior eyes disposed in two recurved rows; ALE almost two times larger than the other eyes; ocular macrosetae may be present only above the ALE or on the MOQ area; sternum heart-shaped with concave anterior border, and clypeus with a pair of macrosetae; labium trapezoidal and endites with rounded edges, longer than wide. Opisthosoma with two projections of different sizes, shapes and angles in relation to the opisthosomal axis, varying from rounded and short ones, disposed horizontally/posteriorly, or long, acute and vertically oriented (Figs 2A–F, 3A–F). Leg formula: 1–2–4–3; anterior tibiae and metatarsi (I and II) ventrally armed with stout macrosetae. Epigynum with membranous and hyaline copulatory ducts, long spermathecae with many chambers or with a single median constriction (Fig. 10D); male palp with RTA rounded or truncated, discoid tegulum and ribbon-like embolus and (Fig. 10C–F).

Composition. Six Neotropical species: *Sidymella excavata* sp. nov., *S. furcillata* (Keyserling, 1880), *S. longispina* (Mello-Leitão, 1943), *S. lucida* (Keyserling, 1880), *S. marmorata* sp. nov., and *S. kolpogaster* (Lise, 1973); 11 additional species from the Australasian region that are not within the scope of the present study.

Distribution. Ecuador, Colombia, Peru, Brazil, Argentina, and Uruguay (Fig. 15).

Sidymella excavata Machado & Guzati, sp. nov.

<http://zoobank.org/4D59E033-C71C-4588-ADBC-6563B92ACDAE>
Figures 2D, 3D, 4, 5

Type material. Holotype ♀, **ECUADOR**: Cerro Troya, Carchi, 0°43'59.7"N, 77°41'00.3"W, L. Pena leg. (MCZ 133396). Paratypes: ♂, **ECUADOR**: Pichincha, 0°15'00.0"S, 78°35'00.0"W, 19.iv.1988, W. Maddison leg. (MCZ 133397); ♀, **COLOMBIA**: Cundinamarca, Mosquera (Mondoñedo), 4°41'0.06"N, 74°15'0.25"W, 20.x.2000, E. Florez & J. Pinzon leg. (ICN 3404).

Material examined. **COLOMBIA**: 2j, Magdalena (Santa Marta), 11°12'54"N, 74°06'01"W, 18.iv.1977, W. Galvis & A.J. Moreno leg. (ICN-Ar 9140); 1♀ 1j, Quindío (Estación Bremen), 4°40'0"N, 75°39'0"W, 14–20.iv.1998, P. Ariza leg. (MPUJ 45511); 1♀, 1j, same data as preceding (MPUJ 11490); 1♀, Cundinamarca, Mosquera (via a La Mesa), 4°40'12.0"N, 74°16'00.7"W, 20.x.2000, E. Florez & J. Pinzon leg. (ICN-Ar 3404); 2♀, Mosquera (Desierto de Zabinsky), 4°44'30"N, 74°14'8"W, 23.ii.2002, L. Benavides, C. Niño, A. Castañeda & G. Mora leg. (ICN-Ar 2157); 2♀, 5j, 06.iv.2002, same locality and collectors (ICN-Ar 2146); 4♀, 7j, same locality, April 2006,

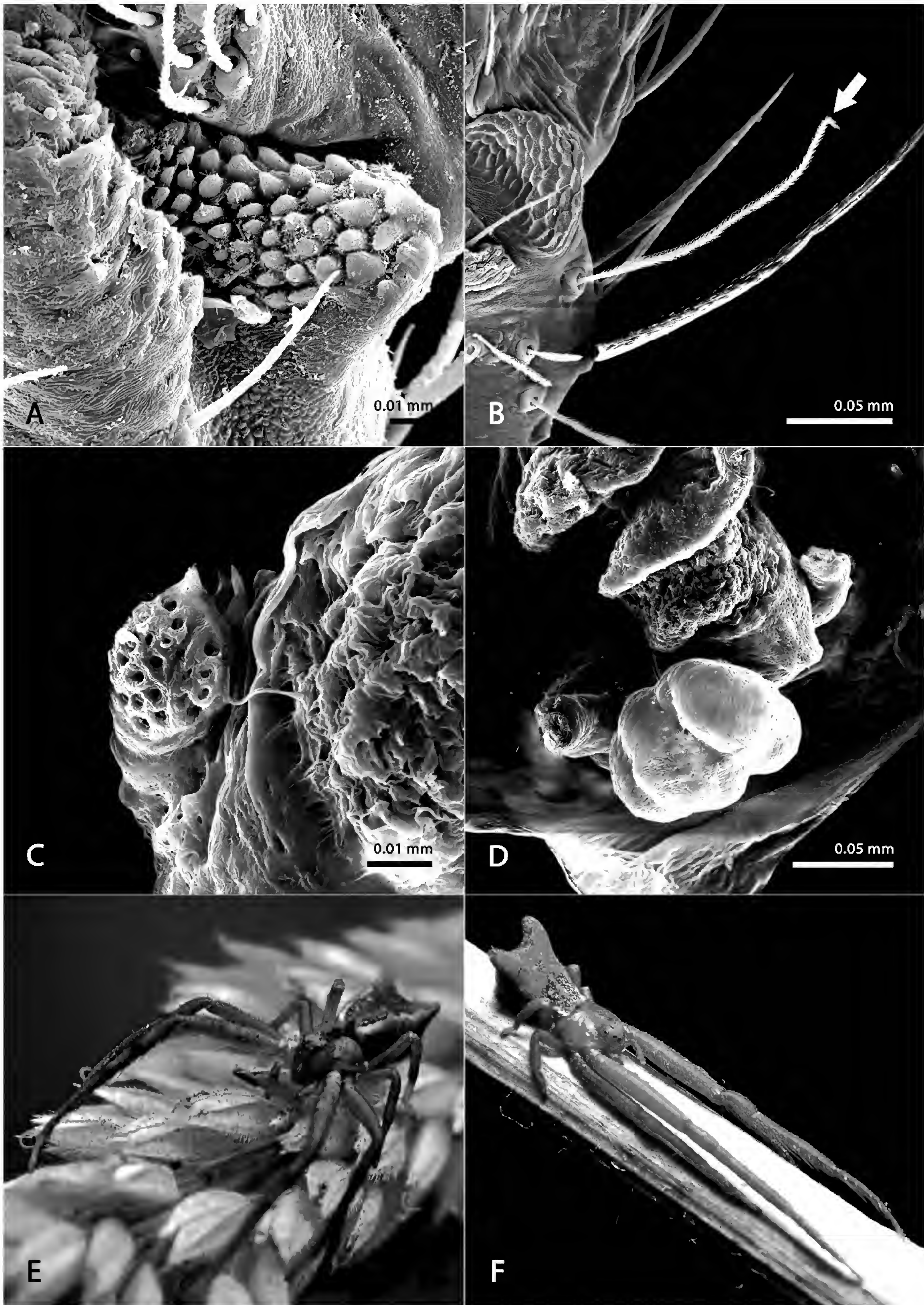


Figure 1. a–d Diagnostic sexual features of *Sidymella* a Detail of the nodose RTA surface on male palp b Tibial trichobothria on male palp (indicated by an arrow) c Glandular head on spermatheca d Walnut-shaped spermatheca e, f Photos of live specimens of *Sidymella lucida*. Photo credits: e Diego Galarraga Sugoniaev; f Damián Hagopían.

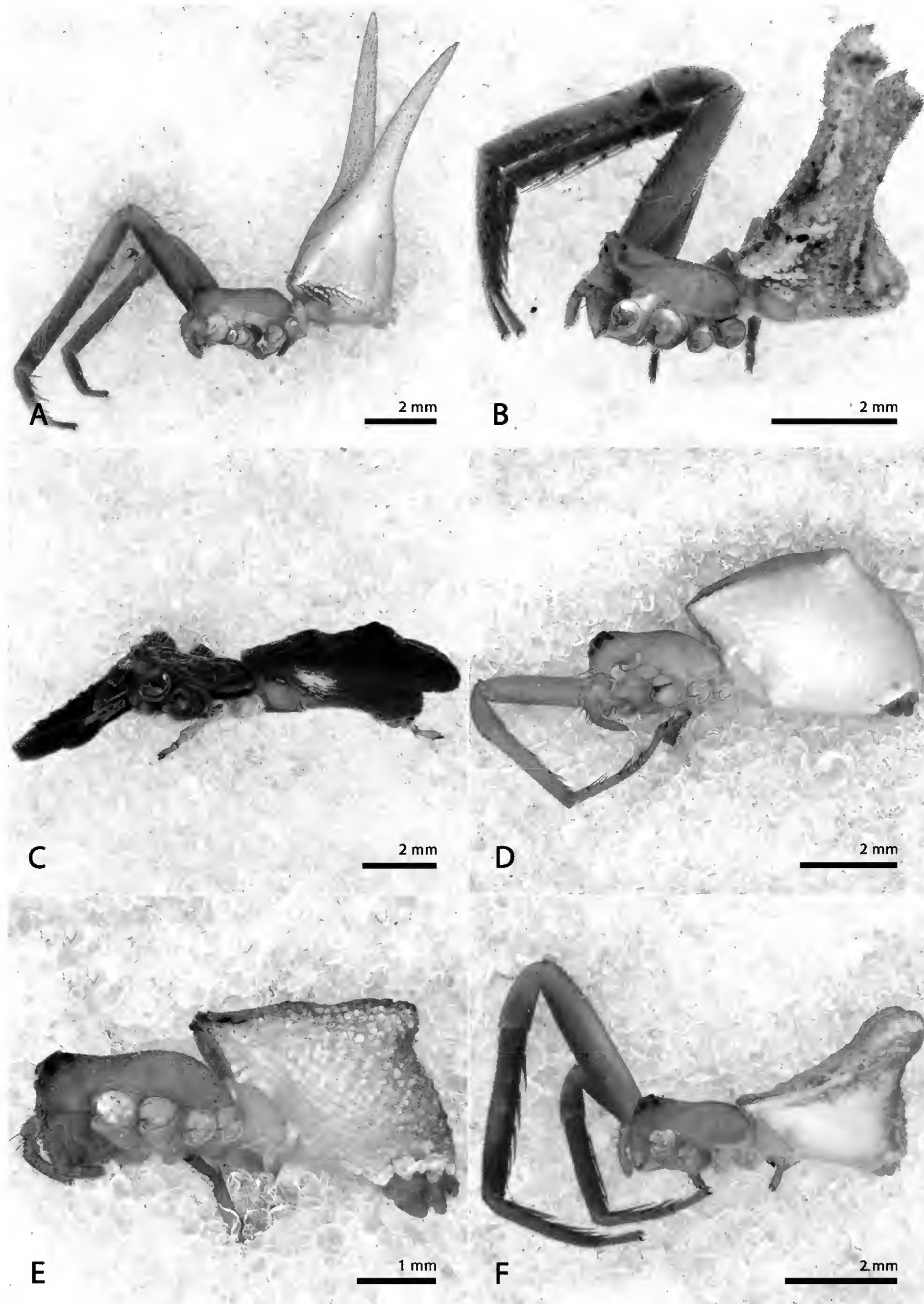


Figure 2. Habitussen of females, lateral **a** *Sidymella longispina* **b** *Sidymella furcillata* **c** *Sidymella kolpogaster* **d** *Sidymella excavata* sp. nov. **e** *Sidymella marmorata* sp. nov. **f** *Sidymella lucida*.

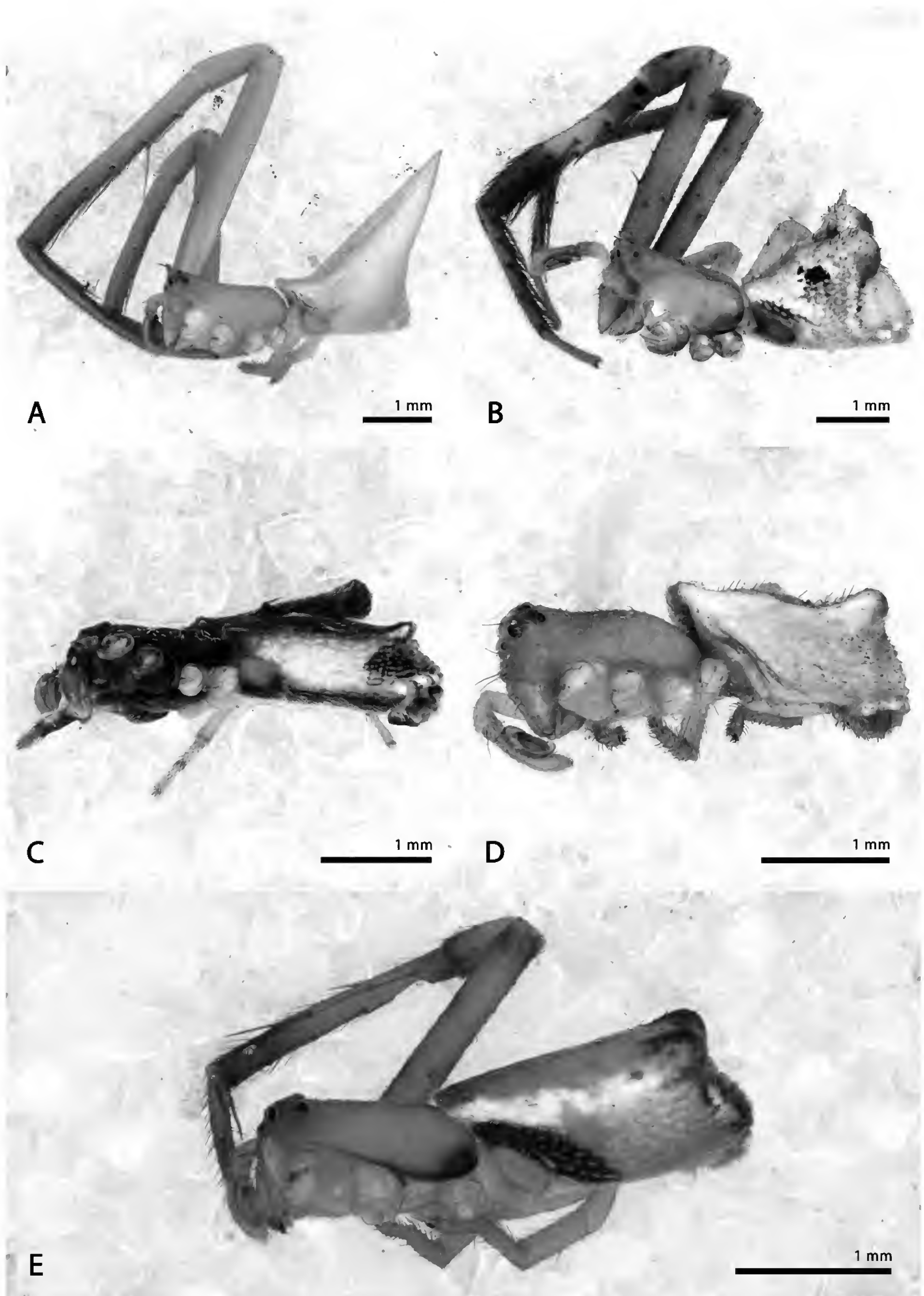


Figure 3. Habitussen of males, lateral **a** *Sidymella longispina* **b** *Sidymella furcillata* **c** *Sidymella kolpogaster* **d** *Sidymella excavata* sp. nov. **e** *Sidymella lucida*.

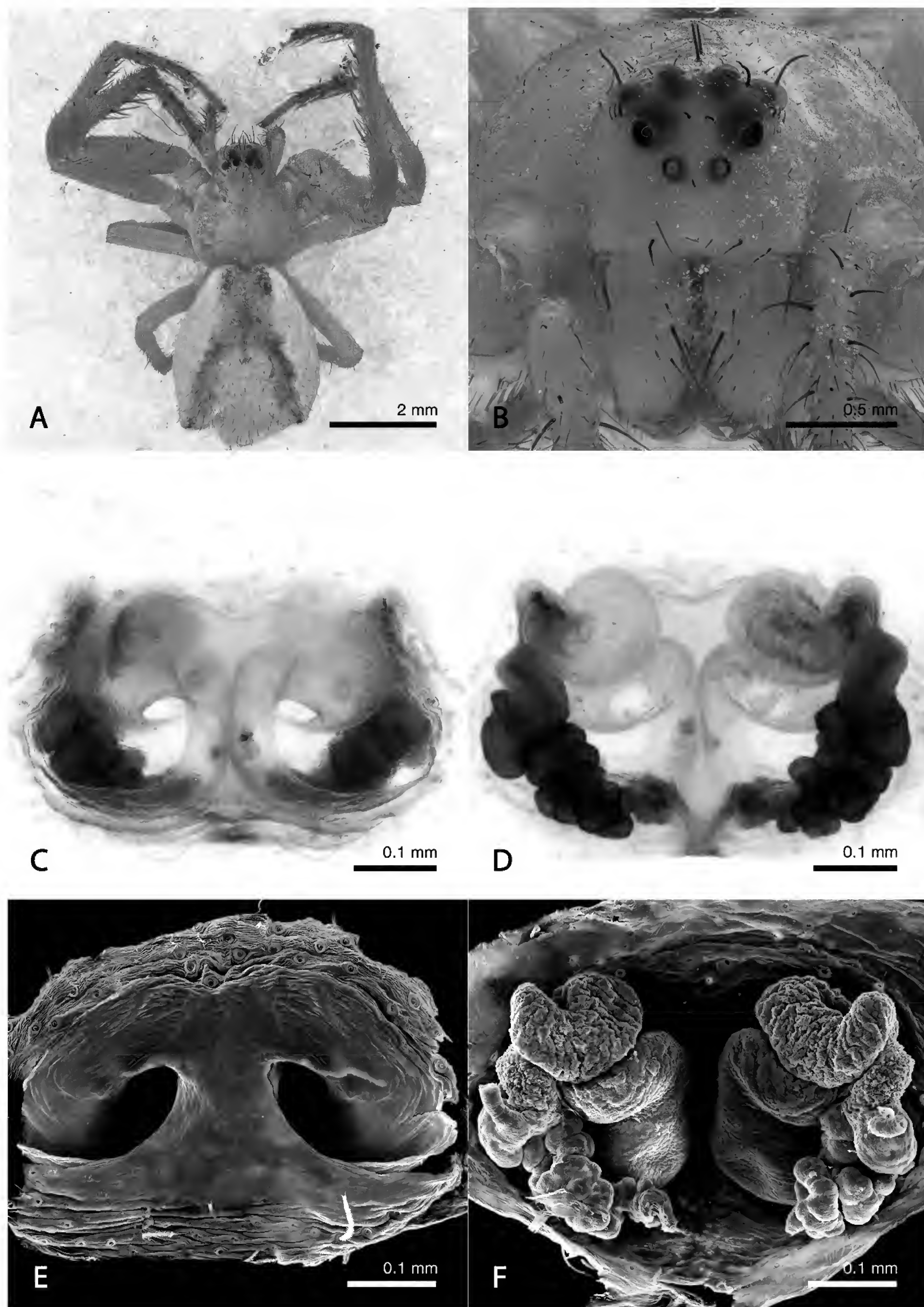


Figure 4. Female of *Sidymella excavata* sp. nov. **a** habitus, dorsal **b** prosoma, anterior **c, e** epigynum, ventral **d, f** epigynum, dorsal.

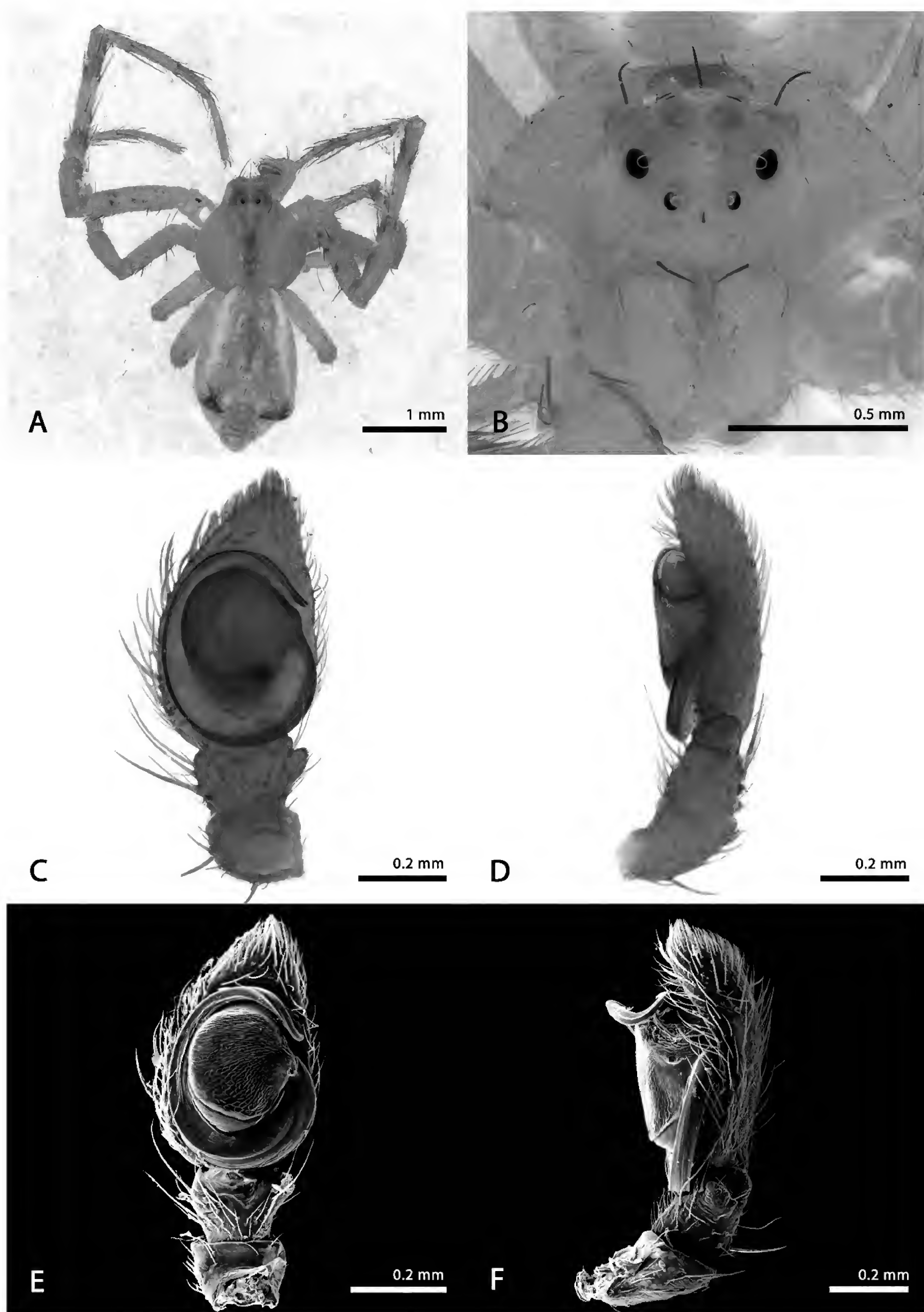


Figure 5. Male of *Sidymella excavata* sp. nov. **a** habitus, dorsal **b** prosoma, anterior **c, e** left palp, ventral view **d, f** left palp, retro-lateral view.

J. Martínez leg. (ICN-Ar 10500); 1♀, 23.ii.2002, same locality, C. Niño, G. Mora, A. Castañeda & J. Martínez leg. (CAUD-216-ARA 139); 1♀, 27.vii.2002, same locality, J. Martínez, C. Niño & G. Mora leg. (CAUD-216-ARA 366); 1♀, iv.2002, same locality, C. Niño, G. Mora, A. Castañeda & J. Martínez leg. (CAUD-216-ARA 1944); 1♀, 08.ix.2016, same locality, D. Molina leg. (ICN-Ar 10449); 1♀, same data as preceding (ICN-Ar 10498). 1♀, 2j, Boyacá, Villa de Levya, 5°40'21"N, 73°27'42"W, 09.vi.2001, L. Benavides leg. (ICN-Ar 1248). 1♂, Valle del Cauca, Saladito, 3°34'15.78"N, 76°36'9.27"W, W. Eberhard leg. (MCZ 133395). **ECUADOR**: 1♂, Quito, Pichincha, 0°15'00"S, 78°35'0"W, 19.iv.1988, W. Maddison leg. (MCZ 133397). 1♂, 2j, Azuay, Cerro Tinajillas, 3°10'60"S, 79°02'00"W, 18–21.iii.1965, L. Pena leg. (MCZ 133403). **PERU**: 1♂, Chavin, Ancash, 9°25'56"S, 77°32'07"W, 14.i.1972 (MACN-Ar 19068). **ARGENTINA**: 3♂, 4 j, Catamarca, Las Chacritas, 27°41'19.25"S, 65°55'24.97"W, 20.i.1987, P. Goloboff leg. (MACN-Ar 19098).

Etymology. The specific name refers to the shape of the anterior border of the opisthosoma with a remarkable median re-entrance/excavation.

Diagnosis. Females of *S. excavata* sp. nov. resemble those of *S. marmorata* sp. nov. by the large body size, short opisthosomal projections and long copulatory ducts; however, they can be distinguished by the presence of long needle-shaped macrosetae on the ocular area (Fig. 4B), and by having five mesial macrosetae on femora I and II (Fig. 4A). Males are similar to those of *S. lucida*, but can be recognized by cephalic setae and a basal branch of the RTA which is truncated instead of conical (Fig. 5C–F).

Description. Female: Prosoma, sternum and legs totally orange; legs I and II covered by numerous spiniform setae; opisthosoma predominantly light-yellow with a dark median stain on the dorsum that splits posteriorly towards the tips of the projections (Fig. 4A). Epigynum with a wide septum formed by the median junction of the posterior folds of the epigynal plate (Fig. 4C, E); copulatory ducts hyaline, long and coiled, leading to a pair of walnut-shaped spermathecae (Fig. 4D, F).

Measurements: eyes sizes and interdistances: AME 0.03, ALE 0.09, PME 0.05, PLE 0.03, AME–AME 0.15, AME–ALE 0.09, PME–PME 0.17, PME–PLE 0.17, MOQ length 0.41, MOQ width 0.17; leg formula: 1–2–4–3: leg I – femur 3.40/ patella 1.36/ tibiae 3.04/ metatarsus 2.04/ tarsus 0.88/ total 10.72; II – 2.68/ 1.12/ 2.08/ 1.72/ 0.68/ 8.28; III – 1.40/ 0.72/ 0.88/ 0.80/ 0.60/ 4.44; IV – 1.76/ 0.76/ 1.12/ 0.96/ 0.60/ 5.20. Total body length 5.48; prosoma 2.48 length, 2.04 wide; opisthosoma length 3.00; clypeus 0.35 height; sternum 1.12 length, 1.04 width; endites 0.56 length, 0.20 width; labium 0.32 length, 0.36 width.

Male: Prosoma yellow with a darker median stain; legs I and II yellow with brownish spots on the femo-

ral setiferous tubercles and at the distal portion of each leg segment; legs III and IV light-yellow. Opisthosoma as in female (Fig. 5A). Palpi with a well-developed pars pendula and embolus emerging at three o'clock, curling at the tip (Fig. 5C–F); basal branch of RTA stout and directed retro laterally while the RTA is short, rounded and oriented vertically (Fig. 5D, F).

Measurements: eyes diameters and eyes interdistances: AME 0.05, ALE 0.07, PME 0.05, PLE 0.05, AME–AME 0.13, AME–ALE 0.05, PME–PME 0.11, PME–PLE 0.13, MOQ length 0.17, MOQ width 0.11; leg formula: 1–2–4–3: leg I – femur 2.04/ patella 0.72/ tibiae 1.92/ metatarsus 1.68/ tarsus 0.76/ total 7.12; II – 1.44/ 0.60/ 1.20/ 1.12/ 0.60/ 4.96; III – 0.72/ 0.60/ 0.56/ 0.40/ 0.40/ 2.68; IV – 0.96/ 0.36/ 0.60/ 0.52/ 0.40/ 2.84. Total body length 3.12; prosoma 1.56 length, 1.24 wide; opisthosoma length 1.56; clypeus 0.19 height; sternum 0.68 length, 0.62 width; endites 0.35 length, 0.13 width; labium 0.17 length, 0.25 width.

Distribution. COLOMBIA: Magdalena, Quindío, Cundinamarca, Boyacá, and Valle del Cauca; ECUADOR: Pichincha and Azuay; PERU: Chavin; ARGENTINA: Catamarca (Fig. 15).

Sidymella furcillata (Mello-Leitão, 1944)

Figures 2B, 3B, 6, 7

Sidyma spinifera Mello-Leitão, 1943: 209, f. 36 (♀; preoccupied by Mello-Leitão 1929).

Sidyma multispinulosa Mello-Leitão, 1944: 4 (replacement name). Lise 1973: 13, figs 24–33 (holotype ♀ from Santa Catarina, Brazil, P. Buck leg., MNRJ 41934, examined). (New synonymy)

Stephanopsis furcillata Keyserling, 1880: 179, pl. 4, fig. 98 (holotype ♀ from Santa Cruz, Rio Grande do Sul, Brazil, Hensel leg., ZMB 2406, examined). (New combination)

Material examined. **ARGENTINA**: 1j, Misiones, San Vicente, 26°55'12"S, 54°31'12"W, 12.i.2005, L. Lopardo et al. leg. (ICN-Ar 27642); 1j, same locality, viii.1954, Schiapelli de Carlo leg. (ICN-Ar 19099); 2j, same locality, 1954, Schiapelli de Carlo leg. (ICN-Ar 19096). **BRAZIL**: 1♂, Bahia: Maracás, 13°28'15"S, 40°26'16"W, 14.iii.2012, E.S. Araújo & A.S. Medeiros leg. (UFMG 15165); 1♂, São Paulo, Botucatu (Rubião Júmior), 22°53'53"S, 48°29'23"W, 15.ii.1966, V.C. Jesus leg. (MNRJ 10391); 1♀, Paraná: Colombo, 25°17'31"S, 49°13'26"W, 02.xii.1990 (MCN 20684); 1♂, Três barras do Paraná, 25°25'08"S, 53°10'51"W, 20–26.ii.1993 (MCN 23043); 1♀, Curitiba (Parque Birigui), 25°25'31.58"S, 49°18'38.69"W, 01.xii.1990, A.B. Bonaldo leg. (MCN 20626); 1♀, Curitiba, 25°25'47"S, 49°16'19"W, 15.iv.2005, J. Ricetti leg. (MCTP 37237); 1♀, Santa Catarina: Itapiranga, 27°10'08"S, 53°42'43"W, Pio Buck leg. (MNRJ 41934); 2♀, 3j, Rancho Queimado, 27°40'22"S, 49°01'19"W, 13–15.i.1995 (MCN 26464); 1♂, Rio Grande do Sul, Tenente Portela, 27°22'25.69"S, 53°47'32.43"W, 11.ix.1976, S. Scherer leg. (MCN 4862);

1♀, Nonoai (Parque Estadual de Nonoai), 27°27'21.25"S, 53°6'46.98"W, 14.i.1985, A.A. Lise leg. (MCN 13077); 1♀, Arroio do Meio, 29°23'47.15"S, 51°56'54.26"W, 09.i.1985, same collector (MCN 13071); 1j, Iraí, 27°11'38"S, 53°15'03"W, 20 September 1975, same collector (MCN 8084); 1♂, Derrubadas (Parque Estadual do Turvo), 27°13'57"S, 53°51'04"W, 16.i.1985, same collector (MCN 13057); 1♀, same locality, 01 February 1996, A.B. Bonaldo, A. Kury & R. Pinto-da-Rocha leg. (MCN 27100); 1j, 27–31.viii.2003, R. Ott leg. (MCN 37827); 1j, Caxias do Sul, 29°07'17"S, 51°01'07"W, 18–21.xi.1993 (MCTP 4176); 1♀, Farroupilha, 29°13'30"S, 51°20'52"W, 29.ix.1978, H. Bischoff leg. (MCN 8268); 1♀, 2j, same data as preceding (MCN 8270); 1♂, Estrela Velha (Barragem de Itaúba), 29°15'19"S, 53°13'36"W, 07.iii. 2001, R. Ott leg. (MCN 33700); 1♀, São Francisco de Paula (Barragem Passo do Inferno), 29°16'29"S, 50°44'15"W, 26.ix.2000, M.A.L. Marques leg. (MCN 33220); 1♀, São Francisco de Paula, 29°27'00"S, 50°34'59"W, 10.xii. 2007, L. Moura & R. Moraes leg. (MCN 43748); 1♀, Parobé (Rio dos Sinos), 29°37'29"S, 50°49'56"W, 11.v. 2008, E.N.L. Rodrigues leg. (MCN 47943); 1♀, Maquiné, 29°39'41"S, 50°12'47"W, 08–09.iii.1998, L.A. Moura leg. (MCN 29060); 1♀, Campo Bom, 29°40'44"S, 51°3'10"W, 19–20.v.1986, C.J. Becker leg. (MCN 15080); 2♀, Santa Maria, 29°40'59"S, 53°48'00"W, 17.iv.1996, C.B. Kotzian & L. Indrusiak leg. (MCTP 40093); 1j, Montenegro, 29°41'20"S, 51°27'39"W, 06.viii.1977, H. Bischoff leg. (MCN 6822); 1j, same locality, 03.xi.1977, A.A. Lise leg. (MCN 7141); 1♂, 1♀, 3j, same locality, 15.xii.1977, same collector (MCN 7510); 1♀, same locality, 20.xii.1977, same collector (MCN 7614); 1j, same locality, 03.xi.1977, same collector (MCN 8089); 2j, same locality, 29.ix.1977, same collector (MCN 9058); 5j, same data as preceding (MCN 9059); 1♀, São Leopoldo, 29°45'36"S, 51°8'49"W, 12.vi.1992 (MCN 24755); 2♀, 3j, Montenegro (Pesqueiro), 29°46'16"S, 51°23'57"W, 12.v.1977, A.A. Lise leg. (MCN 5323); 1♀, Santo Antônio da Patrulha, 29°49'4"S, 50°31'12"W, 18.vii.2000, same collector (MCN 33116); 2♀, Triunfo (Parque Copesul de Proteção Ambiental), 29°51'57"S, 51°21'54"W, 25.i.1990, A.B. Bonaldo leg. (MCN 19344); 1♀, same locality, 13.i.1994, A.F. Franceschini leg. (MCN 24771); 1j, same locality, 25.xi.1994, L.A. Moura leg. (MCN 26116); 1♂, 2♀, same locality, 08.i.1997, E.H. Buckup leg. (MCN 28176); 2♀, 14–15.i.1997, L.A. Moura leg. (MCN 28263); 3♀, same locality, 16–17.iii.1998, L.A. Moura leg. (MCN 29238); 1♀, same locality, 05.ii.2003, R. Ott leg. (MCN 35125); 2♀, same locality, 29–30.iv.2003, R. Ott leg. (MCN 35740); 2♀, same locality, 06.i.2005, R. Ott leg. (MCN 38352); 1♀, same locality, 01.iii.2005, R. Ott leg. (MCN 39924); 1♀, same locality, 28.v. 2007, E.N.L. Rodrigues leg. (MCN 43383); 1♂, 1♀, same locality, 14.ii.2008, R. Moraes leg. (MCN 44009); 1♀, same locality, 03.iv.2008, A. Barcellos leg. (MCN 44127); 1♀, same locality, 26.ii.2010, M.C. Pairet Jr. leg. (MCN 47032); 1♀, same locality, 26.ii.2010, M.A.L. Marques leg. (MCN 47049); 3♀, Canoas, 29°55'12"S, 51°10'48"W, 13.xii.1990 (MCN

20142); 1♂, 1♀, 2j, same locality, 24.i.1991, H. Galileo & E.H. Buckup leg. (MCN 20431); 1j, same locality, 25.xii.1983, A.D. Brescovit leg. (MCN 11904); 3♀, Triunfo, 29°56'34"S, 51°43'4"W, 20.x.1977, H. Bischoff leg. (MCN 6900); 3♀, same locality, 28.xi.1977, same collector (MCN 7314); 1♀, Triunfo (Parque Estadual Delta do Jacuí), 29°57'16"S, 51°12'55"W, 23.ii.1999, A.B. Bonaldo leg. (MCN 30488); 1j, Porto Alegre, 30°01'58"S, 51°13'48"W, 04.ix.1977, A.A. Lise leg. (MCN 6469); 1♀, same locality, 17.xii.1983, A.D. Brescovit leg. (MCN 11882); 2♂, 1♀, same locality, 18.i.1992, A.D. Brescovit leg. (MCN 21958); 1♀, same locality, 2010, biology students leg. (MCTP 41329); 1j, Porto Alegre (Morro Santana), 30°02'34"S, 51°08'39"W, 22.x.1981, A.A. Lise leg. (MCN 11421); 1j, Viamão (Estação Experimental Fitotécnica Águas Belas), 30°02'51"S, 51°00'53"W, 24.i.1977, A.A. Lise leg. (MCN 5140); 1♂, same locality, 06.i.1977, same collector (MCN 5763); 1♀, Viamão (Escola Marista), 30°04'41"S, 51°03'02"W, 1994, A. Braul leg. (MCTP 4726); 3j, Porto Alegre (Ponta Grossa), 30°10'29"S, 51°11'50"W, 03.ix.1975, A.A. Lise leg. (MCN 3029); 1j, same locality, 07.v.1976, same collector (MCN 8086); 3j, Viamão (Morro do Coco), 30°16'11"S, 51°03'15"W, 04.x.1975, A.A. Lise leg. (MCN 8085); 1♀, same locality, 25.vii.1985, same collector (MCN 13378); 1j, Viamão, 30°4'51"S, 51°1'22"W, 12.i.1996, same collector (MCTP 8365); 1♀, same locality, 23.i.1996, same collector (MCTP 9294); 3j, same locality, 02.xii.1994, A.A. Lise & A. Braul leg. (MCTP 5876); 5j, same locality, 12.vii.1994, A.A. Lise leg. (MCTP 5244); 1♀, 1j, Guaíba, 30°6'50"S, 51°19'30"W, 09.i.1996, A.A. Lise leg. (MCTP 8247); 1♂, Cristal (Rio Camaquã), 31°00'12"S, 52°04'02"W, 03.ii.2008, E.N.L. Rodrigues leg. (MCN 48665).

Diagnosis. Females of *S. furcillata* are similar to those of *S. longispina* by having macrosetae above the ALE and long opisthosomal projections that are directed vertically (Fig. 2B); however, in *S. furcillata* the projections are rounded at the apex with a smaller terminal tubercle (Fig. 2B). They can be also distinguished by having a group of clavate setae on the median region of the prosoma (Fig. 6B), a triad of mesial macrosetae on femora I, presence of seven pairs of ventral macrosetae on tibiae I, a dark transversal line on the dorsum of opisthosoma (Fig. 6A), and by the long and coiled copulatory ducts (Fig. 6D, F). Males can be distinguished by having tubercles at the apexes of the opisthosomal projections (Fig. 3B), wide pars pendula (Fig. 7C, E), retrolateral tegular process, and the bifid basal branch of the RTA (Fig. 7D, F).

Description. Female: Prosoma dark-yellow to light-brown, covered by hyaline setae; legs of the same colour as prosoma, with some sparse darker circular taints randomly distributed; dorsal surface of coxae I and II with wide guanine spots (Fig. 6A). Opisthosoma dark-yellow with two transversal dark lines, being the posterior line disposed along the projections (Fig. 6A).

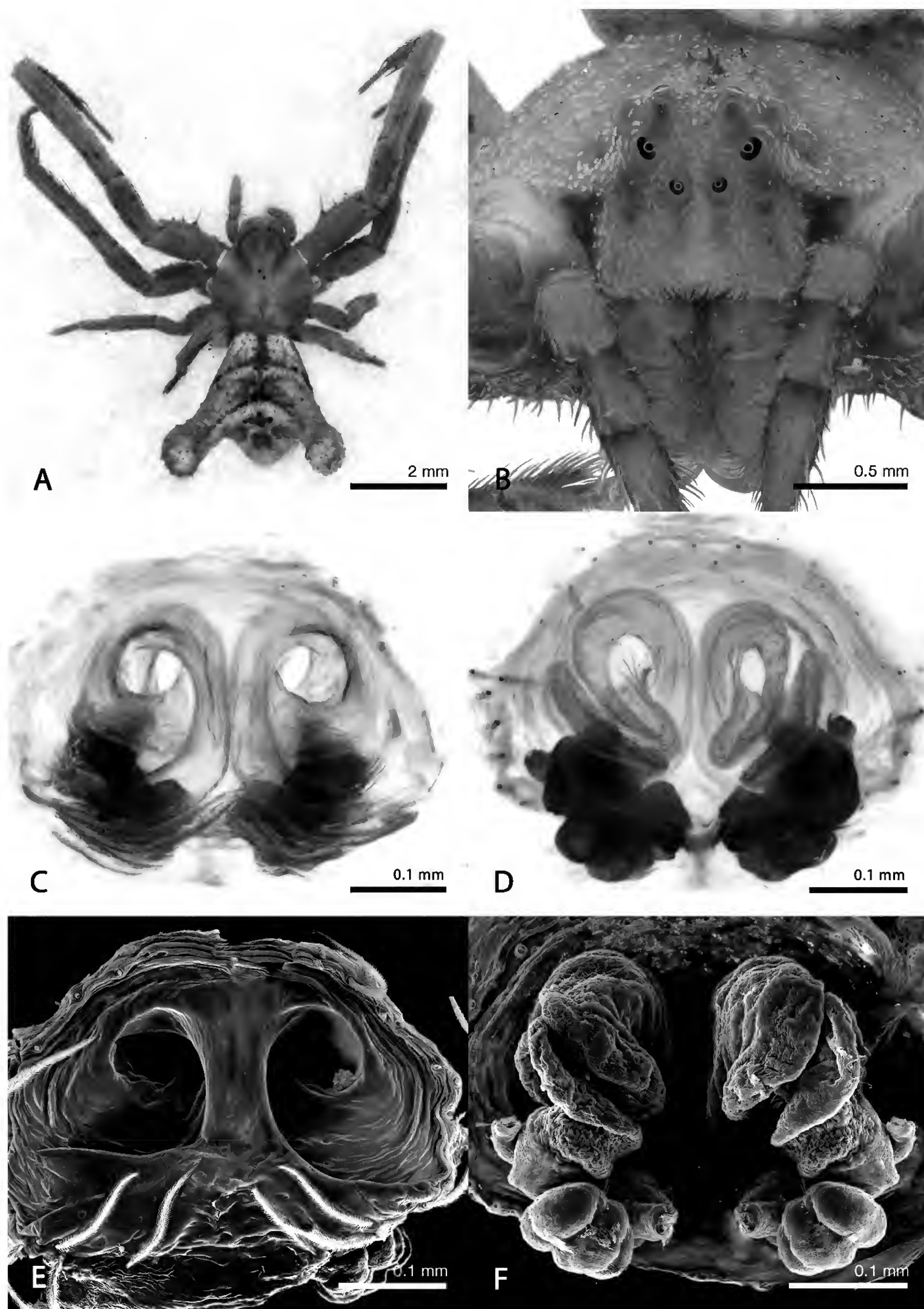


Figure 6. Female of *Sidymella furcillata* **a** habitus, dorsal **b** prosoma, anterior **c**, **e** epigynum, ventral **d**, **f** epigynum, dorsal.

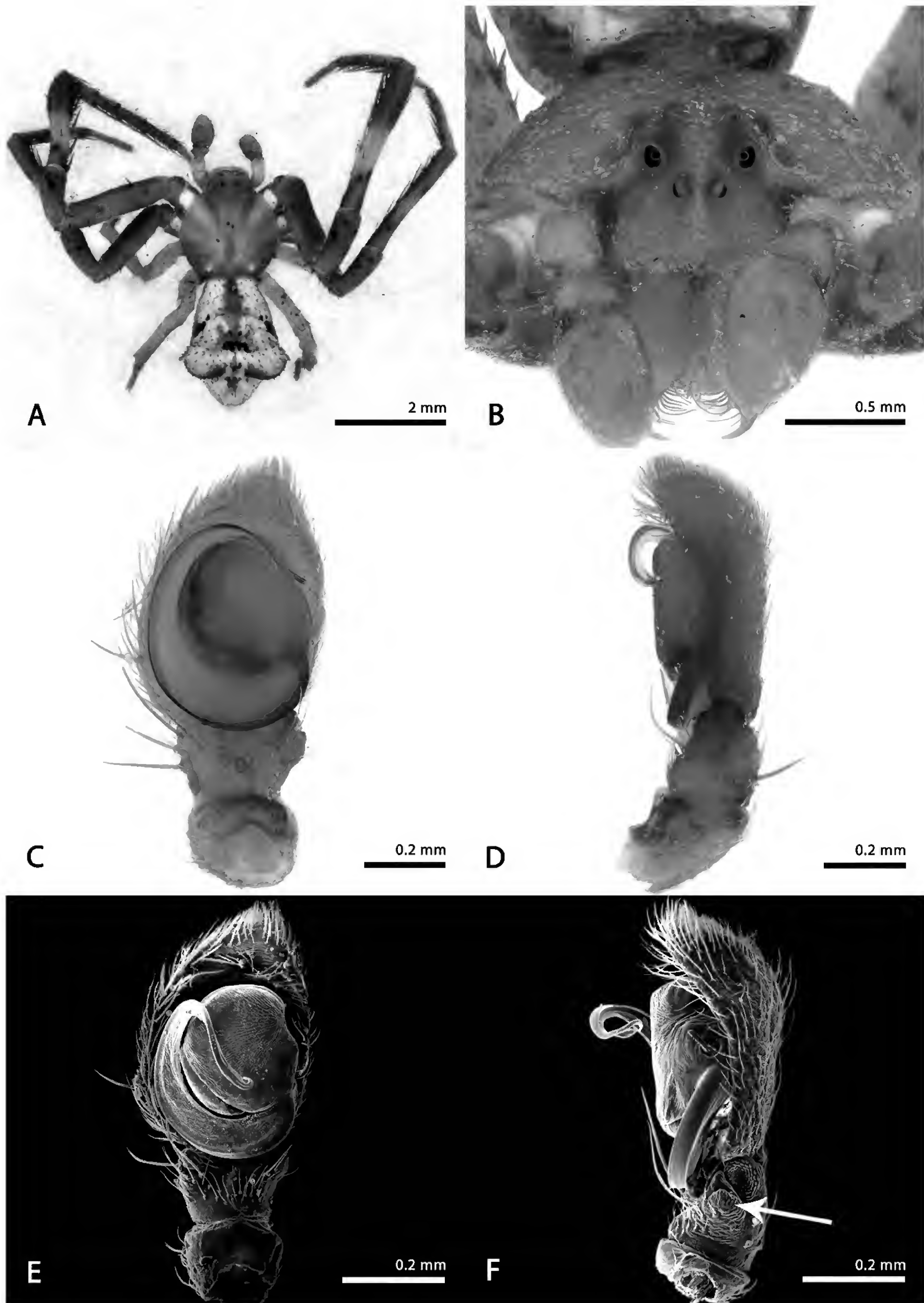


Figure 7. Male of *Sidymella furcillata* **a** habitus, dorsal **b** prosoma, anterior **c**, **e** left palp, ventral view **d**, **f** left palp, retrolateral view (white arrow indicates the basal branch of the RTA).

Measurements: eyes diameters and eyes interdistances: AME 0.05, ALE 0.09, PME 0.05, PLE 0.05, AME–AME 0.13, AME–ALE 0.11, PME–PME 0.15, PME–PLE 0.15, MOQ length 0.33, MOQ width 0.15; leg formula: 1–2–4–3: leg I – femur 3.36/ patella 1.40/ tibiae 3.12/ metatarsus 2.24/ tarsus 0.92/ total 11.04; II – 3.17/ 1.32/ 2.40/ 1.96/ 0.76/ 9.61; III – 1.16/ 0.68/ 0.92/ 0.60/ 0.52/ 3.88; IV – 1.36/ 0.72/ 0.84/ 0.52/ 0.48/ 3.92. Total body length 5.05; prosoma 2.04 length, 2.08 wide; opisthosoma length 3.01 (considering the projections); clypeus 0.29 height; sternum 1.03 length, 0.94 width; endites 0.47 length, 0.29 width; labium 0.27 length, 0.27 width.

Male: Prosoma dark-yellow, legs I and II predominantly light-brown with dark spots; tibiae I yellowish on the median region; legs III and IV yellowish (Fig. 7A). Opisthosoma yellowish with a pair of dorsolateral and a median posterior black spot (Fig. 7A). Embolus long, emerging from tegulum at four o'clock, with wide pars pendula and curled at the tip; RTA rounded and with central excavation (Fig. 7C–F).

Measurements: eyes diameters and eyes interdistances: AME 0.03, ALE 0.07, PME 0.05, PLE 0.05, AME–AME 0.11, AME–ALE 0.09, PME–PME 0.17, PME–PLE 0.13, MOQ length 0.31, MOQ width 0.11; leg formula: 1–2–4–3: leg I – femur 3.08/ patella 1.32/ tibiae 2.88/ metatarsus 2.32/ tarsus 0.88/ total 10.48; II – 2.48/ 1.00/ 2.04/ 1.96/ 0.80/ 8.28; III – 0.76/ 0.52/ 0.76/ 0.56/ 0.48/ 3.08; IV – 1.24/ 0.44/ 0.76/ 0.48/ 0.48/ 3.40. Total body length 3.96; prosoma 1.96 length, 1.88 wide; opisthosoma length 2.00 (considering the projections); clypeus 0.29 height; sternum 0.90 length, 0.82 width; endites 0.43 length, 0.25 width; labium 0.23 length, 0.27 width.

Distribution. ARGENTINA: Misiones; BRAZIL: Bahia, São Paulo, Paraná, Santa Catarina, and Rio Grande do Sul (Fig. 16).

Sidymella kolpogaster Lise, 1973

Figures 2C, 3C, 8, 9

Sidyma kolpogaster Lise, 1973: 5, figs 5–9 (♀); Lise 1981: 130, figs 1–12 (♂,♀).

Sidymella kolpogaster: Brignoli, 1983: 605.

Type material. Holotype ♀, BRAZIL: Paraná, Rio Negro, Franciscanos leg. (MNRJ 58065, examined; lost in the fire of the Museu Nacional do Rio de Janeiro). Neotype ♀, BRAZIL: Paraná, Curitiba (Parque Barigui), 25°25'12"S, 49°18'21"W, A.B. Bonaldo leg., 01.xii.1990 (MCN 20622, designated here).

Other material examined. BRAZIL: 1♀, Paraná, Rio Negro, 26°05'11"S, 49°46'47"W (MNRJ 58065); 1♂, Santa Catarina, Rancho Queimado, 27°40'22"S, 49°01'19"W, 09–13.x.1995, A.A. Lise, A. Braul & M. Silveira leg. (MCTP 7009); 1♀, Rio Grande do Sul, Estrela Velha, 29°15'19"S, 53°13'36"W, 21.x.1998, A.B. Bonaldo leg. (MCN 30791); 1j, Arroio do Tigre (Itaúba), 29°16'47"S,

53°06'34"W, 18.iv.1978, A.A. Lise leg. (MCN 8047); 1j, Arroio do Tigre, 29°19'58"S, 53°05'34"W, 23.iv.1978 (MCN 8150); 1♀, São Francisco de Paula, 29°24'52"S, 50°15'24"W, 20.ix.1998, A.A. Lise leg. (MCTP 14446); 1j, same locality, 21–24.iii.1995, same collector (MCTP 12010); 1j, Montenegro, 29°41'20"S, 51°27'39"W, 20.xii.1977, A.A. Lise leg. (MCN 7613); 1♂, 1♀, Glorinha (Rincão São João), 29°49'00"S, 50°50'00"W, 14.vii.2000, A.B. Bonaldo leg. (MCN 33053); 1♂, Triunfo (Parque Copesul de Proteção Ambiental), 29°51'57"S, 51°21'54"W, 01.ix.2008, E.N.L. Rodrigues leg. (MCN 45434); 1♀, Triunfo (Parque Braskem), 29°51'57"S, 51°21'54"W, 04.xii.2009, E.N.L. Rodrigues leg. (MCN 46847); 1j, Porto Alegre (Morro Santana), 30°02'34"S, 51°08'39"W, 17.v.1980, A.A. Lise leg. (MCN 9065); 1j, Viamão (Estação Experimental Fitotécnica Águas Belas), 30°02'51"S, 51°00'53"W, 12.viii.1994, A.A. Lise leg. (MCTP 5243); 1♀, same locality, 23.ix.1994, same collector (MCTP 5498); 1♂, same locality, 06.v.1994, A.A. Lise & A. Braul leg. (MCTP 4683); 1♀, same locality, 17.i.1977, A.A. Lise leg. (MCN 4995); 1♀, Viamão, 30°04'51"S, 51°01'22"W, 14.v.2005, R. Jalisco leg. (MCTP 19737).

Diagnosis. Females of *S. kolpogaster* are similar to those of *S. lucida* by the general shape of the spermathecae, short copulatory ducts, and femora I with two mesial macrosetae. However, females of *S. kolpogaster* can be easily distinguished from congeners by curved tibiae I and II, flattened prosoma, dark body colouration, varying from dark-brown to black and contrasting with their vivid yellow legs III and IV (Fig. 8A). The males can also be recognized by their body colour pattern, which is the same as in females, and by their truncated RTA fused with basal branch (Fig. 9D, F).

Description. Female: Prosoma dark-brown, lighter on the ocular area and clypeus, covered by hyaline setae and dorsoventrally compressed (Fig. 8B). legs I and II entirely dark-brown, except for the reduced and yellowish tarsi; metatarsi I and II curved; legs III and IV entirely light-yellow (Fig. 8A). Opisthosoma dark-brown with posterior projections stout and conical. Epigynal plate wide and with short septum; copulatory ducts short and hyaline (Fig. 8C–F).

Measurements: eyes diameters and eyes interdistances: AME 0.07, ALE 0.11, PME 0.05, PLE 0.05, AME–AME 0.17, AME–ALE 0.09, PME–PME 0.23, PME–PLE 0.19, MOQ length 0.21, MOQ width 0.15; leg formula: 1–2–4–3: leg I – femur 4.95/ patella 1.80/ tibiae 4.15/ metatarsus 2.95/ tarsus 0.95/ total 14.80; II – 4.45/ 1.75/ 3.20/ 2.65/ 0.85/ 12.90; III – 1.65/ 0.75/ 1.15/ 1.05/ 0.55/ 5.15; IV – 2.05/ 0.75/ 1.25/ 1.15/ 0.55/ 5.75. Total body length 7.65; prosoma 2.80 length, 2.85 wide; opisthosoma length 4.85; clypeus 0.19 height; sternum 1.21 length, 1.20 width; endites 0.68 length, 0.37 width; labium 0.41 length, 0.50 width.

Male: Prosoma and legs colouration as in female (Fig. 9A, B). Palpi with flattened cymbium and dorsal trichobothria on tibiae; tegulum discoid and embolus thin, slightly curved at the tip and emerging from tegulum at four o'clock (Fig. 9C–F).

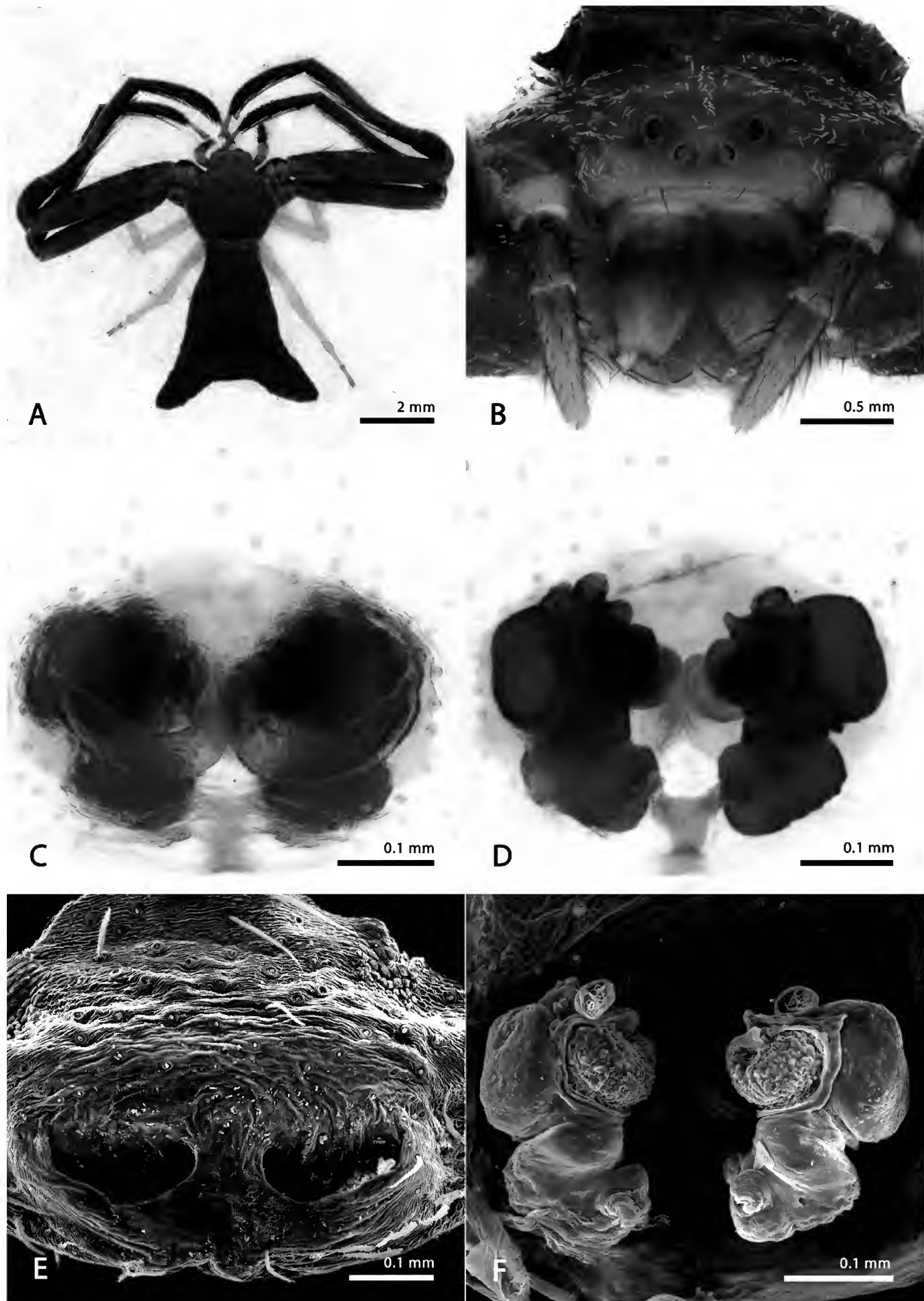


Figure 8. Female of *Sidymella kolpogaster* **a** habitus, dorsal **b** prosoma, anterior **c, e** epigynum, ventral **d, f** epigynum, dorsal.

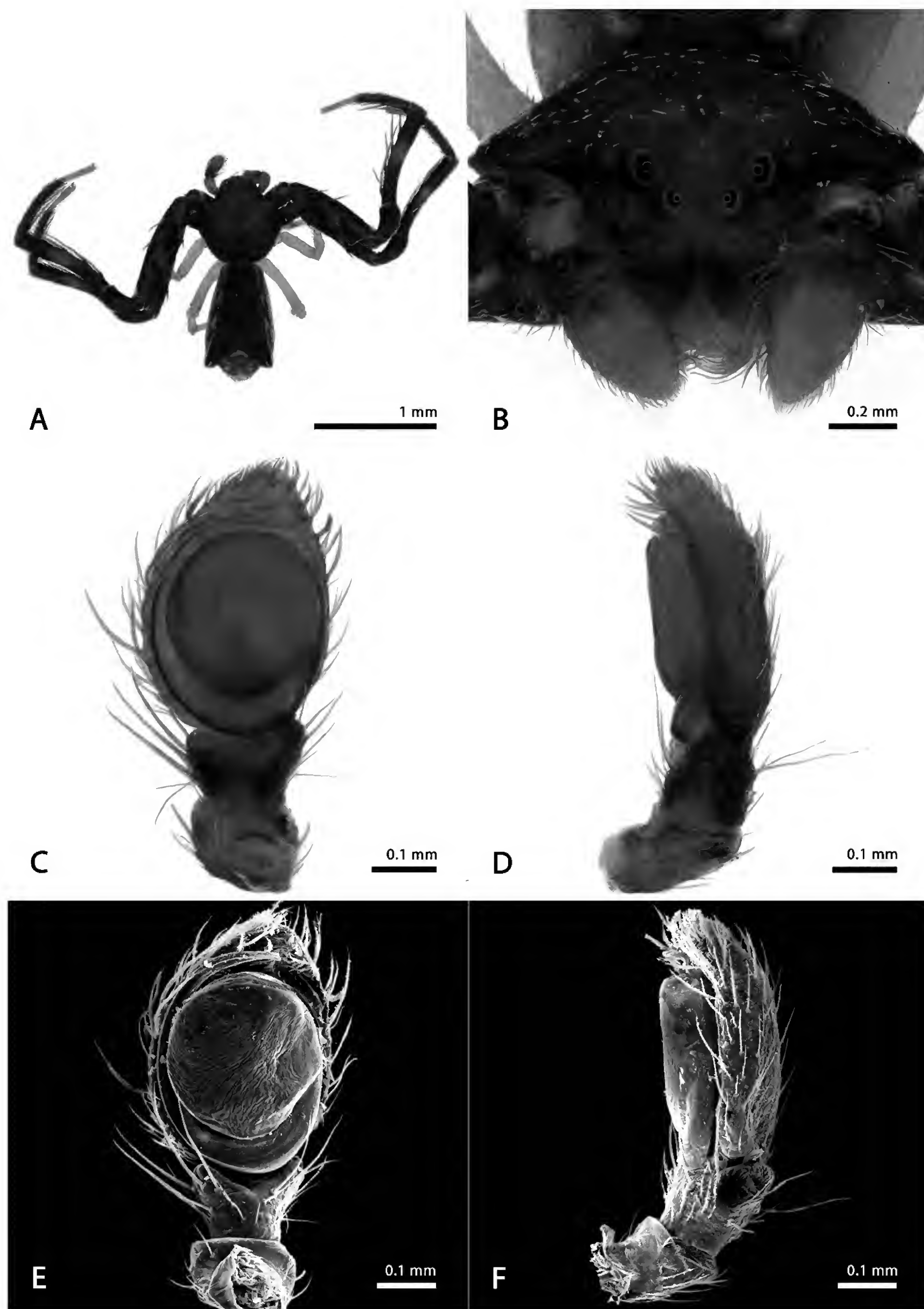


Figure 9. Male of *Sidymella kolpogaster* **a** habitus, dorsal **b** prosoma, anterior **c**, **e** left palp, ventral view **d**, **f** left palp, retro-lateral view.

Measurements: eyes diameters and eyes interdistances: AME 0.03, ALE 0.05, PME 0.03, PLE 0.05, AME–AME 0.11, AME–ALE 0.05, PME–PME 0.09, PME–PLE 0.09, MOQ length 0.21, MOQ width 0.11; leg formula: 1–2–4–3: leg I – femur 2.04/ patella 0.68/ tibiae 1.68/ metatarsus 1.56/ tarsus 0.60/ total 6.56; II – 1.64/ 0.36/ 1.44/ 1.20/ 0.52/ 5.16; III – 0.72/ 0.36/ 0.52/ 0.52/ 0.32/ 2.44; IV – 0.92/ 0.32/ 0.76/ 0.48/ 0.36/ 2.84. Total body length 3.12; prosoma 1.40 length, 1.32 wide; opisthosoma length 1.72; clypeus 0.07 height; sternum 0.64 length, 0.68 width; endites 0.27 length, 0.32 width; labium 0.13 length, 0.25 width.

Distribution. BRAZIL: Paraná, Rio Grande do Sul, Santa Catarina (Fig. 17).

Sidymella longispina (Mello-Leitão, 1943)

Figures 2A, 3A, 10, 11

Sidyma longispina Mello-Leitão, 1943: 208, fig. 35 (♀); Lise 1973: 10, figs 19–23 (♀).

Type material. Holotype ♀, BRAZIL: Rio Grande do Sul, B. Rambo leg. (MNRJ 41911, examined; lost in the fire of the Museu Nacional do Rio de Janeiro). Neotype female, BRAZIL: Rio Grande do Sul, São Francisco de Paula, 29°24'52"S, 50°15'24"W, A.A. Lise et al., 24–26. iv.2006 (MCTP 35899, designated here).

Other material examined. BRAZIL: 1♂, Minas Gerais, Vale Verde (Parque Nacional do Caparaó), 20°25'05"S, 41°50'48"W, 24–30.xi.2014, B.T. Faleiro leg. (UFMG 18264). 1♂, 1j, Paraná, Foz do Iguaçu (Refúgio Biológico de Bela Vista), 25°26'56"S, 54°33'23"W, 09–11. xi.1991, A.B. Bonaldo leg. (MCN 21809). 1♀, Santa Catarina, Rancho Queimado, 27°40'22"S, 49°01'19"W, 08–12.x.1994, A.B. Bonaldo & L.A. Moura leg. (MCTP 5952). 3j, Rio Grande do Sul, Tenente Portela, 27°22'15"S, 53°45'28"W, 17.i.1985, A.A. Lise leg. (MCN 13068); 2j, Iraí, 27°11'38"S, 53°15'03"W, 18.xi.1975, A.A. Lise leg. (MCN 3142); 10j, same locality, 21.xi.1975, same collector (MCN 8082); 1j, Derrubadas (Parque Estadual do Turvo), 27°13'57"S, 53°51'04"W, 04–06.ii.1980, A.A. Lise leg. (MCN 8984); 3♀, same locality, 04–07.v.2004, R. Ott leg. (MCN 38864); 1♀, same locality, 19–22.x.2004. R. Ott leg. (MCN 38878); 1f, Caxias do Sul (Vila Oliva), 29°12'56"S, 50°53'22"W, 14.ix.1976, H. Bischoff leg. (MCN 4485); 1♂, 10.iv.1992, L.A. Moura leg. (MCN 22124); 1j, Canela, 29°21'57"S, 50°48'57"W, 24.viii.1975, A.A. Lise leg. (MCN 3026); 2♀, São Francisco de Paula, 29°27'00"S, 50°34'59"W, 14.v.1993, A. Bräul leg. (MCTP 3213); 3j, same locality, 05.i.1985, A.A. Lise leg. (MCN 13107); 1♀, Maquiné, 29°40'47"S, 50°11'20"W, 22.vi.2008, E.N.L. Rodrigues leg. (MCN 54202); 1♀, Santa Maria, 29°40'59"S, 53°48'00"W, 18.i.1999, C.B. Kotzian & L. Indrusiak leg. (MCTP 40101); 1♂, 1♀, same locality, 30.ix.1992, biology students leg. (MCTP 41330); 1♀, Gravataí (Mato Alto),

29°57'20"S, 50°57'46"W, 13.iii.1985, A.D. Brescovit leg. (MCN 13094); 2♀, Cachoeira do Sul, 30°0'0"S, 53°0'0"W, B. Rambo leg. (MNRJ 41911); 1♀, Pantano Grande, 30°11'27"S, 52°22'26"W, 05.iv.2008, G. Deprá leg. (MCTP 40084); 1♀, Guaíba, 30°6'50"S, 51°19'30"W, 28.iv.1995, A. Bräul leg. (MCTP 7542); 1♀, Cristal (Rio Camaquã), 31°00'12"S, 52°04'02"W, 19.xii.2007, E.N.L. Rodrigues leg. (MCN 48618); 1♂, same locality, 14.ii.2008, same collector (MCN 48832); 1♀, same locality, 21.iv.2008, same collector (MCN 49031); 1j, São Borja, 28°10'16.10"S, 55°26'49.78"W, 06.xii.1975, A.A. Lise leg. (MCN 8088). ARGENTINA: 1♀, Misiones, Puerto Iguazu (Parque Nacional Iguazú), 25°41'01"S, 54°27'14"W, 22–30.viii.1986, M. Ramírez leg. (MACN-Ar 19069); 2j, same locality, 19–20.i.2005, C. Grismado et al. leg. (MACN-Ar 27637); 1♀, same locality, vi.1985, M. Ramírez leg. (MACN-Ar 19067); 1j, Iguazu, 25°50'53.71"S, 54°20'48.17"W, x.1954, Schiapelli de Carlo leg. (MACN-Ar 19070); 1j, Montecarlo, 26°33'58"S, 54°45'25"W, i.1966, same collector (MACN-Ar 19072); 3♂, 2j, Santa Maria, 27°53'39"S, 55°21'20"W, 1952, C. Viana leg. (MCTP 3537).

Diagnosis. Females of *S. longispina* are similar to those of *S. furcillata* by their long and vertically oriented opisthosomal projections (Figs 2A, 10A), and the presence of stout macrosetae above the ALE (Fig. 10B); however, their opisthosomal projections have pointy conical apices instead of being rounded with a small apical protuberance as in *S. furcillata*. The females of *S. longispina* also have shorter copulatory ducts (Fig. 10D, F). Males of *S. longispina* resemble those of *S. furcillata* but their palpi bear a truncated RTA with a conical and well-developed basal branch (larger than the RTA itself) (Fig. 11D, F); the male palp has a long, acute tegular process and a dorso-basal projection (Fig. 11D, F). Both males and females have just one mesial macroseta on femora I (Fig. 11A).

Description. Female: Prosoma yellowish-orange, darker on the cephalic area and presenting a pair of needle-shaped macrosetae on conical projections above the ALE (Fig. 10B). Legs yellowish-orange; femora I with a single pro-lateral macrosetae; both the anterior tibiae and metatarsi (I and II) ventrally armed with five pairs of ventral macrosetae. Opisthosoma light-yellow with posterior projections long, pointed and vertically oriented (Figs 2A, 10A).

Measurements: eyes diameters and eyes interdistances: AME 0.05, ALE 0.09, PME 0.05, PLE 0.05, AME–AME 0.15, AME–ALE 0.11, PME–PME 0.15, PME–PLE 0.17, MOQ length 0.35, MOQ width 0.15; leg formula: 1–2–4–3: leg I – femur 4.45/ patella 1.60/ tibiae 4.20/ metatarsus 3.05/ tarsus 0.85/ total 14.15; II – 3.35/ 1.30/ 2.95/ 1.95/ 0.75/ 10.30; III – 1.25/ 0.65/ 1.05/ 0.55/ 0.55/ 4.05; IV – 1.60/ 0.70/ 0.95/ 0.55/ 0.45/ 4.25. Total body length 7.93; prosoma 2.56 length, 2.12 wide; opisthosoma length 5.37 (considering the projections); clypeus 0.23 height; sternum 1.11 length, 1.00 width; endites 0.60 length, 0.27 width; labium 0.31 length, 0.37 width.

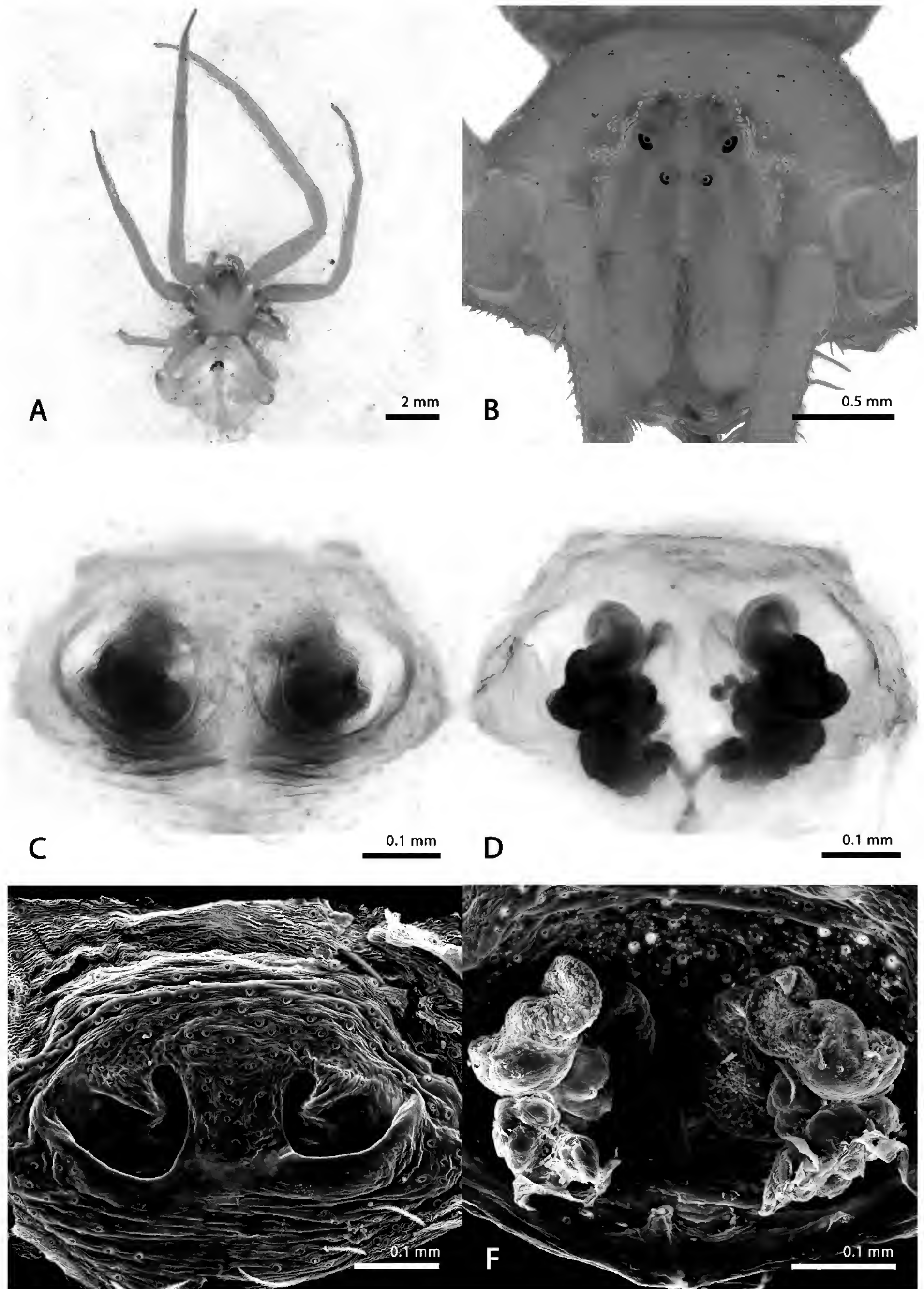


Figure 10. Female of *Sidymella longispina* **a** habitus, dorsal **b** prosoma, anterior **c, e** epigynum, ventral **d, f** epigynum, dorsal.

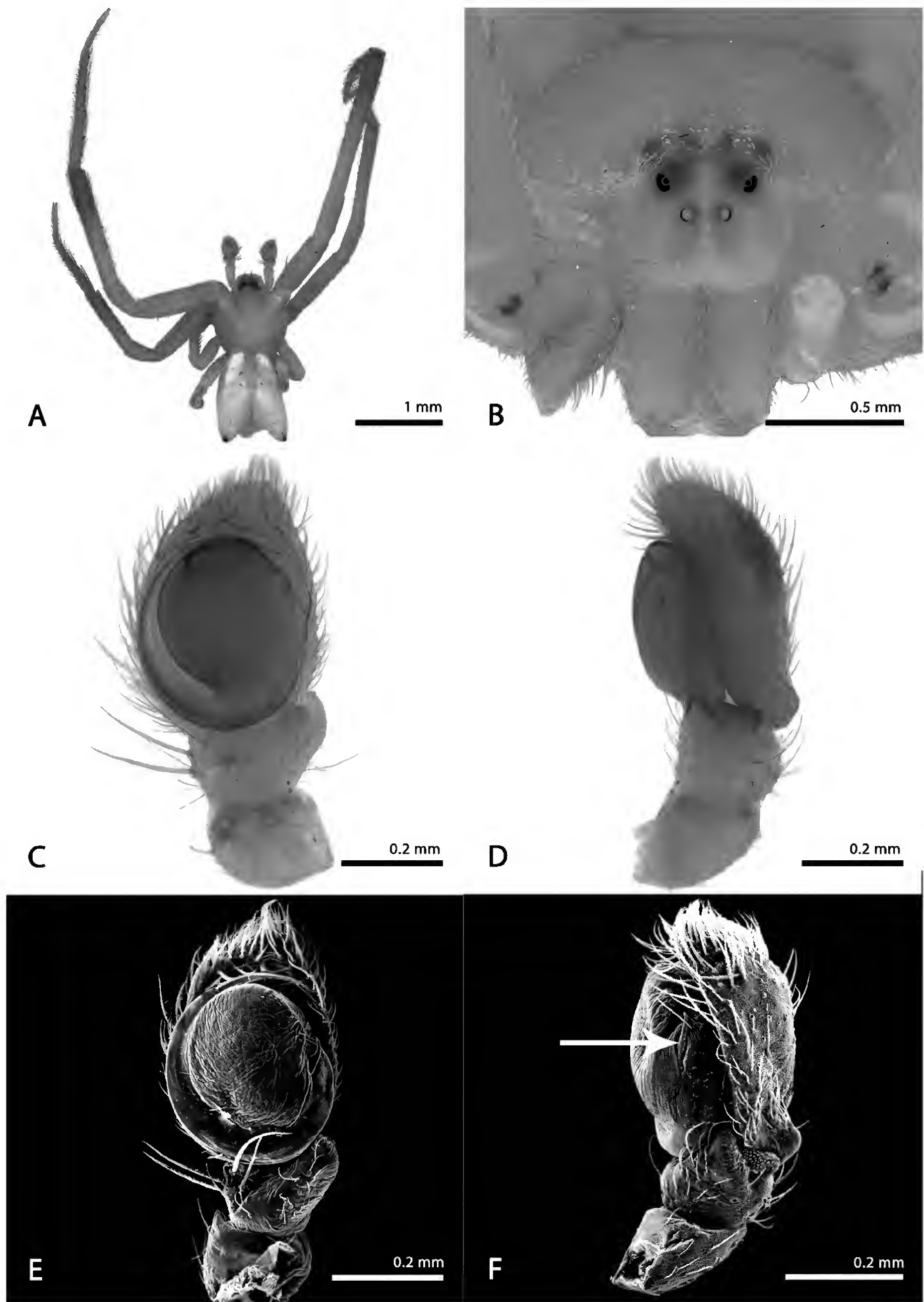


Figure 11. Male of *Sidymella longispina* **a** habitus, dorsal **b** prosoma, anterior **c**, **e** left palp, ventral view **d**, **f** left palp, retrolateral view (white arrow indicates the tegular process).

Male: Body colouration pattern and other characteristics as in female (Fig. 11A, B).

Measurements: eyes diameters and eyes interdistances: AME 0.03, ALE 0.05, PME 0.03, PLE 0.03, AME–AME 0.09, AME–ALE 0.05, PME–PME 0.11, PME–PLE 0.11, MOQ length 0.21, MOQ width 0.13; leg formula: 1–2–4–3: leg I – femur 2.44/ patella 1.12/ tibiae 3.12/ metatarsus 2.28/ tarsus 0.92/ total 9.88; II – 2.08/ 0.76/ 1.64/ 1.48/ 0.72/ 6.68; III – 0.60/ 0.48/ 0.60/ 0.40/ 0.40/ 2.48; IV – 1.04/ 0.44/ 0.60/ 0.40/ 0.40/ 2.88. Total body length 3.04; prosoma 1.40 length, 1.72 wide; opisthosoma length 1.64 (considering the projections); clypeus 0.17 height; sternum 0.76 length, 0.66 width; endites 0.33 length, 0.17 width; labium 0.17 length, 0.25 width.

Distribution. BRAZIL: Minas Gerais, Paraná, Santa Catarina, and Rio Grande do Sul; ARGENTINA: Misiones (Fig. 17).

Sidymella lucida (Keyserling, 1880)

Figures 2F, 3E, 12, 13

Stephanopis lucida Keyserling, 1880: 190, pl. 4, fig. 105 (♀).

Sidyma lucida: Simon 1895: 1056. Berland 1913: 95, pl. 9, figs 51–56 (♂♀).

Sidyma cancellata: Mello-Leitão 1934: 207, fig. 34 (♂).

Sidymella lucida: Strand 1942: 399. Machado et al. 2017: 454, figs S11A, F, S14B (♂).

Sidyma lucida Lise, 1973: 6, figs 10–18 (♂♀).

Type material. Holotype ♂, BRAZIL: Rio Grande do Sul, B. Rambo (MNRJ 41748, examined).

Other material examined. ECUADOR: 1♂, Tunguhua, Baños, 01°23'51"S, 78°25'27"W, 10.iv.1939 (MCZ 133401); 1♂, 1♀, 2j, same locality, iv.1939 (MCZ 133402); COLOMBIA: 1♀, Valle del Cauca, Cali, 3°20'50"N, 76°34'34"W, x.1972 (MCZ), BRAZIL: 1♀, Minas Gerais, Tiradentes (Serra de São José), 21°06'36"S, 44°10'23"W, 28.x.1989, Becker, Johann & Roppa leg. (MNRJ 2694); 1♀, Rio de Janeiro, Santa Maria Madalena, 21°57'18"S, 42°0'28"W, 15.v.2002 (MCN 34671); 1♀, São Paulo, Vale do Ribeira, 24°37'28.68"S, 47°23'33.99"W, vi.2002, E.H. Wienskoski leg. (MNRJ 11513); 1♀, 1j, Paraná, São José dos Pinhais, 25°32'06"S, 49°12'21"W, 09.xii.2015, A.C. Domahovski leg. (MCTP 39092); 1♂, 2♀, Santa Catarina, Rancho Queimado, 27°40'22"S, 49°01'19"W, 13–15.i.1995, L.A. Moura leg. (MCN 26465); 1♀, Alta Feliz, 29°23'31"S, 51°18'43"W, vii.1988, A.A. Lise leg. (MCTP 526); 1♀, Rio Grande do Sul, Derrubadas (Parque Estadual do Turvo), 27°13'57"S, 53°51'04"W, 27–31.x.2003, R. Ott leg. (MCN 37826); 1♀, same locality, 19–22.x.2004, same collector (MCN 38879); 1♀, 1j, São Valentim, 27°33'28"S, 52°31'26"W, 16.x.1976 (MCN 4704); 1♀, Santa Rosa, 27°52'15"S, 54°28'34"W, 02.i.1984, A.D. Brescovit leg. (MCN 11989); 2j, Esmeralda, 28°03'14"S, 51°11'24"W, 24.v.1975, A.D. Brescovit leg. (MCN 2881); 1♀, Esmer-

alda (Estação Ecológica de Esmeralda), 28°03'8.35"S, 51°11'36.92"W, 12.xii.1978, C.J. Becker leg. (MCN 8467); 6♀, 3j, Garruchos, 28°10'16.21"S, 55°26'49.38"W, 08.xii.1975, A.A. Lise leg. (MCN 8083); 1♀, same locality, 08.xi.1979, H. Bischoff leg. (MCN 8965); 4j, Vacaria, 28°30'43"S, 50°56'02"W, 23.v.1981 (MCN 9758); 1♂, Augusto Pestana, 28°31'01"S, 53°59'31"W, 06.ix.2009, L.V. Silva-Leomar & B. Medeiros (MCTP 30588) 1♀, same locality, 12.ix.2008, L.V. Silvia-Leomar et al. leg. (MCTP 27094); 1♀, São Borja (Reserva Biológica de São Donato), 28°39'39"S, 56°00'14"W, 23.i.2012, Machado, M. leg. (MCTP 34729); 2♂, 3♀, Salto do Jacuí (Horta da CEEE), 29°05'21.03"S, 53°12'41.24"W, 19.x.1998, A.B. Bonaldo leg. (MCN 30761); 1♀, Caxias do Sul (Fazenda Souza), 29°07'17"S, 51°01'07"W, 11–12.xi.1995, lab staff leg. (MCTP 7322); 1♂, Muçum, 29°09'54"S, 51°52'04"W, 02.iii.1984 (MCN 12090); 1♀, Caxias do Sul (Água Azul), 29°11'51"S, 50°59'27"W, 15.ix.1976, E.H. Buckup (MCN 4498); 1♂, 4j, Caxias do Sul (Vila Oliva), 29°12'56"S, 50°53'22"W, 05.iv.1975, H. Bischoff leg. (MCN 2872); 1♀, Estrela Velha (Barragem de Itaúba), 29°15'19"S, 53°13'36"W, 20.x.1998, L.A. Moura leg. (MCN 30763); 1♀, same locality, 28.x.1999, A. Silva (MCN 31959); 1♂, São Francisco de Paula, 29°16'29"S, 50°44'15"W, 19.xi.1990, E.H. Buckup leg. (MCN 28841); 1♀, same locality, 16.xii.1999, A.F. Franceschini leg. (MCN 32047); 1j, Canela, 29°21'57"S, 50°48'57"W, 07.x.1967, A.A. Lise leg. (MCN 649); 3j, same locality, 05.ii.1970, same collector (MCN 651); 2♀, same locality, 20.i.1972, same collector (MCN 1025); 1♀, same locality, 31.xii.1973, same collector (MCN 2029); 1♀, same locality, 21.ix.1974, same collector (MCN 2249); 3♀, same locality, 26.xii.1974, same collector (MCN 2492); 1j, same locality, 08.xi.1975, same collector (MCN 5968); 1j, same locality, 05.i.1973, same collector (MCN 9056); 1j, same locality, 11.i.1966, same collector (MCN 9057); 1♀, São Francisco de Paula (FLONA), 29°25'47"S, 50°23'35"W, 19.xii.2010, R.A. Teixeira leg. (MCTP 33303); 1♀, same locality, 10.x.2012, same collector (MCTP 41327); 3j, São Francisco de Paula, 29°27'00"S, 50°34'59"W, 05.i.1985, A.A. Lise leg. (MCN 12723); 1j, Três Coroas, 29°30'55"S, 50°46'46"W, 15.xii.1976, A.A. Lise leg. (MCN 4924); 1♀, São Martinho da Serra, 29°32'16"S, 53°51'18"W, 19.x.1993, L. Indrusiak & R.A. Boelter leg. (MCTP 40116); 1♀, Itaara, 29°36'36"S, 53°45'54"W, 22.xi.2006, L. Indrusiak & R.A. Boelter leg. (MCTP 21356); 2j, same locality, 23.vi.2007, A.A. Lise et al. leg. (MCTP 21357); 1j, same locality, 14.vii.2007, L. Indrusiak leg. (MCTP 21358); 1♀, Agudo, 29°38'31"S, 53°15'10"W, 21.x.1988, L. Indrusiak leg. (MCN 18751); 1♀, Campo Bom, 29°40'44"S, 51°3'10"W, 19.x.1987, L. Indrusiak leg. (MCTP 135); 1♀, Santa Maria, 29°40'59"S, 53°48'00"W, 03.vii.2000, L. Indrusiak leg. (MCTP 40092); 2♀, same locality, 29.vi.1998, same collector (MCTP 40094); 1♀, same locality, 24.iii.1992, same collector (MCTP 40122); 1♂, same locality, 28.vii.1995, C.B. Kotzian & L. Indrusiak leg. (MCTP 40100); 1♀, same locality, 14.x.2004, C.B. Kotzian leg. (MCTP

40091); 1♀, same locality, 03.iv.2013, L. Indrusiak leg. (MCTP 39419); 1♂, 1♀, same locality, 24.v.2007, A. Aued & E. Felzmamm leg. (MCTP 40103); 1♀, 30.vii.2000, L. Indrusiak leg. (MCTP 40090); 1♀, same locality, 15.vii.1998, C.B. Kotzian & L. Indrusiak leg. (MCTP 40102); 1♀, same locality, 22.v.1996, same collector (MCTP 40097); 1♀, same locality, 20.x.1995, same collector (MCTP 40098); 3♂, 1♀, same locality, 19.vi.1998, C. Kotzian & M. Monteiro leg. (MCTP 41324); 1♀, same locality, 17.xii.1992, L. Indrusiak & M. Monteiro leg. (MCTP 41323); 1♀, same locality, 21.xii.1993, L. Indrusiak leg. (MCTP 41322); 1♀, same locality, 17.iii.1998, C. Kotzian & L. Indrusiak leg. (MCTP 41326); 1♂, 3♀, same locality, 21.viii.1994, biology students leg. (MCTP 41325); 1♂, 1♀, same locality, 26.viii.1992, E. Lang & L. Oleques leg. (MCTP 40096); 3♂, 1♀, same locality, 30.ix.1998, L. Indrusiak & M. Monteiro leg. (MCTP 40095); 1♂, same locality, 15.x.1998, C. Kotzian & L. Indrusiak leg. (MCTP 40104); 1j, same locality, 10.x.1979, D. Link leg. (MCN 9548); 3♀, same locality, 02.xi.1985, A.D. Brescovit leg. (MCN 14565); 2♂, same locality, 31.viii.1994, R.G. Buss leg. (MCTP 10254); 5j, Montenegro, 29°41'20"S, 51°27'39"W, 01.ix.1977 (MCN 6362); 1j, same locality, 06.x.1977, T. Arigony leg. (MCN 6808); 1j, same locality, 29.ix.1977, A.A. Lise leg. (MCN 8180); 1♂, Santa Cruz do Sul, 29°43'04"S, 52°25'33"W, 14.viii.1994, A.A. Lise leg. (MCN 33985); 1♂, Novos Cabrais, 29°46'59"S, 52°58'18"W, 01.xi.2008, R.G. Buss leg. (MCTP 27971); 1♂, same locality, 11.ix.2008, same collector (MCTP 28090); 1j, Alegrete, 29°47'26"S, 55°47'43"W, 28.viii.1984, M.A.L. Marques leg. (MCN 9717); 1♂, Morungava, 29°51'11"S, 50°54'31"W, 02.ii.1992, A.D. Brescovit leg. (MCN 23177); 1♂, 3♀, Cachoeira do Sul (Porteira 7), 30°01'18.65"S, 52°55'3.70"W, 31.x.1992, R.G. Buss leg. (MCTP3485); 1♀, 1j, same locality, 26.vii.1992, same collector (MCTP 3488); 1♀, Porto Alegre, 30°01'58"S, 51°13'48"W, 01.xi.2009, I. Martins leg. (MCTP26258); 1♂, 2♀, 1j, Cachoeira do Sul, 30°01'59"S, 52°54'00"W, 10.x.1992, R.G. Buss leg. (MCTP 3491); 1♂, 1♀, same locality, 26.ix.1992, same collector (MCTP 3493); 1♂, 1♀, same locality, 27.ix.1992, same collector (MCTP 3487); 1j, Porto Alegre (Morro Santana), 30°02'34"S, 51°08'39"W, 01.ix.1984, A.A. Lise leg. (MCN 12546); 1j, Viamão (Estação Fitotécnica de Viamão), 30°02'51"S, 51°00'53"W, 12.viii.1994, A.A. Lise leg. (MCTP 5245); 1j, same locality, 30.iii.1976 same collector (MCN 5860); 1♂, Viamão, 30°04'51"S, 51°01'22"W, 22.xi.1995, A.A. Lise leg. (MCTP 12246); 1♂, Guaíba, 30°06'50"S, 51°19'30"W, 04.x.1995, (MCTP 12334); 1♀, São Sepé, 30°09'50"S, 53°34'18"W, iv.1999, E.C. Costa leg. (MCTP 40099); 1♂, same locality, 03.x.2002, C.B. Kotzian leg. (MCTP 41321); 1♀, Cachoeira do Sul (Fazenda das Pedras), 30°12'50"S, 52°50'21"W, 27.x.1992, R.G. Buss leg. (MCTP 3490); 1♀, same locality, 09.ix.1992, same collector (MCTP 3486); 1♂, same locality, 30.xi.1993, same collector (MCTP 4251); 1♀, Cachoeira do Sul (Capanezinho),

30°18'35"S, 52°58'50"W, 29.viii.1992, R.G. Buss leg. (MCTP 3492); 1♂, 2♀, same locality, 17.x.1992, same collector (MCTP 3489); 2♀, Viamão (Morro Fortaleza), 30°20'45"S, 51°01'35"W, 22.xi.1992, A. Braul leg. (MCTP 2656); 2j, Quaraí, 30°23'03"S, 56°26'56"W, 24–28.v.1991, A. Braul leg. (MCTP 461); 4j, Quaraí (Estância São Roberto), 30°25'14"S, 55°51'53"W, 07.ii.1978, J.W. Thomé leg. (MCN 7779). **ARGENTINA:** 7♂, 3♀, Jujuy, Parque Nacional Calilegua, 23°38'20"S, 64°34'17"W, 23–24.ix.1995 (MACN-Ar 19229); 1♂, Misiones, El Piñalito, 25°58'59"S, 53°53'59"W, xi.1954, Schiapelli di Carlo leg. (MACN-Ar 19095); 1♀, Tucuman, Racó, 26°38'15"S, 65°22'43"W (MACN-Ar 19102); 1j, Arroyo Yabebiry (Ruta Nacional 12), 27°17'05"S, 55°32'01"W, vii.1980, P. Goloboff leg. (MACN-Ar 19100); 1♀, Santa Maria, 27°53'39"S, 55°21'20"W, vii.1954, M.J. Viana leg. (MACN-Ar 19097); 1♀, same locality, x.1953, M.J. Viana & Schiapelli di Carlo leg. (MACN-Ar 3804); 3♂, same locality, xii.1952, J. Viana leg. (MACN-Ar 3535); 1j, same locality, xi.1952, J. Viana leg. (MACN-Ar 19071); 1j, same locality, 1954, M. Belgrano & Schiapelli di Carlo leg. (MACN-Ar 19096); 1♀, same locality, xii.1947, J. Viana leg. (MACN-Ar 2455); 2♀, same locality, xi.1952, J. Viana leg. (MACN-Ar 3534); 1♂, Entre Ríos, Rosario del Tala, 32°18'00"S, 59°08'00"W, 20.xi.1988, M. Ramírez leg. (MACN-Ar 19091). **URUGUAY:** 1♀, Lavalleja, Cerro Arequina, 34°17'09"S, 55°16'05"W, 03.xii.1997, A.A. Lise leg. (MCTP 12677).

Diagnosis. Females of *S. lucida* resemble those of *S. excavata* sp. nov. and *S. marmorata* sp. nov. by their short and rounded opisthosomal projections (Figs 2F, 12A). They can be distinguished by shorter copulatory ducts and spermathecae with just a median twisted constriction instead of many chambers (Fig. 12D, F). Males are similar to those of *S. excavata* sp. nov. by the colour pattern of the opisthosoma and the shape of its posterior projections. However, males of *S. lucida* have a roundish RTA with a discrete basal branch (Fig. 13D, F), narrower pars pendula, and a shorter embolus emerging from tegulum at five o'clock (Fig. 13C, E).

Description. Female: Prosoma yellowish, with cephalic ridges delimited by lines of small papules; needle-shaped setae concentrated on the median area of prosoma, being the largest ones disposed right back of the PLE (Fig. 12B). Legs yellowish, with femora I bearing three equal-sized needle-shaped macrosetae on their mesial surface (Fig. 12A); both the anterior tibiae and metatarsi (I and II) ventrally armed with five pairs of ventral macrosetae; tibiae I also bear a pair of smaller macrosetae along their mesial surface (Fig. 12A). Opisthosoma light-yellow with a median black stain on its anterior portion; posterior projections stout, obtuse and vertically oriented (Fig. 12A). Epigynal plate wide, depressed on the median field; posterior folds thick and converging in the middle to form a septum (Fig. 12C, E).

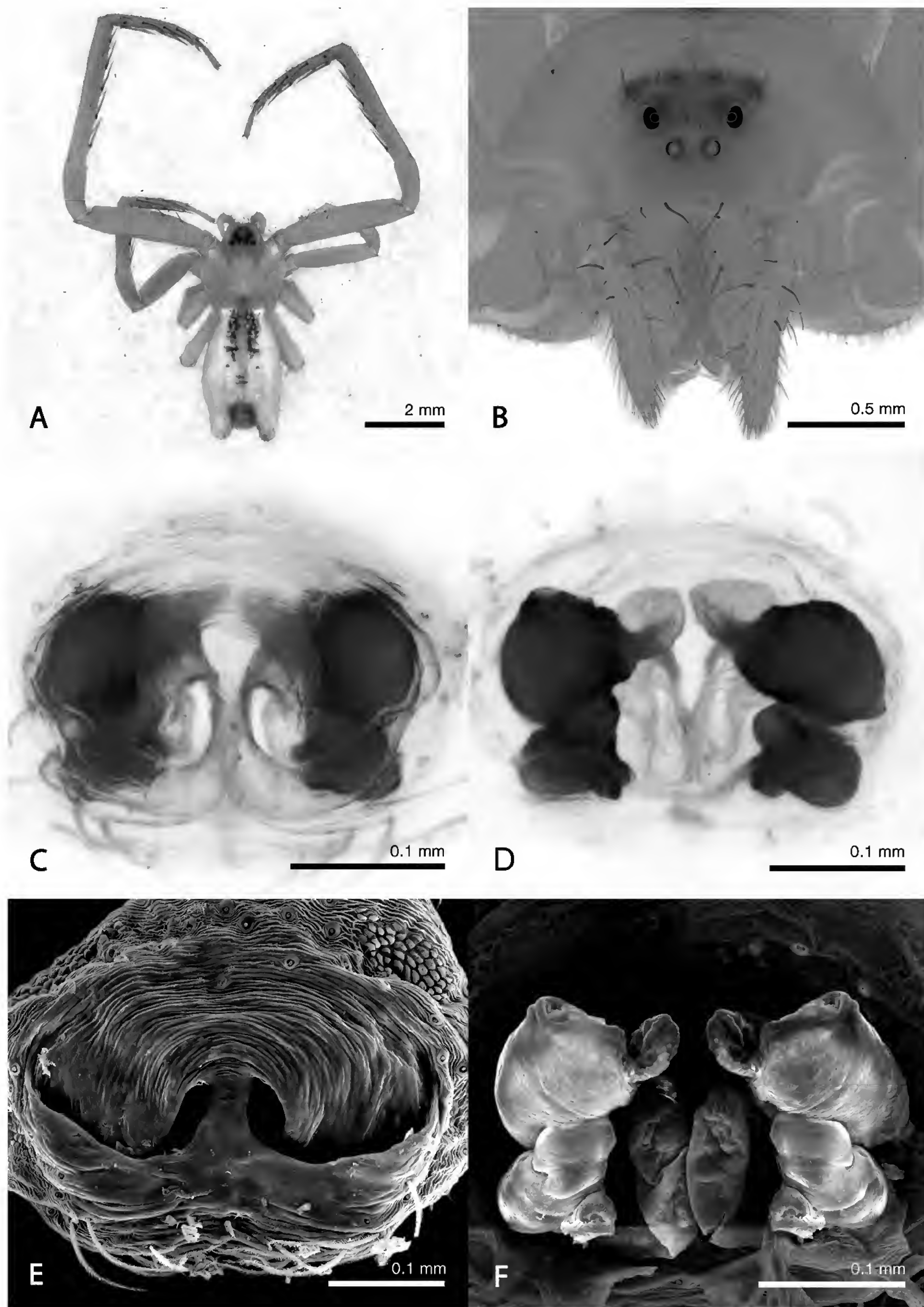


Figure 12. Female of *Sidymella lucida* **a** habitus, dorsal **b** prosoma, anterior **c**, **e** epigynum, ventral **d**, **f** epigynum, dorsal.

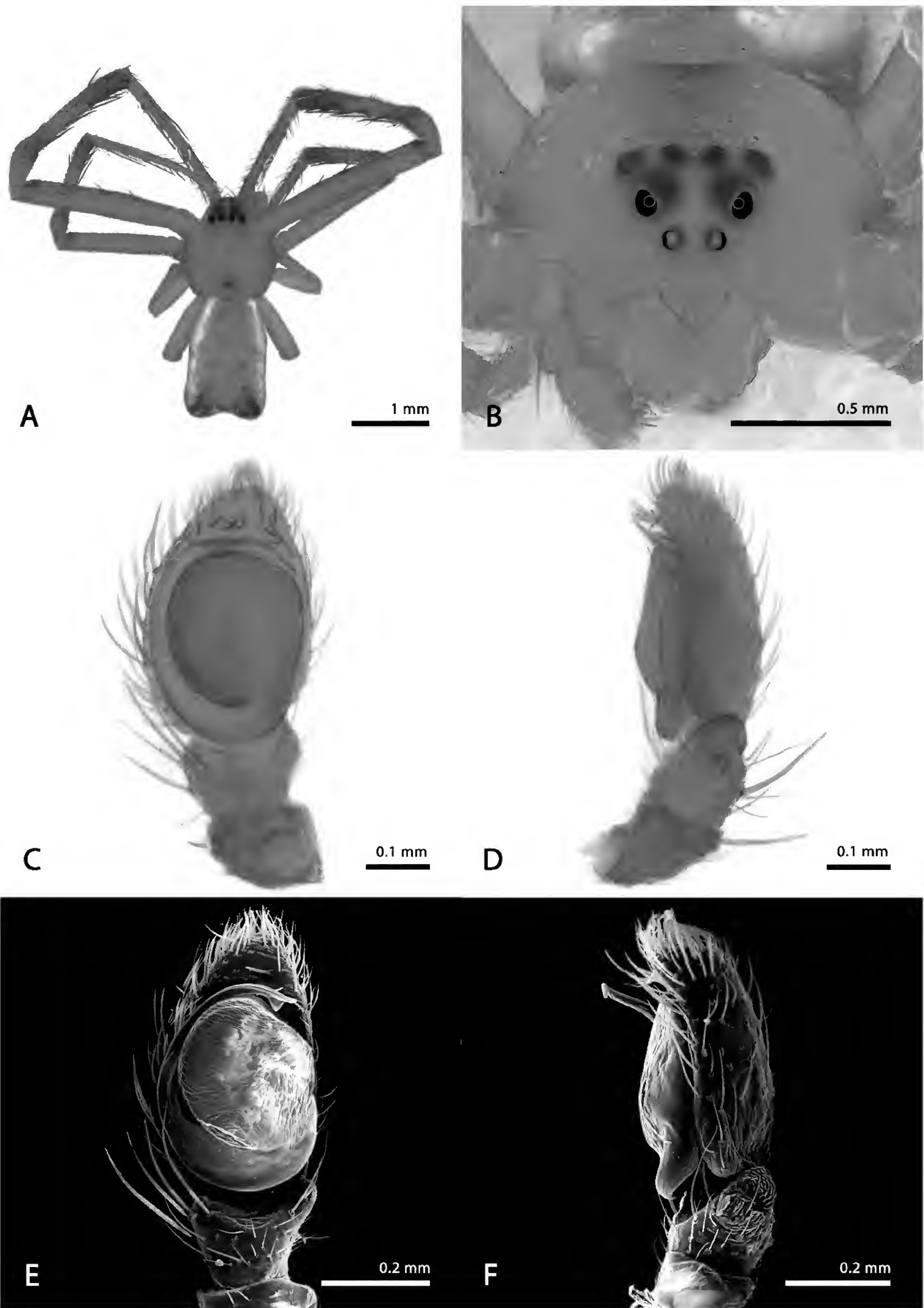


Figure 13. Male of *Sidymella lucida* **a** habitus, dorsal **b** prosoma, anterior **c**, **e** left palp, ventral view **d**, **f** left palp, retrolateral view (black arrow indicates the basal branch of the RTA).

Measurements: eyes diameters and eyes interdistances: AME 0.05, ALE 0.07, PME 0.05, PLE 0.05, AME–AME 0.11, AME–ALE 0.05, PME–PME 0.09, PME–PLE 0.17, MOQ length 0.29, MOQ width 0.23; leg formula: 1–2–4–3: leg I – femur 3.10/ patella 1.28/ tibiae 3.16/ metatarsus 2.32/ tarsus 0.84/ total 10.70; II – 2.00/ 0.96/ 1.64/ 1.48/ 0.56/ 6.64; III – 0.80/ 0.52/ 0.68/ 0.44/ 0.40/ 2.84; IV – 1.04/ 0.60/ 0.68/ 0.52/ 0.36/ 3.20. Total body length 4.68; prosoma 1.96 length, 1.76 wide; opisthosoma length 2.72 (considering the projections); clypeus 0.27 height; sternum 1.08 length, 0.84 width; endites 0.44 length, 0.28 width; labium 0.28 length, 0.32 width.

Male: Prosoma and legs as in female; opisthosoma predominantly yellow with lateral whitish lines, posterior projections dark (Fig. 13A, B). Palp flattened dorsoventrally and elongated; cymbium distally narrowed; tegulum rounded with scaled surface (Fig. 13C–F).

Measurements: eyes diameters and eyes interdistances: AME 0.05, ALE 0.07, PME 0.05, PLE 0.05, AME–AME 0.11, AME–ALE 0.05, PME–PME 0.09, PME–PLE 0.17, MOQ length 0.29, MOQ width 0.23; leg formula: 1–2–4–3: leg I – femur 2.56/ patella 0.88/ tibiae 2.48/ metatarsus 2.12/ tarsus 0.72/ total 8.76; II – 1.68/ 0.60/ 1.36/ 1.28/ 0.56/ 5.48; III – 0.64/ 0.32/ 0.56/ 0.28/ 0.36/ 2.16; IV – 0.84/ 0.44/ 0.48/ 0.24/ 0.36/ 2.36. Total body length 3.00; prosoma 1.40 length, 1.20 wide; opisthosoma length 1.60 (considering the projections); clypeus 0.15 height; sternum 0.58 length, 0.76 width; endites 0.27 length, 0.13 width; labium 0.17 length, 0.15 width.

Distribution. ARGENTINA: Entre Rios, Jujuy, Misiones, and Tucumán. BRAZIL: Paraná, Rio de Janeiro, Rio Grande do Sul, and Santa Catarina. COLOMBIA: Cáli and Nova Granada. ECUADOR: Loja and Tungurahua. URUGUAY: Lavalleja (Fig. 16).

***Sidymella marmorata* Machado & Guzati, sp. nov.**

<http://zoobank.org/0EB278EC-9D36-4D68-8D52-9CE838B66501>

Figures 2E, 14

Type material. Holotype ♀, ECUADOR: Quito (Road to Santo Domingo), 0°19'3.83"S, 79°19.95"W, L. Pena leg. (MCZ 133399). Paratypes. ECUADOR: 1 ♀, Quito (Road to Santo Domingo), 0°19'3.83"S, 79°19.95"W, 24.ii.1965, L. Pena leg. (MCTP 42654); COLOMBIA: 1 ♀, Cundinamarca (Chía, Alto de Yerbabuena), 4°51'53.13"N, 74°3'3.30"W, 09.x.2005, K. Lara & X. Marquínez leg. (ICN 7578)

Other material examined. COLOMBIA: 1 ♀, Cundinamarca, Zipacón, 04°45'44"N, 74°22'46"W, 01.i.2011, D. Luna & C. Romero leg. (ICN-Ar 6379); 1 ♀, 1j, Boyacá, 05°41'14"N, 73°26'9"W, 01.viii.2003 (MPUJ_ENT); 1 ♀, Nariño (La Planada), 01°11'16"N, 78°3'19"W, 29.ii.1991, C. Valderrama leg. (LPN 226); 1 ♀, Valle del Cauca (Chicoral), 03°39'24"N, 76°41'18"W, iii.2005,

J. Cabra leg. (MUSENUV 28231); 1 ♀, Quindío (Buenavista), 04°21'59"N, 75°44'37"W, 13.ii.2010 (CIUQ 9663); 1 ♀, Cundinamarca (Universidad Javeriana), 04°37'44"N, 74°03'51"W, 03.xi.1995 (IAvH 1157); 1 ♀, Quindío (Bengala), 04°40'0"N, 75°39'0"W, 05.v.2003, A. Ardila leg. (MAUQ 1691); 3 ♀, 2j, Cundinamarca (Alto de Yerbabuena), 04°51'55"N, 74°01'27"W, ix.2005, K. Lara & X. Marquínez leg. (ex. ICN-Ar 7578); 1 ♀, Cundinamarca (Suesca), 05°06'12"N, 73°47'56"W, 06.x.2013 (ICN-Ar 7637); 1 ♀, Caldas (Samaná), 05°36'0"N, 75°2'0"W, 23.xi.1995, V. Rueda & H. Piñeros leg. (IAvH 180518); 1 ♀, Boyacá, (Villa de Leyva), 05°40'21"N, 73°27'42"W, 09.vi.2001, L. Benavides & J. Pinzón leg. (ICN-Ar 1249).

Etymology. The epithet means marbled or overlaid with marble and refers to the reticulated colour pattern of the opisthosoma.

Diagnosis. Females of *S. marmorata* sp. nov. resemble those of *S. excavata* sp. nov. by the large body size and the general shape of opisthosoma with an anterior concavity and short posterior projections (Figs 2E, 14A). However, females of *S. marmorata* sp. nov. bear numerous spiniform macrosetae on the mesial surface of femora I and II and five, instead of four, pairs of ventral macrosetae on tibiae I and II (Fig. 14A).

Description. Female: Prosoma and legs I and II entirely orange while the posterior legs (III and IV) are yellowish. Opisthosoma predominantly yellow but with brownish irregular stains distributed randomly, giving a “marbled” aspect to the spider’s dorsum (Fig. 14A); opisthosoma projections short and stout and anal region projected backwards (Figs 2E, 14A). Epigynal plate elevated, with a wide septum and lateral folds concentrically developed towards to the copulatory openings (Fig. 14C, E) copulatory ducts long, hyaline and coiled, leading to a pair of walnut-shaped spermathecae subdivided in chambers and with a tubular glandular-head (Fig. 14D, F).

Measurements: eyes diameters and eyes interdistances: AME 0.07, ALE 0.11, PME 0.07, PLE 0.07, AME–AME 0.17, AME–ALE 0.13, PME–PME 0.19, PME–PLE 0.19, MOQ length 0.37, MOQ width 0.17; leg formula: 1–2–4–3: leg I – femur 3.20/ patella 1.20/ tibiae 2.85/ metatarsus 1.80/ tarsus 0.88/ total 9.93; II – 2.40/ 1.03/ 2.12/ 1.60/ 0.77/ 7.92; III – 1.40/ 0.76/ 0.92/ 0.84/ 0.44/ 4.36; IV – 1.72/ 0.76/ 1.08/ 0.92/ 0.52/ 5.00. Total body length 5.44; prosoma 2.36 length, 2.32 wide; opisthosoma length 3.08; clypeus 0.33 height; sternum 1.03 length, 1.07 width; endites 0.58 length, 0.23 width; labium 0.33 length, 0.41 width.

Male: Unknown.

Distribution. ECUADOR: Quito. COLOMBIA: Cundinamarca, Boyacá, Nariño, Valle del Cauca, and Quindío (Fig. 15).

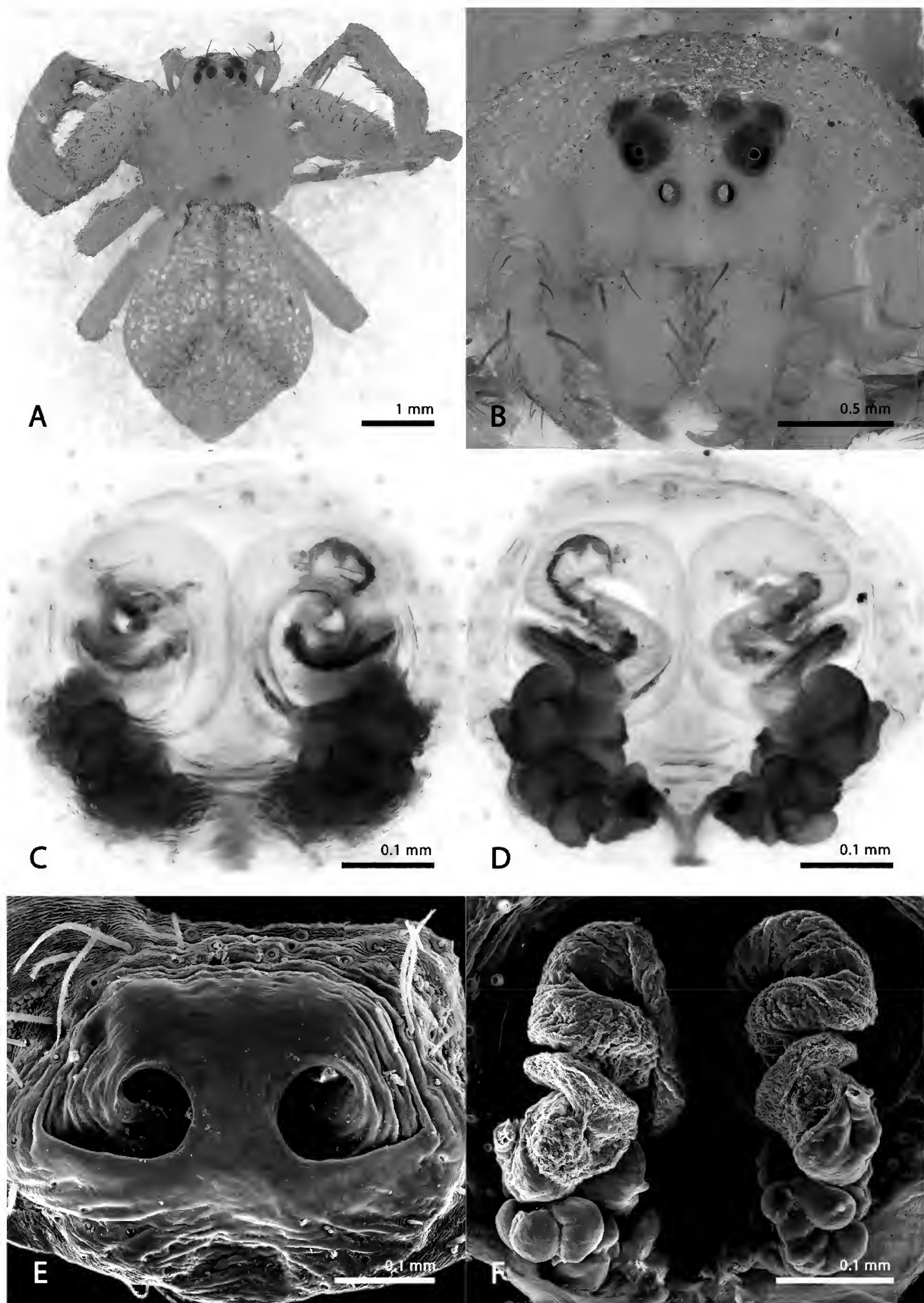


Figure 14. Female of *Sidymella marmorata* sp. nov. **a** habitus, dorsal **b** prosoma, anterior **c, e** epigynum, ventral **d, f** epigynum, dorsal.

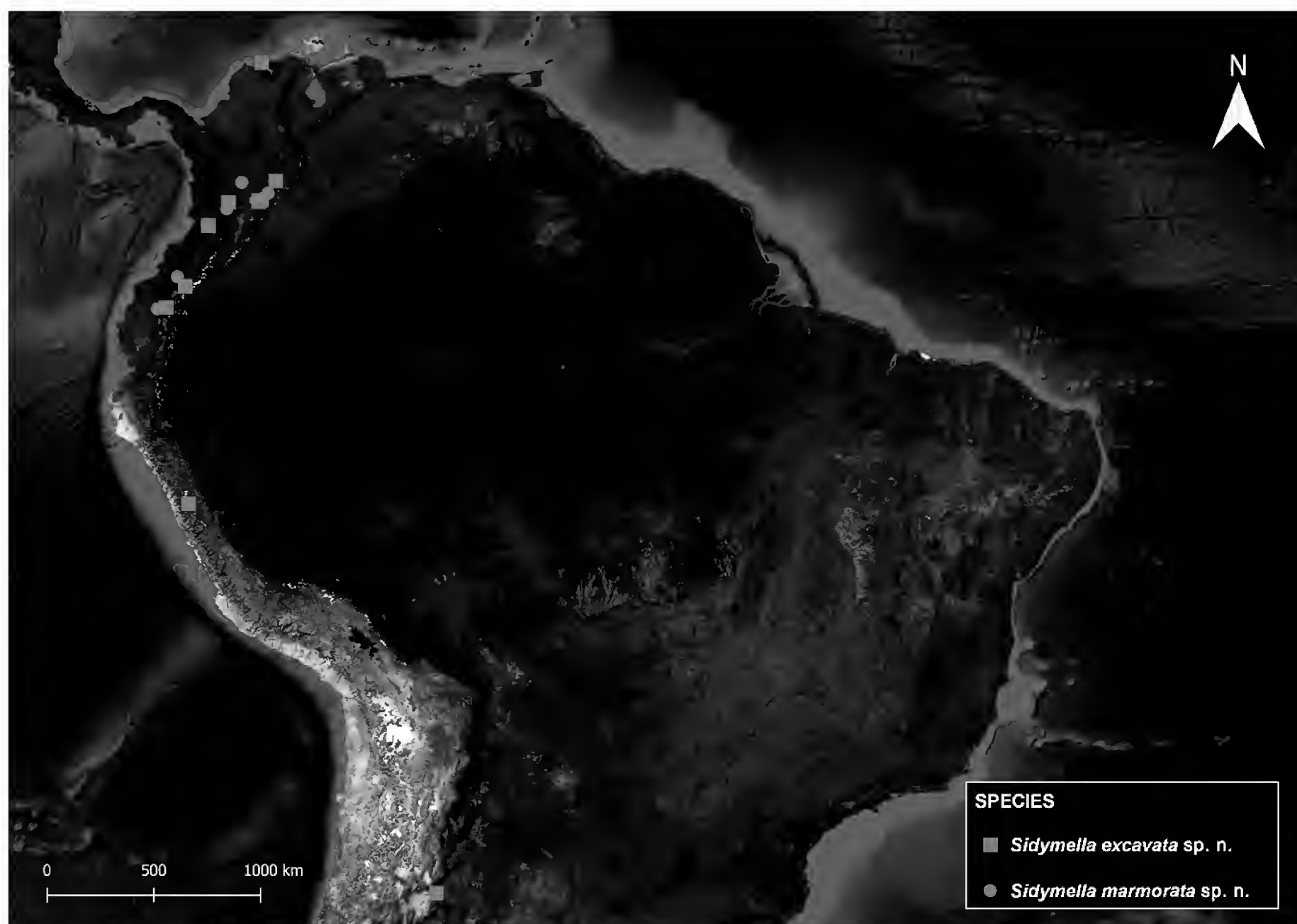


Figure 15. Distribution records of *Sidymella excavata* sp. nov. and *Sidymella marmorata* sp. nov.

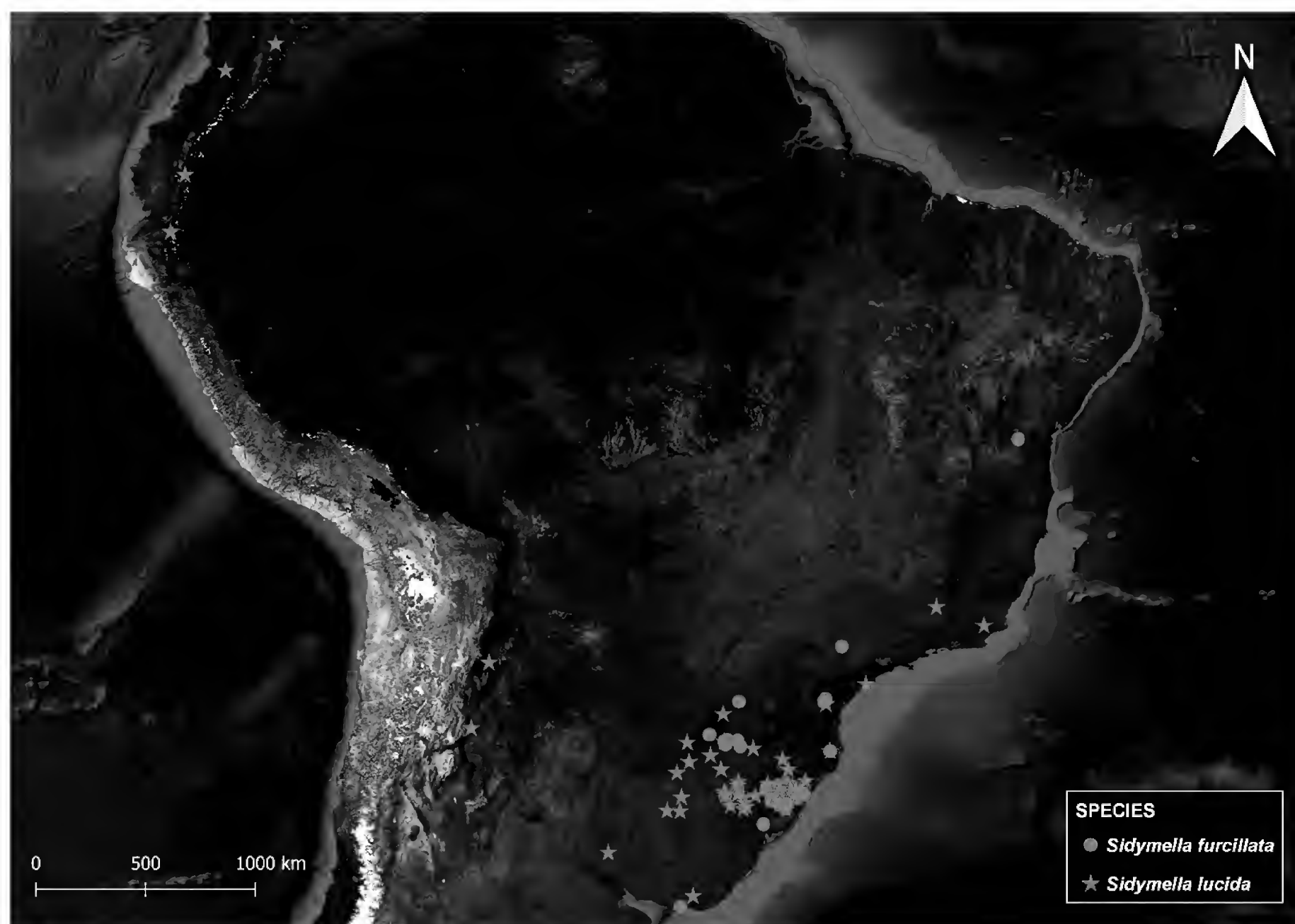


Figure 16. Distribution records of *Sidymella furcillata* and *Sidymella lucida*.

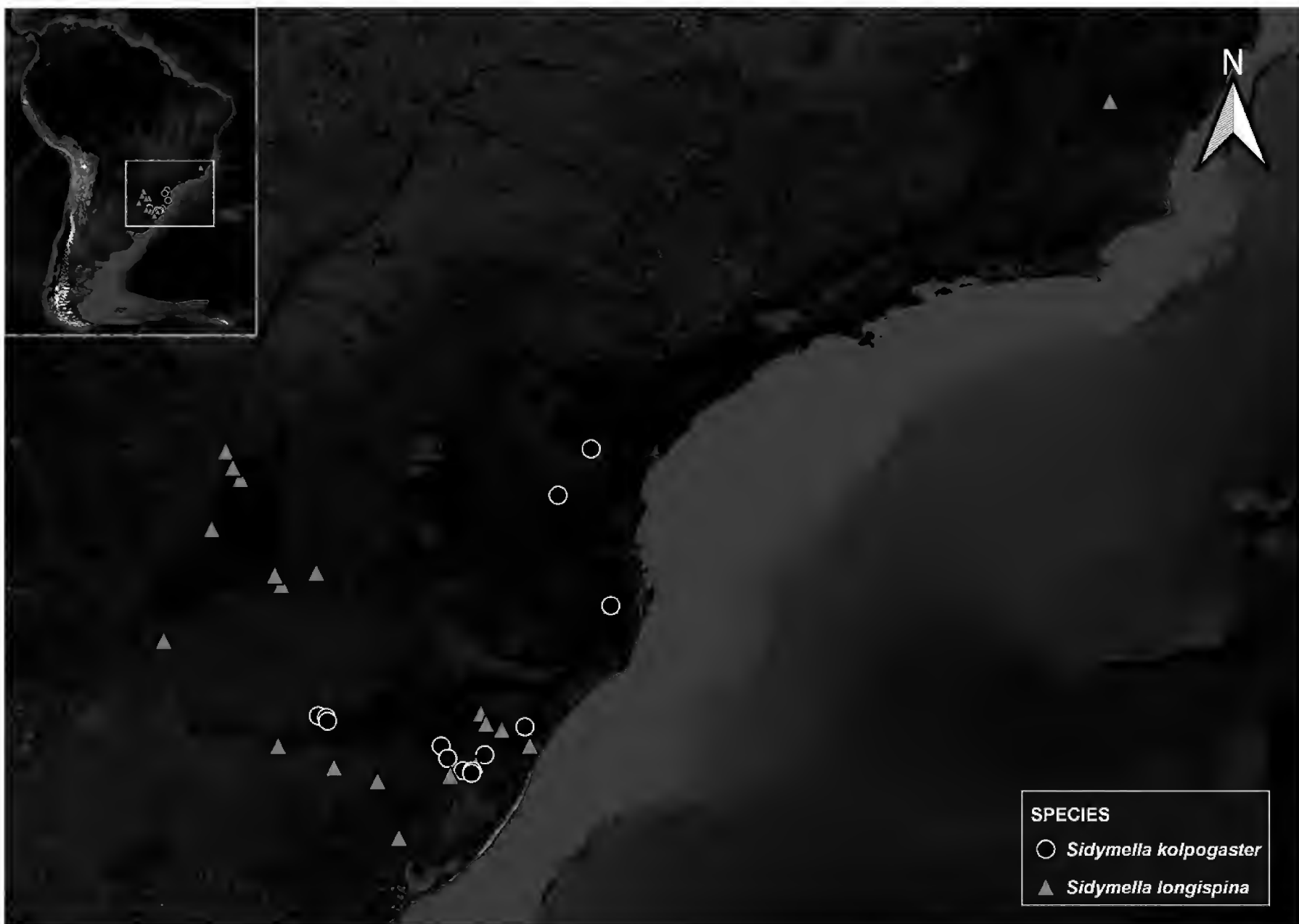


Figure 17. Distribution records of *Sidymella kolpogaster* and *Sidymella longispina*.

Additional taxonomic changes

Sidymella nigripes Mello-Leitão, 1947: 276 (♂). Lise 1973: 16, figs 34–38 (♀).

Note. The holotype female was collected in Curitiba by Padre Moure in April 1942 and deposited in the Instituto de Proteção do Patrimônio Natural da Secretaria da Agricultura do Estado do Paraná under the number 2497. However, this institution has closed and its arthropod collection was transferred to unknown institutions. The repository of this species is unknown, even after we searched for it in all major Brazilian institutions with arachnological collections, and we assume that the holotype of *S. nigripes* is lost. Therefore, we propose that the species should be considered a *species inquirenda*.

Sidymella obscura Mello-Leitão, 1929: 65. Holotype juvenile collected in Serro da Caraça, Minas Gerais, Brazil (MNHN 8263, examined). *Nomen dubium*.

Sidymella parallela Mello-Leitão, 1929: 64. Holotype juvenile collected in Salobro, Bahia, Brazil (MNHN 31114, examined). *Nomen dubium*.

Sidymella spinifera Mello-Leitão, 1929: 66. Lise 1973: 21, figs 47–53. Syntypes, 1 immature ♂ and 1 immature ♀ collected in Serro da Caraça, Minas Gerais, Brazil (MNHN 8202, examined).

Note. In the original work, Mello-Leitão (1929) mentioned both specimens as “type”, but they are labelled as syntypes. Both specimens are juveniles that cannot be diagnostic of any species. *Nomen dubium*.

Acknowledgments

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A new cryptic species of *Hyphessobrycon* Durbin, 1908 (Characiformes, Characidae) from the Eastern Amazon, revealed by integrative taxonomy

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<http://zoobank.org/E45AD907-EFD2-46B9-B056-31250BC8BFEE>

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Abstract

Hyphessobrycon caru **sp. nov.** is described based on five different and independent methods of species delimitation, making the hypothesis of this new species supported by an integrative taxonomy perspective. This new species has a restricted distribution, occurring just in the upper Pindaré river drainage, Mearim river basin, Brazil. It is a member of the rosy tetra clade, which is characterized mainly by the presence of a dark brown or black blotch on dorsal fin and absence of a midlateral stripe on the body. *Hyphessobrycon caru* **sp. nov.** is distinguished from the members of this clade mainly by the shape of its humeral spot, possessing few irregular inconspicuous vertically arranged chromatophores in the humeral region, or sometimes a very thin and inconspicuous humeral spot, and other characters related to teeth count, and color pattern. The phylogenetic position of the new species within the rosy tetra clade was based on molecular phylogenetic analysis using sequences of the mitochondrial gene cytochrome oxidase subunit 1. In addition, a new clade (here termed *Hyphessobrycon micropterus* clade) within the rosy tetra clade is proposed based on molecular data, comprising *H. caru* **sp. nov.**, *H. micropterus*, *H. piorskii*, and *H. simulatus*, and with *H. caru* **sp. nov.** and *H. piorskii* recovered as sister species. Our results suggest cryptic speciation in the rosy tetra clade and, more specifically, in the *H. micropterus* clade. We recommend the use of integrative taxonomy for future taxonomic revisions and species descriptions when dealing with species complexes and groups containing possible cryptic species.

Key Words

bPTP, DNA barcoding, rosy tetra clade, species complex, Stethaprioninae

Introduction

Hyphessobrycon Durbin, 1908 is a species-rich characid genus comprising about 160 valid species (Fricke et al. 2019). It is widely distributed along the river basins of the Neotropical region, from southern Mexico to the La Plata River basin in northeastern Argentina (Carvalho and Malabarba 2015; García-Alzate et al. 2017; Guimarães et al. 2018). The genus was first proposed as a subgenus of *Hemigrammus* Gill, 1858 by Durbin in Eigenmann (1908), differing from the latter only by the absence of scales covering the caudal-fin. *Hyphessobrycon* was reviewed by Eigenmann (1918, 1921) in a work which still constitutes the most comprehensive revisionary studies on the genus. The large number of species included within *Hyphessobrycon* and the poor knowledge of the alpha and beta-taxonomy of species and species groups are among the major challenges for a more comprehensive taxonomic study and phylogenetic analyses of the genus. It is widely known that *Hyphessobrycon* does not constitute a monophyletic group (Weitzman and Palmer 1997a; Mirande 2010, 2018; Oliveira et al. 2011; Carvalho and Malabarba 2015; Carvalho et al. 2017; Moreira and Lima 2017; Betancur-R. et al. 2018; Guimarães et al. 2018). Nevertheless, groups of species have been proposed based primarily on similarities of color pattern and other external features (e.g. Weitzman and Palmer 1997a; García-Alzate et al. 2008; Moreira and Lima 2017). Some of them are probably merely artificial operational assemblages to aid species identification, whereas others represent potential monophyletic groups, delimited by exclusive character states (e.g. Castro-Paz et al. 2014; Carvalho and Malabarba 2015; Guimarães et al. 2018).

Several genetic studies focusing on characoid fishes, such as *Astyanax* Baird & Girard, 1854 (e.g. Ornelas-Garcia et al. 2008), *Caenotropus* Günther, 1864 (e.g. Melo et al. 2014), *Chilodus* Müller & Troschel, 1844 (e.g. Melo et al. 2014), *Curimatopsis* Steindachner, 1876 (e.g. Melo et al. 2016a), *Gymnocorymbus* Eigenmann, 1908 (e.g. Benine et al. 2015), *Hyphessobrycon* (e.g. Castro-Paz et al. 2014, Guimarães et al. 2018), *Piabina* Reinhardt, 1867 (e.g. Pereira et al. 2011), *Prochilodus* Agassiz, 1829 (e.g. Melo et al. 2016b), *Nannostomus* Günther, 1872 (e.g. Benzaquem et al. 2015) and *Tetragonopterus* Bleeker, 1863 (e.g. Melo et al. 2016c) have evidenced that some species may exhibit large discontinuities in their geographic distribution patterns, with high genetic divergences, but little morphological variability among geographically isolated lineages. These results suggest that these groups may represent species complexes or cryptic species, that is, they might even including morphologically quite similar or undistinguishable species that are hidden and erroneously classified (Brown et al. 1995; Bickford et al. 2006; Adams et al. 2014; Souza et al. 2018). Studies relying solely on morphology may be inadequate in recognizing species within groups including cryptic species (Guim-

arães et al. 2018). Integrative studies, using more than one criteria, such as character-based, tree-based, genetic distance and coalescent-based approaches, especially including molecular data, are useful and powerful for the recognition of hidden and/or possible new species in such species complexes (Sytsma and Schaal 1985; Bickford et al. 2006; Goldstein and Desalle 2010; Padial et al. 2010; Adams et al. 2014; Costa-Silva et al. 2015; Souza et al. 2018; Ottoni et al. 2019).

In this context of integrative taxonomy, the present study aims to investigate the diversity within the rosy tetra clade sensu Weitzman and Palmer (1997a). This clade comprises around 30 species, including some species of *Hyphessobrycon* and other allied species, that are appreciated as aquarium fishes due to their attractive color patterns (e.g. Weitzman and Palmer 1997a, 1997b, 1997c, 1997d; Zarske 2008; Hein 2009; Guimarães et al. 2018).

This group has had its composition and name changed over the last decades, and a detailed taxonomic history is presented by Weitzman and Palmer (1997a). Two previous papers (e.g. Castro-Paz et al. 2014; Guimarães et al. 2018) applied molecular approaches to investigate the diversity of rosy tetra clade, and they suggested that its taxonomic resolution should be better investigated as it could include cryptic species or valid species which may have been synonymized. A new species of *Hyphessobrycon* and member of the rosy tetra clade is described from the upper Pindaré river drainage, Mearim river basin, a coastal river basin of the Eastern Amazon region, Brazil, based on both morphology and molecular data. Furthermore, a new clade, within the rosy tetra clade, is proposed based on the phylogenetic tree topology presented.

Materials and methods

Taxa sampling, specimens collection, and preservation

Individuals collected for this study were euthanized with a buffered solution of MS-222 at a concentration of 250 mg L⁻¹ for a period of 10 min or more until opercular movements completely ceased. Specimens selected for morphological analysis were fixed in formalin and left for 10 days, after which they were preserved in 70% ethanol. Molecular data were obtained from specimens that were euthanized, fixed, and preserved in absolute ethanol.

Specimens for morphological analysis are listed in type and comparative material lists. Specimens for molecular approaches are listed in Table 1. We also retrieved sequences from other species of *Hyphessobrycon* and allied species for a comparative analysis from the Barcode of Life Database (BOLD) and the National Center for Biotechnology Information (NCBI) databases (Table 1).

Table 1. List of species, specimens and their respective catalogue numbers, Region/state/country, and BOLD Systems and GenBank sequence accession numbers. Sequences available in the current study are in **Bold**.

N°	Species	Catalogue number	Region/state/country	Accession no.
1	<i>Hyphessobrycon erythrostigma</i>	INPA 37681-HERY1	Tabatinga/Amazonas/Brazil	HYP076-13
2	<i>Hyphessobrycon erythrostigma</i>	INPA 37681-HERY10	Tabatinga/Amazonas/Brazil	HYP077-13
3	<i>Hyphessobrycon erythrostigma</i>	INPA 37681-HERY2	Tabatinga/Amazonas/Brazil	HYP078-13
4	<i>Hyphessobrycon erythrostigma</i>	INPA 37681-HERY3	Tabatinga/Amazonas/Brazil	HYP079-13
5	<i>Hyphessobrycon pyrrhonotus</i>	INPA 37672-TRO10	Santa Isabel do Rio Negro/Amazonas/Brazil	HYP040-13
6	<i>Hyphessobrycon pyrrhonotus</i>	INPA 37672-TRO11	Santa Isabel do Rio Negro/Amazonas/Brazil	HYP041-13
7	<i>Hyphessobrycon pyrrhonotus</i>	–	Barcelos/Amazonas/Brazil	HYP157-13
8	<i>Hyphessobrycon pyrrhonotus</i>	–	Barcelos/Amazonas/Brazil	HYP158-13
9	<i>Hyphessobrycon socolofi</i>	INPA_39530-6152	Barcelos/Amazonas/Brazil	HYP131-13
10	<i>Hyphessobrycon socolofi</i>	INPA_39530-6155	Barcelos/Amazonas/Brazil	HYP134-13
11	<i>Hyphessobrycon socolofi</i>	INPA_39530-6178	Barcelos/Amazonas/Brazil	HYP135-13
12	<i>Hyphessobrycon socolofi</i>	INPA 39530-BCR8	Barcelos/Amazonas/Brazil	HYP148-13
13	<i>Hyphessobrycon copelandi</i>	INPA_37683-TU1	Tabatinga/Amazonas/Brazil	HYP094-13
14	<i>Hyphessobrycon copelandi</i>	INPA_37683-TU2	Tabatinga/Amazonas/Brazil	HYP095-13
15	<i>Hyphessobrycon copelandi</i>	INPA_37683-TU3	Tabatinga/Amazonas/Brazil	HYP096-13
16	<i>Hyphessobrycon eques</i>	INPA_37678-IC2	Santarém/Pará/Brazil	HYP070-13
17	<i>Hyphessobrycon eques</i>	INPA_37679-PE1	Macapá/Amapá/Brazil	HYP071-13
18	<i>Hyphessobrycon eques</i>	INPA_37680-AL1	Parintins/Amazonas/Brazil	HYP072-13
19	<i>Hyphessobrycon eques</i>	OL-0544	Bonito/Mato Grosso do Sul/Brazil	DSMIS077-09
20	<i>Hyphessobrycon epicharis</i>	INPA_37665-JUF1	São Gabriel da Cachoeira/Amazonas/Brazil	HYP002-13
21	<i>Hyphessobrycon epicharis</i>	INPA_37665-JUF3	São Gabriel da Cachoeira/Amazonas/Brazil	HYP004-13
22	<i>Hyphessobrycon epicharis</i>	INPA_37665-JUF4	São Gabriel da Cachoeira/Amazonas/Brazil	HYP005-13
23	<i>Hyphessobrycon epicharis</i>	INPA_37665-JUF8	São Gabriel da Cachoeira/Amazonas/Brazil	HYP006-13
24	<i>Hyphessobrycon compressus</i>	CINV-NEC7411	Flores Magon/Campeche/México	FYPM054-10
25	<i>Hyphessobrycon compressus</i>	ECOCH	Hatie ville/Belize/Belize	MXV765-15
26	<i>Hyphessobrycon compressus</i>	ECOCH	Hatie ville/Belize/Belize	MXV766-15
27	<i>Hyphessobrycon compressus</i>	ECOCH	Hatie ville/Belize/Belize	MXV767-15
28	<i>Hyphessobrycon bentosi</i>	INPA_37684-5939	Barcelos/Amazonas/Brazil	HYP097-13
29	<i>Hyphessobrycon bentosi</i>	INPA_37684-5940	Barcelos/Amazonas/Brazil	HYP098-13
30	<i>Hyphessobrycon bentosi</i>	INPA_39527-BA1	–	HYP116-13
31	<i>Hyphessobrycon bentosi</i>	INPA_39527-BA2	–	HYP117-13
32	<i>Hyphessobrycon bentosi</i>	CICCAA02349	Santarém/Pará/Brazil	MK240339
33	<i>Hyphessobrycon bentosi</i>	CICCAA02350	Santarém/Pará/Brazil	MK240340
34	<i>Hyphessobrycon bentosi</i>	CICCAA02351	Santarém/Pará/Brazil	MK240341
35	<i>Hyphessobrycon simulatus</i>	MHNG 2743.087	Pisiemoengo/Commewijne/Suriname	GBOL761-15
36	<i>Hyphessobrycon simulatus</i>	MHNG 2743.087	Pisiemoengo/Commewijne/Suriname	GBOL762-15
37	<i>Hyphessobrycon simulatus</i>	–	Sinnamary/Cayenne/French Guiana	GBOL1771-17
38	<i>Hyphessobrycon simulatus</i>	MHNG 2735.007	Sinnamary/Cayenne/French Guiana	GBOL3296-18
39	<i>Hyphessobrycon simulatus</i>	MHNG 2757.080	Kourou/Cayenne/French Guiana	GBOL3298-18
40	<i>Hyphessobrycon simulatus</i>	MHNG 2759.026	Kaw/Cayenne/French Guiana	GBOL3300-18
41	<i>Hyphessobrycon simulatus</i>	MHNG 2759.026	Kaw/Cayenne/French Guiana	GBOL3301-18
42	<i>Hyphessobrycon simulatus</i>	MHNG 2759.035	Régina/ Cayenne/French Guiana	GBOL3302-18
43	<i>Hyphessobrycon cf. sweglesi</i>	INPA_37668-JAR3	São Gabriel da Cachoeira/Amazonas/Brazil	HYP026-13
44	<i>Hyphessobrycon cf. sweglesi</i>	INPA_37668-JAR4	São Gabriel da Cachoeira/Amazonas/Brazil	HYP027-13
45	<i>Hyphessobrycon cf. sweglesi</i>	INPA_37668-JAR5	São Gabriel da Cachoeira/Amazonas/Brazil	HYP028-13
46	<i>Hyphessobrycon cf. sweglesi</i>	INPA_37668-JAR7	São Gabriel da Cachoeira/Amazonas/Brazil	HYP030-13
47	<i>Hyphessobrycon micropterus</i>	–	Várzea da Palma/Minas Gerais/Brazil	BSB287-10
48	<i>Hyphessobrycon micropterus</i>	–	Várzea da Palma/Minas Gerais/Brazil	BSB288-10
49	<i>Hyphessobrycon micropterus</i>	–	Várzea da Palma/Minas Gerais/Brazil	BSB289-10
50	<i>Hyphessobrycon micropterus</i>	–	Várzea da Palma/Minas Gerais/Brazil	BSB290-10
51	<i>Hyphessobrycon piorskii</i>	CICCAA00725-1	Chapadinha/Maranhão/Brazil	MF765796
52	<i>Hyphessobrycon piorskii</i>	CICCAA00726-1	Chapadinha/Maranhão/Brazil	MF765797
53	<i>Hyphessobrycon piorskii</i>	CICCAA01650-1	Barreirinhas/Maranhão/Brazil	MG791915
54	<i>Hyphessobrycon piorskii</i>	CICCAA01651-1	Barreirinhas/Maranhão/Brazil	MG791914
55	<i>Hyphessobrycon piorskii</i>	CICCAA02164-1	Codó/Maranhão/Brazil	MK240337
56	<i>Hyphessobrycon piorskii</i>	CICCAA02164-4	Codó/Maranhão/Brazil	MK240338
57	<i>Hyphessobrycon caru</i>	CICCAA00748-1	Buriticupu/Maranhão/Brazil	MH338230
58	<i>Hyphessobrycon caru</i>	CICCAA00749-1	Buriticupu/Maranhão/Brazil	MH338231
59	<i>Hyphessobrycon caru</i>	CICCAA02300-1	Buriticupu/Maranhão/Brazil	MH338232
60	<i>Hyphessobrycon caru</i>	CICCAA02301-1	Buriticupu/Maranhão/Brazil	MH338233
61	<i>Pristella maxillaris</i>	–	–	KU568982.1
62	<i>Pristella maxillaris</i>	–	–	KU568981.1
63	<i>Pristella maxillaris</i>	–	Marlborough/Pomeroon-Supenaam/Guyana	TZGAA025-06
64	<i>Pristella maxillaris</i>	–	Santa Cruz/Barima-Waini/Guyana	TZGAA178-06
65	<i>Moenkhausia hemigrammoides</i>	INPA38532-PR1	Guyana	HYP101-13
66	<i>Moenkhausia hemigrammoides</i>	INPA_38532-PR2	Guyana	HYP102-13
67	<i>Moenkhausia hemigrammoides</i>	INPA_38532-PR3	Guyana	HYP103-13
68	<i>Hyphessobrycon panamensis</i>	STRI-05303	Cocle/Panama	BSFFA760-07
69	<i>Hyphessobrycon flammeus</i>	LBPV-40464	Biritiba-Mirim/São Paulo/Brazil	FUPR988-09

Morphological analysis

Measurements and counts were made according to Fink and Weitzman (1974), with exception of the scale rows below lateral line, which were counted to the insertion of pelvic-fin. Vertical scale rows between the dorsal-fin origin and lateral line do not include the scale of the median predorsal series situated just anterior to the first dorsal-fin ray. Counts of supraneurals, vertebrae, procurent caudal-fin rays, unbranched dorsal and anal-fin rays, branchiostegal rays, gill-rakers, premaxillary, maxillary, and dentary teeth were taken only from cleared and stained paratypes (C&S), prepared according to Taylor and Van Dyke (1985). The four modified vertebrae that constitute the Weberian apparatus were not included in the vertebrae counts and the fused PU1 + U1 was considered as a single element. Osteological nomenclature follows Weitzman (1962). Institutional abbreviations follow Fricke and Eschmeyer (2019), with addition of LIOP.UFAM Coleção Ictiológica do Laboratório de Ictiologia e Ordenamento Pesqueiro do Vale do Rio Madeira da Universidade Federal do Amazonas.

DNA extraction, amplification, and sequencing

DNA was extracted from fin clips using Wizard Genomic DNA Purification kit (Promega) according to the manufacturer's protocol. Fragments of the cytochrome c oxidase subunit 1 gene (hereafter COI) from mitochondrial DNA were amplified, using the universal primers designed by Ward et al. (2005) for fish. Polymerase chain reactions (PCR) comprised a total volume of 15 µl containing 1× Polymerase buffer, 1.5 mM MgCl₂, 200 µM dNTP, 0.2 µM of each primer, 1U of Taq Polymerase (Invitrogen), 100 ng of DNA template, and ultrapure water. The PCR cycles were as follows: 2 min at 94 °C, followed by 35 cycles of 94 °C for 30s, 54 °C for 30s, and 72 °C for 1 min, and 10 min at 72 °C. Amplicons were purified using Illustra GFX PCR DNA and Gel Purification Kit (GE Healthcare Systems) and sequenced using the forward primer by an outsourced sequencing service at the University of São Paulo, using BigDye Terminator kit 3.1 Cycle Sequencing kit in ABI 3730 DNA Analyser (Applied Biosystems).

Data partition, evolution models, and alignment

The dataset included the following gene: COI (680 Base pairs, BP). Sequences were aligned using ClustalW (Chenna et al. 2003). The DNA sequences were translated into amino acids residues to test for the absence of premature stop codons or indels using the program MEGA 7 (Kumar et al. 2016). In the alignment, gaps were coded with a dash (–) and missing data with a question mark (?), but during analyses, both were treated as missing data. Measure Substitution Saturation tests were

performed in DAMBE5 (Xia 2013) according to the algorithm proposed by Xia et al. (2003). The best-fit evolutionary model (GTR+G) was calculated, using the corrected Akaike Information Criterion (AICc) determined by the jModelTest 2.1.7 (Darriba et al. 2012).

Species concept, species delimitation, and diagnoses

The unified species concept is herein adopted by expressing the conceptual definition shared by all traditional species concepts, “species are (segments of) separately evolving metapopulation lineages”, disentangling operational criterion elements to delimit taxa from species concepts (de Queiroz 2005, 2007). According to this concept, species are treated as hypothetical units and could be tested by the application of distinct criteria (species delimitation methods) (de Queiroz 2005, 2007). It allows for any criteria to separately provide evidence about species limits and identities, independently from other criteria (de Queiroz 2005, 2007). However, evidence corroborated from multiple operational criteria is considered to produce stronger support for hypotheses of lineage separation (de Queiroz 2007; Goldstein and Desalle 2010), a practice called “integrative taxonomy” (Dayrat 2005; Goldstein and Desalle 2010; Padial et al. 2010).

Five distinct and independent operational criteria for species delimitation, based on morphological and molecular data, were implemented here: Population Aggregation Analysis (Davis and Nixon 1992) (hereafter PAA); DNA barcoding, as proposed by Hebert et al. (2003a, 2003b, 2004 a, 2004b) (hereafter DBC); a tree-based method as proposed by Wiens and Penkrot (2002) (hereafter WP, following Sites and Marshall 2003); a character-based DNA barcoding as proposed by Desalle et al. (2005) (hereafter CBB); and a coalescent species delimitation method termed the Bayesian implementation of the Poisson tree processes (hereafter bPTP, following Zhang et al. 2013). All species delimitation methods here adopted, except PAA, were performed on cytochrome c oxidase subunit 1 (COI) sequences, as it is a mitochondrial gene with fast evolutionary rate, suitable for single locus species delimitation approaches (Avice 2000).

Population aggregation analysis (PAA)

The PAA (Davis and Nixon 1992) is a character-based method, in which species are delimited by unique combination of morphological character states occurring in one or more populations (Costa et al. 2014). The morphological data was based on both examined material and literature (e.g. Steindachner 1882; Meek 1904; Eigenmann, 1908; Durbin 1909; Eigenmann 1915; Ahl 1937; Fowler 1943; Géry 1960, 1961, 1964, 1977; Géry and Uj 1987; Burgess 1993; Planquette et al. 1996; Weitzman and

Palmer 1997a, 1997b, 1997c, 1997d; Zarske 2008; Hein 2009; Lima et al. 2013; Zarske 2014; Carvalho and Malabarba 2015; Carvalho et al. 2017; Guimarães et al. 2018).

Traditional DNA barcoding (DBC) and Phylogenetic analysis

We used the Kimura-2-parameters model (K2P) (Kimura 1980) to estimate the pairwise genetic distances between species in MEGA 7 software (Kumar et al. 2016). We used DnaSP v. 6 (Rozas et al. 2003) to estimate the number of variable sites and haplotypes. A Bayesian inference-based phylogenetic (BI) tree was estimated in MrBayes (Huelsenbeck and Ronquist 2001) plugin in Geneious 9.0.5 to reconstruct the evolutionary relationships among terminals using General Time Reversible (GTR+G) as evolutionary model. Bayesian tree inference was based in a chain length of 10 million, a burn-in length of 500,000 generations subsampling trees every 10,000 generations. We used a sequence of *Hyphessobrycon flammeus* Myers, 1924 as outgroup.

Wiens and Penkrot analysis (WP)

WP is based on the direct inspection of haplotype trees generated from the phylogenetic analysis having as terminals at least two individuals (haplotypes) of each focal species. In this method, the term “exclusive” is used instead of monophyletic, as the term monophyly is considered inapplicable below the species level (Wiens and Penkrot 2002). Clustered haplotypes with concordant geographic distribution forming mutual and well supported clades (exclusive lineages) are considered strong evidence for species discrimination (absence of gene flow with other lineages). When haplotypes from the same locality fail to cluster together, there is potential evidence for gene flow with other populations (Wiens and Penkrot 2002). Statistical support for clades is assessed by the posterior probability, considered as significant at values about 0.95 or higher (Alfaro and Holder 2006). When only one haplotype (specimen) from one putative population was available, the species delimitation was based on the exclusivity of the sister clade of this single haplotype, supported by significant values, allowing us to perform the test in populations with only one haplotype (Wiens and Penkrot 2002). In addition, the method allows recognition of nonexclusive lineages as species since their sister clades are exclusive and supported by significant values (Wiens and Penkrot 2002).

Character-based DNA barcoding (CBB)

The CBB is similar to the population aggregation analysis proposed by Davis and Nixon (1992), but directed to nucleotides as an alternative method for diagnosing taxa through DNA barcodes, as the original method is based on subjective cut-off distance measures to species

designation (Hebert et al. 2003a, 2003b, 2004a, 2004b). This method delimits species based on a unique combination of nucleotides within a site shared by individuals of the same population or group of populations. In addition, species were diagnosed by nucleotide substitutions following Costa et al. (2014). Optimization of nucleotide substitutions among lineages of the *Hyphessobrycon micropterus* clade were obtained from the Maximum Parsimony topology, using TNT 1.5 (Goloboff and Catalano 2016). Maximum Parsimony analysis (MP) was obtained with the following parameters: traditional search, tree bisection reconnection branch swapping (TBR), 1 random seed, setting random taxon-addition replicates to 1,000, multi-trees in effect, collapsing branches of zero length, characters equally weighted, and 10,000 trees saved per replication. MP tree branch support was given by bootstrap analysis (Felsenstein 1985), using a heuristic search with 1,000 replicates and the same settings used in the MP search, saving a maximum of 1,000 trees in each random taxon-addition replicate. The analysis was rooted on *Hyphessobrycon flammeus* Myers, 1924. Each nucleotide substitution is represented by its relative numeric position determined through sequence alignment with the complete mitochondrial genome of *Astyanax paranae* Eigenmann 1914 (KX609386.1:5503-7062 – mitochondrion complete genome), followed by the specific nucleotide substitution in parentheses. The results of this analysis are presented in Suppl. material 1: Box 1 and molecular diagnosis section.

Bayesian implementation of the poisson tree processes (bPTP)

The bPTP is a coalescent phylogeny-based species delimitation method aimed at delimiting species based on single locus molecular data (Zhang et al. 2013). An advantage of bPTP is that it does not need an ultrametric calibration like other coalescent approaches, avoiding errors and computer intensive processes (Zhang et al. 2013). The method relies on the number of substitutions between haplotypes and assumes that more molecular variability is expected between species than within a species (Zhang et al. 2013). In our analysis the dataset was reduced to include only unique haplotypes from the species of the *H. micropterus* clade. Outgroups were restricted to *Hyphessobrycon bentosi* Durbin, 1908 and *Hyphessobrycon copelandi* Durbin 1908. Sequences were aligned using ClustalW (Chenna et al. 2003). The best-fit evolutionary model (GTR+G) for the reduced dataset was calculated using the corrected Akaike Information Criterion (AICc) determined by the jModelTest 2.1.7 (Darriba et al. 2012). The input phylogenetic tree was performed in MrBayes 3.2.6 (Ronquist et al. 2012), with the following parameters: independent runs of two Markov chain Monte Carlo (MCMC) runs of four chains each for 3 million generations and sampling frequency of 1,000. The bPTP analysis was performed in the Exelixis Lab’s web server <http://species.h-its.org/ptp/>, following the default parameters except for a 20% burn in.

Results

Hyphessobrycon caru sp. nov.

<http://zoobank.org/3BC35EBB-E138-4E24-A06E-DF985F015ED5>

Figures 1, 2a; Table 2

Holotype. CICCAA 02286, 22.2 mm SL, Brazil, Maranhão state, Buriticupu municipality, Buritizinho river, Pindaré river drainage, Mearim river basin, 04°22'52"S, 46°30'35"W, 24 Jan. 2017, Guimarães E. C., Brito P. S.

Paratypes. All from Brazil, Maranhão state: CICCAA 00706, 37, 15.9–25.4 mm SL; CICCAA 0709, 12 C&S, 15.1–20.6 mm SL; LIOP.UFAM 1009, 1, 16.2 mm SL collected with holotype. CICCAA00707, 3, 17.2–22.1 mm SL, Buriticupu municipality, Buritizinho river, Pindaré river drainage, Mearim river basin, 4°25'45"S, 46°29'41"W, 24 Jan. 2017, Guimarães E. C., Brito P. S. CICCAA00708, 2, 19.9–21.6 mm SL, Buriticupu municipality, Buritizinho river, Pindaré river drainage, Mearim river basin, 04°19'45"S, 46°29'46"W, 24 Jan. 2017, Guimarães E. C., Brito P. S. UFRJ11745, 1, 22.4 mm SL, Buriticupu municipality, Buritizinho river, Pindaré river drainage, Mearim river basin, 04°19'45"S, 46°29'46"W, 24 Jan. 2017, Guimarães E. C., Brito P. S.

Diagnosis (PAA). The new species *Hyphessobrycon caru* sp. nov. differs from most of its congeners, except members of the rosy tetra clade, by the presence of a dark brown or black blotch on dorsal-fin (vs absence) and absence of a midlateral stripe on the body (vs presence).

The new species differs from most of its congeners in the rosy tetra clade by possessing few irregular inconspicuous vertically arranged chromatophores in the humeral region, or sometimes a very thin and inconspicuous humeral spot (Fig. 2a) [vs inconspicuous vertically elongated humeral spot in *H. hasemani* Fowler, 1913, *H. piorskii* Guimarães, De Brito, Feitosa, Carvalho-Costa, Ottoni, 2018 (Fig. 2b); approximately rounded humeral spot in *H. erythrostigma* (Fowler, 1943), *H. jackrobertsi* Zarske, 2014, *H. minor* Durbin, 1909, *H. pando* Hein, 2009, *H. paepkei* Zarske, 2014, *H. pyrrhonotus* Burgess, 1993, *H. roseus* (Géry, 1960), *H. socolofi* Weitzman, 1977, and *H. sweglesi* (Géry, 1961) (Fig. 2c); humeral spot horizontally or posteriorly elongated in *H. epicharis* Weitzman & Palmer, 1997, *H. khardinae* Zarske, 2008, and *H. wernerii* Géry & Uj, 1987 (Fig. 2d); conspicuous humeral spot at least on males in *H. copelandi* Durbin, 1908, *H. eques* (Steindachner, 1882), *H. haraldschultzi* Travassos, 1960, *H. micropterus* (Eigenmann, 1915), *H. megalopterus* (Eigenmann, 1915), *H. simulatus* (Géry, 1960) and *H. takasei* Géry, 1964 (Fig. 2e); and absence of humeral spot in *H. compressus* (Meek, 1904), *H. dorsalis* Zarske, 2014, *H. georgettae* Géry, 1961, *H. pulchripinnis* Ahl, 1937, and *H. rosaceus* Durbin, 1909 (Fig. 2f)].

Furthermore, the new species differs from *H. bentosi* Durbin, 1908, *H. erythrostigma*, *H. pyrrhonotus*, *H. rosaceus*, and *H. socolofi* by presenting only one tooth in

the outer row of premaxillary, and this unique tooth just slightly displaced from inner row [vs two or more teeth, displaced from the inner row]; from *H. hasemani* and *H. micropterus* by the dorsal-fin spot located approximately at the middle of the fin's depth, not reaching its tip (vs spot located approximately at the middle of the fin's depth, reaching its tip in adults); from *H. hasemani* by presenting tri to unicuspid teeth in the inner row of premaxillary and dentary (vs tricuspid or pentacuspid teeth); from *H. piorskii* by having the anal-fin profile usually nearly straight (vs anal-fin profile usually falcate). In addition, *H. caru* sp. nov. is easily distinguished from *Pristella maxillaris* (Ulrey, 1894), *Moenkhausia hemigrammoides* Géry, 1965, and *Hemigrammus unilineatus* (Gill, 1858) by the absence of a black oblique stripe or band on the anterior portion of the anal-fin (Fig. 1) (vs presence).

Description. Morphometric data of holotype and paratypes are presented in Table 2. Body small (with maximum SL of 25.4 mm), compressed, moderately deep, greatest body depth slightly anterior to dorsal-fin base. Lateral body profile straight and downward directed from the end of dorsal-fin to adipose-fin, straight or slightly convex between later point and origin of dorsal most procurrent caudal-fin ray. Dorsal profile of head convex from upper lip to vertical through eye; predorsal profile of body roughly straight, dorsal-fin base slightly convex, posteroventrally inclined; ventral profile of head convex from lower jaw to pelvic-fin origin. Ventral profile of body straight or slightly convex from pelvic-fin origin to anal-fin origin; straight and posterodorsally slanted along anal-fin base; and slightly concave on caudal peduncle. Jaws equal, mouth terminal, anteroventral end of dentary protruding. Maxilla reaching vertical to anterior margin of pupil.

Table 2. Morphometric data ($N = 45$) of *Hyphessobrycon caru* sp. nov. SD: Standard deviation.

	Holotype	Paratypes	Mean	SD
Standard length	22.2	14.8–25.4	18.9	–
Percentages of standard length				
Depth at dorsal-fin origin (body depth)	37.3	33.1–38.5	35.2	1.1
Snout to dorsal-fin origin	53.7	49.4–55.0	51.7	1.2
Snout to pectoral-fin origin	29.5	28.2–32.3	29.9	1.0
Snout to pelvic-fin origin	46.0	43.6–48.8	45.6	1.0
Snout to anal-fin origin	62.5	58.5–64.0	61.0	1.3
Caudal peduncle depth	12.3	8.5–12.3	10.3	0.8
Caudal peduncle length	11.7	9.5–12.7	11.2	0.8
Pectoral-fin length	23.2	16.5–23.7	19.6	1.9
Pelvic-fin length	20.6	14.1–20.5	17.4	1.4
Dorsal-fin base length	15.2	12.9–15.7	14.3	0.8
Dorsal-fin height	32.2	27.9–34.1	30.8	1.5
Anal-fin base length	32.4	26.4–32.7	29.6	1.3
Eye to dorsal-fin origin	37.5	34.4–38.8	37.3	0.9
Dorsal-fin origin to caudal-fin base	55.1	50.6–56.1	53.4	1.1
Head length	29.8	27.4–31.1	29.3	1.0
Percentages of head length				
Horizontal eye diameter	39.2	35.4–43.6	39.2	1.7
Snout length	24.4	17.3–24.3	21.5	1.8
Least interorbital width	29.1	22.4–30.7	27.2	1.8
Upper jaw length	37.8	33.1–42.5	37.4	2.1



Figure 1. *Hyphessobrycon caru* sp. nov., CICCAA 02286, holotype, 22.2 mm SL; Brazil: Maranhão state: Buritizinho River, Pindaré river drainage, Mearim river basin.

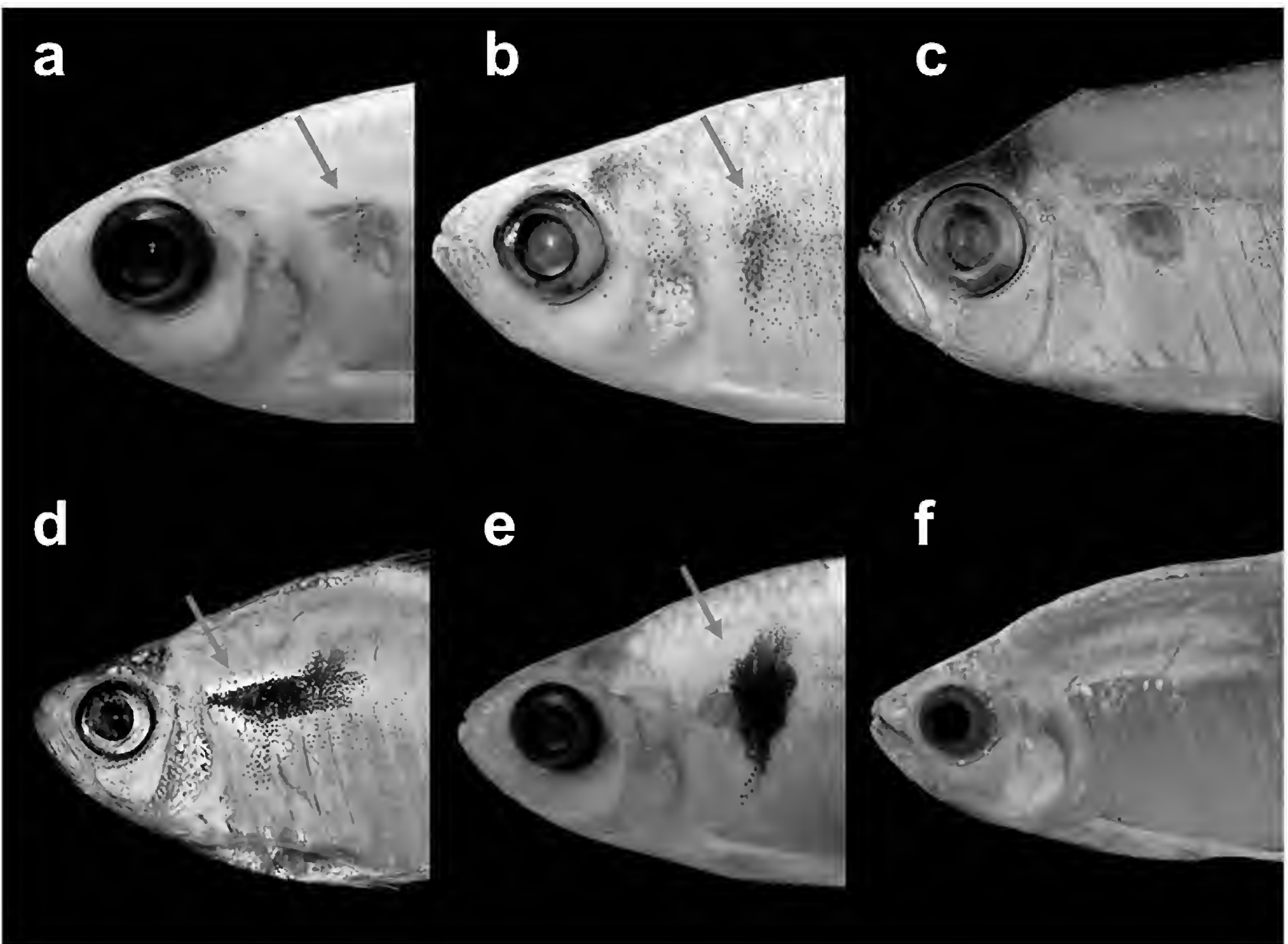


Figure 2. Humeral spot of: **a** *Hyphessobrycon caru*, holotype, CICCAA 02286 **b** *H. piorskii*, holotype, CICCAA 00695 **c** *H. pyr-rhonotus*, holotype, MZUSP 45714 **d** *H. weneri*, holotype, MZUSP 42365 **e** *H. eques*, CICCAA 00300 **f** *H. compressus*, paratype, MHNG 2181.076.

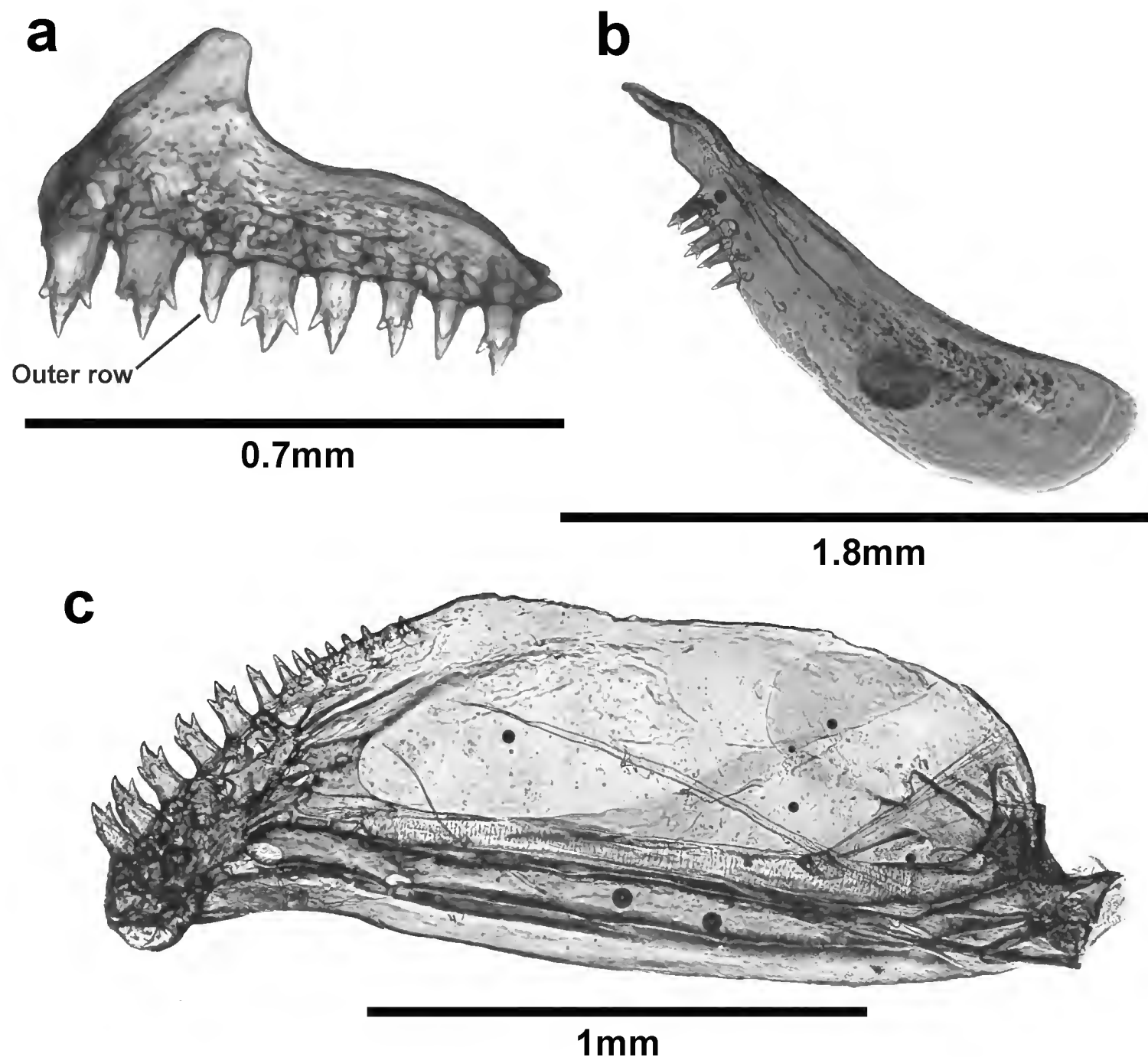


Figure 3. *Hyphessobrycon caru* sp. nov., jaw suspensory, CICCAA 00697, paratype, 19.3 mm SL: premaxillary (a), maxillary (b), and dentary (c).

Premaxillary teeth in two rows. Outer row with one unicuspid or tricuspid tooth, just slightly displaced from inner row; inner row with 6(5), 7(6), or 8(1) tricuspid teeth and one unicuspid tooth. Maxilla with 3(2) tricuspid teeth and two unicuspid teeth, 4(3) tricuspid teeth and two unicuspid teeth or 5(7) tricuspid teeth. Dentary with five (10) or six (1) larger tricuspid teeth followed by one smaller tricuspid teeth 5(2), 6(2), 7(3), and 8(5) smaller unicuspid teeth (Fig. 3).

Scales cycloid, three to eight radii strongly marked, circuli well-marked anteriorly, weakly marked posteriorly; lateral line incompletely pored, with 5(1), 6(2), 7(24), 8(14), or 9(4) perforated scales. Longitudinal scales series including lateral-line scales 31(1), 32(7), 33(14), 34(13), 35(3), or 36(7). Longitudinal scales rows between dorsal-fin origin and lateral line 5(3), 6(32), or 7(10). Horizontal scale rows between lateral line and pelvic-fin origin 4(43) or 5(2). Scales in median series between tip of supraoccipital spine and dorsal-fin origin 10(9), 11(12), 12(21), or 13(3). Circumpeduncular scales 11(6), 12(35), 13(2), or 14(2).

Dorsal-fin origin at midbody. Base of last dorsal-fin ray at vertical through first third of anal-fin. Dorsal-fin rays ii + 9(48), iii + 9(5), ii + 10(4). First dorsal-fin pterygiophore main body located behind neural spine of 4th

vertebrae. Adipose-fin present. Anal-fin origin aligned with vertical line through middle of dorsal-fin, between 6th and 8th dorsal-fin rays base. Anteriormost anal-fin pterygiophore inserting posterior to haemal spine of 11th vertebrae. First anal-fin ray in vertical through the middle of dorsal-fin (with about 7th or 8th ray base). Anal-fin iii + 22(10) or iii + 23(47); anal-fin origin aligned with vertical line through middle of dorsal-fin (between base of 6th and 8th dorsal-fin rays); Anal-fin profile nearly straight; Anal-fin rays with a sexually dimorphic pattern, which is absent in females, described below. Pectoral-fin rays 12(57) total rays. Tip of pectoral-fin surpassing pelvic-fin base. Pelvic-fin rays 8(57) total rays, surpassing anal-fin origin. Pelvic-fin rays with a sexually dimorphic pattern, which are absent in females, described below. Caudal-fin forked, upper and lower lobes similar in size. Principal caudal-fin rays 11+10(50) or 10+9(7); dorsal procurrent rays 8(2), 9(8) or 11(2) and ventral procurrent rays 7(4) or 8(8).

Branchiostegal rays 4(12). First gill arch with 1(11), 2(1) hypobranchial, 11(1), 12(10), or 13(1) ceratobranchial, 1(12) on cartilage between ceratobranchial and epibranchial, and 5(1) or 6(11) epibranchial gill-rakers. Supraneurals 3(2), 4(9), or 5(1). Total vertebrae 28(2) or 29(10).

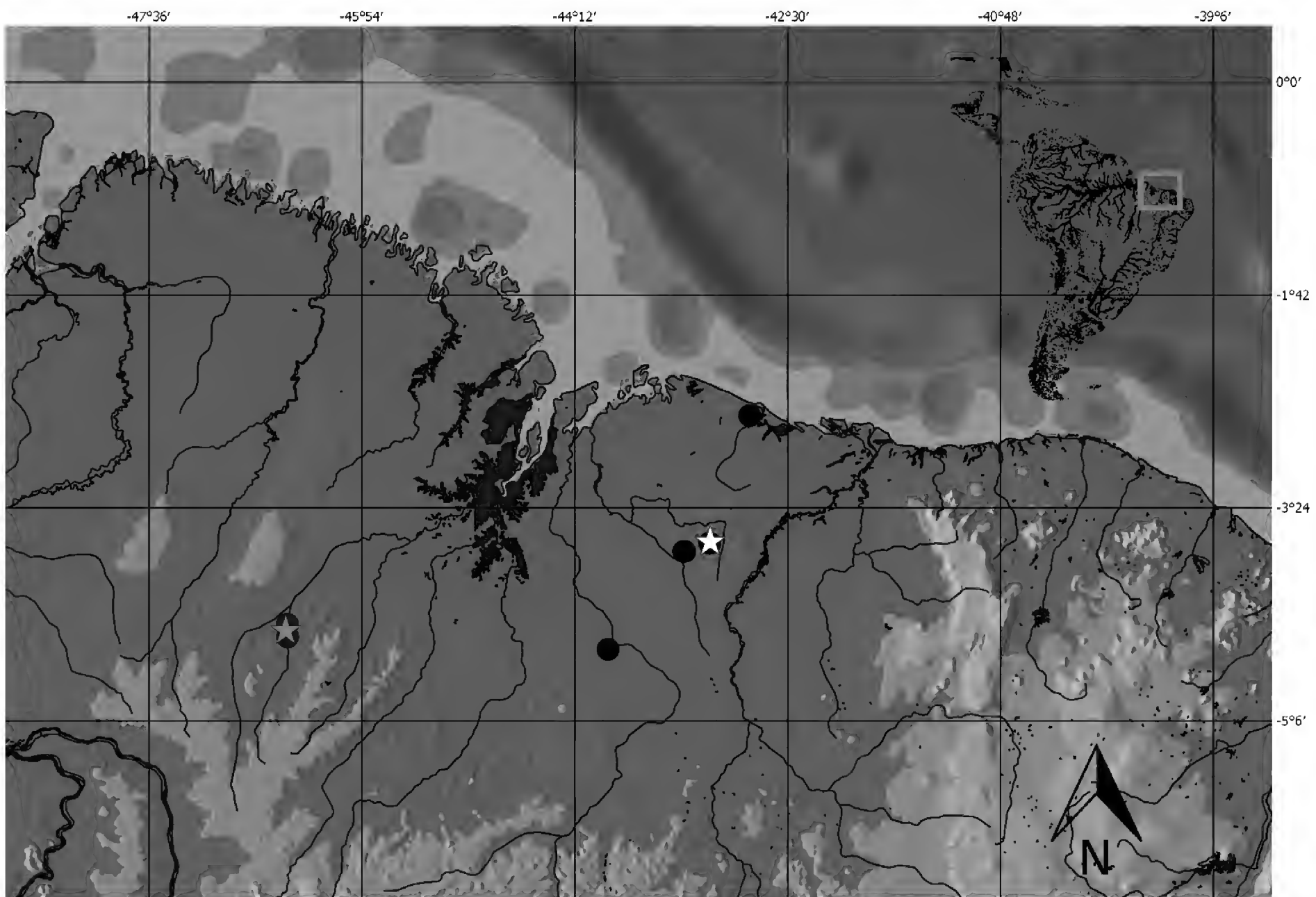


Figure 4. Geographical distribution of *Hyphessobrycon caru* sp. nov. and *H. piorskii*. Red star denotes Holotype and blue circles denote paratypes of *H. caru* sp. nov., and white star denotes Holotype and the black circles denote the known distribution of *H. piorskii*.

Colour in alcohol. Ground coloration light yellowish brown. Humeral region with few irregular inconspicuous vertically arranged chromatophores, sometimes very thin and inconspicuous humeral spot. Flank with chromatophores homogeneously scattered, more concentrated on posterior region to humeral spot, posterior region of dorsal-fin base origin and below mid-portion of trunk, between anal-fin origin and caudal peduncle. Ventral region lacking dark-brown chromatophores. Dark-brown chromatophores present on head and more concentrated on dorsal portion, becoming sparser on cheek and preopercular regions.

Dorsal-fin ground coloration hyaline, with conspicuous black or dark-brown spot located on anterior portion of fin, reaching about 6th ray, approximately between one-half to two-thirds of fin depth. Anal and caudal-fins hyaline. Caudal-fin with a darker, usually dark brown, posterior margin and on its base. Adipose-fin hyaline to light brown, with dark-brown or black chromatophores more concentrated on its dorsal portion, depending on the specimen preservation state. Pectoral and pelvic-fins hyaline; pelvic-fin with variable amounts of dark-brown pigmentation remaining depending on the specimen preservation state.

Sexual dimorphism. Mature males with small bone hooks on anal and pelvic-fin rays. Bone hooks absent on females. Anal-fin presenting bone hooks from 3rd, 4th, or

5th rays to the last ray. Number of hooks variable, increasing from the first to the last rays. Pelvic-fin presenting 2nd, 3rd, 4th, or 5th rays with 5, 6, or 7 smaller hooks.

Etymology. The specific epithet honors the term “Caru”. Caru is the name of an area (about 70.000 ha) inhabited by Brazilian native tribes from the ethnicities Guajá and Guajajara. People from this area use the Tupi language and have suffered consequences of European colonization and are under threat due to the pressure for exploration of the protected territory.

Geographic distribution. *Hyphessobrycon caru* sp. nov. has a restricted geographic distribution, being known only from the upper Pindaré river drainage, Mearim river basin, in the state of Maranhão, northeastern Brazil (Fig. 4). This species was never collected in the lower portions of this river drainage during 8 years of field trips conducted by EG and PB, including about 15 expeditions.

Molecular diagnosis (CBB). *Hyphessobrycon caru* sp. nov. belongs to the *H. micropterus* clade possessing 20 synapomorphic nucleotide substitutions: COI 73 (C→T), COI 88 (T→C), COI 217 (C→T), COI 274 (C→T), COI 298 (C→T), COI 334 (C→G), COI 338 (T→C), COI 370 (A→G), COI 418 (A→G), COI 433 (C→T), COI 439 (C→A), COI

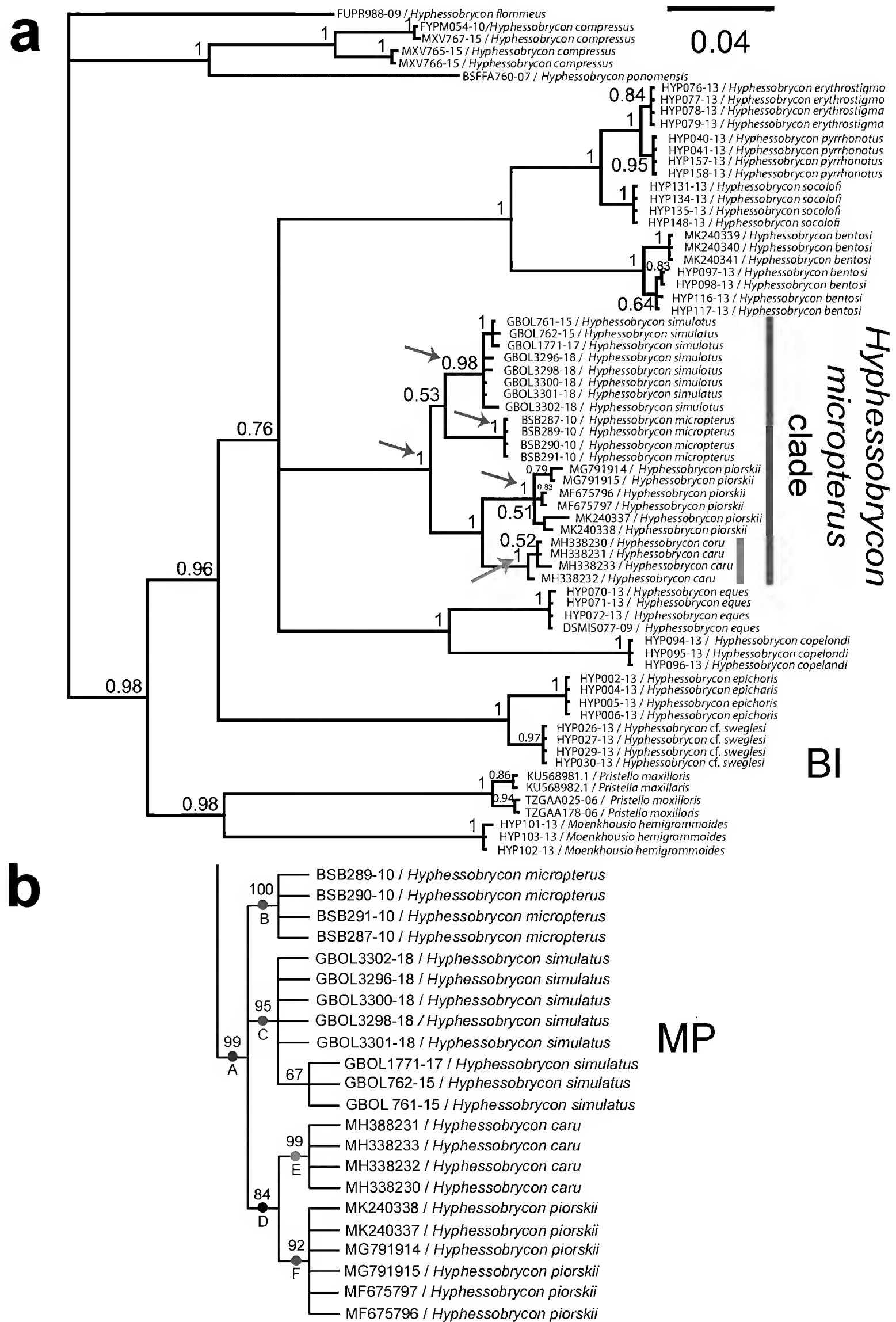


Figure 5. Phylogenetic tree based on Bayesian Inference (BI). Numbers above branches are posterior probability values. Posterior probability value supporting the *Hyphessobrycon micropterus* clade is indicated in green (haplotypes marked with a green bar); posterior probability value supporting the *H. caru* sp. nov. lineage under WP method is indicated in red (haplotypes marked with a red bar); and the other species (lineages) under WP method, within this clade, are indicated in black. **b** Strict consensus phylogenetic tree based on Maximum Parsimony (MP), obtained from the 38 most parsimonious trees, in which 587 characters were constant, 20 variable but parsimony-uninformative, and 248 parsimony-informative (total length 833, consistency index 0.489, retention index 0.901). The image is focusing on the *Hyphessobrycon micropterus* clade. Numbers above branch are bootstrap values and letters below branches correspond to nucleotide substitutions, listed in Suppl. material 1: Box 1, corresponding to the CBB method. Green circle indicating *Hyphessobrycon micropterus* clade, red circle *H. caru* sp. nov., blue circles the other congeners within the clade, and black circle the clade *H. caru* sp. nov. + *H. piorskii*.

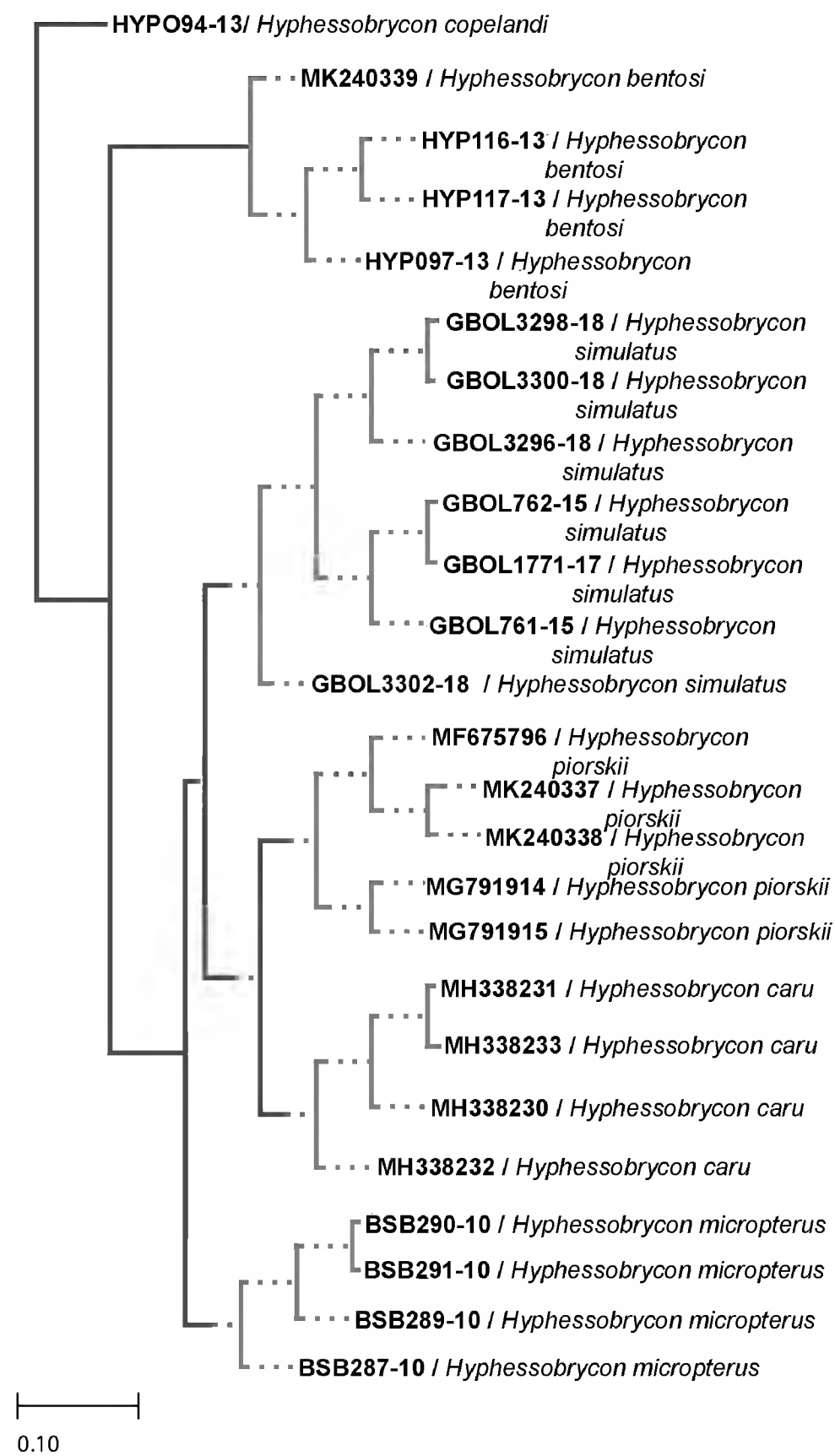


Figure 6. Species delimitation tree generated by the Bayesian Poisson Tree Processes (bPTP) model, using a fragment of the mitochondrial gene COI. The blue lines indicate branching processes among species, while red lines indicate branching processes within species.

457 (A→G), COI 469 (T→C), COI 478 (A→T), COI 559 (A→G), COI 562 (T→A), COI 592(A→G), COI 631 (A→T), COI 655 (A→C), COI 673 (A→C). It shares nine synapomorphic nucleotide substitutions with *H. piorskii*, which separate them from *H. simulatus* and *H. micropterus*: COI 181 (A→C), COI 208 (A→G), COI 245 (C→T), COI 325 (T→C), COI 349 (T→C), COI 436 (A→T), COI 472 (A→G), COI 538 (C→T), COI 556 (T→C). In addition, it has six unique nucleotide substitutions within the *H. micropterus* clade: COI 148 (C→T), COI 154 (C→T), COI 175 (T→C), COI 364 (G→A), COI 487 (T→C), COI 517 (A→G) (Fig. 5; Suppl. material 1: Box 1).

DBC. COI sequences support the existence of a new species of *Hyphessobrycon* inhabiting the Pindaré river basin in Maranhão state. After trimming, the final alignment yielded 680 base pairs with 159 polymorphic sites and 26

haplotypes. Average genetic distances were 18.3%, with the highest values between *H. epicharis* and *H. erythro stigma* (23.4%), while the lowest value (0.7%) was between *H. pyr rhonotus* and *H. erythro stigma* (Table 3). *Hyphessobrycon caru* sp. nov. is divergent on average 17.0% from the other taxa, with a minimum distance of 3.6% to *H. piorskii* and a maximum of 21.8% to *Pristella maxillaris* (Table 3).

WP and CBB. Both phylogenetic analysis based on BI and MP supported a clade comprising *H. caru* sp. nov., *H. micropterus*, *H. piorskii*, and *H. simulatus*, hereafter termed *Hyphessobrycon micropterus* clade, with maximum posterior probability value and 99% bootstrap value in BI and MP, respectively. *Hyphessobrycon caru* sp. nov. formed a single exclusive lineage with maximum posterior probability value (posterior probability = 1) and 99% bootstrap value in BI and MP, respectively.

Table 3. Kimura-2 parameters pairwise genetic distances among species.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1 <i>H. erythro stigma</i>																
2 <i>H. pyrrhonotus</i>	0.007															
3 <i>H. socolofi</i>	0.037	0.035														
4 <i>H. simulatus</i>	0.192	0.194	0.179													
5 <i>H. micropterus</i>	0.205	0.202	0.198	0.041												
6 <i>H. piorskii</i>	0.188	0.185	0.178	0.063	0.064											
7 <i>H. caru</i>	0.206	0.210	0.203	0.062	0.057	0.036										
8 <i>H. eques</i>	0.175	0.178	0.163	0.154	0.157	0.160	0.160									
9 <i>H. copelandi</i>	0.192	0.189	0.186	0.170	0.176	0.158	0.168	0.102								
10 <i>H. epicharis</i>	0.234	0.230	0.220	0.170	0.175	0.189	0.190	0.187	0.197							
11 <i>H. bentosi</i>	0.106	0.103	0.112	0.197	0.194	0.205	0.204	0.195	0.220	0.219						
12 <i>H. cf. sweglesi</i>	0.210	0.207	0.197	0.182	0.187	0.201	0.209	0.181	0.197	0.030	0.222					
13 <i>P. maxillaris</i>	0.225	0.232	0.206	0.201	0.211	0.220	0.218	0.194	0.213	0.180	0.202	0.183				
14 <i>M. hemigrammoides</i>	0.219	0.219	0.209	0.179	0.185	0.178	0.179	0.203	0.211	0.196	0.221	0.199	0.166			
15 <i>H. compressus</i>	0.214	0.218	0.215	0.202	0.208	0.198	0.208	0.198	0.201	0.212	0.212	0.212	0.203	0.215		
16 <i>H. panamensis</i>	0.210	0.213	0.209	0.202	0.199	0.179	0.187	0.215	0.229	0.221	0.213	0.218	0.204	0.208	0.145	
17 <i>H. flammeus</i>	0.201	0.201	0.198	0.169	0.174	0.186	0.204	0.203	0.205	0.192	0.200	0.189	0.206	0.200	0.170	0.196

These species delimitation analysis (WP and CBB) have identical results, delimitating four species within the *Hyphessobrycon micropterus* clade: *H. caru* sp. nov., *H. micropterus*, *H. piorskii*, and *H. simulatus* (Fig. 5a, b). The nucleotide substitutions supporting these four lineages within the *H. micropterus* clade, and the nucleotide substitutions supporting this clade are presented in Figure 5b and Suppl. material 1: Box 1. The combination of nucleotide substitutions diagnosing *H. caru* sp. nov. are presented in the molecular diagnosis section.

bPTP. This species delimitation analysis also indicates four lineages (species) within the *Hyphessobrycon micropterus* clade: *H. caru* sp.n., *H. micropterus*, *H. piorskii*, and *H. simulatus* (Fig. 6). This outcome was similar to the aforementioned results. The species included as outgroups (*H. bentosi* and *H. copelandi*) were also supported as independent lineages.

Discussion

Currently molecular techniques are frequently useful for solve species complexes and discover cryptic species (e.g. Bickford et al. 2006; Costa and Amorim 2011; Pereira et al. 2011; Adams et al. 2014; Costa-Silva 2015; Costa et al. 2012, 2014, 2017; Amorim 2018; Guimarães et al. 2018; Ottoni et al. 2019) and could be an excellent complement for traditional taxonomy (Kekkonen and Hebert 2014). DNA barcoding has demonstrated to be very efficient for delimiting species of *Hyphessobrycon*, mainly in groups with little morphological variation (i.e., cryptic species) (see Castro-Paz et al. 2014; Guimarães et al. 2018), preferably when applied together with other species delimitation methods, such as PAA, DBC, CBB, bPTP, and WP in an integrative taxonomy perspective (Guimarães et al. 2018). The recognition of different genetic patterns and lineages in groups with very similar morphology has been a common pattern in the tree of eukaryotic life. This is observed particularly often in species-rich genera, such

as in several Neotropical fishes (e.g. Pereira et al. 2011; Roxo et al. 2012; Castro-Paz et al. 2014; Melo et al. 2014, 2016a; Benzaquem et al. 2015; Benine et al. 2015; Ottoni et al. 2019). DNA techniques can help to uncover morphological hidden diversity (Bickford et al. 2006; Adams et al. 2014), delimiting a putative population or group of populations as an independent lineage (species), and, subsequently, through a more meticulous analysis of morphological features, morphological differences between cryptic species can be found.

The large number of the described *Hyphessobrycon* species (about 160 spp.), with new species described every year, reveal an astonishing diversity within the genus. During the past 10 years, about 50 new species have been described (Fricke et al. 2019). However, historically *Hyphessobrycon* species have been described only on the basis of morphological features, including differences in the pigmentation patterns and teeth numbers and morphology, using few individuals per species (e.g. Steindachner 1882; Eigenmann 1915; Zarske 2008, 2014; Bragança et al. 2015). Recently, DNA barcoding in characoid fishes has been used to discriminate species, identify new ones, and reveal that it is not always possible to differentiate species based solely on their morphology (Ornelas-Garcia et al. 2008; Pereira et al. 2011; Castro-Paz et al. 2014; Melo et al. 2014, 2016a; Benine et al. 2015).

Our results suggest a cryptic speciation in the rosy tetra clade, more specifically in a new clade here defined, the *Hyphessobrycon micropterus* clade, including *H. caru* sp. nov., *H. micropterus*, *H. piorskii*, and *H. simulatus*, so far only known from the Pindaré, Itapecuru, Munim, Preguiças, and São Francisco river drainages of Brazil and the coastal river basins of French Guiana and Suriname (Guimarães et al. 2018; Brito et al. 2019; Fricke et al. 2019; this study). The clade proposed here is supported by high node support values (maximum posterior probability value and 99% of bootstrap value in BI and MP, respectively). In addition, this clade was corroborated by 20 synapomorphic nucleotide substitutions (Fig. 5; Suppl. material 1: Box 1).

Hyphessobrycon caru sp. nov. is herein described within the *Hyphessobrycon micropterus* clade based on five different and independent methods of species delimitation (PAA, DBC, WP, CBB and bPTP), characterized by different criteria and assumptions. *Hyphessobrycon caru* sp. nov. is distinguished from all its congeners by a combination of unambiguous morphological character states [see Diagnosis (PAA)]. In our Bayesian phylogenetic analysis (Fig. 5A), haplotypes of *H. caru* sp. nov. formed a single exclusive clade with maximum posterior probability value (posterior probability = 1) (WP). Furthermore, the COI average genetic distance of *H. caru* sp. nov. when compared with the other taxa herein analyzed was 19.6% and its minimum COI genetic distance was 3.6% to *H. piorskii* (DBC). Considering this value, the threshold of *H. caru* sp. nov. would be greater than that inferred by delimitations among Neotropical fish species (2% according to Pereira et al. 2011). Moreover, *H. caru* sp. nov. was also molecularly diagnosed by six synapomorphic nucleotide substitutions (Fig. 5b; Suppl. material 1: Box 1), as well as, by a combination of other nucleotide substitutions (see CBB - molecular diagnosis), and corroborated by a bPTP analysis. Thus, it makes the hypothesis of this new species stronger from an integrative taxonomy perspective (see Dayrat 2005; de Queiroz 2007; Goldstein and Desalle 2010; Padial et al. 2010). Therefore, we recommend the use of integrative taxonomy for future taxonomic revisions and species descriptions when dealing with species complexes and groups containing possible cryptic species.

Comparative material

***Hyphessobrycon amandae*:** UFRJ 1557, 5 spcms, Jussara municipality, Goiás state, Brazil. ***H. bentosi*:** MCZ 20842, 1 spcm (Syntype), Óbidos municipality, Pará state, Brazil. ***H. bifasciatus*:** UFRJ 0068, 6 spcms, Marataízes and Guarapari municipality, Espírito Santo state, Brazil. ***H. compressus*:** BMNH 1905.12.6.4-5, 2 spcms (Paratypes), Oaxaca state, México. ***H. copelandi*:** CAS 42683, 1 spcm (Syntype); MCZ 20771, 1 spcm (Syntype), Tabatinga municipality, Amazonas state, Brazil. ***H. eques*:** CICCAA 00715, 4 spcms (C&S); CICCAA 00710, 51 spcms, Tombos municipality Carangola river, Minas Gerais state, Brazil. ***H. erythrostigma*:** ANSP 70208, 1 spcm (Holotype), Peru and Brazil. ***H. epicharis*:** FMNH100609, 1 spcm (Paratype), Baria river, Amazonas, Venezuela. ***H. haraldschultzi*:** CICCAA 00873, 20 spcms, Ilha do Bananal municipality, Javaés river, Tocantins state, Brazil. ***H. hasemani*:** ANSP 39230, 1 spcm (Holotype), Guajaramirim municipality, Madeira river, Rondônia state, Brazil. ***H. micropterus*:** FMNH 57916, 1 spcm (Holotype), São Francisco river at Lagoa de Porto, Minas Gerais state, Brazil. ***H. piorskii*:** CICCAA 00695, 1 spcm (Holotype); CICCAA 00430, 15 spcms (Paratype); CICCAA 00431, 21 spcms (Para-

type); CICCAA 00696, 15 spcms (Paratype); CICCAA 00697, 16 spcms (C&S) (Paratype); CICCAA 00698, 6 spcms, 1 spcm (C&S) (Paratype); CICCAA 00750, 9 spcms (Paratype); CICCAA01654, 1 spcm (Paratype); CPUFMA 171664, 15 spcms (Paratype); UFRJ 11553, 6 spcms (Paratype), stream at the Anapurus municipality, Munim river, Maranhão state, Brazil. CICCAA 00089, 1 spcm (C&S) (Paratype); CICCAA 00881, 1 spcm (Paratype); CICCAA 01563, 1 spcm (Paratype); stream at Mata de Itamaçoca, Chapadinha municipality, Munim river, Maranhão state, Brazil. CICCAA 01382, 5 spcms (Paratype); CICCAA 02008, 12 (C&S) spcms (Paratype), stream at Mata Fome, Barreirinhas municipality, Preguiças river, Maranhão state, Brazil. ***H. pyrrhonotus*:** MZUSP 45714, 1 spcm (Holotype), Ereré river, Brazil. ***H. rosaceus*:** FMNH 52791, 1 spcm (Holotype), Gluck Island, Essequibo River, Guyana. ***H. weneri*:** MZUSP 42365, 1 spcm (Holotype), Santa Maria do Pará and São Miguel de Guamá municipality, Guamá river, Pará state, Brazil. CICCAA 00751, 1 spcm, Paragominas municipality, Candiru river, Pará state, Brazil. ***H. socolofi*:** MZUSP 13181, 1 spcm (Holotype), Barcelos municipality, Negro river, Amazonas state, Brazil.

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Supplementary material 1

Box 1

Authors: Erick Cristofore Guimarães, Pâmella Silva de Brito, Leonardo Manir Feitosa, Luis Fernando Carvalho Costa, Felipe Polivanov Otoni

Data type: DOCX file

Explanation note: List of nucleotide substitutions (synapomorphies and autapomorphies) from each lineage (species) and some crucial points of the cladogram of the Fig. 5B.

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Type specimens of Aplysiida (Gastropoda, Heterobranchia) in the Academy of Natural Sciences of Philadelphia, with taxonomic remarks

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Abstract

The type specimens of 15 nominal species of Aplysiida (Gastropoda, Heterobranchia) at the Academy of Natural Sciences of Philadelphia are listed and their primary types are illustrated. Type materials described by the following authors are present: Henry A. Pilsbry (9 names), Angelo Heilprin (2), Charles N. E. Eliot (1), William H. Pease (2) and Elizabeth J. Letson (1). Some taxonomic notes are provided. *Aplysia perviridis* (Pilsbry, 1895), **comb. nov.**, *Aplysia pilsbryi* (Letson, 1898), and *Aplysia pulmonica* Gould, 1852 are reinstated as valid.

Key Words

Mollusca, Anaspidea, Aplysiomorpha, morphology, new combinations, biodiversity, Curatorial methods, malacology, nomenclature, type specimens

Introduction

Since the publication of Pilsbry's *Manual of Conchology* (1895, 1896a, 1896b), where a number of new taxa were described, little has been published about the types of Aplysiida (e.g. Valdés and Héros 1998). Systematic revisions of several aplysiidan groups are needed (Gosliner 1994; Valdés et al. 2006; Uribe et al. 2013), and information about type materials is essential for determining the status of species-group taxa. As the aplysiidan material that Pilsbry studied as well as that of other authors is housed at the Academy of Natural Sciences (ANSP), evaluation of the type materials held there is important. We follow Bouchet et al. (2017) for the name of the order; it has also been called Anaspidea and Aplysiomorpha.

Material and methods

To find putative type material of aplysiidans, we searched the ANSP collection database for items indicated as having a type status; this database includes digitized records from the handwritten ledgers. We also searched the dry collection for specimens indicated as type specimens on their labels and relevant literature (e.g. Pilsbry 1896; Eales 1960) for indications of type materials held by ANSP.

Where ethanol-preserved material was verified as part of a type series, the animals were dissected by standard techniques, under a stereomicroscope, with the specimen immersed in ethanol. Digital photography of the whole animals was obtained with the specimen immersed in ethanol an acrylic container with rubber bottom. After

dissections, photographs were taken of the specimen carefully pinned into the container in the desired position.

Digital photographs of shells were made using either a standard digital macro-lens system with single photos of each view for specimens larger than ~10 mm in maximum dimension, or a computer-operated motorized StackShot™ system (Cognisys, Inc.), coupled with Helicon Remote and Helicon Focus software (HeliconSoft Ltd.), allowing digital combination (i.e., “stacking”) of multiple individual shots of each view for specimens less than 10 mm.

The figures of shells are not shown to scale, but the maximum dimension of each specimen is given in the corresponding figure legend. The photographs of types published here are also available in the online database for the ANSP Mollusca collection.

Catalogue numbers in the ANSP malacology collection were originally assigned in a single sequence, started in 1889 by Henry Pilsbry. Around 1970, George M. Davis established a separate number sequence prefixed with “A” for alcohol-preserved material. Many samples with catalogue numbers in the original sequence were given new numbers in the A sequence. This renumbering affected all of the nominal taxa of Aplysiida for which ANSP has type material in alcohol. In some cases, the shell is stored under the dry collection under the original number and body from which it was dissected is preserved in the alcohol collection under an “A” number. We have traced these associations to ensure that we have recognized the components of each lot.

The list of nominal taxa is arranged alphabetically by the original epithet (in **bold**) with the taxon name written as in the original description, except that capitalization is adjusted to current standards.

Institutional Acronyms: ANSP, Academy of Natural Science of Philadelphia, USA; CPIC, research collection of the Department of Biological Sciences of the California State Polytechnic University, Pomona, USA; MCZ, Museum of Comparative Zoology, Harvard University, Boston, USA.

Results and discussion

Search of the ANSP collection, the collection database and relevant literature found potential type material of 18 names. Three of these proved to be false leads: a lot of *Dolabrifera maillardi* Deshayes, 1863 (ANSP 114205) from Reunion was erroneously flagged in the database as a type; one was a manuscript name of Pilsbry (ANSP 84337, A7044, currently *Aplysia* sp.) from Zanzibar [we do not mention the name to avoid creating a nude name]; and one labeled as “Co-type?” of *Dolabrifera marmorea* Pease (ANSP 247112), but Sowerby (1868), not Pease introduced this name.

For 15 nominal taxa, we verified the presence of type material in ANSP. This includes holotypes for 3 taxa and syntypes for 11, along with 1 (*Aplysia badistes*) where we could not determine in the specimen was the holo-

type or a paratype. The names were introduced by Henry A. Pilsbry (9), Angelo Heilprin (2), Charles N. E. Eliot (1), William H. Pease (2), and Elizabeth J. Letson (1). The type localities are Western Atlantic (7), South Pacific Ocean (3), North Pacific Ocean (4), and Indian Ocean (2). Currently 18 valid species with 10 synonyms are recognized for Aplysiida in the Western Atlantic. This catalog is especially important to that region, as it represents 25% of the 28 nominal taxa.

In the following section, the type material and current status of each nominal species is included. Two species were previously considered valid and 13 held as synonymous. *Aplysia perviridis* (Pilsbry, 1895) new comb., *Aplysia pilsbryi* (Letson, 1898), and *Aplysia pulmonica* (Gould, 1852) are herein are reinstated as valid and *Tethys pulmonica* var. *tryoniana* is returned to the synonymy of *Aplysia pulmonica* Gould, 1852 rather than *A. argus* Rüppell & Leuckart, 1830.

Nominal taxa

Aplysia aequorea Heilprin, 1888

Figure 1A, B

Aplysia aequorea Heilprin, 1888: 325–327, pl. 16, figs 2–2b.

Type locality. South side of Castle Harbor, opposite Tucker’s Town, Bermuda.

Type material. Holotype (monotypy), ANSP A7030, 1 specimen (dehydrated but subsequently put back on alcohol, 33.2 mm long preserved); ANSP 66519, 1 shell (35 mm) (A. Heilprin coll. 1888), removed from body of holotype by Heilprin.

Remarks. Heilprin (1888) stated that he examined a single specimen. We do not illustrate the rehydrated alcohol specimen as it is a blackened mass without visible distinguishing features.

Current systematic position. *Aplysia dactylomela* Rang, 1828 (*fide* Valdés et al. 2013).

Aplysia (Metaplysia) badistes Pilsbry, 1951

Figure 1C–G

Aplysia (Metaplysia) badistes Pilsbry, 1951: 1–6, figs 1–9.

Type locality. Venetian Causeway, Biscayne Bay, Florida, USA.

Type material. Holotype and paratype: ANSP A7028, 2 specimens (one whole except for removal of buccal mass, measuring 45.8 mm long preserved and the other dissected, measuring 46.7 mm long preserved); ANSP 187712, 1 shell (18.7 mm) and gizzard plates of dissected specimen of A7028 (H. A. Pilsbry coll., iv/1951), 1 slide with radulas of dissected specimens.

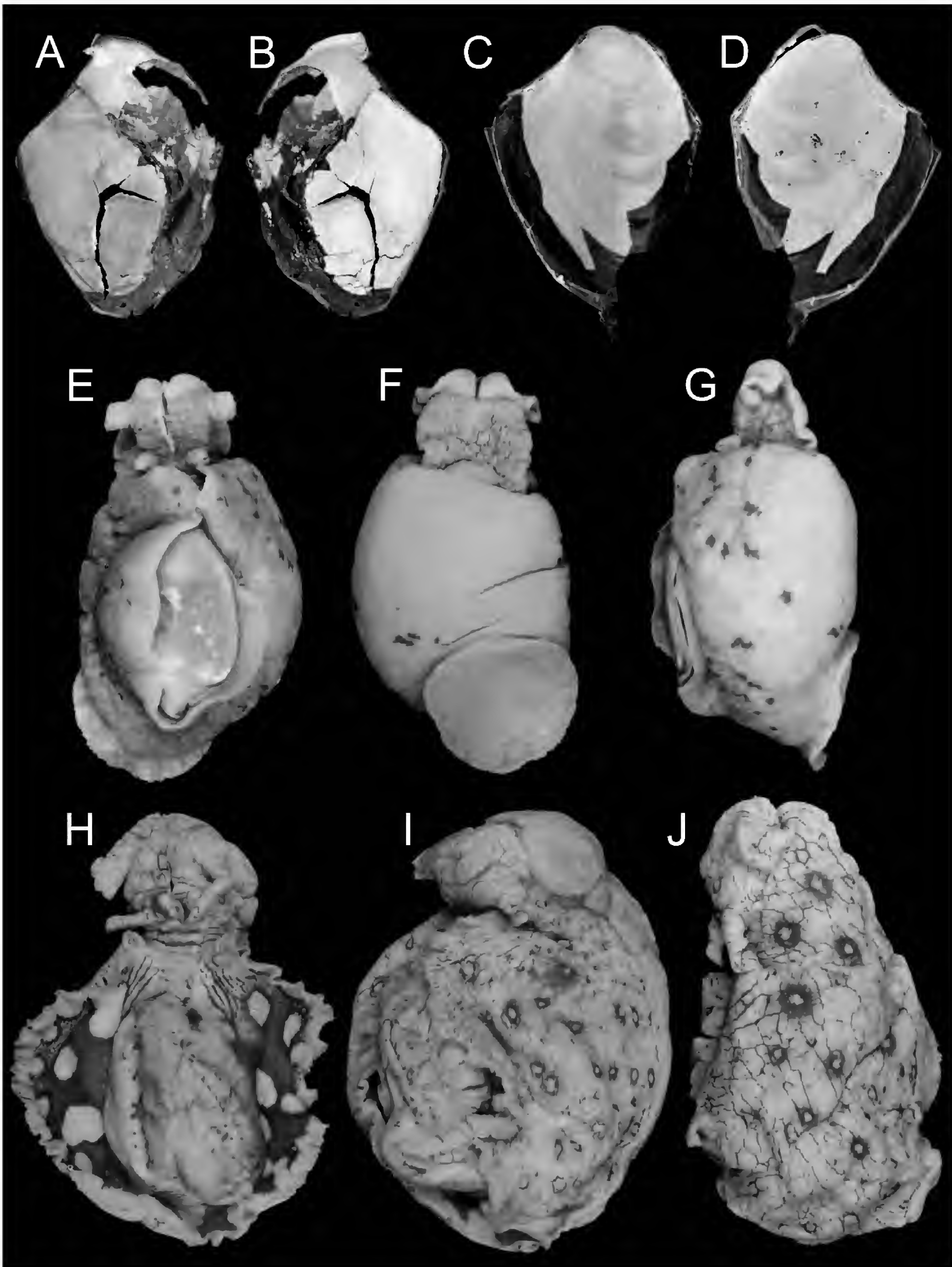


Figure 1. Aplysiida types. **A.** Holotype of *Aplysia aequorea* (= *A. dactylomela*), shell, L 35 mm, ANSP 66519 in dorsal view. **B.** Same, in ventral view. **C–G.** Types of *A. badistes*, **C.** Shell, L 18.7 mm, ANSP 187712 in dorsal view. **D.** Same, in ventral view. **E.** Same species, whole specimen, L 45.8mm, ANSPA7028 in dorsal view. **F.** Same, in ventral view. **G.** Same, in right lateral view. **H–J.** Syntypes of *A. benedicti* (= *Aplysia argus*), whole specimens ANSPA7027. **H.** Specimen L 79 mm in dorsal view. **I.** Same, in right lateral view. **J.** Specimen L 76 mm in right lateral view.

Remarks. *Aplysia badistes* Pilsbry, 1951 is the type species of subgenus *Metaplysia* Pilsbry, 1951. Pilsbry stated “Type and another specimen are 187712 ANSP”. Pilsbry described the internal anatomy from one specimen but extracted the radula from both. Someone separated the shell and gizzard plates as ANSP 188279, and labeled them “Paratype”, a term not used in the publication. We have restored them to the original catalogue number (187712) as it is not possible to tell which specimen Pilsbry intended to be the holotype.

Current systematic position. *A. juliana* Quoy & Gaimard, 1832 (*fide* Eales 1960).

Aplysia (Tethys) benedicti Eliot, 1900

Figure 1H–J

Aplysia (Tethys) benedicti Eliot, 1900: 513–515, pl. 19, fig. 2a, b.

Type locality. Apia Harbor, Upolu, Samoa.

Type material. Syntypes: ANSP A7027, 2 specimens + 1 slide with radulae and jaw mounted (leg., C. N. E. Eliot, 19–21/vii/1899) [1 specimen (Eliot 1900: fig 2a), preserved 76 mm long, whole, not dissected; another specimen, preserved 79 mm long, with radula removed].

Current systematic position. *Aplysia argus* Rüppell & Leuckart, 1830 (*fide* Alexander & Valdes, 2013).

Syphonota elongata Pease, 1860

Figure 2A, B

Syphonota elongata Pease, 1860: 24.

Type locality. Sandwich Islands [Hawaii, USA].

Type material. Potential syntypes: ANSP 20686, 1 shell + 2 fragments (11.3 mm long, “ex auct”), ANSP 20687, 3 shells (7.1, 7.2 and 7.5 mm long, “ex auct”), MCZ 31442 and 298486 (Johnson 1994).

Remarks. It is not known whether Pease collected the specimens deposited at ANSP and MCZ before or after the species description was published. Therefore, we consider them potential syntypes.

Current systematic position. *Aplysia parvula* Mörch, 1863 (*fide* Eales 1960).

Tethys floridensis Pilsbry, 1895

Figure 2C–E

Tethys floridensis Pilsbry, 1895: 82–83; 1896a, pl. 37, figs 15–19.

Type locality. Key West, Florida, USA.

Type material. Syntypes: ANSP A7034, 2 specimens (one 90 mm long preserved, with shell, not dissected;

other 76 mm long preserved, shell removed, penis everted) (H. C. Machette, leg. 1893) [1 specimen (Fig. 2C, D), penis not everted; another specimen, penis everted (Fig. 2E)]; ANSP 63529, 1 shell (fragmented, ca 45 mm long).

Remarks. Pilsbry (1895) stated that “the types are two well preserved alcohol specimens”. We judge the original drawing of a whole animal (Pilsbry 1896a: pl. 37, fig. 19) to be a composite of the two specimens.

Current systematic position. *Aplysia fasciata* Poiret, 1789 (*fide* Medina et al. 2005).

Dolabrifera fusca Pease, 1868a

Figure 2F, G

Dolabrifera fusca Pease, 1868a: 76, pl. 8, fig. 4; 1868b, pl. 12, fig. 27.

Type locality. Polynesia.

Type material. Syntype: ANSP 20710 (Pease 1868b: pl. 12, fig. 27; Valdés et al 2017: fig. 5I, J), 1 shell (7.7 mm long) “ex auct”, no locality data. Syntypes, MCZ 297870, 3 shells, from Tahiti (Johnson 1994).

Remarks. Pease (1868a) neglected to state a locality within Polynesia, although he described the habitat as “under stones, in the upper region of the laminarian zone”.

Current systematic position. *Dolabrifera dolabrifera* Rang, 1828 (*fide* Valdés et al. 2017).

Dolabrifera jacksoniensis Pilsbry, 1896a

Figure 2H–K

Dolabrifera jacksoniensis Pilsbry, 1896a: 120–121; 1896b, pl. 44, figs 38–41.

Type locality. Port Jackson, New South Wales, Australia.

Type material. Syntypes: ANSP A7040, 2 specimens (one 16.7 and another 11.3 mm long preserved); ANSP 64931 (Pilsbry 1896b: pl. 44, figs 38–41; Valdés et al. 2017: fig. 8E, F), 1 shell (6.7 mm long; ex J. C. Cox 1893).

Remarks. Both alcohol specimens have had the shell removed, but only one shell is present in the corresponding dry lot.

Current systematic position. *Dolabrifera brazieri* G. B. Sowerby II, 1870 (*fide* Valdés et al. 2017).

Dolabrifera nicaraguana Pilsbry, 1896a

Figure 3A–E

Dolabrifera nicaraguana Pilsbry, 1896a: 124–125; 1896b pl. 63, figs 12–16.

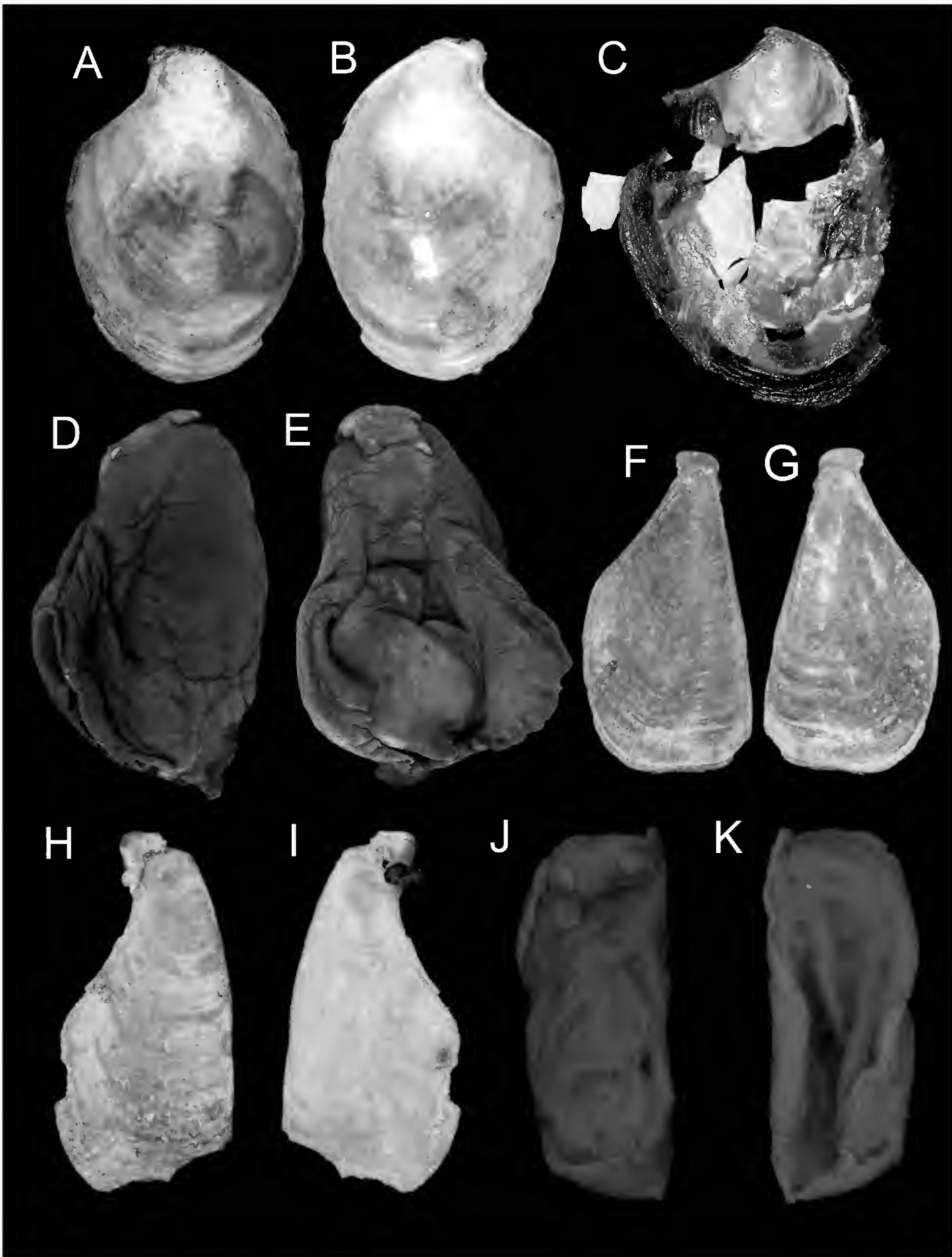


Figure 2. Aplysiida types. **A–B.** Syntype of *Syphonota elongata* (= *Aplysia parvula*), **A.** Shell, L 11.3 mm, ANSP 20686 in dorsal view. **B.** Same, in ventral view. **C–E.** Syntypes of *Tethys floridensis* (= *A. fasciata*), **C.** Shell, L ca 45 mm, ANSP 63529 in dorsal view. **D.** Same species, whole specimen, L ca 90 mm, ANSP A7034 in right lateral view. **E.** Same, in dorsal view. **F.** Syntype of *Dolabrifera fusca* (= *D. dolabrifera*), shell, L 7.7, ANSP 20710 in dorsal view. **G.** Same, in ventral view. **H–K.** Syntypes of *D. jacksoniensis* (= *D. brazieri*), **H.** Shell, L 6.7 mm, ANSP 64931 in dorsal view. **I.** Same, in ventral view. **J.** Same species, whole specimen, L ca 16.7 mm, ANSP A7040 in dorsal view. **K.** Same in ventral view.

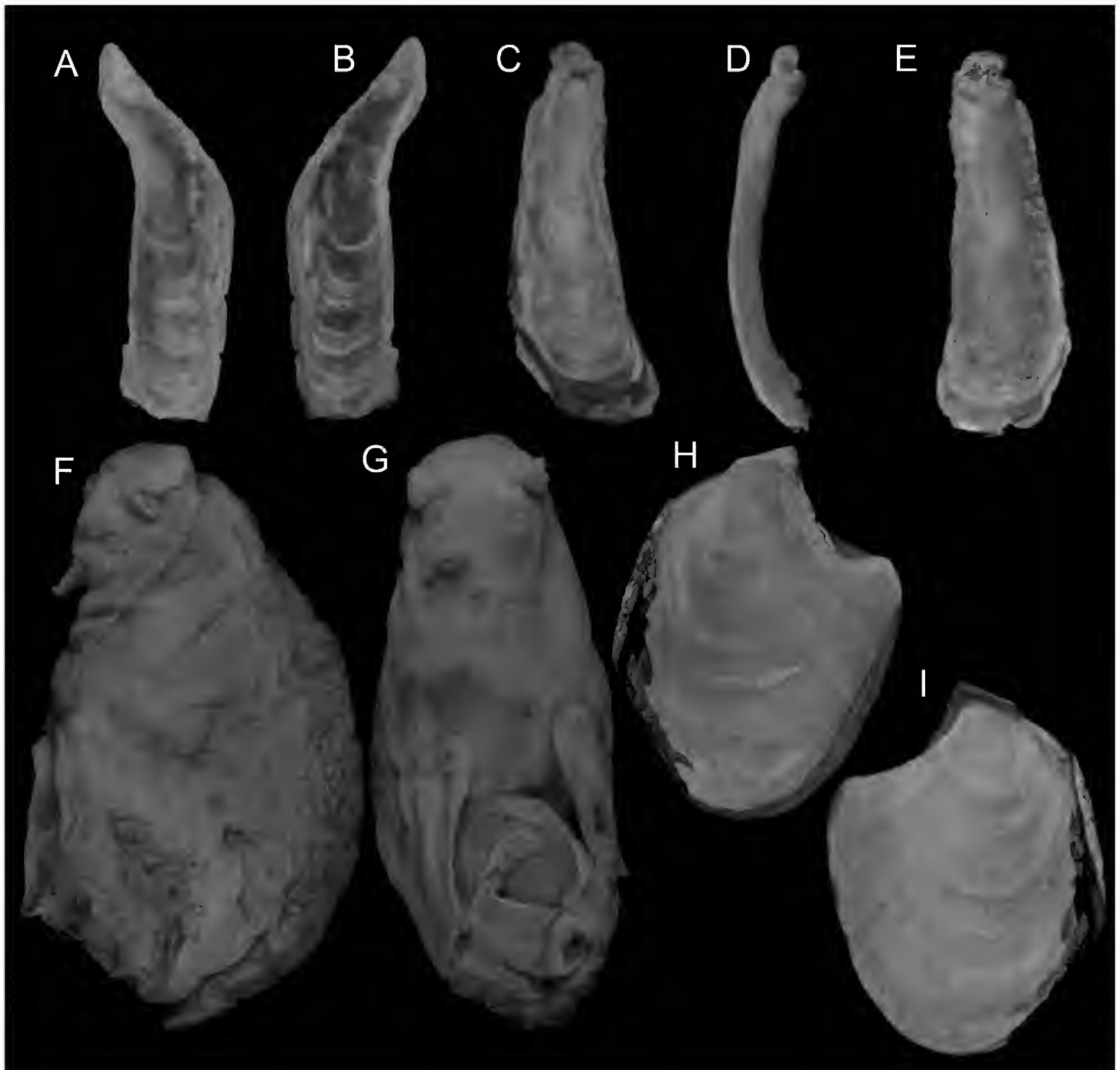


Figure 3. Aplysiida types. **A–E.** Syntypes of *Dolabrifera nicaraguana*, **A.** Shell, L 8.2 mm, ANSP 67518 in dorsal view. **B.** Same, in ventral view. **C.** Same species, shell, L 9.2 mm, ANSP 67517 in dorsal view. **D.** Same in lateral view. **E.** Same in ventral view. **F–I.** Syntypes of *Tethys panamensis* (= *A. dactylomela*), **F.** whole specimen, L ca 52 mm, ANSP A7042 in right lateral view. **G.** Same in dorsal view. **H.** Shell, L 16 mm, ANSP 20693 in ventral view. **I.** Same in dorsal view.

Type locality. San Juan del Sur, Nicaragua.

Type material. Syntypes (all leg. J. E. Bransford): ANSP A7048, 2 specimens (both dry, one ca 25.5 mm long preserved with shell 7.8 mm long and another ca 24.6 mm long preserved, shell removed); ANSP 67517 (Pilsbry, 1896b: figs 12–14; Valdés et al 2017: fig. 15A, B), 1 shell (9.2 mm long), taken from body in A7048; ANSP 67518 (Pilsbry 1896b: fig. 15), 1 shell (8.2 mm long), corresponding alcohol specimen missing.

Remarks. Pilsbry (1896a) gave measurements for two specimens preserved in ethanol, but three shells and two

bodies are present in the ANSP collection. The ANSP ledger lists 63517 from “San Juan Del Sur Nicaragua” (the type locality) as containing two alcohol specimens and one dry and 63518 from “Nicaragua” as having one alcohol and one dry. These were catalogued on 21 January 1896 and so are part of the material that Pilsbry examined as the description was published on 13 March 1896. The ledger lists 63517 as “Types” but does not list 63518 as a “type”. The original ANSP label for 63517 says “Shell of the TYPE”; whereas that for 63518 does not mention type status. Although Pilsbry intended 63517 to be the holotype, he did not designate a holotype in the original description, so we consider all of the material to be syntypes.

ANSP A7048 contains a note saying, “August 1969 badly dried” and the back of the most recent Academy label says “Treated with Tri-sodium phosphate and stepped up to 70% ETOH. Unfortunately, the sample subsequently dried out again, and so has been combined with the dry lot.

Current systematic position. *Dolabrifera nicaraguana* Pilsbry, 1896 (fide Valdés et al. 2017).

Tethys panamensis Pilsbry, 1895

Figure 3F–I

Tethys panamensis Pilsbry, 1895: 88–89; 1896b, pl. 60, figs 45–48

Type locality. Panama.

Type material. Syntype: ANSP A7042 (Pilsbry 1896b: fig. 45), 1 specimen (52 mm long preserved), ANSP 20693 (Pilsbry, 1896b: figs 46–48), 1 shell (16 mm long; J. A. McNeil coll.).

Remarks. Recently, the Caribbean species *Aplysia dactylomela* was genetically differentiated from Indo-Pacific ones (Alexander and Valdés 2013), while the East Pacific remains unsampled (Uribe et al. 2013). *Aplysia panamensis* (Pilsbry, 1895) is the representative synonym of this area.

Current systematic position. *Aplysia dactylomela* Rang, 1828 (fide Eales 1960).

Tethys willcoxi var. *perviridis* Pilsbry, 1895

Figure 4A–E

Tethys willcoxi var. *perviridis* Pilsbry, 1895: 81–82; 1896b, pl. 55, figs 1–4.

Type locality. Cape May, New Jersey [USA].

Type material. Holotype (monotypy): ANSP A2250 (ca 105 mm long preserved, shell 60 mm long; H. Lemon coll., 25/x/1894). Pilsbry stated that he examined a single specimen.

Remarks. Aplysiidans possess a large gland near the mantle floor, called the opaline gland (or gland of Bohadsch), that produces a milky liquid when the animal is disturbed (Gosliner 1994). The gland can be multiporous (e.g. *A. depilans*, *A. juliana* and *A. parvula*) or uniporous (e.g. *A. dactylomela* and *A. fasciata*) (Beeman 1968; Cunha and Simone 2019; pers obs.). The opaline gland in *Aplysia perviridis* is unique in having both conditions, uniporous and multiporous (figs 32, 33). Pilsbry (1895) described the opaline gland as “projecting externally as a pedunculated oval body”, but that appears to be the result of contraction upon fixation, as suggested by Pilsbry:

“but perhaps evaginated, in which case it would have one large orifice”.

The opaline gland of a single young specimen collected in 1950 from Sea Isle City, New Jersey, which is about 35 km north of the type locality was dissected to confirm this condition (ANSP A2235, ~60 mm long preserved). Despite the lack of a “pedunculated oval body” the condition of gland is the same (Fig. 4B, C). The multiporous part is more developed in the holotype than in the young specimen.

Aplysia perviridis (Pilsbry, 1895) was accepted as a synonym of *A. willcoxi* Heilprin, 1886 by Eales (1960). However, with the anatomical differences of the opaline gland, we treat it as a valid species herein.

Current systematic position. *Aplysia perviridis* (Pilsbry, 1895) comb. nov.

Tethys pilsbryi Letson, 1898

Figure 4F–H

Tethys pilsbryi Letson, 1898: 193, pl. 8, figs 1–4.

Type locality. Silam, north coast of Yucatan, Mexico.

Type material. Syntypes, ANSP A7036, 2 specimens (one 97 mm long preserved with shell and other 94 mm long preserved with shell removed, both dissected and radula removed) + 1 slide with radulae and jaw mounted (Heilprin Expedition, 1890) [one specimen (Letson 1898: figs 2–3), whole, lacking the left rhinophore (added in the figure), dissected ventrally, shell and radula not removed; other specimen, shell and radula removed].

Remarks. Eales (1960) synonymized this species with *A. cervina* Dall & Simpson, 1901 because of general morphological similarity, but it differs in having an upturned edge to the rim of the mantle where the purple gland lies (Fig. 4H: ed). This remarkable characteristic is unique in the genus *Aplysia*. Letson (1898) also described the presence of “a few inconspicuous scattered warts” on the integument, not reported by Eales (1960). However, both features were confirmed in juvenile specimens from Yucatan (ANSP A1993, 10 specimens measuring 25–50 mm). Additionally, *A. pilsbryi* has a shorter shell (ca 1.2 times long as wide), while the shell of *A. cervina* is more elongated (ca 1.6 times long as wide) (MacFarland 1909).

Current systematic position. *Aplysia pilsbryi* (Letson, 1898). Kobelt (1897: 240) introduced the combination to the genus *Aplysia*.

Tethys robertsi Pilsbry, 1895

Figure 5A–D

Tethys robertsi Pilsbry, 1895: 89; 1896b, pl. 55, figs 5, 6.

Type locality. West coast of Mexico.

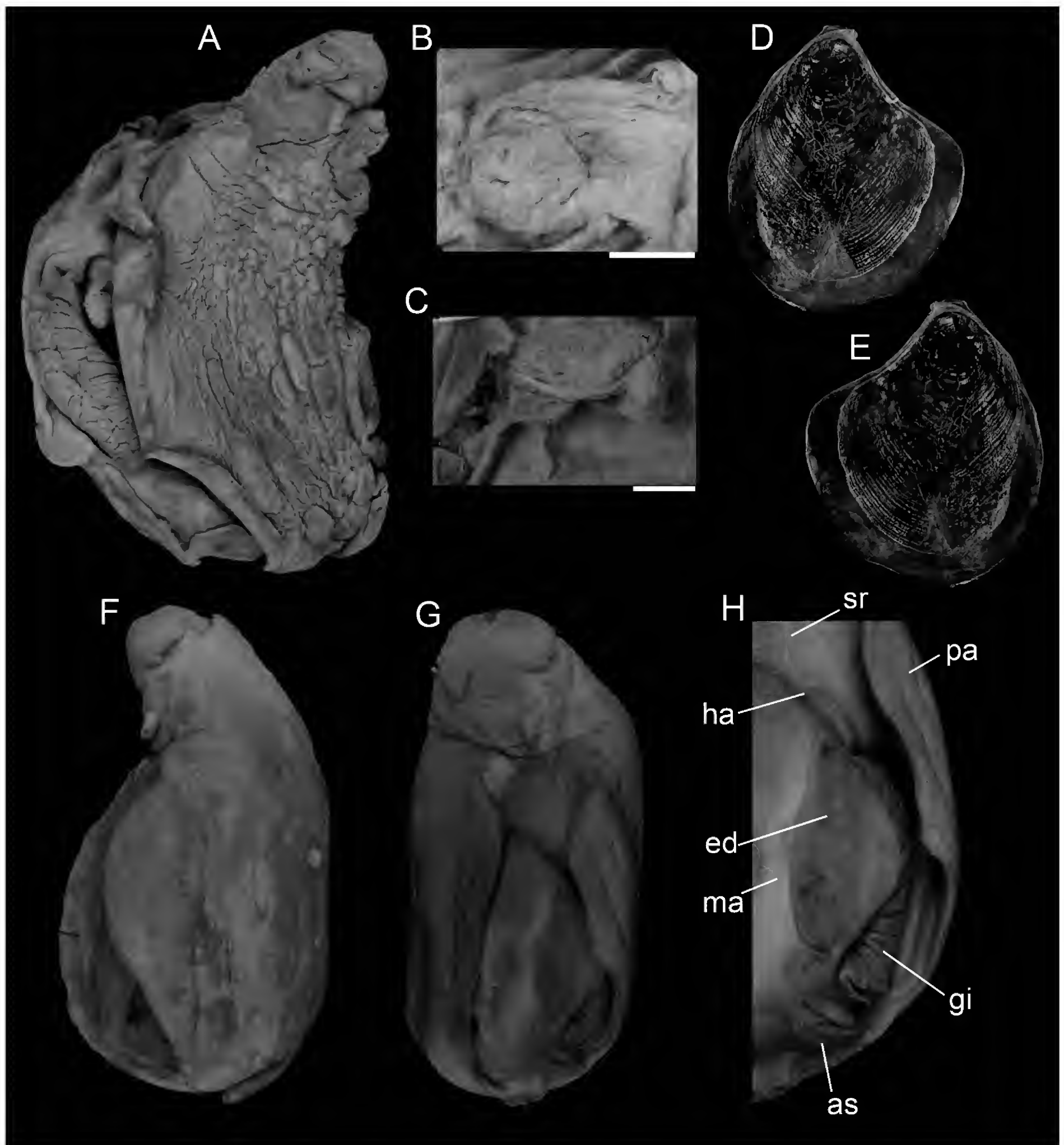


Figure 4. Aplysiida types. **A–E.** Holotype of *Tethys willcoxi* var. *perviridis* (= *A. perviridis*), **A.** Whole specimen, L. ca 105 mm, ANSPA2250 in right lateral view. **B.** Same, detail of opaline gland in dorsal view showing the uniporous and multiparous apertures. **C.** Same, opaline deflected showing the opaline gland spread on the roof of haemocoel. **D.** Shell of the same, L 60 mm, in ventral view. **E.** Same in dorsal view. **F–H.** Syntype of *Tethys pilsbryi* (= *A. pilsbryi*). **F.** Whole specimen, L 97 mm, ANSPA7036 in right lateral view. **G.** Same in dorsal view. **H.** Same, detail of pallial cavity showing the upturned edge to the rim of the mantle border (ed); legend: pa - parapodium, sr - seminal groove, ha - hermaphrodite aperture, ed - upturned edge, ma - mantle; gi - gill, as - anal siphon. Scale bar: 5 mm.

Type material. Holotype (original designation, “the type”): ANSP A7029, 1 specimen (ca 92 mm long preserved; W.H. Jones, leg.) [shell removed and figured by Pilsbry (1896b: pl. 55, fig. 5) but not found, should be ANSP 66307].

Remarks. Pilsbry (1895) cited plate 55, figures 4 and 5, but when the plate was published the next year, the captions showed figures 5 and 6, the latter being correct. The specimen has the sole covered by small black dots (Fig. 5D), which is not mentioned in the original description nor by Eales (1960).



Figure 5. Aplysiida types. **A–D.** Holotype of *Tethys robertsi* (= *A. robertsi*), **A.** Whole specimen, L ca 92 mm, ANSP A7029 in dorsal view. **B.** Same in right lateral view. **C.** Same in ventral view. **D.** Same, detail showing the sole covered by small black dots. **E–G.** Syntype of *Dolabrifera swiftii* (= *D. dolabrifera*), **D.** Shell, L 10.5 mm, ANSP 67519 in dorsal view. **F.** Same in ventral view. **G.** Same in lateral view. **H–L.** Syntype of *Tethys pulmonica* var. *tryoniana* (= *A. pulmonica*), **H.** Whole specimen, L ca 122 mm, ANSP A7037 in right lateral view. **I.** Same in dorsal view. **J.** Same in ventral view. **K.** Shell, L ca 58 mm, ANSP 66306, in dorsal view. **L.** Same in ventral view. Scale bar: 5 mm

Current systematic position. *Aplysia robertsi* (Pilsbry, 1895) (*vide* Eales 1960).

***Dolabrifera swiftii* Pilsbry, 1896a**

Figure 5E–G

Dolabrifera swiftii Pilsbry, 1896a: 125; 1896b, pl. 67, figs 19, 20.

Type locality. West Indies.

Type material. Syntype: ANSP 67519 (Valdés et al 2017: fig. 12K, L), 1 shell (10.5 mm long, donated by Robert Swift).

Remarks. In the plate caption, which was published later than the description (September 23 vs March 13), Pilsbry suggested the name may be a synonym of *D. ascifera* Rang.

Current systematic position. *Dolabrifera ascifera* (Rang, 1828) (*vide* Valdés et al. 2017).

***Tethys pulmonica* var. *tryoniana* Pilsbry, 1895**

Figure 5H–L

Tethys pulmonica var. *tryoniana* Pilsbry, 1895: 96–97; 1896b, pl. 57, figs 24–27.

Type locality. Upolu, Samoa Island.

Type material. Syntype, ANSP A7037 (Pilsbry, 1896b: pl. 57, fig. 27), 1 specimen (ca 122 mm long preserved), ANSP 66306 (Pilsbry, 1896b: pl. 57, figs 24–26), 1 shell (fragmented, ca 58 mm long; ex G. W. Tryon from Dr Gräffe, Museum Godeffroy).

Remarks. In 1895 Pilsbry cited plate 57, figures 54–57, but when the plate was published the next year, the captions showed figures 24–27, the latter being correct. The specimen was purchased by G. W. Tryon from the Godeffroy Museum Catalogue. Pilsbry cited “*Aplysia* sp.? Museum Godeffroy, Catalog IV, p. 105, No. 1107a”, but apparently examined only one specimen. Pilsbry did not dissect the specimen but removed the shell.

Current systematic position. According to Pilsbry (1895), *A. pulmonica* and *Tethys pulmonica* var. *tryoniana* (both from Samoa) are similar, differing just in that *A. pulmonica* lacks black maculations and has a more extensive posterior junction of the parapodia. We follow Eales (1960), keeping *Tethys pulmonica* var. *tryoniana* as a synonym of *A. pulmonica* until more material is available.

According to a recent study by Alexander and Valdes (2013), suggesting that “the ring doesn’t mean a thing”, *A. pulmonica* Pease, 1860 is a synonym of *A. argus* Ruppell & Leuckart, 1830. The photographs of Hawaiian specimens identified as *A. dactylomela* and *A. pulmonica* in their paper (Alexander and Valdes 2013: fig. 2) suggest that the material of *A. pulmonica* has rings in the color

pattern, although it is supposed to lack them. Photographs of live specimens of the main material used in that publication (*A. dactylomela*, CPIC 00297 and *A. pulmonica*, CPIC 00313) confirm that both possess black rings in the body color. The black rings are more evident in the material they identified as *A. dactylomela* (paler) than in the ones they identified as *A. pulmonica* (darker).

Their Hawaiian material does belong to a single species, as they concluded based on their molecular data. The dark morph is consistent with the description of *A. grandis* Pease, 1860 (type locality Hawaii), which was not cited by the authors, in having a purplish-brown color, pale along the flanks, everywhere above densely crowded with minute white dots, and foot projecting posteriorly, where it is rounded. The dark morph is not consistent with the original description and illustration of *A. pulmonica*, which differs in being coarsely reticulated with black veins, lacking white dots, having oral tentacles short, and the posterior junction of the parapodia producing a sac-like structure. Bebbington (1977) included *A. grandis* in the synonymy of *A. dactylomela*, and not of *A. pulmonica*. In synonymizing *A. pulmonica* with *A. argus*, Alexander and Valdes (2013) ignored that most previous authors regarded *A. dactylomela* and *A. pulmonica* in the Indo-Pacific as distinct species. We regard their use of *A. pulmonica* for their Hawaiian material as a misidentification, and resume use of *A. pulmonica* as a valid species.

***Aplysia willcoxi* Heilprin, 1887a**

Figure 6A–D

Aplysia willcoxi Heilprin, 1887a: 364; Heilprin 1887b: 20, pl. 19.

Type locality. Little Gasparilla Bay, west coast of Florida, USA.

Type material. Syntypes (ex Heilprin 1887): A2262, 5 specimens with radula associated and 3 loose shells; ANSP 64260, SEM stub with fragment of radula.

Remarks. The ledger entry for ANSP 64260 says six specimens in alcohol. Heilprin (1887b: 20) noted that a half dozen specimens were collected with dip-nets by Joseph Willcox and the expedition cook (Moses Natteal, p. iii), so one syntype is currently missing. The alcohol lot was subsequently renumbered as A2262, but we retained the dry number for an SEM stub with a radular fragment. All specimens were previously dissected, with the radula having been removed and kept with the specimens.

ANSP 63628 contains shells (and fragments) of about seven individuals collected by Willcox, from Marco, Florida donated by Joseph Leidy. We do not consider these parts of the type series as the locality was not mentioned in the original description.

Current systematic position. *Aplysia fasciata* Poiret, 1789 (*vide* Medina et al. 2005; Rosenberg et al. 2009).

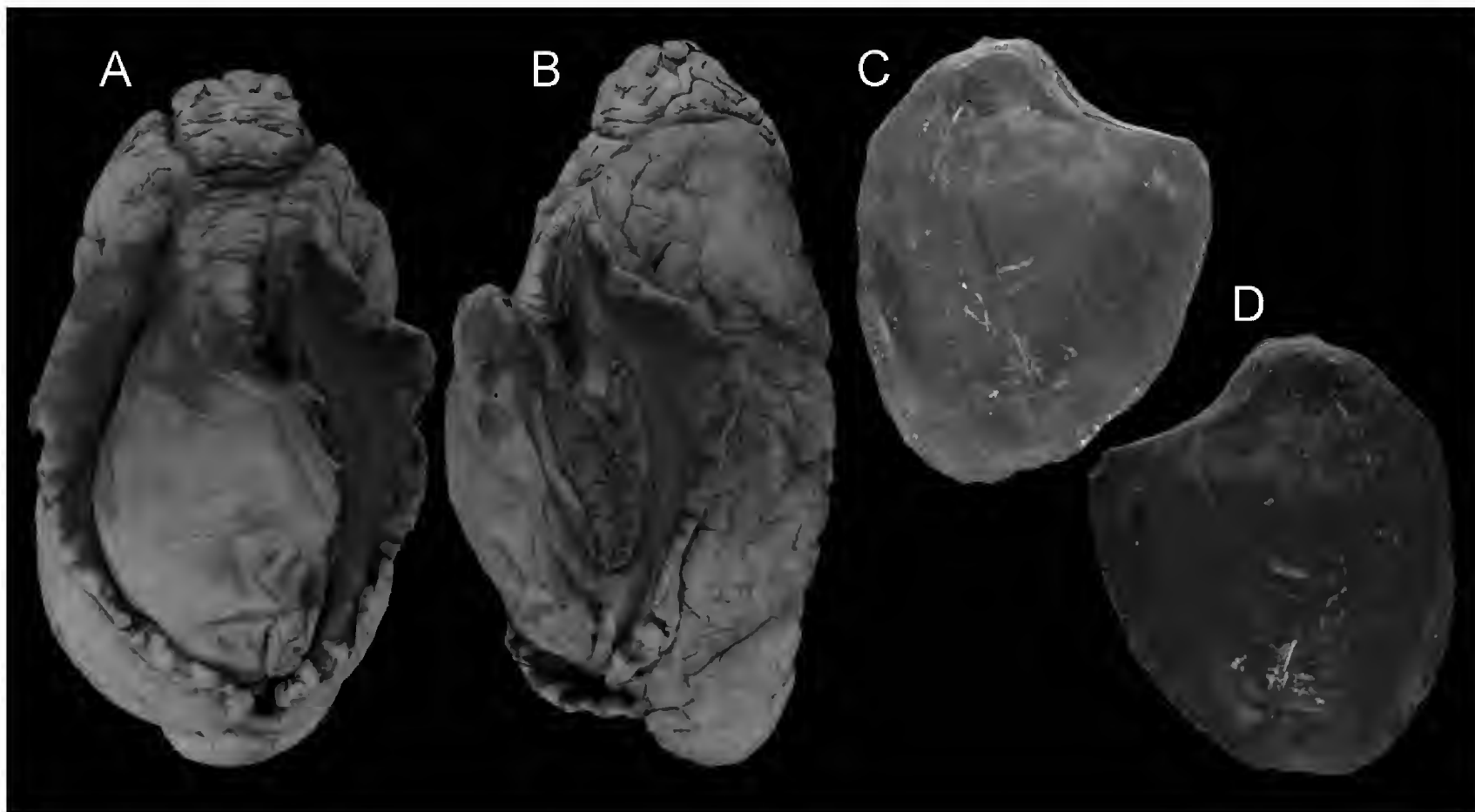


Figure 6. Aplysiida types. **A–D.** Syntype of *Aplysia willcoxi* (= *A. fasciata*). **A.** Whole specimen, L = ca 114 mm, ANSP A2262, in dorsal view. **B.** Same in right lateral view. **C.** Shell in ventral view, L = 50 mm. **D.** Same, in dorsal view.

List of taxa by species-group names

Here is presented a list of the species whose types can be found in the ANSP collection, arranged alphabetically by specific epithet. Species appear first in their original generic allocation and then in their current systematic position.

- aequorea*, *Aplysia* Heilprin, 1888. *Aplysia dactylomela* Rang, 1828
badistes, *Aplysia* (*Metaplysia*) Pilsbry, 1951. *Aplysia juliana* Quoy & Gaimard, 1832
benedicti, *Aplysia* (*Tethys*) Eliot, 1900. *Aplysia argus* Rüppell & Leuckart, 1830
elongata, *Syphonota* Pease, 1860. *Aplysia parvula* Mörch, 1863
floridensis, *Tethys* Pilsbry, 1895. *Aplysia fasciata* Poiret, 1789
fusca, *Dolabrifera* Pease, 1868. *Dolabrifera dolabrifera* Rang, 1828
jacksoniensis, *Dolabrifera* Pilsbry, 1896. *Dolabrifera brazieri* G. B. Sowerby II, 1870
nicaraguana, *Dolabrifera* Pilsbry, 1896. *Dolabrifera nicaraguana* Pilsbry, 1896
panamensis, *Tethys* Pilsbry, 1895. *Aplysia dactylomela* Rang, 1828
perviridis, *Tethys willcoxi* var. Pilsbry, 1895. *Aplysia perviridis* Pilsbry, 1895
pilsbryi, *Tethys* Letson, 1898. *Aplysia pilsbryi* (Letson, 1898)
robertsi, *Tethys* Pilsbry, 1895. *Aplysia robertsi* (Pilsbry, 1895)
swiftii, *Dolabrifera* Pilsbry, 1896. *Dolabrifera ascifera* (Rang, 1828)

tryoniana, *Tethys pulmonica* var. Pilsbry, 1895. *Aplysia pulmonica* Pease, 1860

willcoxi, *Aplysia* Heilprin, 1887. *Aplysia fasciata* Poiret, 1789

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A glimpse in the dark? A first phylogenetic approach in a widespread freshwater snail from tropical Asia and northern Australia (Cerithioidea, Thiaridae)

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Abstract

Thiaridae are a speciose group of freshwater snails in tropical areas including a high number of described nominal taxa for which modern revisions are mostly lacking. Using an integrative approach, the systematic status of a group of thiarids from the Oriental region, including the nominal species *Melania aspera* and *M. rudis*, is reassessed on the basis of shell morphology and biometry, radula dentition patterns, and reproductive biology along with molecular genetic methods. Our results suggest that populations from the Oriental region cannot be distinguished on the basis of shell morphology, radula characters and their reproductive mode and are monophyletic based on mitochondrial sequences. Hence, *M. rudis* with *M. aspera* are regarded as belonging to the same species along with several other nominal taxa that were previously included in *M. rudis*. Moreover, populations from Thailand and Australia, from where the species was not previously recorded, could be shown to form a monophyletic group together with samples from Indonesia. However, a generic affiliation with *Thiara*, in which the investigated taxa were often included in the past, was not supported in our phylogenetic analyses, highlighting the need for a comprehensive revision of the genus-group systematics of Thiaridae as a whole.

Key Words

Cerithioidea, evolutionary systematics, Oriental region, Thailand

Introduction

Despite advances in the understanding of the family-level phylogeny of Cerithioidea Fleming, 1822, the taxonomical diversity in Thiaridae Gill, 1871 (1823) is still not well understood, and evolutionary systematic research in the sense of Glaubrecht (2010) in this particular family is still in its infancy. The Thiaridae, in earlier treatments subsumed under the name Melaniidae Children, 1823, have been used as a “rubbish bin” to accommodate all freshwater lineages belonging to the Cerithioidea. Only after the removal of the families Pachychilidae Fischer & Crosse, 1892, Melanopsidae Adams & Adams, 1854, Paludomidae Stoliczka, 1868, Pleuroceridae Fischer, 1885

(1863), and Semisulcospiridae Morrison, 1952) (Campbell 2019; Neiber and Glaubrecht 2019b, 2019c, 2019d; Strong and Lydeard 2019 and references therein) and recently the Neotropical Hemisinidae Fischer & Crosse, 1891 (Glaubrecht and Neiber 2019a), a more accurate circumscription of “core” Thiaridae began to emerge on the basis of molecular and/or morphological evidence (e.g., Glaubrecht 1993, 1996, 2011; Holznagel and Lydeard 2000; Lydeard et al. 2002; Glaubrecht et al. 2009; Strong 2011; Strong et al. 2011).

In addition to uncertainties in the delimitation of genera, research on thiarids is further complicated by the large disparity of shell characters among species, a large phenotypic plasticity within species and a high ecologi-

cal adaptability that is, however, also known from other limnic Cerithioidea. This conchological variability has certainly led to an overestimation of the number of species in the past, as specifically shown for limnic lineages in the superfamily (Glaubrecht 1993, 1996; Köhler and Glaubrecht 2001, 2003, 2006; Glaubrecht and Köhler 2004; Glaubrecht et al. 2009), but may also cause problems in delimiting species resulting in an underestimation of the actual morphological disparity versus the taxonomical diversity, at least in some cases. These problems are exacerbated by the putatively widespread occurrence of parthenogenesis in different lineages of Thiaridae (Glaubrecht 1996) and the associated problems of what is actually meant by “species” in this case (e.g. Hausdorf 2011). Additionally, Thiaridae have also realised different life history strategies that were characterised by Glaubrecht (1996, 1999, 2006, 2011) by the duration of ontogenetic stages to remain within a specialised structure of the female, viz. the subhaemocoelic brood pouch. While in some thiarids only very early ontogenetic stages, i.e. embryos without shell, develop and are released as veligers (ovoviviparity), other thiarid species brood and even transform their subhaemocoelic brood pouch into a matrotrophic organ or “pseudoplacenta” that apparently nourishes the developing juveniles, as e.g. in the Southeast Asian thiarid *Tarebia granifera* (Lamarck, 1816) (eu-viviparity, see Glaubrecht 1996; Glaubrecht et al. 2009; Maaß and Glaubrecht 2012; Veeravechskij et al. 2018b). Finally, some thiarids also have an extraordinarily high invasive potential, such as *Melanoides tuberculata* (Müller, 1774) and *Tarebia granifera* and today have an almost pantropical distribution (e.g., Brown 1994; Glaubrecht 1996).

To date, only few of the several dozen thiarid taxa have seen closer investigation. Glaubrecht et al. (2009) and Maaß and Glaubrecht (2012) surveyed the thiarid fauna of Australia. Dechruska et al. (2013) evaluated the status and identity of the nominal taxon *Melania jugicostis* Hanley & Theobald, 1876 from the Southeast Asian mainland, and Veeravechskij et al. (2018a, 2018b) investigated the phylogeography and reproductive biology of *T. granifera* and its trematode parasites. However, many other named taxa have been rarely studied and, thus, remain enigmatic and even pure nomenclatorial “ghosts” with highly questionable status as evolutionary relevant entities, which hampers further insights into the systematics, biogeography, and evolution of these freshwater gastropods otherwise under scrutiny, e.g., in speciation and/or radiation studies.

Melania aspera Lesson, 1831, which was originally described from New Guinea (Lesson 1830–1831), is such an “enigmatic” taxon (Fig. 1), which Glaubrecht and Podlacha (2010) regarded as a possible senior synonym of the nominal species *Melania rudis* Lea & Lea, 1851. The latter taxon is usually regarded as belonging to *Thiara* Röding, 1798 and thought to be relatively widespread, being reported from several countries, occurring from India and Sri Lanka to Southeast Asia and the Indo-Australian

archipelago (Schepman 1892, 1915; Rensch 1934; van Benthem Jutting 1937; Subba Rao 1989; Ramakrishna and Dey 2007; Budha 2010; Patil and Talmale 2011, see also Fig. 2). However, actual distribution records are relatively scarce in the literature and the distinction from other nominal thiarid taxa remains uncertain so far.

As a further contribution towards a better understanding of thiarid diversity, we here re-evaluate the identity of *M. aspera* and *M. rudis* on the basis of museum samples including available type material as well as material collected during ongoing surveys in Southeast Asia using shell morphology and biometry, radula dentition patterns, and reproductive biology along with molecular genetic methods. Nomenclatural issues and the synonymy of the genus *Thiara* are also discussed.

Material and methods

This study is mainly based on the examination of specimens in the collections of the Parasitology and Medical Malacology Research Unit, Department of Biology, Faculty of Science, Silpakorn University, Thailand and the Museum für Naturkunde, Berlin, Germany, and supplemented by material from other museums (see below). Additionally, new samples were collected using hand picking and scooping methods in Thailand and Australia. Specimens were fixed in 75–96% ethanol.

Collection acronyms

MNHN	Muséum National d’Histoire Naturelle de Paris, France
SUT	Silpakorn University, Nakhon Pathom, Thailand
USNM	National Museum of Natural History, Washington, USA
ZMB	Museum für Naturkunde, Berlin, Germany (formerly Zoologisches Museum Berlin)

Coordinates (WGS84) of localities were taken with a GPS device or determined as accurately as possible from a map. Sampling sites were then mapped on a dot-by-dot basis to a digitally reduced version of the drainage pattern map of the Indo-Australian region. This map was prepared using a relief map on the basis of the Global30-Arc-Second Elevation Data (GTOPO30) from the U.S. Geological Survey and a river map from the map server Aquarius Geomar; and then compiled using Adobe Photoshop CS3 and Adobe Illustrator. For the exact locality data, see the material examined section.

Shell characters

Specimens were photographed using a digital EOS 350D camera (Canon, Tokyo, Japan). Standard biometric parameters were taken from each shell using electronic cal-

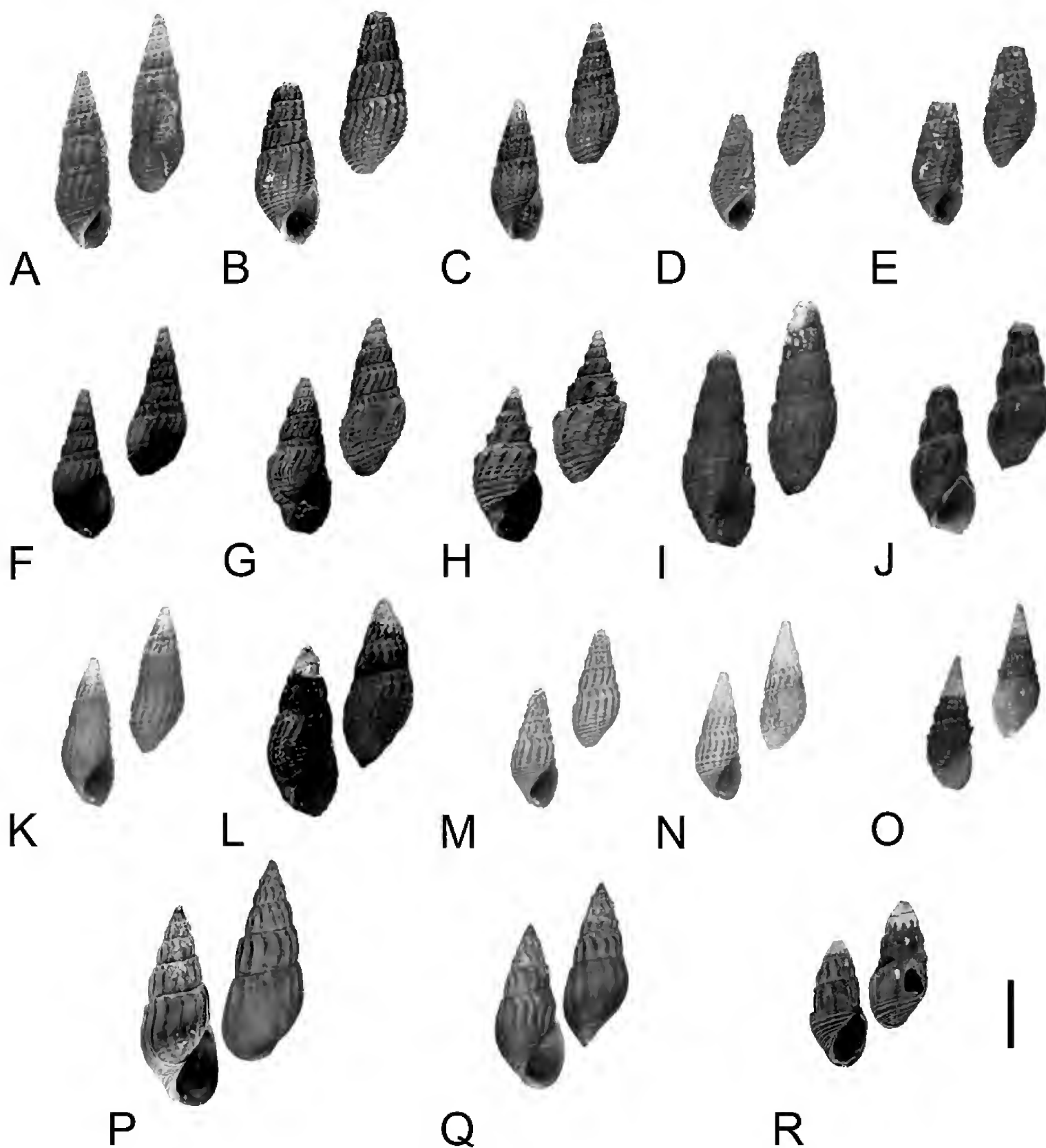


Figure 1. Shells of “*Thiara*” *aspera* (Lesson, 1831). **A.** Holotype of *Melania aspera* Lesson, 1831, MNHN 21098, ‘La Nouvelle-Guinée’ [more specifically Manokwari on New Guinea Island, West Papua, Indonesia, see Glaubrecht and Podlacha 2010]; **B.** Syntype of *Melania rudis* Lea & Lea, 1851, USNM 119778, Amboyna; **C.** Syntype of *Melania microstoma* Lea & Lea, 1851, USNM 119722, mountain streams, isle of Negros, Philippines; **D.** ZMB 107002, Calcutta, India; **E.** ZMB 107003, Ceylon, Sri Lanka; **F.** ZMB 127534, Don Ko Canal, Nakhon Pathom, Thailand; **G.** ZMB 127535, Don Ko Canal, Nakhon Pathom, Thailand; **H.** ZMB 127535, Don Ko Canal, Nakhon Pathom, Thailand; **I.** ZMB 191279, Yehembang River, Bali, Indonesia; **J.** ZMB 191279, Yehembang River, Bali, Indonesia; **K.** ZMB 106472, Yehembang, Bali, Indonesia; **L.** East of Munday, stream southwest of Gunicik, Bali, Indonesia; **M.** ZMB 191278, stream at Tembeeha, road Tirobus-Kendari, Southwest Sulawesi, Indonesia; **N.** ZMB 107378, Banggai Islands, Peleng Island, West of Peninsula, Tataban river, Central Sulawesi, Indonesia; **O.** ZMB 107377, Banggai Islands, Peleng Island, West of Peninsula, Tataban river, Central Sulawesi, Indonesia; **P, Q.** ZMB 107617, Wabalarr, Roper River, Northern Territory, Australia; **R.** ZMB 106599, Berry Springs, Northern Territory, Australia. Scale bar: 1 cm.

lipers (accuracy 0.1 mm): shell height (H), shell width (W), aperture length (AL; measured from the upper apertural angle to the farthest point on the basal margin of the aperture), aperture width (AW; measured perpendicular to AL as the widest distance between outer apertural margin and outer margin of parietal callous), height of the body whorl (BW), and number of whorls (NW) as shown in Figure 3A. To reduce dimensionality a principal component analysis was conducted on log-transformed shell measurements using R 3.3.2 (R Core Team 2016).

Only the minimal number of PCA axes that accounted for more than 95% of the cumulative variation were used for further testing.

The Shapiro-Wilk test was conducted in R to test for normal distributions of PCA 1 and PCA 2 values, respectively, for the here proposed geographic subgroups, i.e., samples from 1) Thailand, 2) Indonesia, 3) India, and Sri Lanka, and 4) Australia. Since some of the Shapiro-Wilk tests were significant ($p \leq 0.05$), the non-parametric Kruskal-Wallis rank sum test was conducted for PCA 1 and

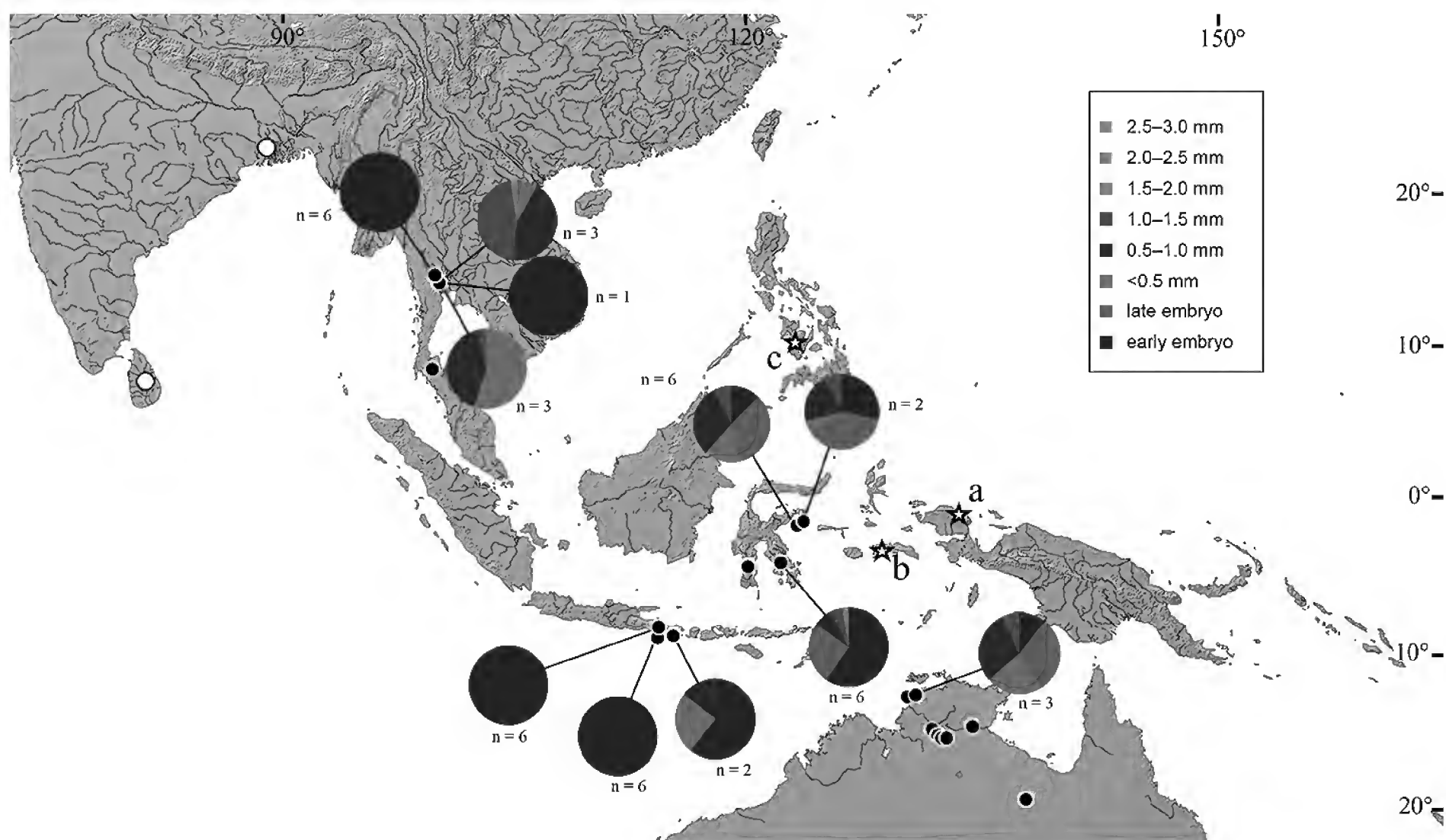


Figure 2. Distribution and reproductive strategy of “*Thiara*” *aspera* (Lesson, 1831). Stars: type localities of a) *Melania aspera* Lesson, 1831, Monokwari, New Guinea, b) *Melania rudis* Lea & Lea, 1851, Amboyna and c) *Melania microstoma* Lea & Lea, 1851, mountain streams, isle of Negros, Philippines. Pie charts show the percentages of offspring in the brood pouch of female *T. aspera* in different size classes as defined in Glaubrecht et al. (2009), see inset. The numbers near the pie charts refer to the number of individuals examined per population. Filled circles: material preserved in ethanol; open circles: dry shells.

PCA 2 assuming the grouping of specimens according to geography followed by Dunn’s test (Bonferroni-corrected) as post-hoc test as implemented in the R package “dunn.test 1.3.5” (Dinno 2017) in case that the Kruskal-Wallis-rank-sum tests were significant.

Radula preparation

Shells of representative specimens were cracked with a small vice and removed from the soft body parts, which were afterwards examined and dissected with the aid of a Leica Wild MZ 9.5 stereo microscope (Leica Microsystems, Wetzlar, Germany). Radulae were extracted following the protocol of Holznagel (1998), fixed on aluminium stubs, and coated with platinum using a Polaron SC 7640 Sputter Coater (Quorum Technologies, East Grinstead, UK). Radulae were then viewed and photographed (oriented so that denticles on the teeth were well visible) with a scanning electron microscope (SEM) EVO LS10 (Zeiss, Oberkochen, Germany).

Content of brood pouch

The brood pouch was opened after removing the mantle and its content was counted under a Leica Wild MZ 9.5 stereo microscope. Both, shelled juveniles and embryos,

were grouped into standard size classes as described in Glaubrecht et al. (2009). Embryos and juveniles from representative specimens were fixed on aluminium stubs, air-dried, coated with platinum using a Polaron SC 7640 Sputter Coater, and then viewed, photographed, and measured (Fig. 3B) with a EVO LS10 SEM. Parameters of the embryonic shell were measured from SEM images as shown in Figure 3B: diameter of first half whorl (de; measured as the maximal width of the shell after 0.75 turns of the suture line), width of first quarter whorl (he; measured parallel to de as the distance from the starting point of the suture to the point after 0.25 turns of the suture line), width of first half whorl (we; measured perpendicular to de as the distance from the starting point of the suture to the point after 0.5 turns of the suture line).

Molecular methods and phylogenetic analyses

Total genomic DNA was extracted from ethanol-preserved foot muscle tissue using a CTAB protocol as described by Winnepenninckx et al. (1993) from 31 thiarid specimens and *Paludomus siamensis* Blanford, 1903 as outgroup representing one of the cerithioidean families, which have been shown to be closely related to the Thiaridae (Wilson et al. 2004; Strong et al. 2011).

For phylogenetic analyses, fragments of the mitochondrial cytochrome c oxidase subunit 1 (*cox1*) gene and the

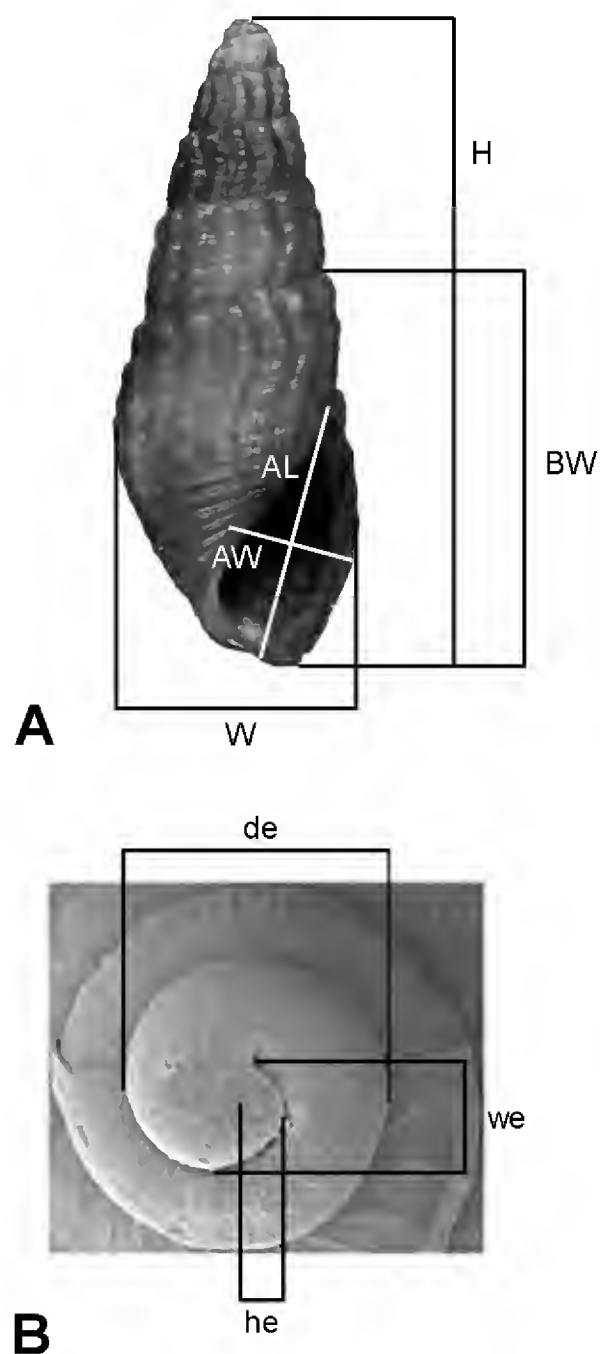


Figure 3. Measured shell parameters. **A:** H – shell height; W – shell width; BW – body whorl height; AL – aperture length; AW – aperture width. **B:** he – height of embryonic shell; we – width of embryonic shell; de – maximum diameter at one whorl.

16 S rRNA (16S) gene were amplified by polymerase chain reaction (PCR) using the primer pairs LCO1490 (5'-GGT CAA CAA ATC ATA AAG ATA TTG G-3'; Folmer et al. 1994) plus HCO2198var (5'-TAW ACT TCT GGG TGK CCA AAR AAT-3'; Rintelen et al. 2004) and 16S_F_Thia2 (5'-CTT YCG CAC TGA TGA TAG CTA G-3'; Neiber and Glaubrecht 2019a, see also Gimnich 2015) plus H3059var (5'-CCG GTY TGA ACT CAG ATC ATG T-3'; Wilson et al. 2004), respectively. Amplifications were conducted in 25 µl volumes containing 50–100 ng DNA, 1× PCR buffer, 200 mM of each dNTP, 0.5 mM of each primer and 1 U of *Taq* polymerase. After an initial denaturation step of 3 min at 94 °C, 35 cycles of 30 s at 94 °C, 60 s at 45–62°C and 60–120 s at 72°C were performed, followed by a final extension step of 5 min at 72°C. PCR products were purified using a NucleoSpin Extract II Kit (Macherey–Nagel, Bethlehem, PA, USA). Both strands of the amplified gene fragments were cycle-sequenced using the primers employed in PCR with the Big Dye Terminator chemistry version 1.1 (Applied Biosystems, Inc., Waltham, MA, USA). Sequences were visualised on an ABI 3130xl or ABI 3730xl Genetic Analyzer (Applied Biosystems, Inc.).

Forward and reverse sequence reads were assembled with CODONCODE ALIGNER v. 3.7.1 (CodonCode Corporation, Dedham, MA, USA) and corrected by eye. For information on vouchers, see Table 1. The protein coding *cox1* sequences were aligned with MUSCLE (Edgar 2004) as implemented in MEGA 6 (Tamura et al. 2013) under default settings. The 16S sequences were aligned with MAFFT (Kato and Standley 2013) using the Q-INS-i iterative refinement algorithm and otherwise default settings, because this algorithm has been described to perform better for the alignment of sequence data sets that may contain deletions and insertions than alternative multiple sequence alignment methods (Golubchik et al. 2007).

Maximum likelihood (ML), Bayesian Inference (BI), and maximum parsimony (MP) approaches were used to reconstruct the phylogenetic relationships. The sequence data set was initially divided into four partitions for the nucleotide model-based ML and BI approaches: 1) 1st codon positions of *cox1*, 2) 2nd codon positions of *cox1*, 3) 3rd codon positions of the *cox1*, and 4) the 16S. To select an appropriate partitioning scheme and evolutionary models the sequence data set was analysed with PARTITIONFINDER v. 1.1.1 (Lanfear et al. 2012) conducting an exhaustive search and allowing for separate estimation of branch lengths for each partition using the Bayesian information criterion as recommended by Luo et al. (2010). Models to choose from were restricted to those available in MRBAYES v. 3.2.6 (Ronquist et al. 2012) as well as in GARLI v. 2.1 (Zwickl 2006). As best-fit partitioning scheme, the PARTITIONFINDER analysis suggested to combine the 1st and 2nd codon positions of *cox1* and the 16S sequences together in one partition (GTR + G model) and the 3rd codon positions of *cox1* in a second partition (HKY + G model).

The BI analysis was performed using MRBAYES v. 3.2.6. Metropolis-coupled Monte Carlo Markov chain (MC³) searches in MRBAYES were run with four chains in two separate runs for 50,000,000 generations with default priors, trees and parameters sampled every 1000 generations under default heating using the best-fit model as suggested by PARTITIONFINDER. Diagnostic tools in MRBAYES, including Estimated Sample Size (ESS) values > 200, were used to ensure that the MC³ searches had reached stationarity and convergence. The first 5,000,000 generations of each run were discarded as burn-in.

Heuristic ML analysis was performed with GARLI using the best-fit models as suggested by PARTITIONFINDER. Support values were computed by bootstrapping (BS) with 1,000 replicates.

Heuristic MP searches were carried out with PAUP v. 4.0b10 (Swofford 2002) using 100 random-addition-sequence replicates and TBR branch swapping. Support values were computed by bootstrapping with 1,000 replications.

Alternative phylogenetic hypotheses were tested using the approximately unbiased (AU) test (Shimodeira 2002) as implemented in the program CONSEL (Shimodeira and Hasegawa 2001). Information on vouchers and GENBANK accession numbers are listed in Table 1.

Table 1. Museum registration numbers, GenBank accession numbers and locality data for the specimens used in the molecular phylogenetic analyses. Abbreviations for countries: AUS – Australia, IDN – Indonesia, IND – India, THA – Thailand.

Taxon	Museum number	Extraction number	Country	Latitude	Longitude	GenBank accession number		
						cox1	16 S rRNA gene	
<i>Thiara</i> "aspera"	SUT 0311020	11449	THA	13°38'08"N	100°05'03"E	MK879291	MK879427	
	SUT 0312070	11446	THA	13°48'08"N	100°02'06"E	MK879292	MK879428	
	SUT 0311044	9603	THA	13°38'08"N	100°05'03"E	MK879290	–	
	ZMB 191268	2200	IDN	03°39'28"S	122°13'52"E	MK879296	MK879434	
	ZMB 191488	4558	IDN	08°38'39"S	115°16'38"E	MK879297	MK879435	
	ZMB 107377	6494	IDN	01°32'18"S	122°51'28"E	MK879293	MK879429	
	ZMB 107378	6495	IDN	01°32'18"S	122°51'28"E	MK879294	MK879430	
	ZMB 107617	7586	AUS	14°56'02"S	133°10'26"E	MK879295	MK879433	
	ZMB 107617	8743	AUS	14°56'02"S	133°10'26"E	–	MK879431	
	ZMB 107617	8744	AUS	14°56'02"S	133°10'26"E	–	MK879432	
	<i>Stenomelania</i> "denisoniensis"	ZMB 106682	7599	AUS	14°55'47"S	133°08'44"E	MK879288	MK879425
		ZMB 106632	7602	AUS	15°00'42"S	133°14'25"E	MK879287	MK879424
<i>Thiara amarula</i>	ZMB 191489	2886	IDN	01°26'43"S	127°29'01"E	MK879289 ^a	MK879426 ^a	
	ZMB 107472	6496	IDN	03°35'28"S	128°08'42"E	MK094074	MK098355	
<i>Thiara winteri</i>	ZMB 106554	1043	IDN	08°23'38"S	114°45'04"E	MK879301	MK879439	
	ZMB 190261	1055	IDN	02°35'34"S	120°54'10"E	MK879302	MK879440	
<i>Thiara</i> cf. <i>winteri</i>	ZMB 106472	1001	IDN	08°23'38"S	114°45'04"E	MK879298	MK879436	
	ZMB 191279	2232	IDN	08°23'36"S	114°45'04"E	MK879299	MK879437	
	ZMB 191279	4559	IDN	08°23'36"S	114°45'04"E	MK879300	MK879438	
<i>Mieniplotia scabra</i>	ZMB 107382	6514	IDN	00°48'33"N	127°17'40"E	MK879279	MK879416	
	ZMB 107564	7340	AUS	14°55'38"S	133°07'06"E	MK879280	MK879417	
	ZMB 127495	9574	THA	07°55'15"N	099°15'47"E	MK879285	MK879422	
	SUT 0312060	9578	THA	12°51'15"N	099°59'49"E	MK879278	MK879415	
	SUT 0311024	9580	THA	14°54'04"N	100°03'48"E	MK879276	MK879413	
	SUT 0311040	9582	THA	13°25'07"N	099°57'18"E	MK879277	MK879414	
	ZMB 127470	9589	THA	08°27'09"N	098°28'01"E	MK879284	MK879421	
	ZMB 127468	9599	THA	12°56'54"N	099°28'52"E	MK879283	MK879420	
	ZMB 107962	9779	THA	16°37'38"N	100°56'43"E	MK879282	MK879419	
	ZMB 107869	9781	THA	08°38'18"N	099°44'59"E	MK879281	MK879418	
	SUT 0311009	9787	THA	16°11'33"N	099°15'51"E	MK879275	MK879412	
	<i>Melanoides tuberculata</i>	ZMB 200313	7530	IND	11°34'45"N	076°34'55"E	MK879274	MK879411
	<i>Paludomus siamensis</i>	ZMB 107721	7334	THA	14°26'15"N	098°51'11"E	MK879286	MK879423

^a From Neiber and Glaubrecht (2019a).

Results

Biometric analyses

The first two principal components (PCA 1 and PCA 2) account for > 95% of the cumulative variation in shell parameters. The plot of PCA 1 vs PCA 2 (Fig. 4A) shows that the clusters of specimens that were grouped according to geographic origin widely overlap. Especially the clusters of specimens from Thailand and Indonesia (corresponding to mitochondrial Clades A and B, Fig. 4) and the clusters of specimens from Australia (corresponding to mitochondrial Clade C, Fig. 4) also widely overlap. The Kruskal–Wallis rank sum tests were significant for PCA 1 ($p < 5.0 \times 10^{-6}$) and PCA 2 ($p < 2.0 \times 10^{-16}$), i.e., at least one group stochastically dominates one other group in each of the tests. Dunn's test for PCA 1 found significant differences between the groups including samples from Indonesia and Australia ($p < 0.0001$) as well as between the groups including samples from Australia and Thailand ($p < 0.0075$), respectively, but not for pairwise comparisons of the other groups (Fig. 4B). Dunn's test for PCA 2 found significant differences between the following groups: Indonesia vs Australia ($p < 0.0031$), Indo-

nesia vs Thailand ($p < 0.0001$), Australia vs Thailand ($p < 0.0007$), Australia vs India/Sri Lanka ($p < 0.0004$), and Thailand vs India/Sri Lanka ($p < 0.0001$), but not for Indonesia vs India/Sri Lanka (Fig. 4C). However, both for PCA 1 and PCA 2 the comparison of ranges shows that the ranges of all pairs of geographic groups overlap and therefore do not allow a diagnostic separation of these groups on the basis of the biometric data. The included type specimens of the nominal taxa *M. rudis* and *M. microstoma* fall within the convex hull spanned by specimens sampled from Thailand, Indonesia, Australia, India, and Sri Lanka in the PCA 1 vs PCA 2 plot; only the holotype of the nominal taxon *M. aspera* lies outside this area (Fig. 4A), although closely resembling the examined syntypes of *M. rudis* and *M. microstoma* with respect to shell sculpture and overall shape.

Phylogenetic analyses

A clade including *Thiara amarula* (Linnaeus, 1758) (the type species of *Thiara* Röding, 1798), *T. winteri* (Busch, 1842) in Philippi (1842–1844), *T. cf. winteri* from Bali, and the specimens identified as *Thiara aspera* from Thai-

land, Indonesia, and Australia as well as “*Stenomelania*” *denisoniensis* (Brot, 1877) in Brot (1874–1879) was recovered in all three analyses (BI: 1.00, BS (ML): 92, BS (MP): 96). However, *Thiara* is paraphyletic with respect to “*S.*” *denisoniensis*. *Thiara amarula* grouped together with *T. winteri* and *T. cf. winteri* from Bali in a clade (BI: 1.00, BS (ML): 97, BS (MP): 93). A sister group relationship of *T. amarula* and *T. winteri* was recovered in the BI and ML analyses (BI: 0.99, BS (ML): 83) but not in the MP analysis (BS (MP): < 50). Within this clade, the clades including specimens of *T. amarula*, *T. winteri*, and *T. cf. winteri* from Bali, respectively, were supported (BI: 1.00, BS (ML): 96–100, BS (MP): 100). The clade containing *T. amarula*, *T. winteri*, and *T. cf. winteri* was recovered as the sister group of a clade containing “*S.*” *denisoniensis* and specimens from Thailand, Australia, and Indonesia (including also a single specimen from Bali) assigned to the *T. aspera* on basis of conchological similarity with rather high support (BI: 1.00, BS (ML): 92, BS (MP): 96). Within this clade, “*S.*” *denisoniensis* was recovered as the sister group (BI: 1.00, BS (ML): 94, BS (MP): 90) of *T. aspera*, which in turn formed a rather well-supported clade (BI: 1.00, BS (ML): 90, BS (MP): 79). *Thiara aspera* specimens from Australia (Clade C) formed a maximally supported clade. The *T. aspera* specimens from Thailand grouped together with a single individual from Bali in a well-supported clade (Clade A; BI: 1.00, BS (ML): 92, BS (MP): 100), which was sister to another supported clade (Clade B; BI: 1.00, BS (ML): 77, BS (MP): 100) that included *T. aspera* specimens from Sulawesi.

The included specimens of *Mieniplotia scabra* (Müller, 1774) formed the sister clade of a specimen of *Melanoides tuberculata* from India in the BI analysis, albeit without support. To test alternative phylogenetic hypotheses, we conducted four AU tests: 1) the monophyly of *M. scabra* ($p = 0.252$) and 2) the monophyly of *T. winteri* plus the *T. cf. winteri* specimens from Bali ($p = 0.156$) could not be rejected, whereas 3) the monophyly of *T. aspera*, *T. winteri* and *T. cf. winteri* ($p < 0.001$) and 4) the monophyly of *Thiara* excl. “*S.*” *denisoniensis* ($p = 0.033$) but including the *T. aspera* specimens was rejected at a confidence level of $\alpha = 0.05$.

Systematic account

Thiaridae Gill, 1871 (1823)

Thiara Röding, 1798*

Vesica Humphrey, 1797: 58 [unavailable, published in a work rejected for nomenclatural purposes, see International Commission on Zoological Nomenclature 1912: 116–117; among the mentioned species is *Vesica thiara* Humphrey, 1797 (unavailable) = *Helix amarula* Linnaeus, 1758].

Thiara Röding, 1798: 109 [type species: *Helix amarula* Linnaeus, 1758, by subsequent designation of Herrmannsen 1849 in Herrmannsen 1847–1849: 576].

Melania Lamarck, 1799: 75 [type species: *Helix amarula* Linnaeus, 1758, by monotypy].

Melanigemus Renier, 1807: pl. 8 [unavailable, published in a work rejected for nomenclatural purposes, see International Commission on Zoological Nomenclature 1956: 290].

Melas Montfort, 1810: 322–324 [unjustified emendation of *Melania* Lamarck, 1799].

Melanidia Rafinesque, 1815: 144 [unjustified emendation of *Melania* Lamarck, 1799].

Melanea – Sowerby 1818 in Sowerby 1818–1822: 33 [incorrect subsequent spelling of *Melania* Lamarck, 1799].

? *Spirilla* Gray, 1824: 254 [unavailable, published in synonymy; mentioned as *Spirilla spinosa* (quoting a label or note attributed to G. Humphrey as “*Spirilla spinosa*, freshwater spiral spined shell, from Admiralty Island, New Guinea”) under *Melania setosa* Swainson, 1824 (= *Thiara cancellata* Röding, 1798, see Swainson 1824: 13–15 and Wilkins 1957: 167–169) and as being conspecific with the nomenclaturally unavailable *Buccinum aculeatum* Lister, 1692: pl. 1055, fig. 8. Mentioned as a synonym by Férussac 1824: 318, Gray 1825: 524, Oken 1833: 133, Gray 1847: 152, Wilkins 1957: 167 as well as by Agassiz 1842: 84, Agassiz 1847: 348 and Herrmannsen 1848 in Herrmannsen 1847–1849: 491 in nomenclators, with the name attributed to Humphrey 1797 (where it could not be found). Used by Favre 1869: 79 (attributing the name to G. Humphrey but without reference to the work of Gray 1824) for a subgenus of *Fusus* Bruguière 1789 in Bruguière 1789–1792 and in a very different meaning from that of Gray 1824 and therefore not regarded here as having been made available from that work].

Spirella – Oken 1833: 61 [incorrect subsequent spelling of the unavailable *Spirilla* Gray, 1824].

Melacantha Swainson, 1840: 341 [type species: *Helix amarula* Linnaeus, 1758 by subsequent designation of Herrmannsen 1849 in Herrmannsen 1847–1849: 26].

Thaira – Gray 1840: 148 [incorrect subsequent spelling of *Thiara* Röding, 1798].

Amarula Sowerby, 1842: 61 [type species: *Helix amarula* Linnaeus, 1758, by monotypy].

Melanium – Busch 1842 in Philippi 1842–1845: 4 [incorrect subsequent spelling of *Melania* Lamarck, 1799].

Tiara – Gray 1847: 152 [incorrect subsequent spelling of *Thiara* Röding, 1798].

Thaera – Agassiz 1847: 367 [unavailable, emendation for *Thaira* as used by Gray 1840: 148 proposed in synonymy in a nomenclator].

Lithoparches Gistel, 1848: ix [nom. nov. pro *Melania* Lamarck, 1799; type species: *Helix amarula* Linnaeus, 1758, by typification of the replaced name].

Hydrognoma Gistel, 1848: 169 [nom. nov. pro *Melania* Lamarck, 1799, type species: *Helix amarula* Linnaeus, 1758, by typification of the replaced name].

Tiaropsis Brot, 1871: 298 [non Agassiz 1849: 289–298; type species: *Melania winteri* Busch, 1842 in Philippi 1842–1844: *Melania*, 1, pl. 1 figs 1, 2 by subsequent designation of Brot 1874 in Brot 1874–1879: 7].

Cerithomelania Moore, 1899: 233–234 [type species: *Helix amarula* Linnaeus, 1758 by original designation].

? *Ripalania* Iredale, 1943: 209 [type species: *Melania queenslandica* Smith, 1882 by monotypy].

? *Setaeara* Morrison, 1952: 8 [type species: *Thiara cancellata* Röding, 1798 by original designation].

* a question mark indicates a tentative synonymisation

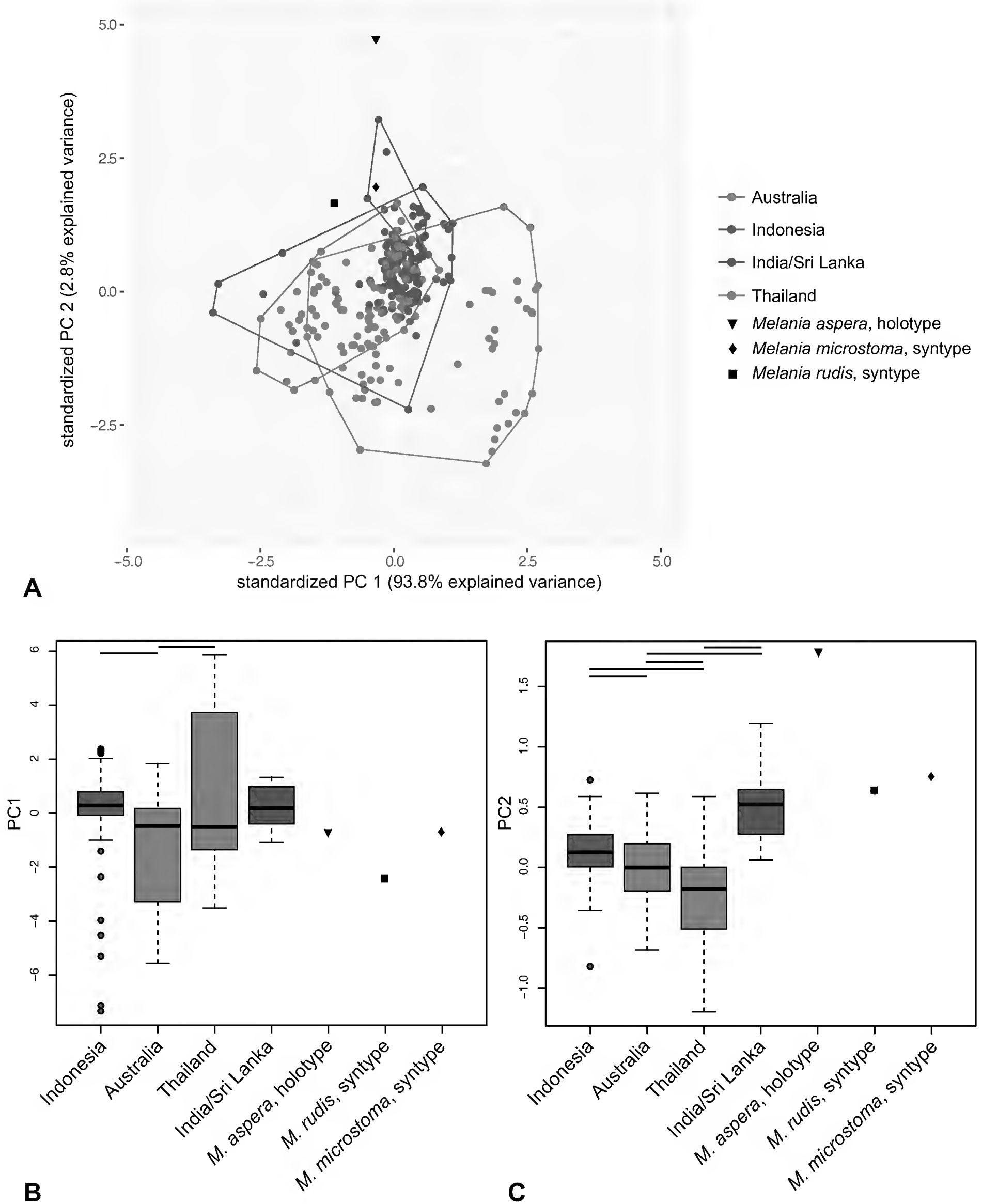


Figure 4. Results of the analysis of biometric data of “*Thiara*” *aspera* (Lesson, 1831) specimens from Australia (yellow), Indonesia (green), Thailand (red) and India/Sri Lanka (blue) and type material of *Melania aspera* Lesson, 1831 (holotype, triangle), *Melania rudis* Lea & Lea, 1851 (syntype, square) and *Melania microstoma* Lea & Lea, 1851 (syntype, diamond). **A.** Scatter plot of the first two axes of the principal component analysis (PCA) of biometric data. Coloured lines indicate the outline of the convex hull for each geographic group; **B, C.** Boxplots of PCA 1 (**B**) and PCA 2 (**C**); bars above the box plots indicate significant differences of groups resulting from testing with Dunn’s test.

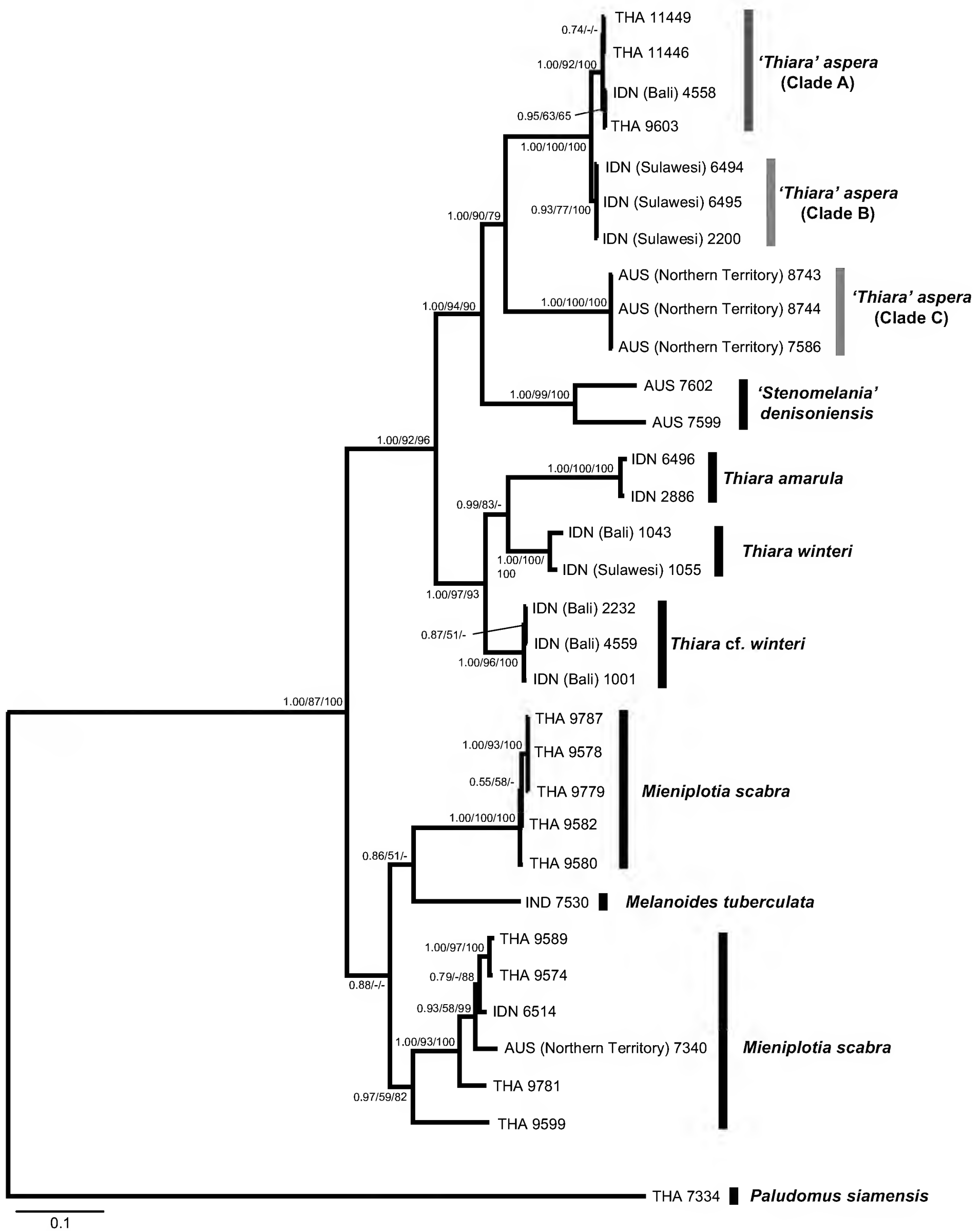


Figure 5. Bayesian 50% majority-rule consensus tree based on partial sequences mitochondrial cytochrome c oxidase subunit 1 (*coxI*) and 16S rRNA (16S) genes. Support values at nodes refer to Bayesian posterior probabilities (left), Maximum Likelihood (middle) and Maximum Parsimony (right) bootstrap values. AUS: Australia, IDN: Indonesia, THA: Thailand. Numbers at tips refer to DNA vouchers in the collection of the ZMB, see also Table 1.

Remarks. Many names have been proposed for the group of Thiariidae that is currently regarded as representing *Thiara* Röding, 1798. Several of these names are objective junior synonyms of *Thiara* having the same type species (*Helix amarula* Linnaeus, 1758), and several others are nomenclaturally unavailable. A few, like *Ripalania* Iredale, 1943 or *Setaeara* Morrison, 1952, may actually be synonyms of *Thiara*. However, those hypotheses should be further tested using molecular genetic approaches. Therefore, these nominal genera were only tentatively included in the synonymy of *Thiara*.

“*Thiara*” *aspera* (Lesson, 1831)*

Figs 1, 6, 7

Melania aspera Lesson, 1831 in Lesson (1830–1831: 357–358) [type locality: “La Nouvelle-Guinée” (= New Guinea), restricted to Manokwari by Glaubrecht and Podlacha (2010)].

Melania rudis Lea & Lea, 1851: 186 [type locality: ‘Amboyna’ (= Amboyn)].

Melania microstoma Lea & Lea, 1851: 186 [type locality: mountain streams, isle of Negros, Philippines].

? *Melania armillata* Lea & Lea, 1851: 195–196 [type locality: India].

? *Melania broti* Reeve, 1859 in Reeve (1859–1861: pl. 22 fig. 160) [type locality: Ceylon (= Sri Lanka)].

? *Melania hybrida* Reeve, 1859 in Reeve (1859–1861: pl. 13 fig. 163) [type locality: not given].

? *Melania chocolatum* Brot, 1860: 256–257, pl. 16, fig 2 [type locality: “Ceylon” (= Sri Lanka)].

? *Melania (Tiaropsis) rudis* var. *spinosa* Brot, 1877 in Brot (1874–1879: 306) [type locality: not given, see also Brot (1868: 33, pl. 1, fig. 7)].

? *Melania (Tiaropsis) drilliiformis* Martens, 1897: 305 [nomen nudum].

? *Melania fortitudinis* Fulton, 1904: 51–52, pl. 4, fig. 3 [type locality: “Soekaboemi, Java” (= Sukabumi, Java)].

? *Melania rudis* var. *cylindrica* Schepman, 1915: 27 [type locality: West Ceram, Kairatu (= West Seram Island, Kairatu)].

Diagnosis. Thiariid with a turreted, subcylindrical to elongate-ovoid, strongly ornamented high-spired shell with usually rather flattened whorls and a narrowly pyriform aperture that at most reaches half the total shell height, but usually less. Ornamentation of the shell consisting of sinuous axial ribs that usually reach to the base of the body whorl and spiral chords that form nodes where they intersect the ribs; spiral chords usually present on the entire whorl but strongest at the base of body whorl.

Remarks. The examined type specimens of *M. aspera*, *M. rudis*, and *M. microstoma* correspond well to each other in overall shell shape and sculpture and are here regarded as conspecific because of this. As already noted by Brot (1874–1879: 307) and Glaubrecht and Podlacha (2010: 200), the name *Melania aspera* Lesson, 1830 has priority over the somewhat more fre-

quently used name *Melania rudis* (e.g., van Benthem Jutting 1937, 1956; Subba Rao 1989; Ramakrishna and Dey 2007; Budha 2010; Patil and Talmale 2011 as *T. rudis*). The holotype of *Melania aspera* is unusual in possessing a very small aperture in relation to overall shell height, possibly explaining its isolated position in the PCA 1 vs PCA 2 scatter plot (Fig. 4A). The nominal taxa *M. armillata*, *M. broti*, and *M. chocolatum* described from India or Sri Lanka were regarded by Brot (1874–1879) as closely related to *M. rudis* and are here tentatively synonymised with *M. aspera*, largely following the views of Rensch (1934) and van Benthem Jutting (1937, 1956) who synonymised these taxa with *M. rudis*. According to Brot (1874–1879: 307–308) *Melania hybrida* is based on a teratological specimen with an unusual aperture formation and is here tentatively synonymised with *M. aspera*. The nominal taxon *Melania (Tiaropsis) rudis* var. *spinosa* Brot, 1877 is an individual variation of *M. aspera* with somewhat longer shoulder spines. The original figures and descriptions of *Melania fortitudinis* and *M. (Tiaropsis) rudis* var. *cylindrica* from Java and West Seram Island also correspond well with the holotype of *M. aspera* and are herein treated as synonyms of the former.

Type material examined. Holotype of *Melania aspera* Lesson, 1831, MNHN 21098, “La Nouvelle-Guinée”; syntype of *Melania rudis* Lea & Lea, 1851, USNM 119778, “Amboyna”; syntype of *Melania microstoma* Lea & Lea, 1851, USNM 119722, ‘mountain streams, isle of Negros, Philippines’.

Additional material examined (w: ethanol preserved samples). **India:** Kolkata, ZMB 107002. **Sri Lanka:** Colombo, ZMB 107003. **Thailand:** Samut Sakhon Province, Klong Don Ko, SUT 0311020, ZMB 127535, SUT 0311044, SUT 0311053, ZMB 127534, w; Nakhon Pathom province, Pond in Silpakorn University campus, SUT 0312069, SUT 0312070 = ZMB 127536, w. **Indonesia:** Bali: South Bali, Yehembang River, ZMB 191279, ZMB 191279a, w, South Bali, at Yehembang, ZMB 106472, w; east of Mendaya, stream southwest of Gumicik, ZMB 191488; Sulawesi: South Sulawesi, Kalena catchment, Angkona river, ZMB 192751, w; southeast Sulawesi, Pohara river, at Pohara, road Kendair to Kolaka, ZMB 191261, w; southeast Sulawesi, Simbune river, 1 km northeast of Raterate, road Kendari to Kolaka, ZMB 191262, ZMB 191262a, w; southeast Sulawesi, stream at Tembeeha, road Tirobus to Kendari, ZMB 191278, w; central Sulawesi, Banggai Islands, Peleng Island, West Peninsula, Tataban river, ZMB 107378, w, ZMB 107377, w. **Australia:** Northern Territory: Berry Springs, ZMB 106704, w, ZMB 106599a, w, ZMB 127616, w; Wabalaar, Roper River, ZMB 107617, w, ZMB 107614, w, ZMB 127645, w; Salt creek, ZMB 127619, w, ZMB 127636, w, ZMB 127637, w; Roper Bar, ZMB 127620, w; Queensland: O’Shanassy, ZMB 107280.

* a question mark indicates a tentative synonymisation

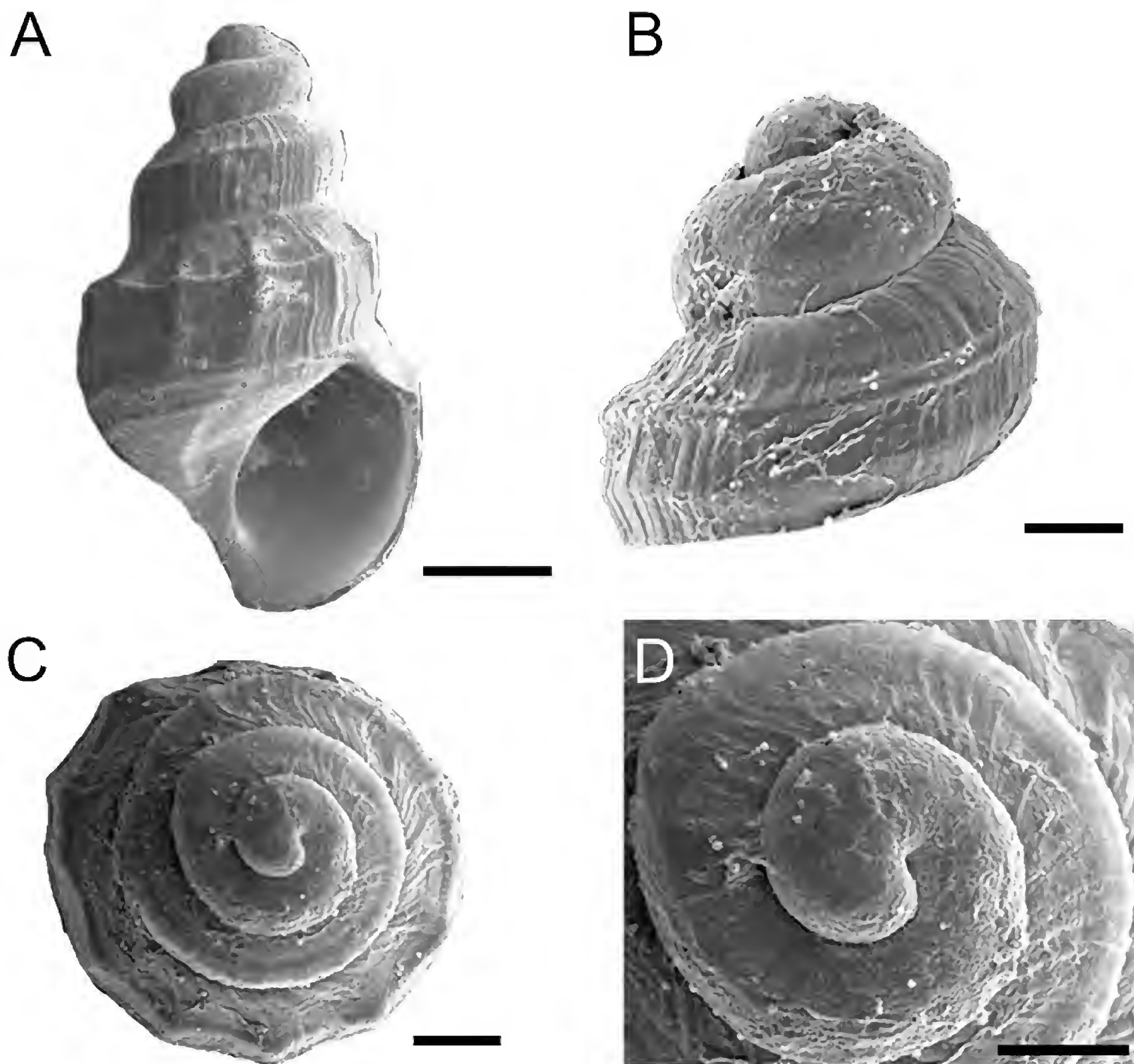


Figure 6. Juvenile and embryonic shells of “*Thiara*” *aspera* (Lesson, 1831), SUT 0311020, Samut Sakhon Province, Klong Don Ko. **A.** Lateral view; **B.** Apical whorls, lateral, **C.** Apical view. **D.** Details of the protoconch. Scale bars: 450 μm (**A**); 250 μm (**B**); 200 μm (**C**); 100 μm (**D**).

Shell. Turreted, subcylindrical to elongate-ovoid, corneous to dark brown, with up to nine whorls (the early whorls usually eroded) (Fig. 1; for juvenile shells, see Fig. 6). Whorls rather flat to convex, separated by a slightly impressed to distinctly impressed, undulating suture. Whorls slightly constricted below the suture, ornamented with sinuous ribs and spiral chords that usually form nodules at their intersections. Radial sculpture usually strongest on the upper half of the whorls, with the nodules at the shoulder of the whorls usually largest, sometimes forming spines. Towards the lower part of the body whorl the spiral sculpture often becomes the dominant sculptural element, forming distinct parallel chords. Aperture pyriform, angled in its upper part and rather narrow, wider at the base and appearing truncated in frontal view. Columella thickened, almost straight to curved, abruptly terminating basally. Shell size $H = 7.6\text{--}48.0\text{ mm}$, $W = 3.1\text{--}22.0\text{ mm}$ (Table 2).

Operculum. The operculum is typical for thiarids, oval and paucispiral, light to dark brown, and with the nucleus being excentric in the lower left corner.

Juvenile shell. The shells of the juveniles in the brood pouch had up to five whorls, with a maximum height of about 2.5 mm. The protoconch is smooth, with the radial and spiral sculpture developing on the first teleoconch whorls (Fig. 6). For measurements of the embryonic shell, see Table 3.

Radula. Taenioglossate (Fig. 7), resembling other thiarids. As in all thiarids the central tooth or rachidian is significantly wider than tall; all specimens have a central cusp flanked by three to six triangular denticles on both sides, resulting in up to 12 denticles and a typically 4–5/1/4–5 pattern at the upper cutting edge (Fig. 7A, C, E, Table 4). The laterals are equipped with three to six

Table 2. Shell parameters of “*Thiara aspera* (Lesson, 1831) specimens from Thailand, Indonesia and Australia, with min./max. values, mean, standard deviation (SD), and number of whorls.

Voucher	Country, region	n		Measurements (mm)					NW
				H	W	AL	AW	BW	
USNM 119778	Indonesia, Ambon Island	1		23.7	9.7	9.8	5.1	15.5	4
USNM 119722	Philippines, Negros Island	1		20.3	7.7	7.1	3.3	12.3	6
MNHN 21098	Indonesia, West Papua	1		25.0	7.8	6.9	3.5	12.6	7
GSUBg 14265	Indonesia, Java	1		48.0	22.0	22.0	10.0	28.1	7
ZMB 107002	India, Calcutta	1		17.4	7.5	5.7	2.5	12.0	3
ZMB 107003	Sri Lanka, Colombo	5	Range	13.3–16.6	5.3–6.6	4.3–5.3	2.3–2.5	9.0–11.3	4–5
			Mean	14.3	5.9	4.8	2.4	9.8	
			SD	1.2	0.4	0.3	0.1	0.8	
SUT 0311053	Thailand, Samut Sakhon	30	Range	7.6–12.8	3.1–5.5	2.8–6.2	1.6–3.4	4.4–7.8	4–7
			Mean	9.5	3.9	4.0	2.3	5.7	
			SD	1.1	0.6	0.6	0.4	0.9	
SUT 0311020	Thailand, Samut Sakhon	52	Range	14.1–24.3	7.1–11.1	7.0–11.1	3.2–5.4	9.7–16.2	6–7
			Mean	17.7	8.7	8.7	4.2	12.0	
			SD	2.5	1.0	1.0	0.5	1.5	
SUT 0311044	Thailand, Samut Sakhon	1		22.9	10.9	10.5	4.8	15.2	6
SUT 0312070	Thailand, Nakhon Pathom	12	Range	14.4–19.8	5.3–7.9	5.7–6.8	2.4–4.2	7.6–12.0	5–8
			Mean	17.1	6.8	7.0	3.4	9.9	
			SD	1.5	0.7	0.9	0.5	1.2	
ZMB 191488	Indonesia, Bali	2	Range	19.8–22.1	8.3–9.4	8.0–8.8	4.1–4.7	12.8–14.5	5
			Mean	20.9	8.9	8.4	4.4	13.7	
			SD	1.1	0.6	0.4	0.3	0.9	
ZMB 191278	Indonesia, Sulawesi	19	Range	14.3–18.2	6.2–7.8	6.1–8.9	3.1–3.9	9.3–12.3	4–5
			Mean	16.1	6.7	7.2	3.6	10.4	
			SD	1.0	0.3	0.6	0.2	0.7	
ZMB 107377	Indonesia, Sulawesi	10	Range	13.6–20.3	5.5–7.5	4.5–7.3	2.7–4.0	7.7–11.7	4–5
			Mean	16.8	6.5	6.2	3.4	9.6	
			SD	2.1	0.7	0.8	0.4	1.3	
ZMB 107378	Indonesia, Sulawesi	19	Range	12.9–19.6	5.2–7.1	5.1–7.8	2.6–3.9	7.7–11.2	4–5
			Mean	16.9	6.3	6.3	3.2	9.9	
			SD	1.5	0.4	0.7	0.4	0.8	
ZMB 191279	Indonesia, Bali	17	Range	16.8–27.0	7.0–9.9	7.9–12.0	3.3–5.1	11.0–17.2	4–6
			Mean	22.7	8.6	9.9	4.3	14.5	
			SD	3.7	1.0	1.4	0.6	2.2	
ZMB 106472	Indonesia, Bali	16	Range	17.9–22.8	6.4–9.3	7.0–10.6	3.1–5.0	11.4–16.2	4–7
			Mean	20.1	7.5	8.5	3.8	12.7	
			SD	1.4	0.6	0.9	0.4	1.2	
ZMB 127538	Indonesia, Bali	20	Range	18.4–30.4	8.6–13.7	9.3–14.9	4.4–7.4	12.8–20.7	4–6
			Mean	24.8	11.0	11.8	5.6	16.8	
			SD	3.0	1.2	1.4	0.7	1.9	
ZMB 191268	Indonesia, Sulawesi	5	Range	29.3–41.5	11.5–16.0	12.1–18.7	5.7–8.4	12.3–26.8	4–6
			Mean	35.3	13.5	15.3	6.9	20.9	
			SD	4.9	2.0	2.5	1.1	5.3	

Table 3. Measurements of parameters of the juvenile protoconch of “*Thiara aspera* (Lesson, 1831) of specimens obtained from the brood pouch.

Voucher	Country, region	n		Measurements (µm)		
				he	we	de
ZMB 127534	Thailand, Samut Sakhon	3	Range	48.0–63.2	96.0–120.0	312.7–395.7
			Mean	54.0	106.7	352.8
ZMB 127535	Thailand, Samut Sakhon	2	Range	56.3–71.4	107.0–114.3	354.3–366.2
			Mean	63.9	110.7	352.8
ZMB 191278	Indonesia, Sulawesi	2	Range	34.0–72.4	76.0–91.1	202.0–252.4
			Mean	53.2	84.6	227.2
ZMB 191488	Indonesia, Bali	1	–	83.3	95.2	259.5

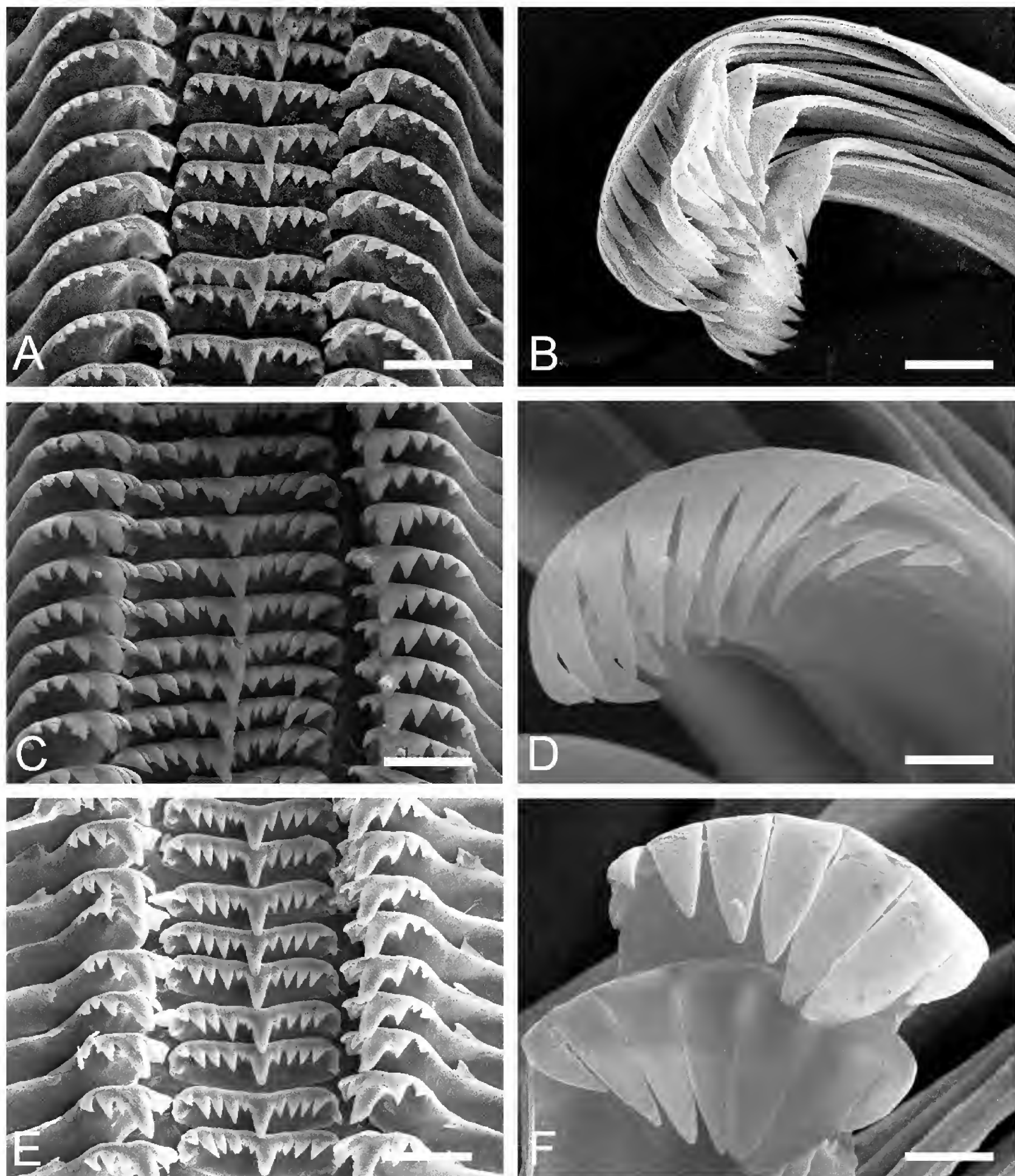


Figure 7. Radulae of “*Thiara*” *aspera* (Lesson, 1831) from Thailand. **A, B.** SUT 0312070, Nakhon Pathom province, pond at Silpakorn University campus; **A.** Central and lateral teeth; **B.** Marginal teeth; **C, D.** SUT 0311020, Samut Sakhon province, Klong Don Ko; **C.** Central and lateral teeth; **D.** Marginal teeth. **E, F:** SUT 0311053, Samut Sakhon Province, Klong Don Ko; **E.** Central and lateral teeth; **F.** Marginal teeth. Scale bars: 35 μm (**A, E**); 5 μm (**B, F**); 25 μm (**C**); 10 μm (**D**).

Table 4. Variation of cusps on the radula teeth of “*Thiara*” *aspera* (Lesson, 1831) specimens.

Voucher	Country, region	n	Marginal teeth	Lateral teeth (left)	Lateral teeth (right)	Rachidian
SUT 0311053	Thailand, Samut Sakhon	4	6–8	3-1-3	3-1-3	4-5-1-4-5
SUT 0311020	Thailand, Samut Sakhon	4	6–8	3-1-3	3-1-3	4-5-1-4-5
SUT 0312070	Thailand, Nakhon Pathom	2	7–8	5-1-5	4-1-4	4-1-4
SUT 0312069	Thailand, Nakhon Pathom	2	9–10	3-1-3	3-1-3	3-1-3
ZMB 191278	Indonesia, Sulawesi	2	7–8	3-1-3	3-1-3	4-1-4
ZMB 191488	Indonesia, Bali	1	10	6-1-6	6-1-6	6-1-5
ZMB 191279	Indonesia, Bali	3	6–7	4-1-4	4-1-4	4-5-1-4-5
ZMB 106472	Indonesia, Bali	2	6–7	3-1-3	3-1-3	4-1-4

smaller denticles on the inner side, and three to six denticles outside from the large main cusps (Fig. 7A, C, E, Table 4). The marginal teeth are moderately long, spoon-shaped, with a varying number of 6–10 denticles (Fig. 7B, D, F, Table 4).

Reproductive strategy. The results of the analysis of brood pouch content are summarised in Figure 2. Juveniles of up to 2 mm (rarely also larger) were found in the populations from Thailand, Indonesia (Bali and Sulawesi) and Australia (Northern Territory) suggesting an euviviparous reproductive strategy for “*T.*” *aspera*, i.e., the taxon was found to give birth to crawling and shelled juveniles in accordance with the definitions in Glaubrecht et al. (2009). In a few populations in Thailand and on Bali, gravid females with only early embryos, i.e., veliger larvae in the brood pouch were found.

Distribution. “*Thiara*” *aspera* as here understood is a widespread species, with records from Sri Lanka and India (Subba Rao 1989), Myanmar and Cambodia (van Benthem Jutting 1956), Indonesia (Rensch 1934; van Benthem Jutting 1956), and the Philippines (Lea and Lea 1851; van Benthem Jutting 1956). As our results indicate, the taxon is also present in Thailand and northern Australia, from where it was not previously reported (Fig. 2).

Discussion

The results of our phylogenetic analyses show that the nominal taxon *Melania winteri* Busch, 1842 is closely related to *Thiara amarula* and can be classified with the same genus. However, the nominal species *Melania aspera* Lesson, 1830 (= *Melania rudis* Lea & Lea, 1851), which has often been classified as a member of *Thiara* (e.g., van Benthem Jutting 1937, 1956; Subba Rao 1989; Ramakrishna and Dey 2007; Budha 2010; Patil and Talmale 2011 under the name *T. rudis*) cannot be included within that genus on the basis of our data without broadening the concept of *Thiara* to an extent that it encompasses almost the entire conchological diversity of Thiaridae because “*Stenomelania*” *denisoniensis* Brot, 1877, which is conchologically similar to *Stenomelania* Fischer, 1885 or *Melanooides* Olivier, 1804, clusters within *Thiara* s. lat. in our phylogenetic analyses and an approximately unbiased test rejected the monophyly of *T. amarula*, *T. winteri*, *T. cf. winteri*, and “*T.*” *aspera*, i.e., excluding “*Stenomelania*” *denisoniensis*. Pending a phylogenetic analysis of the entire family, we here retain the species in *Thiara*, but indicate the tentative placement by quotation marks.

Our phylogenetic analyses further show that “*T.*” *aspera* exhibits little genetic variation throughout the Indo-Malayan Archipelago and the Southeast Asian mainland, although populations vary considerably with regard to shell shape, and especially sculpture, confirming previous surveys on thiarid species, which showed also an extraordinary plasticity of the shell (Glaubrecht et al. 2009).

We here report the presence of “*T.*” *aspera* in Thailand for the first time, albeit in anthropogenic habitats. Previous surveys of the Thai freshwater snail fauna, e.g., by Brandt (1974) did not record the species. Thus, as his years-long surveys were exhaustive it is safe to assume that the species is probably introduced but additional surveys should be carried out to clarify whether the taxon also occurs in natural habitats in this country and was only overlooked in the past.

We also report “*T.*” *aspera* here for Australia for the first time, where the taxon was found in natural habitats in the Northern Territory and in north-western Queensland. The populations from Australia were found to be somewhat differentiated genetically from the remaining specimens of “*T.*” *aspera* from Thailand and Indonesia included in the phylogenetic analyses and also slightly differ conchologically, i.e., the spiral sculpture almost disappears on the upper half of the teleoconch whorls. Further analysis should therefore confirm whether these differences are constant and would allow a taxonomic separation of the Australian populations.

Unfortunately, no samples could be included in the phylogenetic analyses from either India or Sri Lanka. However, as the examined material closely resembles the holotype of *Melania aspera* in shell characters (although this specimen is exceptional because of its very small aperture in relation to total shell height which may explain its isolate position in Fig. 4A), the populations from these two countries are here regarded as belonging to the species. Therefore, “*T.*” *aspera* has to be considered as a widespread species, ranging from India and Sri Lanka across the Southeast Asian mainland and islands into Australia (Fig. 2).

At present, our data on “*T.*” *aspera* do not allow to assess whether the observed differences of juvenile stages in the brood pouch of the female indicate differences in the reproductive strategy, or rather individual or seasonal variations. The close phylogenetic relationships among these populations (Fig. 5), however, let the latter two explanations appear more likely in our opinion. Therefore, we consider “*T.*” *aspera* a euviviparous species, although it has to be stated that repeated periodic sampling would be necessary to resolve this issue conclusively.

Conclusions

These results highlight the need for a comprehensive revision of the genus-group systematics of Thiaridae as a whole. However, mitochondrial DNA markers are fraught with difficulties in some freshwater cerithioideans (Köhler and Deen 2010; Whelan and Strong 2015; Köhler 2016) and probably also in Thiaridae. Likewise, there appears to be a confusing variability in shell and reproductive features in thiarids, which is in stark contrast to a conserved radular morphology as compared to some other cerithioidean families (Glaubrecht 1996). A stable system of the family, which ought to include the

type species of all named genus-group taxa, can be expected to emerge only after phylogenetic analyses based on suitable molecular markers and/or detailed morphological data become available. A stable system of the family then could serve as a basis for a better understanding of the evolutionary systematics and phylogeography of the group.

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Establishment of a new shrimp family Chlorotocellidae for four genera previously assigned to Pandalidae (Decapoda, Caridea, Pandaloidea)

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Abstract

A new caridean shrimp family, Chlorotocellidae, is established to accommodate four genera previously assigned to Pandalidae, viz., *Chlorotocella* Balss, 1914 (type genus), *Chlorocurtis* Kemp, 1925, *Anachlorocurtis* Hayashi, 1975, and *Miropandalus* Bruce, 1983, which represents the sister clade to a clade consisting of all other pandalid genera (including the two genera previously assigned to Thalassocarididae) in a recent comprehensive phylogenetic analysis of Pandaloidea. Diagnoses are provided for the new family and its constituent genera, and a comparison with Pandalidae is provided, for which a new diagnosis is given.

Key Words

Anachlorocurtis, ASR analysis, *Chlorotocella*, *Chlorocurtis*, *Miropandalus*

Introduction

The caridean family Pandalidae Haworth, 1825 is predominantly composed of cold-water and deep-sea taxa, including several species of commercial importance (Holthuis 1980). An extensive multimarker molecular phylogenetic analyses of the family and the closely related Thalassocarididae by Liao et al. (2019) clarified that Thalassocarididae, represented by two genera, *Thalassocaris* Stimpson, 1860 and *Chlorotocoides* Kemp, 1925, are deeply nested within Pandalidae, and that four genera, *Chlorotocella* Balss, 1914, *Chlorocurtis* Kemp, 1925, *Anachlorocurtis* Hayashi, 1975, and *Miropandalus* Bruce, 1983, comprise the sister clade to the remaining clade consisting of all other pandalid genera. These four genera are represented by small-sized species inhabiting shallow subtidal waters in tropical to subtropical and often associated with cnidarians (Hayashi and Miyake 1968; Hayashi 1975; Bruce 1983; Okuno and Yokota 1995; Minemizu 2000, 2013; Kato and Okuno 2001; Kawamoto and Okuno 2003; Humann and DeLoach

2010; Horká et al. 2014; Anker and De Grave 2016) in sharp contrast to the ecologies of most Pandalidae. To incorporate the documented phylogenetic pattern into the formal classification of Caridea, together with considerations on the morphological distinctness and ecological traits of these taxa, we hereby propose a new family, Chlorotocellidae fam. nov. for these four genera and redefine the family Pandalidae.

Materials and methods

The morphological data assembled following an examination of the literature and direct examination of specimens of relevant taxa formed the basis of the phylogenetic analysis by Liao et al. (2019) and can be found in the online supplementary material for that study. Aside from the family diagnosis, diagnoses are provided for each genus in the new family; to shorten diagnoses, synapomorphies for the family are not repeated in generic diagnosis; autapomorphies are in bold italics.

Illustrations showing diagnostic characters are given for *Chlorotocella* (*C. gracilis* Balss, 1914) and *Chlorocurtis* (*C. jactans* (Nobili, 1904)), as no published modern illustrations are available in easily accessible literature for those taxa. The three species of *Anachlorocurtis* and the monotypic *Miropandalus* have been well illustrated in their respective type description, and thus, no additional figures are presented.

Details of specimens used for preparation of drawings are listed below. These specimens are deposited in the Laboratory of Marine Zoology, Faculty of Fisheries, Hokkaido University, Hakodate, Japan (HUMZ), National Research Institute for Far Seas Fisheries, Shizuoka, Japan (NRIFS), and the Natural History Museum and Institute, Chiba, Japan (CBM).

Chlorotocellidae fam. nov.

Chlorocurtis jactans (Nobili, 1904): CBM-ZC 11596, 1 ovigerous female (cl 1.3 mm), Uehara, Iriomote Island, Yaeyama Islands, Ryukyu Islands, sea grass beds, 0.5–1 m at low tide, 18 July 2007, dip net, coll. T. Komai.

Chlorotocella gracilis Balss, 1914: CBM-ZC 12534, 1 male (cl 5.0 mm), TRV “Toyoshio-maru”, 2001-6 cruise, stn 4, W of Tanegashima Island, Ohsumi Islands, 30°33.50'N, 130°53.30'E, 47 m, 26 May 2001, dredge, coll. T. Komai; HUMZ-C 1556, 1 male (cl 4.1 mm), Tosa Bay, 40 m, 22 May 1960, coll. M. Toriyama.

Pandalidae Haworth, 1825

Chlorotocus novaezealandiae (Borradaile, 1916): NRIFS 578, 1 male (cl 17.0 mm), New Zealand, no other data.

Heterocarpus ensifer A. Milne-Edwards, 1881: HUMZ-C 255, 1 male (cl 33.0 mm), no data.

Pandalus montagui Leach, 1814: CBM-ZC 3422, 1 transitional male (cl 10.5 mm), Texel, The Netherlands, 8 April 1991.

Systematics

Infraorder Caridea Dana, 1852

Superfamily Pandaloidea Haworth, 1825

Family Pandalidae Haworth, 1825

Type genus. *Pandalus* Leach, 1814, by original designation.

Composition. *Atlantopandalus* Komai, 1999, *Austropandalus* Holthuis, 1950, *Bitias* Fransen, 1990, *Chelonika* Fransen, 1997, *Chlorotocoides* Kemp, 1925, *Chlorotocus* A. Milne-Edwards, 1882, *Dichelopandalus* Caullery, 1896, *Dorodotes* Bate, 1888, *Heterocarpus* A. Milne-Edwards, 1881, *Heteronika* Hendrickx, 2019, *Notopandalus* Yaldwyn, 1960, *Pandalina* Calman, 1899, *Pandalus* Leach, 1814, *Pantomus* A. Milne-Edwards, 1883, *Peripandalus* de Man, 1917, *Plesionika* Bate, 1888, *Procletes* Bate, 1888, *Pseudopandalus* Crosnier, 1997, and *Thalassocarid* Stimpson, 1860.

Diagnosis. Rostrum well developed, usually ventrally with teeth or rows of setae. Thoracic sternites 6–8 each with paired conspicuous prominences, teeth or protuberances (Fig. 3A). Pleomere 6 posterolateral process usually terminating in small tooth. Telson with longitudinal row of spiniform setae located on dorso-lateral ridges. Eystalks subpyriform or kidney-shaped, cornea distinctly longer and wider than eystalk. Antennular stylocerite with proximolateral projection, distally acuminate or rounded; article 2 usually with minute spiniform setae (Fig. 6A); outer flagellum with distal portion (distal to aesthetasc-bearing portion) usually well developed, consisting of numerous articles. Article 1 of mandibular palp with prominent expansion on inner distal margin (Fig. 6B). Maxilliped 2 with podobranch. Maxilliped 3 with or without exopod. Pereopod 1 fingers minute or completely reduced. Pereopod 2 subequal or unequal; basis with small process on lateral surface (Fig. 6C); carpal articulation greatly variable, but never tri-articulated. Arthrobranchs usually present on maxilliped 3 and pereopods.

Chlorotocellidae fam. nov.

<http://zoobank.org/CBE45390-043A-46E8-9743-7F5B167255AD>

Type genus. *Chlorotocella* Balss, 1914, by present designation.

Composition. *Chlorotocella* Balss, 1914 (two species), *Chlorocurtis* Kemp, 1925 (monotypic), *Anachlorocurtis* Hayashi, 1975 (three species) and *Miropandalus* Bruce, 1983 (monotypic).

Diagnosis. Rostrum, if present, without teeth or fringe of setae on ventral margin (Figs 1A, 4A). Thoracic sternites without conspicuous ornamentation, such as prominences, teeth or protuberances (Fig. 3B). Pleomere 6 posterolateral process rounded or truncate (Figs 1C, 4B). Telson with dorsolateral spiniform setae located adjacent to lateral margins (Figs 1D, 4C). Eystalks subcylindrical, cornea distinctly shorter than eystalk (Figs 1E, 4D). Antennular stylocerite devoid of proximolateral projection, distally obliquely truncate, bi- or tridentate (Figs 1A, F, 4E); outer flagellum with distal portion (distal to aesthetasc-bearing portion) reduced, consisting only of few articles (Figs 1A, 4E). Maxilliped 2 without podobranch (Figs 1L). Maxilliped 3 with no exopod (Figs 2A, 5A). Pereopod 1 fingers absent (Figs 2B, 5B, C). Pereopod 2 always subequal; basis without small process on lateral surface of basis; carpus consistently divided into three articles (Figs 2C, 5D, 6D). Arthrobranchs always absent from maxilliped 3 and pereopods.

Remarks. Characters differentiating Chlorotocellidae fam. nov. and Pandalidae are summarized in Table 1, with the character states of Chlorotocellidae fam. nov. being synapomorphic against Pandalidae (see Liao et al. 2019).

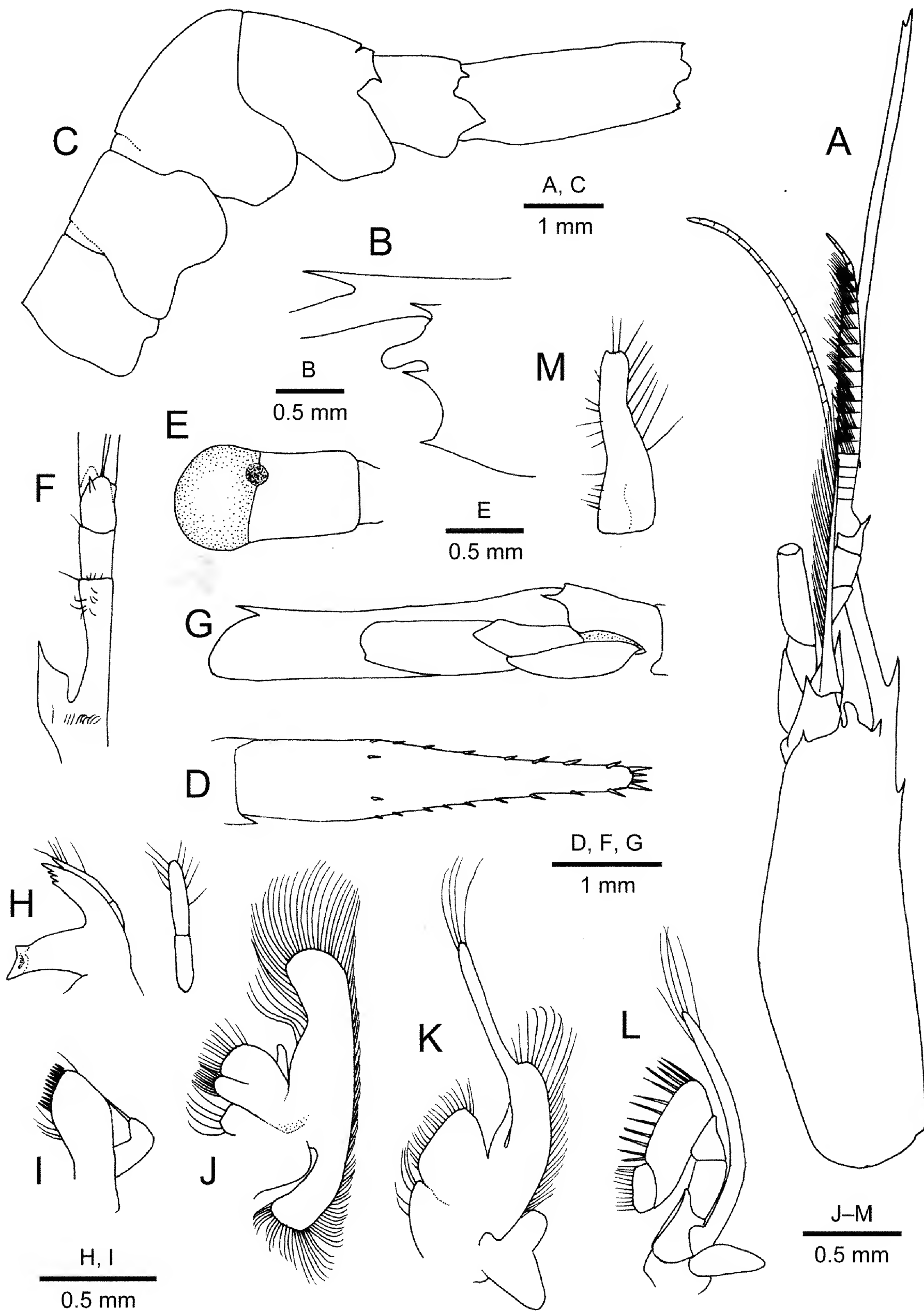


Figure 1. *Chlorotocella gracilis* Balss, 1914, male (cl 5.0 mm), CBM-ZC 12534. **A.** Carapace, antennule and antenna, lateral view (left eye removed); **B.** Anterior part of carapace, lateral view; **C.** Pleon, lateral view; **D.** Telson, dorsal view; **E.** Left eye, dorsal view; **F.** Left antennular peduncle, dorsal view; **G.** Left antenna, ventral view; **H.** Left mandible, outer view; inset, palp, outer view; **I.** Left maxillule, outer view (coxal endite missing); **J.** Left maxilla, outer view; **K.** Left maxilliped 1, outer view; **L.** Left maxilliped 2, outer view; **M.** Endopod of left pleopod 1, ventral view.

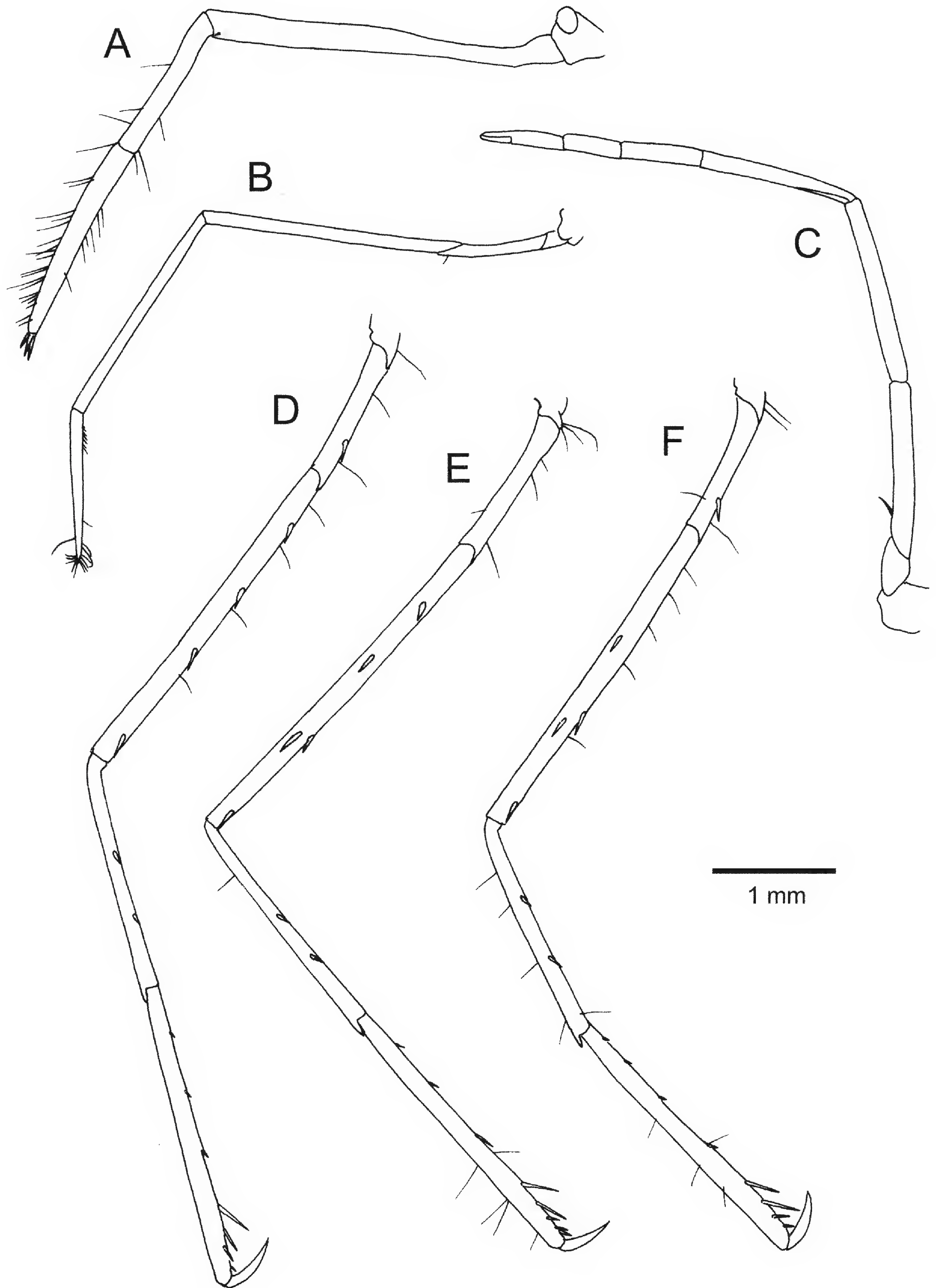


Figure 2. *Chlorotocella gracilis* Balss, 1914, male (cl 5.0 mm), CBM-ZC 12534. Left thoracic appendages in lateral view. **A.** Maxilliped 3; **B–F.** Pereopods 1–5, respectively.

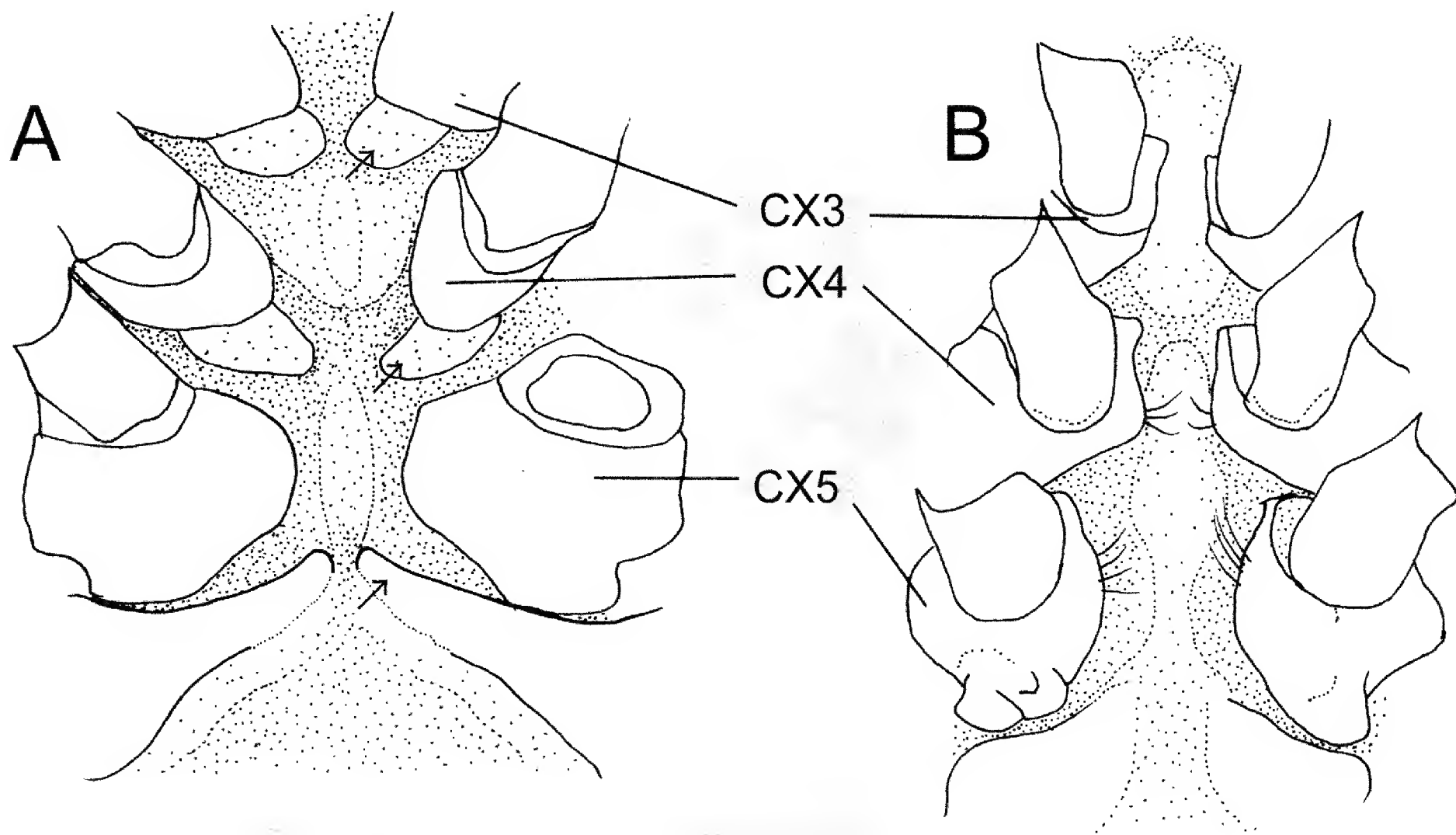


Figure 3. Thoracic sternites 6–8 and coxae (cx) of pereopods 3–5, ventral view. **A.** *Chlorotocus novaezealandiae* (Borradaile, 1916), male (17.0 mm), NRIFSF 578 (arrows indicating prominences on sternites 6–8); **B.** *Chlorotocella gracilis* Balss, 1914, male (cl 4.1 mm), HUMZ-C 1556.

Table 1. Comparison of diagnostic characters between Chlorotocellidae fam. nov. and Pandalidae. Character states of Chlorotocellidae are apomorphic against those of Pandalidae.

	Chlorotocellidae fam. nov.	Pandalidae
1	Rostrum, if present, without teeth or fringe of setae on ventral margin (Figs 1A, 4A).	Rostrum usually well developed, ventral margin armed with a few or series of teeth accompanied by row(s) of short setae.
2	Thoracic sternites without conspicuous ornamentation, such as keels, teeth or protuberances (Fig. 3B).	Thoracic sternites 6 and 7 each with paired prominences on either side of median keel; thoracic sternite 8 with transverse carina bearing submedian spines or teeth (Fig. 3A).
3	Pleomere 6 without posteroventral tooth; posterolateral process rounded or truncate (Figs 1C, 4B).	Pleomere 6 with small posteroventral tooth; posterolateral process terminating in small tooth.
4	Telson with dorsolateral spiniform setae located adjacent to lateral margins (Figs 1D, 4C).	Telson with dorsolateral spiniform setae located on dorsolateral ridges.
5	Eyestalks subcylindrical, cornea distinctly shorter than eyestalk (Figs 1E, 4D).	Eyestalks pyriform or subpyriform, cornea distinctly wider than eyestalk.
6	Antennular stylocerite distally obliquely truncate, bi- or tridentate, devoid of proximolateral projection (1F, 4E).	Antennular stylocerite acuminate or rounded, usually having small proximolateral projection (Fig. 6A).
7	Outer antennular flagellum with distal portion (distal to thickened aesthetasc-bearing portion) reduced, consisting of few articles (Figs 1A, 4E).	Outer antennular flagellum with distal portion (distal to aesthetasc-bearing portion) long and slender, consisting of 10 or more articles.
8	Maxilliped 2 without podobranch (Fig. 1L).	Maxilliped 2 with podobranch.
9	Maxilliped 3 without exopod (Figs 2A, 5A).	Maxilliped 3 with or without exopod.
10	Pereopod 1 fingers absent (Figs 2B, 5B, C).	Pereopod 1 fingers minute or completely reduced.
11	Pereopods 2 always subequal; basis without small process on lateral surface of basis; carpus consistently divided into 3 articles (Figs 2C, 5D, 6D).	Pereopods 2 subequal or unequal; basis without small process on lateral surface of basis; division of carpus highly variable, but never 3-articulated.
12	Arthrobranchs absent from maxilliped 3 and pereopods.	Arthrobranchs usually present on maxilliped 3 and pereopods 1–4.

Supplementary figures of diagnostic characters can be found in Hayashi (1975: figs 1–3), Bruce (1983: figs 1–5), Hayashi (2007a: figs 538, 539, 542a–f), Hayashi (2007c: figs 557–559a–e), Horká et al. (2014: figs 1–8), and Ahyong (2015: figs 9, 10).

Amongst these characters, the division of the carpus of pereopod 2 and quite possibly the absence of ventral rostral teeth can readily be used to differentiate the two families, although determination of their polarity is not straightforward. In Chlorotocellidae the pereopod 2 car-

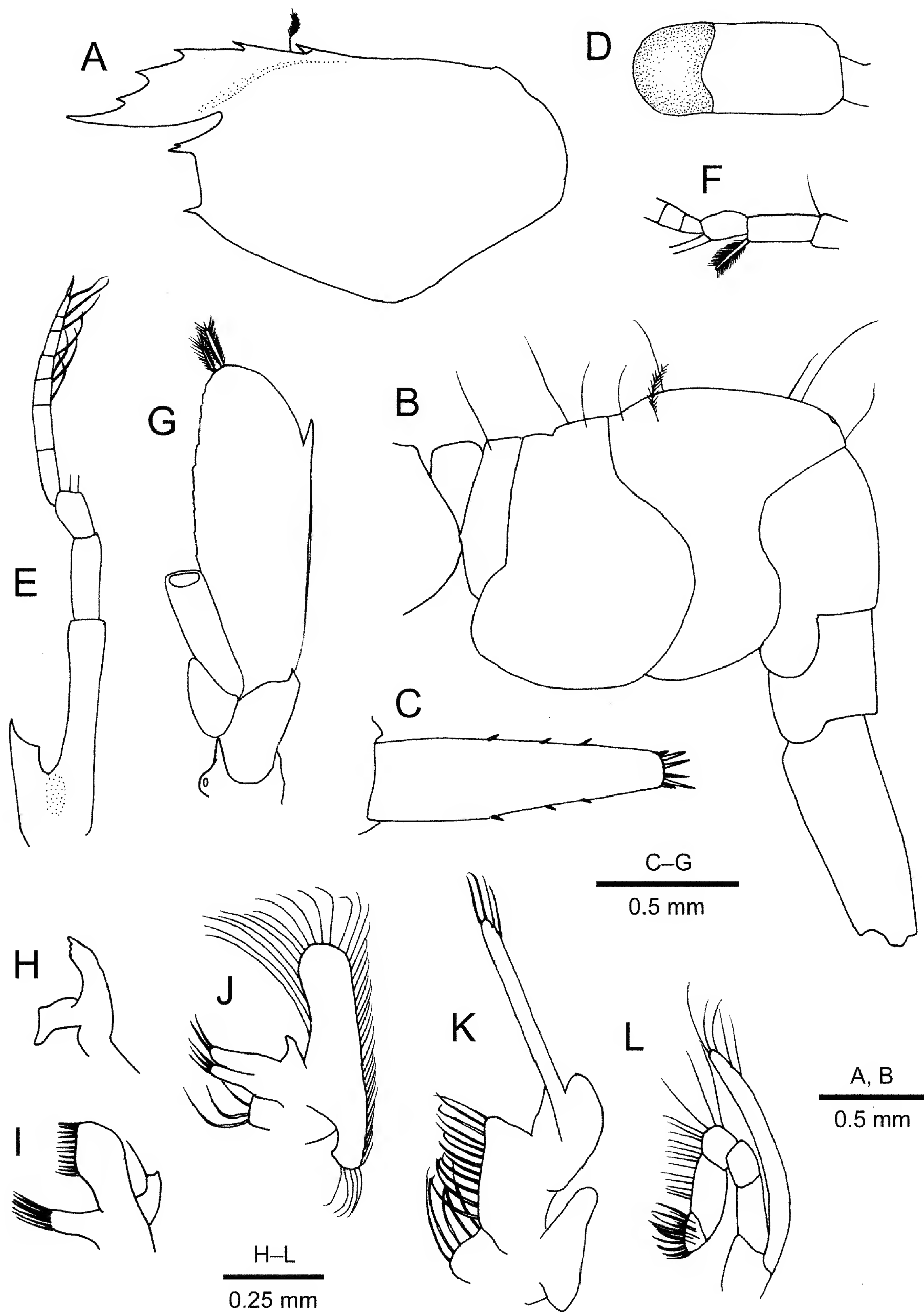


Figure 4. *Chlorocurtis jactans* (Nobili, 1904), ovigerous female (cl 1.3 mm), CBM-ZC 11596. **A.** Carapace, lateral view; **B.** Pleon, lateral view; **C.** telson, dorsal view; **D.** Left eye, dorsal view; **E.** Left antennule, dorsal view (inner flagellum damaged); **F.** Right antennular peduncle, distal 2 articles, mesial view; **G.** Left antenna, ventral view (flagellum missing); **H.** Left mandible, outer view; **I.** Left maxillule, outer view; **J.** Left maxilla, outer view; **K.** Left maxilliped 1, outer view; **L.** Left maxilliped 2, outer view (epipod broken off).

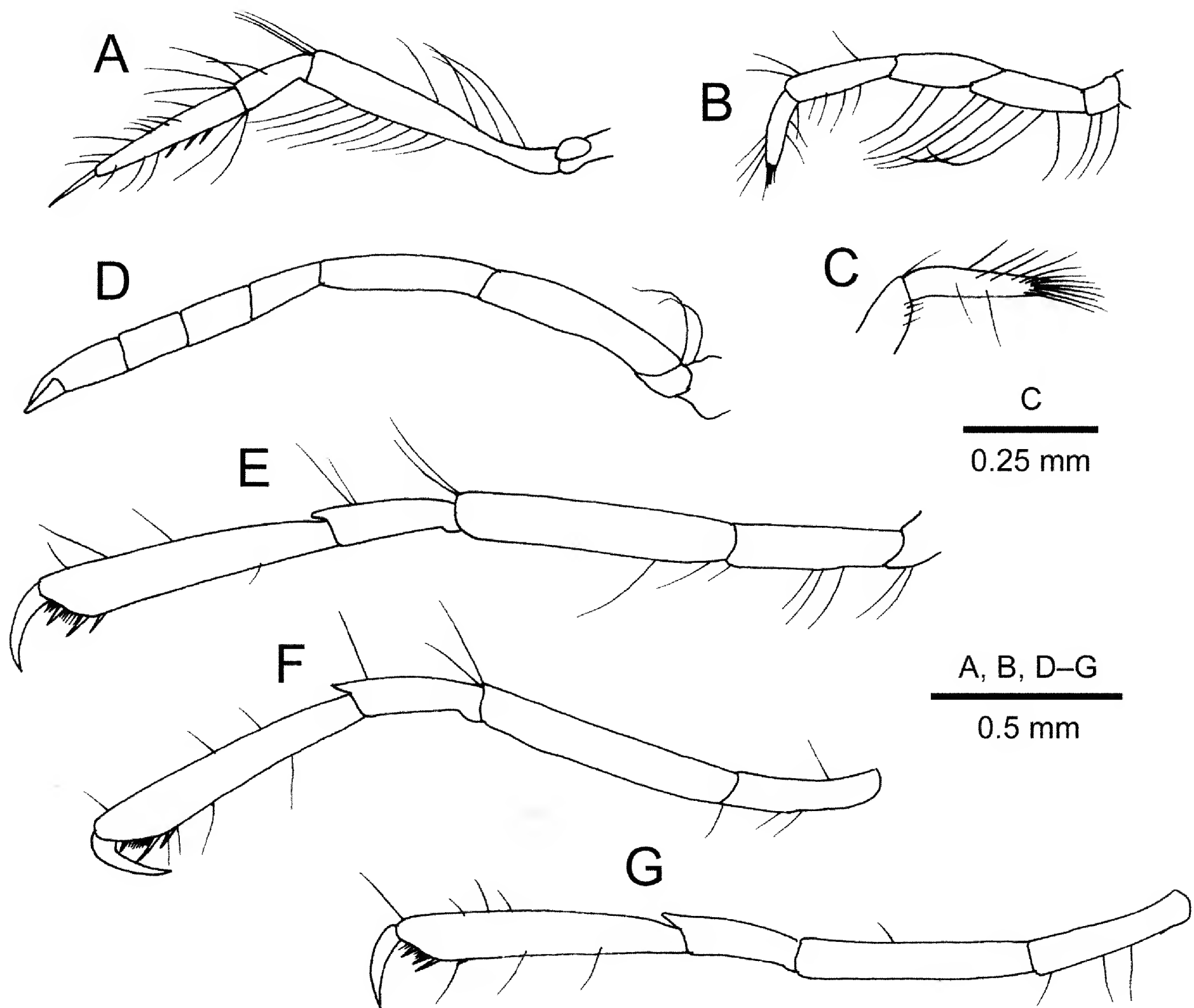


Figure 5. *Chlorocurtis jactans* (Nobili, 1904), ovigerous female (cl 1.3 mm), CBM-ZC 11596, left thoracic appendages in lateral view (except for C). **A.** Maxilliped 3; **B.** Pereopod 1; **C.** Same, propodus, mesial view; **D–G.** Pereopods 2–5, respectively.

pus is consistently divided into three articles, whereas in Pandalidae, the number of the carpal articles is quite variable according to taxa, but none are tri-articulate (cf. Komai 1994). The absence of ventral rostral teeth is also reported in three taxa of the pandalid genus *Plesionika* (Chace 1985) but with doubt (see Chace 1985; Komai et al. 2005; Hayashi 2009; Komai 2011; Li and Chan 2013). Such a similarity, if really present, can be resulted from homoplasy (Liao et al. 2019).

According to the Ancestral State Reconstruction (ASR) analysis by Liao et al. (2019), Pandalidae is characterized by the following synapomorphic features: (1) second article of the antennular peduncle with a few minute spiniform setae on the dorsodistal margin (Fig. 6A); (2) mandibular palp consisting of three articles (Fig. 6B); and (3) basis of pereopod 2 bearing a small process on the lateral surface (Fig. 6C). In these regards, Chlorotocellidae shows the following plesiomorphic states: (1) mandibular palp tends to be reduced, being absent or consisting of two articles at most (Figs 1H, 4H); (2)

second article of the antennular peduncle is unarmed on the dorsodistal margin (Figs 1A, F, 4E); and (3) basis of pereopod 2 being unarmed (Fig. 6D).

Nevertheless, an assessment of the polarity of the development of the mandibular palp is fraught with difficulty and heavily dependent on outgroup selection. In Caridea in general, however, a reduction of the mandibular palp is considered to be derived (e.g., Christoffersen 1987, 1989), as compared to the well-developed palp in Dendrobranchiata and most other Decapoda.

Furthermore, the other two characters are subject to reversal within Pandalidae (Komai 1994; Liao et al. 2019). In species of *Thalassocaris* and *Chlorotocoides* (previously in their own family Thalassocarididae, but now considered part of Pandalidae), the second article of the antennular peduncle is devoid of spiniform setae and the basis of the second pereopods unarmed (Komai 1994).

In addition to the three aforementioned characters, the possession of a rounded laminar expansion at the inner distal angle of the first article of the mandibular palp

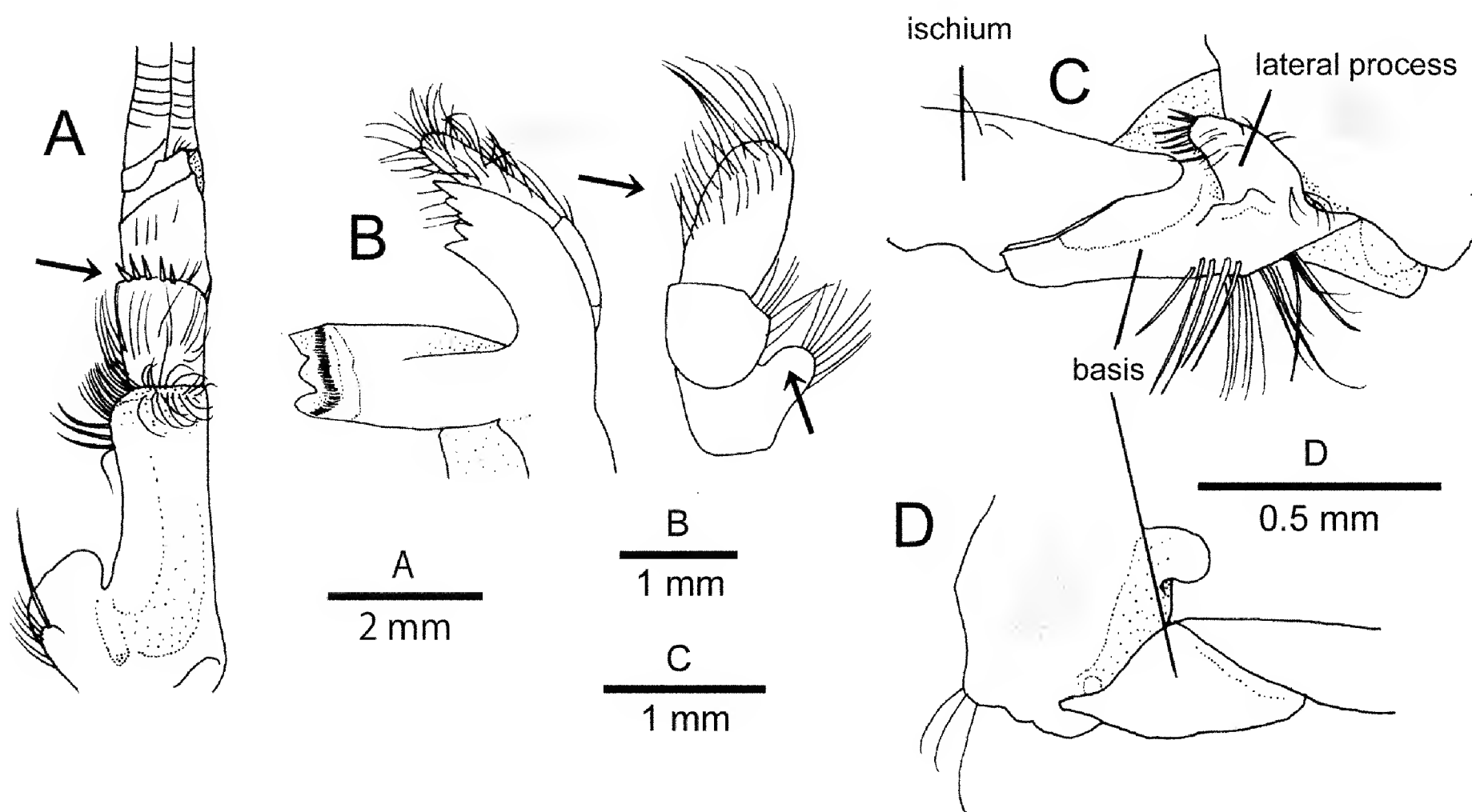


Figure 6. **A, B.** *Pandalus montagui* Leach, 1814, transitional male (cl 10.5 mm), CBM-ZC 3422; **C.** *Heterocarpus ensifer* A. Milne-Edwards, 1881, male (cl 33.0 mm), HUMZ-C 255; **D.** *Chlorotocella gracilis* Balss, 1914, male (cl 4.1 mm), HUMZ-C 1556. **A.** Left antennular peduncle, dorsal view; **B.** Left mandible, outer view; inset, palp, lateral view; **C.** Basis of left pereopod 2; **D.** Basis of right pereopod 2.

(Fig. 6B, inset) might be synapomorphic to Pandalidae (Komai 1994; Liao et al. 2019), although a secondary loss of this structure is observed in *Thalassocaris* and *Chlorotocoides* (Komai 1994; Liao et al. 2019). It is impossible to evaluate the homology of this character for the taxa assigned to Chlorotocellidae, because in those taxa, the mandibular palp only comprises two articles (*Chlorotocella*) or is absent (*Chlorocurtis*, *Anachlorocurtis* and *Miropandalus*), and the homology of the articles has not been established in taxa with different numbers.

Genus *Chlorotocella* Balss, 1914

Chlorotocella Balss 1914: 33; Holthuis 1955: 118, 127; 1993: 263, 266; Hayashi 2007a: 150.

Type species. *Chlorotocella gracilis* Balss, 1914.

Diagnosis. Rostrum elongate, very slender, gently upturned, exceeding far beyond distal margin of antennal scaphocerite, dorsally armed with two teeth around rostral base (one postrostral); ventral margin unarmed (Fig. 1A). Carapace without projections on dorsal midline; **supraorbital tooth present; suborbital lobe prominent, longer than antennal tooth, distally rounded, slightly constricted at base;** pterygostomial tooth moderately small (Fig. 1A, B). Pleomeres 1–6 dorsally rounded; **pleomeres 4 and 5 each with pair of posterolateral teeth; pleomere 5 with deep transverse groove near posterodorsal margin;** pleuron with small posteroventral

tooth (Fig. 1C). **Pleomere 6 with minute postero-median tooth;** posteroventral angle with minute tooth (Fig. 1C). **Telson with additional anterior pair of spiniform setae located more mesial to other lateral series of spiniform setae;** posterior margin narrow, slightly produced medially, with two pairs of unequal spiniform setae (Fig. 1D). Eye with ocellar spot (nebenauge) (Fig. 1E). **Antennular peduncle article 1 armed with tooth on dorsodistal margin** (Fig. 1A, F). Mandible with two-articulated palp (Fig. 1H). **Maxillule palp without distal outer lobule** (Fig. 1I). Maxilla with short, moderately slender endopod (Fig. 1J). Maxilliped 1 with coxal and basal endites well developed, both with row of setae on mesial margin; exopodal flagellum well developed (Fig. 1K). Maxilliped 2 endopod with dactylus located at distal portion of propodus; exopod well developed (Fig. 1L). Pereopod 1 fingers completely reduced (Fig. 2B). Pereopods 3–5 propodi each with closely spaced, short to long spiniform setae in distal 0.2; carpi each with few spiniform setae on lateral surface; meri usually with spiniform setae arranged in two rows; ischia each with spiniform seta on ventral surface in pereopods 3 and 4 (Fig. 2D–F). Male pleopod 1 endopod without appendix interna (Fig. 1M).

Composition. *Chlorotocella gracilis*; *C. spinicaudus* (H. Milne Edwards, 1837).

Distribution. Indo-West Pacific, South Australia; shallow subtidal to 60 m; free living in algal-rich habitats or facultatively associated with gorgonarians and hydroids.

Remarks. At present, two species are assigned to *Chlorotocella* (De Grave and Fransen 2011), viz., *C. gracilis* (type species) and *C. spinicaudus*. Holthuis (1995) clarified that *Hippolyte spinicaudus* H. Milne Edwards, 1837 was a senior subjective synonym of *Pandalus leptorhynchus* Stimpson, 1860. In addition, a third taxon, which was placed in the synonymy of *C. spinicaudus* by De Grave and Fransen (2011), *Pandalus (Parapandalus) leptorhynchus* var. *gibber* Hale, 1924, was described from Gulf St Vincent, South Australia, characterized mainly by the prominently crested tergite of pleomere 3 (see Hale 1927). This taxon has been seldom mentioned in more recent literature. Ledoyer (1984) illustrated a specimen with a weakly crested tergite from Nouméa (New Caledonia), which he assigned to *C. gracilis*, but left it open as to whether this should be a distinct species or merely a “forme *gibber*” of *C. gracilis*. In contrast, Poore (2004) treated the taxon as a distinct species, *C. gibber* (Hale), noting it was restricted to the Gulf St Vincent (South Australia).

Because no modern descriptions are available for *C. spinicaudus*, the above generic diagnosis is largely based on *C. gracilis* and the summary information available on the other species. It seems possible that Hale’s (1924) taxon might be distinct from *C. gracilis* and *C. spinicaudus* as it is characteristic by having a highly crested tergite of the pleomere 3 (Hale 1924: pl. 4, fig. 6; 1927: fig. 35). Re-assessment of the taxonomic status of *C. spinicaudus* and *Pandalus (Parapandalus) leptorhynchus* var. *gibber* will be necessary to fully clarify the taxonomy of the genus.

Genus *Chlorocurtis* Kemp, 1925

Chlorocurtis Kemp 1925: 272, 279; Holthuis 1955: 118, 127; 1993: 263, 265; Hayashi 2007b: 248.

Type species. *Chlorocurtis miser* Kemp, 1925.

Diagnosis. Rostrum short but well developed, directed forward, reaching midlength of article 1 of antennular peduncle; **dorsal margin crested**, with five to seven teeth including two or three postrostral; ventral margin unarmed (Fig. 4A). Carapace without conspicuous projections on dorsal midline; no supraorbital tooth; suborbital lobe absent; pterygostomial tooth moderately small (Fig. 4A). Pleomeres 1–5 dorsally rounded; **pleomeres 1–3 with long, erect setae on dorsal surface**; pleomeres 4 and 5 each without pair of posterolateral teeth; pleomere 5 without deep transverse groove near posterodorsal margin, pleuron rounded posteriorly; pleomere 6 without posteromedian tooth, posteroventral angle unarmed (Fig. 4B). Telson posterior margin rather broad, convex, with three pairs of unequal spiniform setae (Fig. 4C). Eye without ocellar spot (nebenauge) (Fig. 4D). Antennular peduncle article 1 unarmed on dorsodistal margin; stylocerite obliquely truncate distally, distolateral angle terminating in tooth, distomesial angle subacute or blunt; outer

flagellum shorter than peduncle, distal portion reduced to single article (Fig. 4E). **Short, club-like, modified setae present at ventrodistal margin of article 2 of antennular peduncle (one seta) and distal margin of antennal scaphocerite (two setae)** (Fig. 4F, G.). Mandible without palp (Fig. 4H). Maxillule palp with well-developed distal outer lobule (Fig. 4I). Maxilla with short, distally tapering endopod (Fig. 4J). Maxilliped 1 with coxal and basal endites well developed, both with row of setae on mesial margin; exopodal flagellum well developed (Fig. 4K). Maxilliped 2 endopod with dactylus located at distal portion of propodus; exopod well developed (Fig. 4L). **Pereopods 3–5 propodi broadened distally, oblique flexor distal margins each with short rows of narrowly spaced long spiniform setae flanking field of short setae, forming prehensile structure together with dactylus folded back**; carpi without spiniform setae on lateral surface; meri without spiniform setae; ischia without spiniform seta on ventral surface (Fig. 5E–G). Male pleopod 1 endopod without appendix interna.

Composition. Monotypic.

Distribution. Indo-West Pacific, intertidal to 10 m; sea-grass beds.

Remarks. *Chlorocurtis* was originally established for *Chlorocurtis miser* by Kemp (1925).

Later, Holthuis (1947) synonymized *Chlorocurtis miser* with *Virbius (?) jactans* (Nobili, 1904) without any argumentation, although clearly correct. This synonymy has since been widely adopted (e.g., Holthuis 1955; Ledoyer 1968, 1984; Bruce 1976; Hayashi 2007b; Holthuis 1993; De Grave and Fransen 2011; Gan and Li 2018).

Genus *Anachlorocurtis* Hayashi, 1975

Anachlorocurtis Hayashi 1975: 173; 2007a; 147; Holthuis 1993: 263; Horká et al. 2014: 12.

Type species. *Anachlorocurtis commensalis* Hayashi, 1975.

Diagnosis. Rostrum short, ascending in adults, reaching midlength of article 1 of antennular peduncle, terminating in acute tip or obliquely truncate distally with irregular dentition; dorsal and ventral margins usually unarmed. Carapace without supraorbital tooth; dorsal midline with two prominent processes, anterior one postrostral, irregularly denticulate anteriorly, posterior one cardiac in position, directed forward, acuminate; suborbital lobe absent; pterygostomial angle rounded, unarmed. Pleomeres 1–5 dorsally rounded; pleomeres 4 and 5 each without pair of posterolateral teeth. Pleomere 5 without deep transverse groove near posterodorsal margin; pleuron rounded posteriorly. Pleomere 6 without posteromedian tooth; posteroventral angle without tooth. Telson posterior margin truncate or rounded, with five pairs of unequal spiniform

setae. Eye without ocellar spot (nebenauge); *cornea with papilla-like tubercle*. Antennular peduncle article 1 unarmed on dorsodistal margin; stylocerite obliquely truncate distally, both distal angles dentate; outer flagellum shorter than peduncle, distal portion reduced to one or two articles. Mandible without palp. Maxillule palp with well-developed distal outer lobule bearing apical seta. Maxilliped 1 with coxal and basal endites poorly developed, narrow; exopodal flagellum absent. Maxilliped 2 endopod with dactylus located at mesial portion of propodus or fused to propodus; exopod absent. Articulation between carpal article 1 and 2 of pereopod 2 strongly oblique. Pereopods 3–5 propodi slightly narrowing distally, with few widely spaced minute spiniform setae on flexor margin; carpi without spiniform setae on lateral surface; meri of pereopods 3 and 4 each with one spiniform seta distolaterally and one minute spiniform seta at midlength of ventral surface. Male pleopod 1 endopod with small rounded lateral lobe far exceeded by well-developed appendix interna.

For illustrations see Hayashi (1975: figs 1–3), Hayashi (2007a: figs 538, 539, 542a–f); Horká et al. (2014: figs 1–8) and Ahyong (2015: figs 9, 10).

Composition. *Anachlorocurtis commensalis*, *A. occidentalis* Horká, De Grave & Āuriš, 2014, and *A. australis* Ahyong, 2015.

Distribution. Indo-West Pacific, shallow subtidal to 40 m; associated with antipatharian corals.

Genus *Miopandalus* Bruce, 1983

Miopandalus Bruce, 1983: 482; Holthuis 1993: 263, 269; Hayashi 2007c: 585.

Type species. *Miopandalus hardingi* Bruce, 1983.

Diagnosis. *Rostrum absent*. Carapace without supra-orbital tooth; *dorsal midline with two very prominent, erect processes, anterior one postrostral, tapering, posterior one cardiac in position, slightly curved, anteriorly, blunt*; suborbital lobe absent; pterygostomial angle rounded or angular. *Pleomere 1 with prominent protuberance; pleomere 3 with triangular crest on posterior half of dorsal midline*; pleomeres 4 and 5 each without pair of posterolateral teeth; pleomere 5 without deep transverse groove near posterodorsal margin; pleuron rounded posteriorly. Pleomere 6 without posteromedian tooth; posteroventral angle unarmed. Telson posterior margin rounded, with several short spiniform setae. Eye without ocellar spot (nebenauge); cornea without papilla-like tubercle. Antennular peduncle article 1 unarmed on dorsodistal margin; *stylocerite subtruncate distally, bi- or tridentate*; outer flagellum shorter than peduncle, distal portion completely reduced. Mandible without palp. Maxillule palp with well-developed distal outer lobule, without apical seta. Maxilliped 1 with coxal and

basal endites poorly developed, narrow; endopod stout; exopodal flagellum absent. Maxilliped 2 endopod with dactylus fused to propodus; exopod absent. Articulation between carpal article 1 and 2 of pereopod 2 strongly oblique. Pereopods 3–5 propodi narrowing distally, with few minute spiniform setae on flexor margin; carpi without spiniform setae on lateral surface; meri of pereopods 3 and 4 unarmed. Male pleopod 1 endopod with small rounded lateral lobe far exceeded by well-developed appendix interna.

For illustrations, see Bruce (1983: figs 1–5) and Hayashi (2007c: figs 557–559a–e).

Composition. Monotypic.

Distribution. West Pacific, subtidal to 58 m; associated with antipatharian corals.

Acknowledgements

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Eulimacrostoma gen. nov., a new genus of Eulimidae (Gastropoda, Caenogastropoda) with description of a new species and reevaluation of other western Atlantic species

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Abstract

A new genus and a new species of Eulimidae are described based on the shell morphology and on the host-parasite relationship of the type species. *Eulimacrostoma microsculpturata* Souza & Pimenta **gen. nov.** and **sp. nov.** parasitizes a starfish of the genus *Luidia* and has an elongated, conical, straight, or slightly curved shell, a protoconch with a brownish spiral band and convex whorls, a peculiar large and broad aperture with a strongly protruding outer lip, and microsculpture of axial lines on the teleoconch. Four other species are included in the genus, all from the western Atlantic: *Eulimacrostoma chascanon* (Watson, 1883), **comb. nov.**, *Eulimacrostoma fusus* (Dall, 1889), **comb. nov.**, *Eulimacrostoma lutescens* (Simone, 2002), **comb. nov.**, and *Eulimacrostoma patula* (Dall & Simpson, 1901), **comb. nov.** Newly available material of *Eulimacrostoma patula* expands the known geographic distribution of this species in the Caribbean to the north coast of Brazil. *Eulimacrostoma chascanon* and *Eulimacrostoma fusus* and *Eulimacrostoma lutescens* are known only by the type series which was re-examined. A redescription is provided for *Eulimacrostoma chascanon* and *Eulimacrostoma fusus*. Species within *Eulimacrostoma* differ mainly by teleoconch sculpture, the presence or absence of an umbilical fissure, and shell dimensions. Lectotypes are designated for *Eulimacrostoma chascanon*, *Eulimacrostoma fusus*, and *Eulimacrostoma patula*.

Key Words

biodiversity, micromolluscs, parasitic snails shell morphology, taxonomy, Vanikoroidea

Introduction

Eulimidae Philippi, 1853 is a diverse group of marine gastropods comprising more than 1,000 valid species and more than 90 valid genera (MolluscaBase 2018). A massive collection effort in New Caledonia included eulimids as one of the most species-rich families of marine gastropods and about 80% of the species were possibly new to science (Bouchet et al. 2002). Eulimids are parasites of the five extant classes of Echinodermata and shows different life strategies (e.g., ectoparasitism, endoparasitism, gall formers) (Warén 1983; Takano and Kano 2014).

Warén (1983) suggested that all species in a given genus parasitize a single class of Echinodermata, with

the exception of *Vitreolina* Monterosato, 1884, which is known to exploit ophiuroids and echinoids. Takano et al. (2018: 215) suggested that *Vitreolina* contains distantly related lineages and, thus, it is probably not monophyletic and Warén's (1983) rule would apply without exceptions.

Genera of Eulimidae that parasitize echinoderms of the class Asterozoa are *Apicalia* A. Adams, 1862, *Asterolamia* Warén, 1980, *Asterophila* Randall & Heath, 1912, *Niso* Risso, 1826, *Paramegadenus* Humphreys & Lützen, 1972, *Parvioris* Warén, 1981, *Stilifer* Broderip, 1832, and *Thyca* H. Adams & A. Adams, 1854 (Warén 1983). The shell shape in these genera varies from the usual conical format to capuliform, or the animal is shell-less. All kinds of life strategies are present among them.

Recently, one eulimid attached to the starfish *Luidia ludwigi scotti* Bell, 1917 (Luidiidae), collected in the upper bathyal zone off Florida, USA, was studied by the authors and did not correspond to any other species and genus known to parasitize asteroids or other echinoderms. The availability of a single specimen hampered the description of the taxa, but recently we identified shells of the same species from nearby localities in malacological collections, which enabled the present description.

Material and methods

The material examined is housed in the following malacological collections: Academy of Natural Sciences of Philadelphia, Drexel University, Philadelphia, Pennsylvania, USA (ANSP); Florida Museum of Natural History, Florida University, Gainesville, Florida, USA (FLMNH); Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA (MCZ); Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Rio de Janeiro, Brazil (MNRJ); Natural History Museum, London, United Kingdom (NHMUK); Smithsonian National Museum of Natural History, Washington DC, USA (USNM).

During the course of this study, a fire destroyed several collections of MNRJ (Zamudio et al. 2018), including material cited herein. Some vouchers and types from other institutions on loan were also at the MNRJ and were destroyed. These lots are indicated with an asterisk (*) in the material examined.

Some samples were collected by large projects and oceanographic expeditions, such as: (1) Eolis Cruises, organized by John B. Henderson, collected by the yacht *Eolis* between 1910–1916 in the Florida Keys, USA (see Bieler and Mikkelsen 2002 for approximate coordinates of the collecting stations); (2) Johnson–Smithsonian Deep-sea expedition, collected by the yacht *Caroline* in 1933, in deep waters of Puerto Rico, and sponsored by Eldridge R. Johnson (see Bartsch 1933); (3) “A Multidisciplinary Amazon Shelf Sediment Study” (AMASSEDs), collected by the Research Vessel (R/V) *Columbus Iselin* in 1990 near the mouth of the Amazon River, northern Brazil; (4) “Terres Australes et Antarctiques Françaises, cruise MD55” (TAAF MD55), a joint project of the “Muséum National d’Histoire Naturelle”, France, and the “Universidade Santa Úrsula”, Brazil, collected by the R/V *Marion Dufresne* between May and June 1987 (Tavares 1999).

Taxonomic identifications were based on conchological features in comparison with original descriptions and illustrations and examination of type material. Terminology of shell features follows Bouchet and Warén (1986) and Souza and Pimenta (2019). The outer lip may be opisthocline (connection at the suture behind the distal region), prosocline (connection in front of the distal region) or orthocline (in the same plane). Incremental scars are older positions of the outer lip and when present are

usually deep and well demarcated; they are formed during the periodical growth of the eulimids (see Bouchet and Warén 1986: 310 for details). Microsculpture of axial lines usually appears in regular intervals, from suture to suture in each whorl and do not interrupt the suture as do the incremental scars. Growth lines are usually present at irregular intervals and do not reach from one suture to the other. Measurements of the shell are based on Souza and Pimenta (2019): shell length (SL); body whorl length (BWL); aperture length (AL); shell width (SW); aperture width (AW).

Abbreviations of generic names: *Eulima* Risso, 1826 (*E.*); *Eulimacrostoma* gen. nov. (*Eu.*).

Systematics

Family Eulimidae Philippi, 1853

Genus *Eulimacrostoma* Souza & Pimenta, gen. nov.

<http://zoobank.org/8C4C4750-0C97-4AB1-B092-1D37ADB4E3FE>

Type species. *Eulimacrostoma microsculpturata* Souza & Pimenta, sp. nov. Recent, northwestern Atlantic and Caribbean.

Diagnosis. Eulimids parasitic on asteroids. Shell elongated, conical, straight or slightly curved. Protoconch subcylindrical, smooth. Teleoconch with slightly convex whorls, several incremental scars and microsculpture of axial lines, wide brownish spiral bands, a large and spread aperture, occupying between 60–70% of the body whorl length, and an orthocline outer lip, strongly protruding.

Etymology. *Eulima*, due to the systematic affinity and for being one of the most common names of the family, in combination with *Macros*, Gr. = long; and *Stomatos*, Gr. = mouth; in reference to the broad shape of the shell aperture.

Eulimacrostoma microsculpturata Souza & Pimenta, sp. nov.

<http://zoobank.org/F45DF003-4D73-4689-A283-20B0CD5131A6>

Figures 1A–G, 2A–G

Melanella patula auct. non. (Dall & Simpson, 1901): Dall (1927, in part.: 67).

Type material. Holotype: USNM 429762. Paratypes: USA: Florida: Eolis stn. 307, off Fowey Light (~25°35'26"N, 80°05'48"W, 128 m): USNM 417624 [1 shell]; Eolis stn. 362, off Fowey Light (~25°35'26"N, 80°05'48"W, 174 m): USNM 417511* [3 shells]; Eolis stn. 370, off Ajax Reef (~25°24'00"N, 80°08'00"W, 128–165 m): USNM 417497 [3 shells]; Eolis stn. 376, off Caesars Creek (~25°23'02"N, 80°12'37"W, 165 m): USNM 433081* [7 dd]; off Alligator Reef Light, Lower Florida Keys (183 m), coll. 21/iv/1967: ANSP 312431* [1 shell];

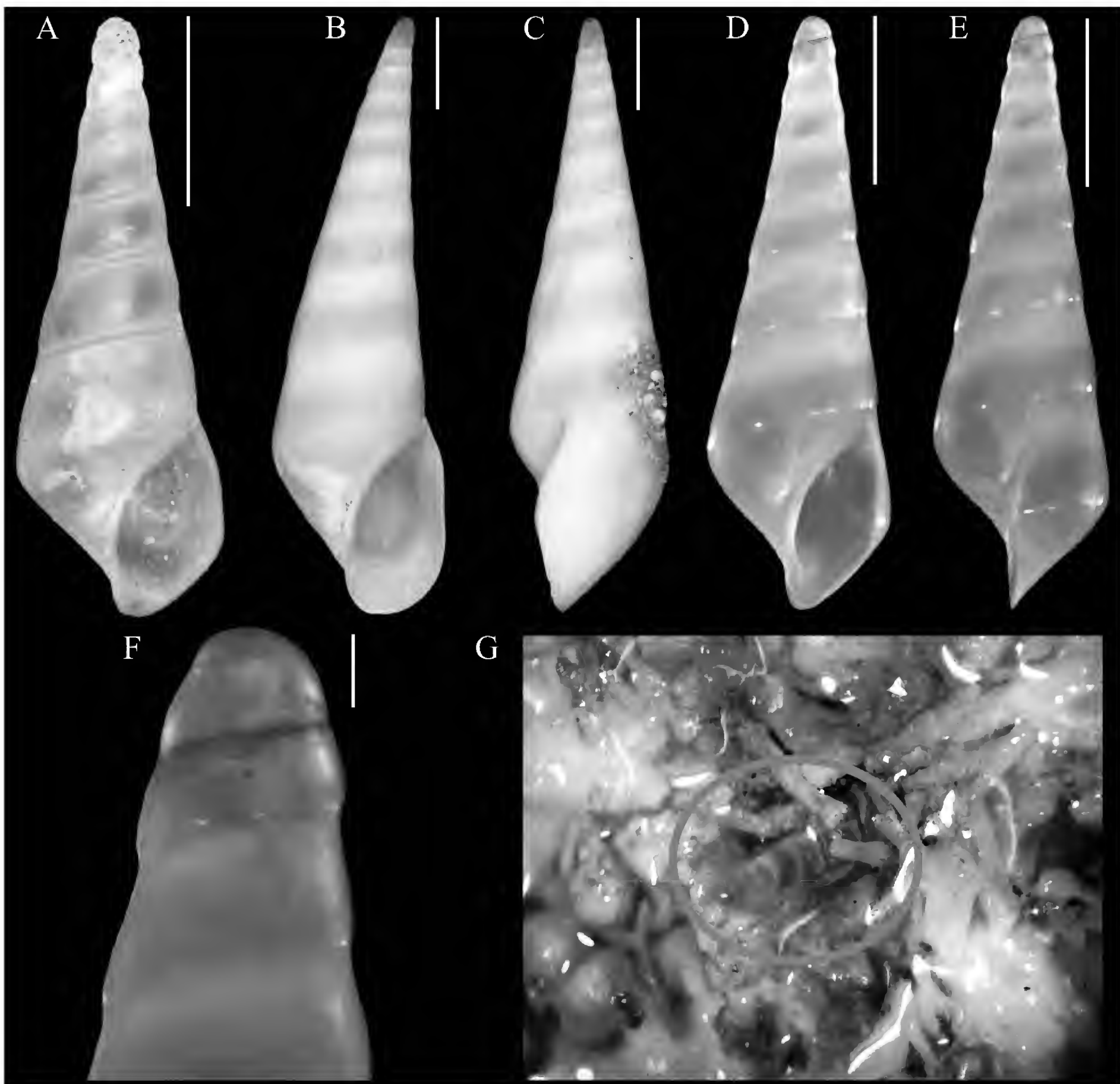


Figure 1. *Eulimacrostoma microsculpturata* gen. nov. and sp. nov. **A.** Holotype (USNM 429762); **B, C.** Paratype (USNM 433081); **D–G.** Paratype (FLMNH uncatalogued.) **A, B, D.** Shell in frontal view; **C, E.** Shell in lateral view; **F.** Detail of apical whorls in frontal view; **G.** Specimen attached to the host *Luidia ludwigi scotti* Bell, 1917 (Echinoderm collection, FLMNH 5042), red ellipse indicates the eulimid. Scale bars: 1 mm (A–E); 100 μ m (F).

Eolis stn. 300, off Sand Key ($\sim 24^{\circ}27'16''\text{N}$, $81^{\circ}52'28''\text{W}$, 132 m): USNM 433039 [1 shell]; Florida Straits ($24^{\circ}30'48.60''\text{N}$, $83^{\circ}30'1.44''\text{W}$, 280 m), attached around the mouth of *Luidia ludwigi scotti* Bell, 1917 (FLMNH 5042, Echinodermata collection), coll. F. Michonneau, 13/iii/2007: FLMNH* (uncatalogued) [1 specimen].

Etymology. The epithet alludes to the microsculpture characteristic of the present species.

Type locality. Puerto Rico: off San Juan, Johnson–Smithsonian Deep-sea expedition stn. 10 ($18^{\circ}29'20''\text{N}$ – $18^{\circ}30'24''\text{N}$,

$66^{\circ}05'30''\text{W}$ – $66^{\circ}04'15''\text{W}$, 219–293 m), coll. Yacht *Caroline*, 02/ii/1933.

Diagnosis. Eulimid parasitic on starfish, with an elongated shell, presenting microsculpture of axial lines, dome-shaped apex, a narrow brownish spiral band close to the suture in the protoconch and a wide brownish spiral band along the teleoconch, a high, wide and spread aperture. Umbilicus absent.

Description. Shell conical with an obtuse apex, reaching about 7.3 mm long and 2.0 mm wide. Protoconch vit-

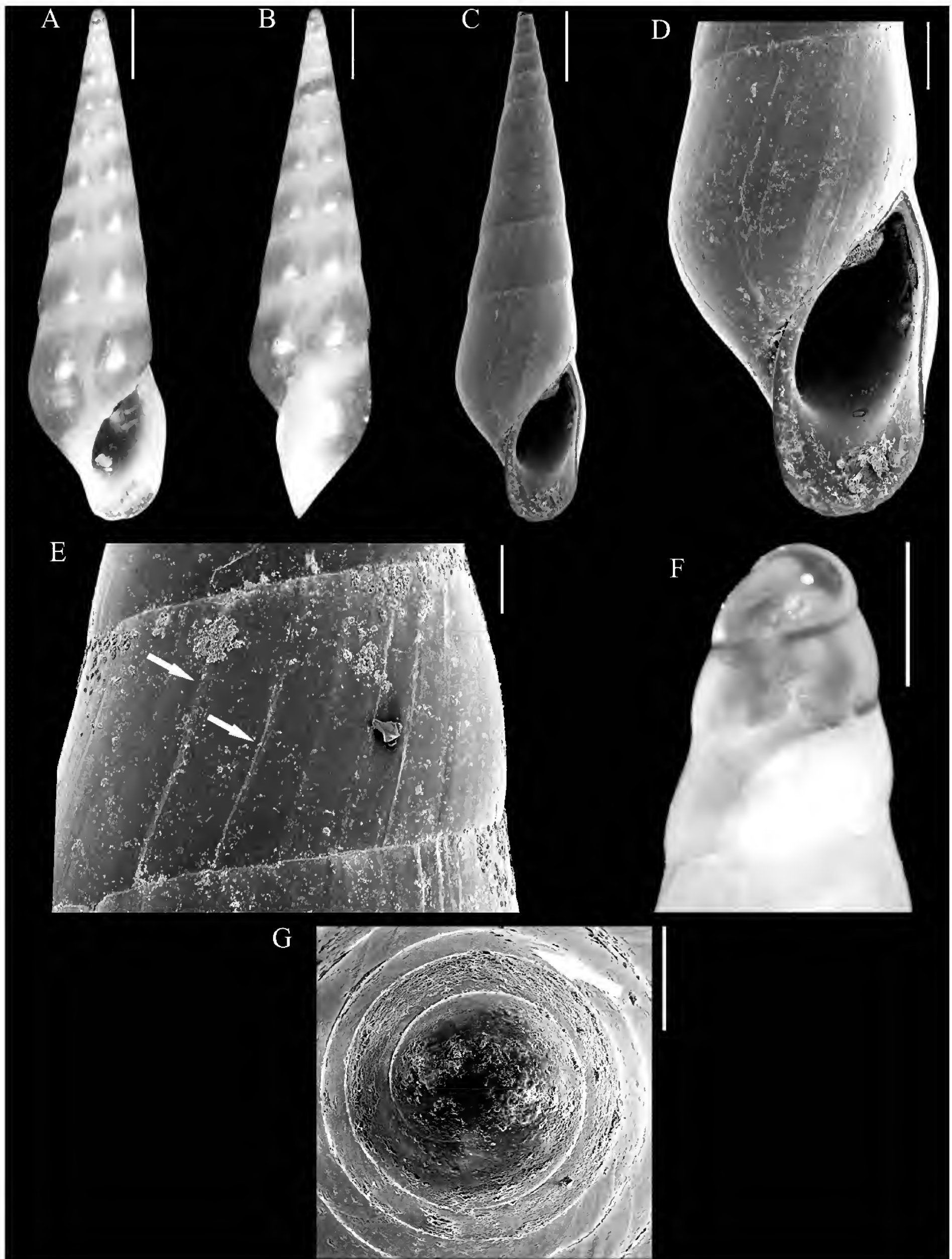


Figure 2. *Eulimacrostoma microsculpturata* gen. nov. and sp. nov. **A–E.** Paratype (ANSP 312431); **F.** Paratype (USNM 433081); **G.** Paratype (USNM 417511). **A, C.** whole shell in ventral view; **B.** Shell in lateral view; **D.** Detail of body whorl in frontal view; **E.** Detail of teleoconch surface, white arrows indicates the microsculpture of axial lines; **F.** Detail of apical whorls in frontal view; **G.** Detail of protoconch in apical view, white arrow indicates the transition protoconch-teleoconch. Scale bars: 1 mm (A–C); 500 μ m (D); 100 μ m (E, G); 200 μ m (F).

Table 1. Measurements (in mm, except for number of whorls) of *Eulimacrostoma* species studied.

Taxon	Catalog number	Status	Wh	SL	BWL	AL	SW	AW
<i>Eu. microsculpturata</i>	USNM 429762	Holotype	8	3.16	1.60	1.06	1.08	0.60
	ANSP 312431	Paratype	12	7.28	3.34	2.21	1.97	1.17
	USNM 433081	Paratype	11	6.50	3.09	2.10	1.88	1.10
	USNM 1273894	Paratype	11	6.55	3.04	1.99	1.79	1.15
	USNM 1273894	Paratype	10.5	6.32	2.88	1.90	1.80	1.06
	USNM 433081	Paratype	10	6.03	2.94	1.97	1.75	1.03
	USNM 433081	Paratype	10	6.10	2.94	1.97	1.75	1.03
<i>Eu. chascanon</i>	NHMUK 1887.2.9.1587	Lectotype	13	4.49	1.96	1.23	1.15	0.65
<i>Eu. fusus</i>	USNM 87273	Lectotype	12	11.24	5.28	3.55	2.78	1.55
	MCZ 7515	Paralectotype	13	12.29	5.63	3.81	2.75	1.62
<i>Eu. lutescens</i>	MNHN-IM 2000-5662	Holotype	10	8.88	4.47	3.05	2.90	1.60
	MZSP 34514	Paratype	10†	10.62	5.00	3.22	3.15	1.82
	MNHN-IM		9	7.58	3.75	2.69	2.28	1.41
<i>Eu. patula</i>	USNM 160202	Lectotype	9	4.53	2.20	1.50	1.50	0.91
	MNRJ 34479		8.5	3.99	2.07	1.42	1.50	0.89
	MNRJ 34476		9	4.24	2.07	1.37	1.42	0.83

† Apex broken. Abbreviations: AL: aperture length; AW: aperture width; BWL: body whorl length; SL: shell length; SW: shell width.; Wh: whorls

reous, with a brownish spiral band close to the suture, subcylindrical, about 2.5 whorls, 300 µm wide, 400 µm in height, smooth, transition to teleoconch marked by a subtle incremental scar and the end of the brownish spiral band. Teleoconch with about nine whorls of sinuous outline, convexity more attenuated on the lower region of each whorl; suture deep, well impressed, sloping; sub-sutural zone occupying about 1/5 of the whorl height; surface glossy, presenting several incremental scars and microsculpture of opisthocline axial lines; incremental scars well developed, appearing in irregular intervals; microsculpture of axial lines present at fairly regular intervals between 80–110 µm. Last whorl occupying about 45% of the shell length; base rounded in outline, elongated. Aperture high, occupying about 70% of the body whorl length, wide, pear-shaped, expanded laterally, acute posteriorly, rounded and spread anteriorly; outer lip thin, very sinuous, orthocline, retracted near the suture, after strongly protruding, and retracted in the distal region, maximum projection at the middle of the outer lip height; inner lip sinuous, sloping and well demarcated. Umbilicus absent. Teleoconch whitish or vitreous, fresh specimens usually have the region near the suture uncoloured and the rest of the whorl yellowish to brownish.

Measurements. Holotype USNM 429762: whorls = 8; SL = 3.16 mm; BWL = 1.60 mm; AL = 1.06 mm; SW = 1.08 mm; AW = 0.60 mm. Paratype USNM 433081: Whorls = 11; SL = 6.50 mm; BWL = 3.09 mm; AL = 2.10 mm; SW = 1.88 mm; AW = 1.10 mm.

Geographic distribution. USA: Florida; Puerto Rico.

Bathymetric distribution. From 128 m to 293 m.

Remarks. Dall (1927: 67) cited 20 specimens of “*Melanella patula*” from “off Georgia”. The USNM houses two lots (USNM 108031, USNM 108380, respectively from Fernandina, Florida, USFC stn. 2668, and from Georgia, USFC stn. 2415), that can be attributed to the material stud-

ied by Dall (1927) due to the labels. USNM 108031 contains a single shell with a broken protoconch and an eroded surface. Although the shell is not in perfect condition, it is possible to affirm that it is actually *Eulimacrostoma microsculpturata* sp. nov. by the general shape and teleoconch sculpture. USNM 108380 contains seven shells, most of them immature, which can neither be identified with certainty as *Eulimacrostoma patula* (Dall & Simpson, 1901), comb. nov. nor as *Eulimacrostoma microsculpturata*.

Most specimens of *Eu. microsculpturata* have a straight spire (Figs 1A, 2A), but individuals of the lot USNM 433081 (Fig. 1B) have a slightly curved spire. The curvature is a growth phenomenon related with the position of the incremental scars and usually helps to distinguish species (Bouchet and Warén 1986: 312). However, in the case of *Eu. microsculpturata* the protoconch, color pattern, shape of the aperture, and dimensions are very similar in all individuals and we consider all of them belonging to the same taxon. The holotype USNM 429762 and paratype FLMNH are young individuals and shows a more rhomboid aperture and angulated body whorl, which is a common feature at this stage of growth (Bouchet and Warén 1986: 310; Souza et al. 2018: 926).

Eulimacrostoma chascanon (Watson, 1883), comb. nov. (Fig. 3A–C) differs by the colorless shell, an aperture not so gaping anteriorly and by the proportionally smaller dimensions (Table 1). The lectotype of *E. chascanon* (Fig. 3A, B) is not fresh and the color pattern may have disappeared over time despite the good preservation of the shell surface.

Eulimacrostoma fusus (Dall, 1889), comb. nov. (Fig. 3D–I) differs by being proportionally greater in shell size: the lectotype with about 12 whorls is 11.24 mm long, whereas the holotype of *Eu. microsculpturata* with about 11 whorls is 6.50 mm long. *Eulimacrostoma fusus* has no color pattern and the protoconch is wider than in *Eu. microsculpturata*.

Eulimacrostoma lutescens (Simone, 2002), comb. nov. (Fig. 3J–N) differs by the flatter teleoconch whorls and by the relatively wider and longer shell (holotype MNHN-

IM 2000-5662, 10 whorls, 8.88 mm long, 2.90 mm wide vs paratype USNM 433081 of *Eu. microsculpturata*, 11 whorls, 6.50 mm long).

Eulimacrostoma patula (Fig. 4A–J) has a more truncated base, like some specimens of *Eu. microsculpturata* (Fig. 1A–E), but differs by the presence of an umbilical fissure and by the slightly wider spire angle.

***Eulimacrostoma chascanon* (Watson, 1883), comb. nov.**

Figure 3A–C

Eulima chascanon Watson 1883: 114–115.

E. chascanon: Watson 1886: pl. 35, fig. 4.

Type material. Lectotype (herein designated) NHMUK 1887.2.9.1587. Paralectotype: from type locality: NHMUK Norman Coll. 1979225 [1 shell].

Material examined. Type material.

Type locality. Puerto Rico: North of Culebra Island, off St. Thomas, *Challenger* Expedition stn. 24 (18°38'30"N, 65°05'30"W, 713 m).

Redescription. Shell whitish, conical with an obtuse apex, reaching about 4.5 mm long and 1.2 mm wide, about 13 whorls. Protoconch vitreous, subcylindrical. Shell with about 13 whorls of slightly sinuous outline, with convexity more attenuated on the lower region of each whorl; suture slightly impressed, sloping; subsutural zone not visible; surface glossy, showing axial lines and incremental scars; incremental scars slightly impressed, appearing in irregular intervals. Last whorl occupying about 45% of the shell length; base rounded, elongated. Aperture high, occupying about 60% of the body whorl length, wide, pear-shaped, expanded laterally, acute posteriorly, rounded and spread anteriorly; outer lip thin, very sinuous, orthocone, strongly retracted near the suture, after strongly project, and retracted in the distal region, maximum projection below the middle of the outer lip height; inner lip sinuous, sloping and well demarcated. Umbilicus absent.

Measurements. Lectotype NHMUK 1887.2.9.1587: whorls = 13; SL = 4.49 mm; BWL = 1.96 mm; AL = 1.23 mm; SW = 1.15 mm; AW = 0.65 mm.

Geographic distribution. Known only from the type locality.

Bathymetric distribution. Known only from 713 m.

Remarks. *Eulimacrostoma chascanon* comb. nov. (Fig. 3A–C) presents some similarities to the new genus, such as the elongated shell with moderately convex whorls and the wide aperture with an orthocone outer lip, strongly protruding. The shell surface is very polished, but some axial lines can be observed in the types. An analysis under

SEM would confirm whether these impressions are like the kind of sculpture present in *Eu. microsculpturata*.

The type material of *Eu. chascanon* formerly consisted of two syntypes (Fig. 3A–C) housed in the NHMUK collection. The shell of NHMUK 1887.2.9.1587 is the best preserved one and seems to be the shell figured by Watson (1886: pl. 35, fig. 4), which is here selected as the lectotype (Fig. 3A, B).

Eulimacrostoma fusus (Fig. 3D–I) differs mainly by the proportionally longer shell (lectotype USNM 87273, 12 whorls, 11.24 mm long vs lectotype NHMUK 1887.2.9.1587 of *Eu. chascanon*, 13 whorls, 4.49 mm long) and wider apex.

Eulimacrostoma lutescens (Fig. 3J–N) differs by the much wider protoconch and by the wider and longer teleoconch (holotype MNHN-IM 2000-5662, 10 whorls, 8.88 mm long, 2.90 mm wide vs lectotype NHMUK 1887.2.9.1587, 13 whorls, 4.49 mm long, 1.15 mm wide).

***Eulimacrostoma fusus* (Dall, 1889), comb. nov.**

Figure 3D–I

Eulima fusus Dall 1889: 329, pl. 19, fig. 11B.

Strombiformis fusus: Abbott 1974: 127, fig. 1392 [reproduced from original illustration].

Type material. Lectotype (herein designated) USNM 87273. Paralectotype: Cuba: off Morro Light, “Blake” stn. 100 (457–732 m), coll. R/V *Blake*, xii/1878: MCZ 7515.

Material examined. Type material.

Type locality. Yucatan Strait (1170 m).

Redescription. Shell whitish, conical with an obtuse apex, reaching about 12.4 mm long and 2.8 mm wide, about 12 whorls, apical whorls slightly bent, aperture broad. Protoconch whitish, subcylindrical. Shell with about 12 whorls of slightly sinuous outline, with convexity more attenuated on the lower region of each whorl; suture well impressed, sloping; subsutural zone occupying about 1/5 of the whorl height; surface glossy, showing microsculpture of axial lines and incremental scars; incremental scars well impressed, appearing in irregular intervals. Last whorl occupying about 45% of the shell length; base rounded, slightly truncated. Aperture high, occupying about 65% of the body whorl length, wide, slightly acute and spread anteriorly and acute posteriorly; outer lip thin, very sinuous, orthocone, strongly retracted near the suture, after strongly protruding, and retracted in the distal region; inner lip almost straight, well demarcated. Umbilicus absent.

Measurements. Lectotype USNM 87273: whorls = 12; SL = 11.24 mm; BWL = 5.28 mm; AL = 3.55 mm; SW = 2.78 mm; AW = 1.55 mm.

Geographic distribution. Yucatan Strait and off Cuba.

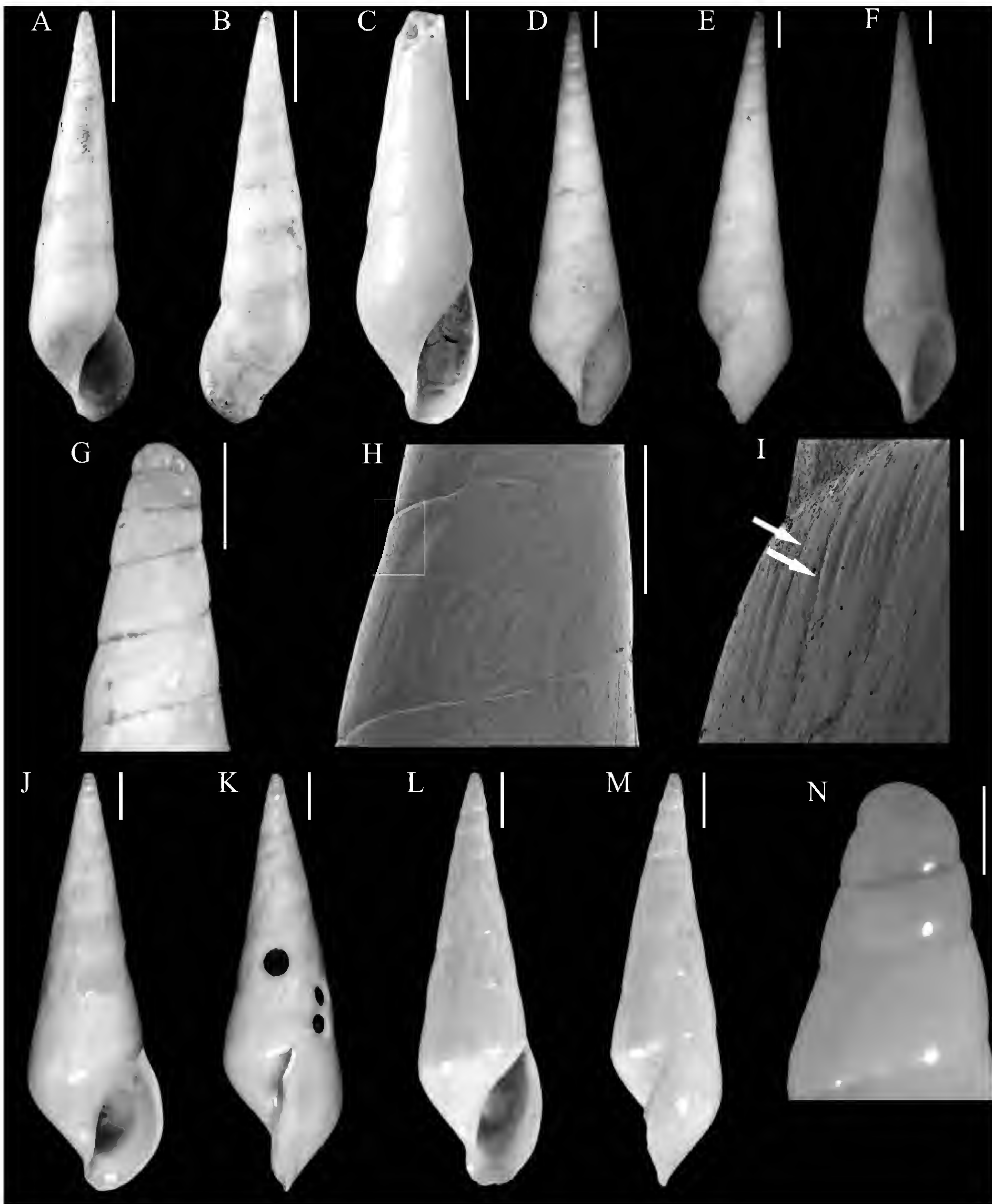


Figure 3. *Eulimacrostoma* spp. **A–C.** *Eulimacrostoma chascanon* (Watson, 1883), comb. nov.: **A, B.** Lectotype herein designated (NHMUK 1887.2.9.1587); **C.** Paralectotype (NHMUK Norman Coll. 1979225); **D–I.** *Eulimacrostoma fusus* (Dall, 1889), comb. nov.: **D, E, G–I.** Lectotype herein designated (USNM 87273); **G.** Paralectotype (MCZ 7515). **J–N.** *Eulimacrostoma lutescens* (Simone, 2002), comb. nov.: **J, K.** Holotype (MNHN-IM 2000-5662); **L–N.** (MNHN-IM uncatalogued), from type locality. **A, C–E, G, K, M.** Shell in frontal view; **B.** Shell in dorsal view; **F, L, N.** Shell in lateral view; **H, O.** Detail of apical whorls in frontal view; **I, J.** Detail of teleoconch surface, white square in I indicates detail in J, white arrows in J indicates microsculpture of axial lines. Scale bars: 1 mm (A–G, I, K–N); 400 μ m (H); 50 μ m (J); 200 μ m (O). Credits: A–C: NHMUK; H, I: USNM; J, K: MNHN-IM.

Bathymetric distribution. From 457 to 1170 m (Dall 1889).

Remarks. The types of *Eulimacrostoma fusus* comb. nov. (Fig. 3D–I) have a partially broken aperture, resembling a channeled aperture (Dall 1889). This condition does not allow for the aperture to be perfectly described, but it is very elongated. The shell is conical, very elongated, with moderately convex and slightly distorted whorls. This species has well-demarcated axial lines in the teleoconch surface (Fig. 3H, I) and a broad subcylindrical protoconch (Figure 3G), which resembles *Eu. microsculpturata*.

Dall (1889) referred to two specimens from different localities, and thus these shells are originally syntypes. Here, USNM 87273 is selected as the lectotype (Fig. 3D, E, G–I).

Dall (1927: 68) recorded 18 shells off Fernandina, Florida, USA, without illustrations. The material cited by Dall was not found in the USNM and is considered dubious. There is no other additional record of the species.

Odé (1989: 67) recorded “*Polygireulima fusus* (Dall, 1889)” without illustrations from Texas, USA, at a depth of 110 m. This record was based on a single specimen with 2.9 mm long, a very small length for the species. We could not find the voucher of Odé’s record. Because there are no illustrations and the length reported by him is small in comparison to the types, we consider this a dubious record.

Eulimacrostoma lutescens (Fig. 3J–N) differs by the wider spire angle of the teleoconch in comparison to the slowly increasing diameter of the teleoconch in *Eu. fusus*.

***Eulimacrostoma lutescens* (Simone, 2002), comb. nov.**

Figure 3J–N

Batheulima lutescens Simone 2002: 56, figs 5–8.

B. lutescens: Rios 2009: 194 (text figure reproduced from original illustration); Dornellas and Simone 2011: 25.

Type material. Holotype MNHN-IM 2000-5662. Paratypes: Brazil: Espírito Santo state: MD55 stn. 42 CB76 (18°58'59"S, 37°49'59"W, 637 m), coll. R/V *Marion Dufresne*, 27/v/1987: MNHN-IM 2000-5664 [1 shell]; Rio de Janeiro state: MD55 stn. 64 CB105 (23°46'59"S, 42°10'00"W, 610 m), coll. R/V *Marion Dufresne*, 02/vi/1987: MNHN-IM 2000-5663 [2 shells]; São Paulo state: Off São Sebastião Island (23°47'S, 42°10'W, 610 m): MZSP 34514 [1 shell], MZSP 34515 [1 shell].

Material examined. Type material. Brazil: from type locality: MNHN-IM* (uncatalogued) [2 shells].

Type locality. Brazil: Espírito Santo: MD55 stn. 54 CB93 (19°36'00"S, 38°53'18"W, 640 m), coll. R/V *Marion Dufresne*, 30/v/1987.

Measurements. Holotype MNHN-IM 2000-5662: whorls = 10; SL = 8.88 mm; BWL = 4.47 mm; AL = 3.05 mm; SW = 2.90 mm; AW = 1.60 mm.

Geographic distribution. Brazil: Espírito Santo, Rio de Janeiro, São Paulo (Simone 2002).

Bathymetric distribution. From 610 to 640 m.

Remarks. Simone (2002) originally included this species in *Batheulima* Nordsieck, 1968, but the species do not present the typical dark-brown protoconch and the sigmoidal axial lines in the protoconch like *Batheulima fuscoapicata* (Jeffreys, 1884), type species of the genus. *Eulimacrostoma lutescens* comb. nov. fits the shape of the genus erected here by the very elongated and slender shell, with an elongated, anteriorly spread aperture, and a similar color pattern. The protoconch and teleoconch of the latter species has a weak brownish spiral band (Fig. 3L, N). Additionally, the shell of *Eu. lutescens* has several axial lines (Simone 2002).

In addition to the type series of *Eu. lutescens*, we find two other shells collected from the type locality. One of them is figured here (Fig. 3L–N), and it is slightly smaller than the holotype but has one less whorl (Table 1). The initial whorls of the holotype (Fig. 3J) are straighter than in the topotype (Fig. 3L, M), but it may be variable. The topotype has a similar conical shape, with a spire angle of 21° (the holotype has 23°), presence of axial lines very evident, faint brownish spiral bands in the protoconch (Fig. 3N) and teleoconch (Fig. 3L, M), a similar aperture (Fig. 3L) and a strongly protruding outer lip (Fig. 3M).

***Eulimacrostoma patula* (Dall & Simpson, 1901), comb. nov.**

Figure 4A–K

Eulima (Leiostraca) patula Dall and Simpson 1901: 413, pl. 57, fig. 3.

Strombiformis patula: Abbott 1974: 127, fig. 1390 (reproduced from original illustration).

E. patula: Lamy and Pointier 2017: 277, pl. 88, fig. 3A, B.

Type material. Lectotype USNM 160202a (herein designated). Paralectotypes USNM 160202b [4 shells], from type locality.

Material examined. Type material. Brazil: Amapá state: mouth of Amazonas River, outer shelf (~03°58'42"N, 49°33'24"W), coll. 30/vii/2001: MNRJ 34476* [4 shells], MNRJ 34477* [2 shells], MNRJ 34478* [3 shells], MNRJ 34479* [8 shells]; AMASSEDS stn. 4134 (02°21'12"N, 48°29'54"W, 72 m), coll. R/V *Columbus Iselin*, 05/xi/1990: MNRJ 34589* [2 shells], MNRJ 35284* [1 shell].

Type locality. Puerto Rico: Mayaguez Harbour, Fish Hawk stn. 6062 (46–55 m).

Redescription. Shell vitreous or with wide brownish spiral bands, conical with an obtuse apex, reaching about 4.5 mm long and 1.5 mm wide, about eight whorls, aperture broad. Protoconch vitreous, subcylindrical, about two whorls, 330 µm in width, smooth, transition to teleo-

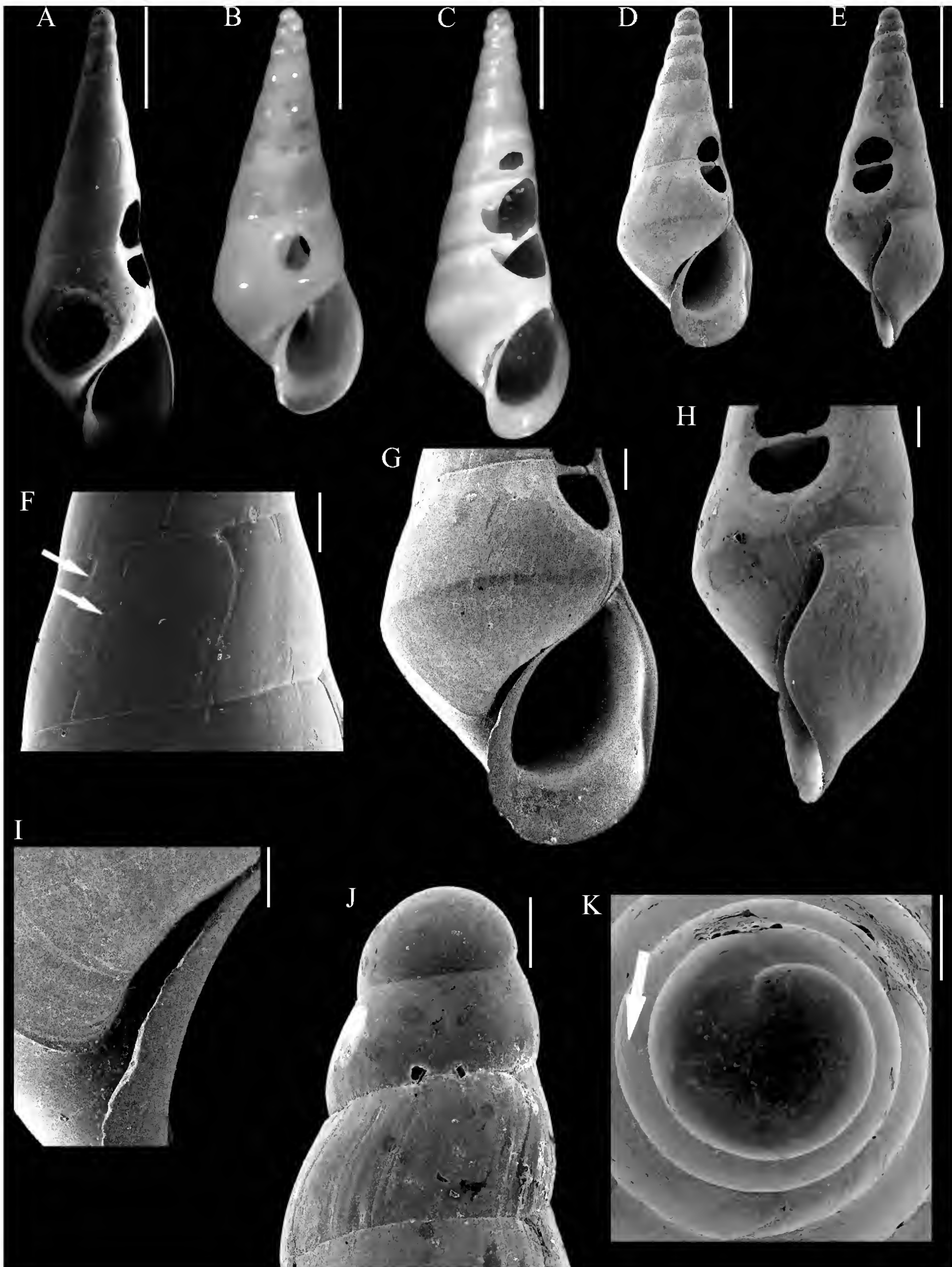


Figure 4. *Eulimacrostoma patula* (Dall & Simpson, 1901), comb. nov. **A.** Lectotype herein designated (USNM 160202), **B, F.** (MNRJ 34479); **C.** (MNRJ 34476). **D–E, G–K.** (MNRJ 34589). **A–D.** Shell in frontal view; **E.** Shell in lateral view; **F.** Detail of teleoconch surface, white arrows indicates microsculpture of axial lines; **G.** Detail of body whorl in ventral view; **H.** detail of body whorl in lateral view; **I.** Detail of umbilical fissure; **J.** Detail of apical whorls in frontal view; **K.** Detail of protoconch in apical view, white arrow indicates the transition from protoconch to teleoconch. Scale bars: 1 mm (A–E); 200 μ m (F–H); 100 μ m (I–K). Credits: A: USNM.

conch marked by a subtle incremental scar. Teleoconch with about six whorls of sinuous outline, with convexity more attenuated on the lower region of each whorl; suture deep, well impressed, sloping; subsutural zone occupying about 1/5 of the whorl height; surface glossy and smooth, except for microsculpture of axial lines and incremental scars; incremental scars well developed, appearing in intervals of about 0.5 whorl. Last whorl occupying about 50% of the shell length; base slightly abrupt in outline. Aperture high, occupying about 70% of the body whorl length, wide, pear-shaped, expanded laterally, acute posteriorly, rounded and spread anteriorly; outer lip thin, very sinuous, orthocline, strongly retracted near the suture, after strongly protruding, and retracted in the distal region, maximum projection at the middle of the outer lip height; inner lip sinuous, sloping and well demarcated. Umbilical fissure present. Shell whitish or vitreous, usually with a wide brownish spiral band along the teleoconch.

Measurements. Lectotype USNM 160202: whorls = 9; SL = 4.53 mm; BWL = 2.20 mm; AL = 1.50 mm; SW = 1.50 mm; AW = 0.91 mm.

Geographic distribution. Puerto Rico (Dall and Simpson 1901); Guadeloupe (Lamy and Pointier 2017); Brazil: Amapá (this study).

Bathymetric distribution. From 46 m (Dall and Simpson 1901) to 300 m (Lamy and Pointier 2017).

Remarks. *Eulimacrostoma patula* comb. nov. (Fig. 4A–K) has a combination of shell features that fit the morphology of the newly described genus, such as the elongated aperture spread anteriorly, a orthocline outer lip strongly protruding (Fig. 4G, H) and moderately convex teleoconch whorls (Fig. 4A–E). Additionally, this species usually has a weak brownish spiral band in the teleoconch (Fig. 4C).

Dall and Simpson (1901) referred to five specimens in the original description without the selection of a holotype and, thus, all shells are syntypes. We select the shell of USNM 160202 (Fig. 4A) as the lectotype.

The material from the north coast of Brazil fits perfectly with the lectotype of *Eu. patula* in shape and reaches a similar size (lectotype USNM 160202, 9 whorls, 4.53 mm long vs MNRJ 34479, 8 whorls, 3.99 mm long). The record of *Eu. patula* from the north coast of Brazil represents the southernmost record of this species and is more than 2,500 km from the type locality and about 1,800 km from the recent record from Guadeloupe (Lamy and Pointier 2017). This species is currently known only by empty shells.

As commented above, one shell recorded by Dall (1927: 67) is actually *Eu. microsculpturata* and the remaining shells found cannot be identified with certainty due to their poor condition. We did not find more material to reassess the record of *Eu. patula* by Dall (1927).

Parker and Curray (1956) recorded *Eu. patula* (as “*Melanella patula*”) from calcareous banks off Texas and Louisiana, USA, in a depth of about 55 m, in a checklist of species without illustrations. Odé (1989) recorded *Eu. patula* (as “*Sabinella patula*”) from Texas also with no illustrations. The source of material of these records could not be traced in malacological collections and the presence of this species in the Gulf of Mexico is considered dubious.

Eulimacrostoma patula differ from the congeners mainly by the presence of an umbilical fissure and by the more truncated base.

Discussion

Eulimacrostoma gen. nov. is erected to group the eulimids with an elongated, conical shell, possessing a smooth protoconch, a teleoconch with slightly convex whorls and an elongate and strongly anteriorly spread aperture. The species usually share a similar color pattern of brownish spiral bands in the protoconch and teleoconch, and microsculpture of axial lines in teleoconch. These latter features are more developed in the type species and in *Eu. fusus* and *Eu. lutescens*. The anatomy of *Eu. microsculpturata* is not described, as only one young specimen with soft parts was identified. However, the kind of host (a starfish) and the combination of shell features corroborate the distinction of this genus.

Among the eulimid genera that parasitize asteroids, the most similar to *Eulimacrostoma* is *Niso* Risso, 1826, due to its conical shape, presence of brownish spiral bands in several species and axial lines on the shell surface. However, *Eulimacrostoma* can be distinguished from *Niso* by the shape of the aperture, which gapes anteriorly and is more elongated in the former, whereas it is usually rhomboid in the latter. In addition, *Niso* usually has a well-developed umbilicus. The type species of *Eulimacrostoma* does not present an umbilicus, but *Eu. patula* has an umbilical fissure, which is a variable feature in relation to its presence or absence in some Eulimidae genera (e.g., *Eulimetta* Warén, 1992, *Fusceulima* Laseron, 1955) (Souza and Pimenta 2014, 2015).

Other similar genera, in relation to conchological features, that parasitize other classes of echinoderms or of unknown hosts are *Batheulima*, *Eulima*, and *Haliella* Monterosato, 1878.

Eulimacrostoma is similar to *Batheulima*, whose host is unknown (Bouchet and Warén 1986); they have an elongated aperture, with a strongly protruding outer lip and sigmoidal axial lines in the teleoconch. However, *Eulimacrostoma* can be distinguished by features of the protoconch, which is smooth, not completely colored.

Eulimacrostoma is also similar to *Eulima*, but the more typical forms of this species-rich genus that parasitizes ophiuroids have a narrower aperture, that is not so spread anteriorly, and the outline of teleoconch whorls of *Eulima* is usually flat.

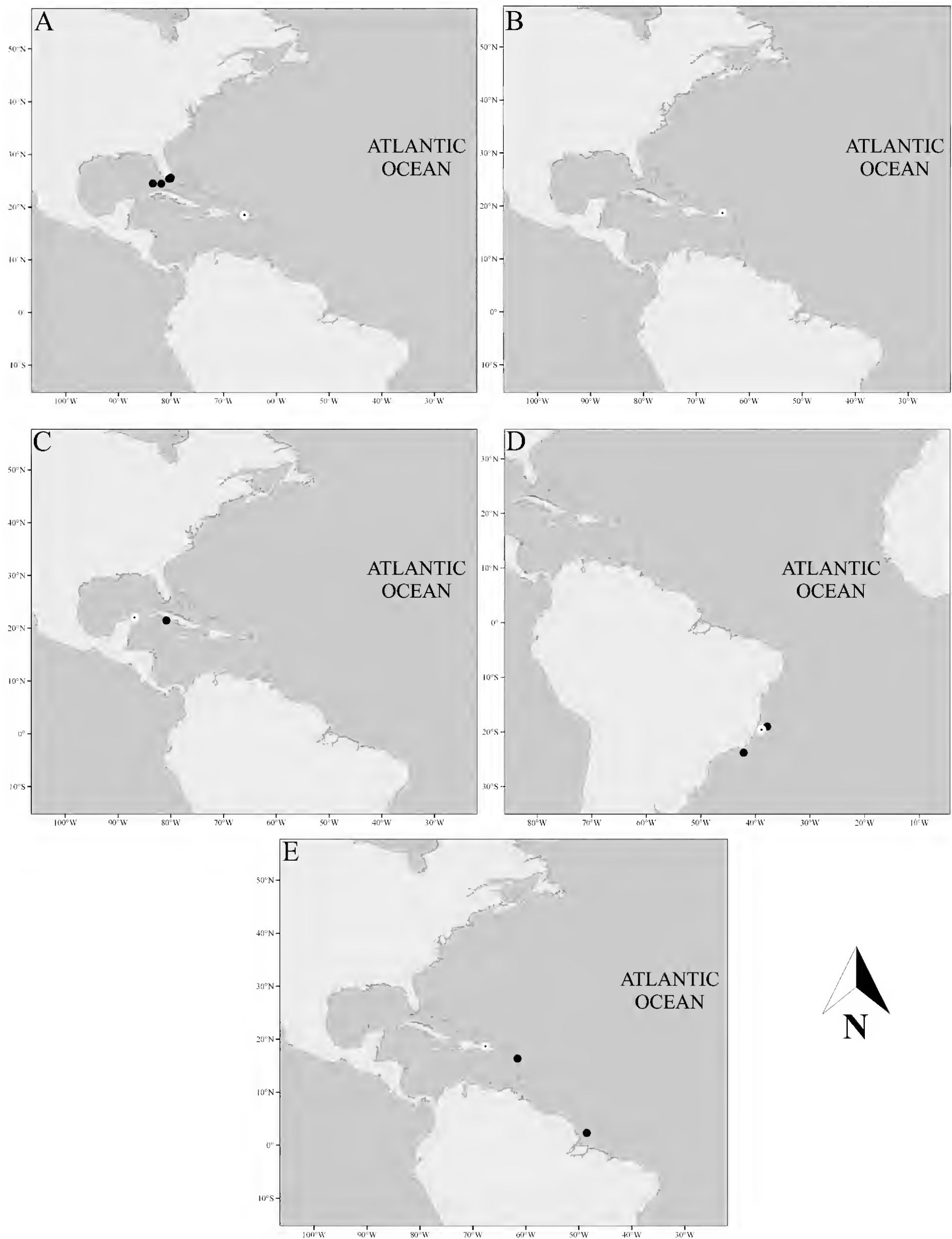


Figure 5. Geographical distributions of *Eulimacrostoma* spp. based on confirmed identifications. **A.** *Eulimacrostoma microsculpturata* sp. nov.; **B.** *Eulimacrostoma chascanon* (Watson, 1883), comb. nov.; **C.** *Eulimacrostoma fusus* (Dall, 1889), comb. nov.; **D.** *Eulimacrostoma lutescens* (Simone, 2002), comb. nov.; **E.** *Eulimacrostoma patula* (Dall & Simpson, 1901), comb. nov. White circle: type locality; black circle: additional records. Records without geographic coordinates are approximate.

Eulimacrostoma can also be compared to *Haliella* Monterosato, 1878 by possessing a high aperture, but the latter can be distinguished by having a more cylindrical shell, a more obtuse apex, and by being colorless. The host of *Haliella* species is doubtful, Warén (1983) commented that the genus possibly includes parasites of ophiuroids (Warén 1983: 47), while Hasegawa (2009: 276) noted irregular sea urchins. Hasegawa (2009) identified *Haliella* sp. collected in the same haul of several irregular sea urchins and ophiuroids. Despite these hypotheses, the species of *Haliella* have never been found on the host.

Delimitation of genera is a hard task in Eulimidae (Bouchet and Warén 1986: 310), with some exceptions. Several species and genera are known only from empty shells and/or have no data about the host and/or anatomy (e.g., *Batheulima*, *Eulimetta*, *Oceanida* de Folin, 1870) (Warén 1983, 1992; Bouchet and Warén 1986; Souza and Pimenta 2014, 2015).

In a revision of the family in the northeast Atlantic, Bouchet and Warén (1986) established eight new genera (including *Acrochalix*, *Bulimeulima*, *Campylorhaphion*, and *Halielloides*) known only from shell morphology and argued that they can introduce 10 more genera based exclusively on shell morphology. The introduction of these genera was justified by consistent features of the shell and the author's experience on the eulimid fauna of other regions.

The description of *Eulimacrostoma* is based on the combination of shell features and on data about the host of *Eu. microsculpturata*. Albeit only one species has the host known, all species included in *Eulimacrostoma* have very similar conchological features.

Recent efforts with molecular data are elucidating many aspects of the evolution of Eulimidae (Takano and Kano 2014; Takano et al. 2018), but the family is too species-rich and to reach a high percentage of DNA-sequenced taxa is a challenge. Takano et al. (2018) proposed a new methodology to identify the hosts of eulimids by extracting DNA from the proboscis of the eulimid in an attempt to find DNA traces of the host and reached successful results. This is an interesting technique, especially if the record of the eulimid attached to the host is not available.

We expect that the description of *Eulimacrostoma* calls the attention of researchers to congeners from other parts of the world. By now, *Eulimacrostoma* is known only from the western Atlantic (Fig. 5A–E). Several genera of Eulimidae have a worldwide distribution (e.g., *Eulima*, *Fusceulima*, *Melanella* Bowdich, 1822). The only known host of *Eulimacrostoma* is a starfish of the genus *Luidia* Forbes, 1839, which has a worldwide distribution (Mah 2019), occurring mainly in shallow waters of tropical and subtropical seas and inhabiting soft bottoms (Clark and McKnight 2000). The current state of knowledge is not sufficient to establish a specificity in the parasite–host relationship at the species or genus level. Thus, more data is necessary to reach a better comprehension about the biology of *Eulimacrostoma*.

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Three new species of *Macrophya* Dahlbom (Hymenoptera, Tenthredinidae) with a key to species of the *Macrophya imitator* group in China

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Abstract

The *Macrophya imitator* group was proposed by Liu et al. in 2015. Three new species, *Macrophya longlingensis* sp. nov., *M. nieshuaiguo* sp. nov. and *M. zejiani* sp. nov. from China are described. A key to all Chinese species and a geographical distribution map of the *M. imitator* group in China are provided.

Key Words

Hymenoptera, *Macrophya imitator* group, Sawflies, taxonomy, Tenthredinoidea

Introduction

Macrophya Dahlbom, 1835 is the third largest genus in the subfamily Tenthredininae (Hymenoptera, Tenthredinidae). It contains 306 species worldwide, of which 167 have been recorded for China up to April 2019 (Li et al. 2019a, 2019b; Liu et al. 2019a, 2019b). The taxonomy and distribution of the genus in China has been studied by the last author and his co-workers since 1994 and a division of *Macrophya* in species groups was given by Liu et al. (2015, 2018, 2019b).

The *Macrophya imitator* group is the second largest species group in *Macrophya*, with 17 species worldwide, all of which are present in China. Among them, *M. imitator* Takeuchi is also distributed in Japan, Korea and Russia (Takeuchi 1937), and *M. postscutellaris* Malaise in Myanmar (Malaise 1945). The species of the *Macrophya imitator* group are all similar in general morphology and

constitute a clearly defined species group in *Macrophya*. In this study, three new species belonging to this species group are described from China, namely: *M. longlingensis* Li, Liu & Wei, sp. nov., *M. nieshuaiguo* Li, Liu & Wei, sp. nov. and *M. zejiani* Liu & Wei, sp. nov. A key to all species found in China is provided.

Materials and methods

All specimens of the newly described species were obtained by sweeping in wooded bog and forest fringe zones in Yunnan Province (southern China) from 1994 to present. Eight specimens of three new species and 788 specimens of known species were examined and studied

for this work. The specimens were examined with a Motic-SMZ-171 stereomicroscope. Images of the imagines were taken with a Nikon D700 digital camera and a Leica Z16APO. The genitalia were examined with a Motic BA410E microscope and photographed with Motic Moti-cam Pro 285A. Images were focus-stacked using Helicon Focus (HeliconSoft, Kharkiv, Ukraine) and further processed with Adobe Photoshop CS 11.0.

The terminology of genitalia follows Ross (1945) and that of general morphology follows Viitasaari (2002). For a few terms (e.g. middle fovea and lateral fovea), we follow Takeuchi (1952).

All types are deposited in the Insect Collection of Central South University of Forestry and Technology, Changsha, Hunan, China (CSCS).

Abbreviations:

- OCL** The distance between a lateral ocellus and the occipital carina, or the hind margin of the head where this carina would be if it were developed (Benson 1954).
- OOL** The shortest distance between an eye and a lateral ocellus.
- POL** The distance between the mesal margins of the two lateral ocelli.

Results

Macrophya imitator species group

Remarks. The *Macrophya imitator* group is morphologically very similar to the *M. maculitibia* group, a

diagnosis to which was provided by Li et al. (2019b). Species of the *M. imitator* group can be recognized using the diagnosis provided by Liu et al. (2015), here restated: the body mainly black, without metallic tinge; the antenna slender and black; the posterior margin of metepimeron straight or slightly concave, the appendage (= posterior corner of metepimeron) differentiated but not elongated, at least partly punctate and evenly pilose, without basin; the abdominal tergum 1 not reticulate and the penis valve oval, narrowed toward apex, ergot short.

Description. Body slender and mainly black, without metallic tinge; white maculae to varying extents on pronotum, hind trochanter and dorsal surface of hind tibia subapically; fore wing without smoky macula below pterostigma; clypeus at its greatest breadth slightly broader than the shortest distance between lower inner orbits of eyes; lateral margins convergent anteriorly, anterior margin incised to approximately 1/5–1/3 length of clypeus, apex of lateral lobe obtuse; malar space narrower than diameter of an ocellus; postocellar area broader than long; vertex with minute and dense punctures, interspaces between punctures narrow usually; antenna slender and black, antennomere 3 clearly longer than antennomere 4; posterior margin of metepimeron straight or slightly concave, appendage (posterior corner of metepimeron) differentiated but not elongated, at least partly punctate and evenly pilose, without basin; inner spur of hind leg slightly longer than half length of metabasitarsus, metabasitarsus always slender, slightly longer than following four tarsomeres together; claw with inner tooth slightly shorter than outer tooth; abdominal tergum 1 not reticulate; penis valve oval, narrowed towards apex, ergot short.

Key to the Chinese species of the *Macrophya imitator* group

- | | | |
|---|---|--|
| 1 | Female..... | 2 |
| – | Male..... | 21 |
| 2 | Ovipositor sheath much longer than middle tibia..... | 3 |
| – | Ovipositor sheath clearly shorter than middle tibia..... | 5 |
| 3 | Posterior margin of pronotum with narrow white band; dorsal surface of hind tibia with a large white macula subapically. China (Beijing, Gansu, Hebei, Henan, Hubei, Ningxia, Qinghai, Shaanxi, Shanxi, Sichuan)..... | <i>M. weni</i> Wei, 1998 |
| – | Pronotum entirely black; dorsal surface of hind tibia with a subapical white macula smaller than above..... | 4 |
| 4 | Postocellar area 2.5× broader than long; POL: OOL: OCL = 4.5: 10: 5.5 (Figure 3B); antennomere 3 approximately 1.4× longer than antennomere 4 (13: 9) (Figure 3D); distance between cenchri twice breadth of a cenchrus; middle serrulae with 2 or 3 proximal and 9 or 10 distal teeth (Figure 3H); cell 2Rs as long as cell 1R ₁ , petiole of anal cell in hind wing 0.6× as long as cross-vein cu-a (Figure 3A). China (Yunnan)..... | <i>M. zejjani</i> Liu & Wei, sp. nov. |
| – | Postocellar area twice broader than long; POL: OOL: OCL = 3: 10: 7; antennomere 3 approximately 1.8× longer than antennomere 4 (11: 6); distance between cenchri 2.5× breadth of a cenchrus; middle serrulae with 2 proximal and 9–12 distal teeth; cell 2Rs clearly shorter than cell 1R ₁ , petiole of anal cell in hind wing only slightly shorter than cross-vein cu-a. China (Sichuan)..... | <i>M. omeialpina</i> Li, Jiang & Wei, 2018 |
| 5 | Apex of middle tibia with a distinct white macula on dorsal surface; punctures on middle part of mesepisternum minute, much smaller than punctures on vertex..... | 6 |
| – | Apex of middle tibia without white macula on dorsal surface, but sometimes with a white spot or stripe on anterior surface; punctures on middle part of mesepisternum about as large as or somewhat smaller than punctures on vertex..... | 12 |
| 6 | Hind trochanter entirely white..... | 7 |
| – | Hind trochanter partly white, with a distinct black macula..... | 8 |

- 7 Ovipositor sheath longer than fore tibia, with lateral setae very short, not distinctly curved; middle serrulae with 20 fine distal teeth. China (Henan, Hubei, Hunan, Shaanxi) *M. flactoserrula* Chen & Wei, 2002
- Ovipositor sheath shorter than fore tibia, with lateral setae long and curved; middle serrulae with 10–12 distal teeth. China (Gansu, Henan, Hubei, Shaanxi)..... *M. funiushana* Wei, 1998
- 8 Pronotum entirely black 9
- Posterior margin of pronotum white 10
- 9 Postocellar area 1.7× broader than long; fore and middle trochanters entirely black; hind trochanter entirely black; subapical white macula on dorsal surface of hind tibia about 2/5 length of tibia; posterior margin of metepimeronal appendage with a distinct shiny and obtuse carina toward the longitudinal axis of body; ovipositor sheath as long as fore tibia; the middle serrulae with 13–16 distal teeth. China (Jilin, Shaanxi) *M. bui* Wei & Li, 2012
- Postocellar area twice broader than long; fore and middle trochanters largely black; hind trochanter largely white, ventral surface with black macula; subapical white macula on dorsal surface of hind tibia shorter than 1/3 length of tibia; the inner side of metepimeronal appendage without a shiny and obtuse carina; ovipositor sheath distinctly longer than fore tibia; lancet oblique and weakly protruding, with several larger teeth, the middle serrulae with 5–7 distal teeth. China (Gansu, Hebei, Henan, Jilin, Liaoning, Ningxia, Shaanxi, Shanxi)..... *M. parimitator* Wei, 1998
- 10 Hind tibia with broad white ring at mid-length, as long as half length of hind tibia. China (Shaanxi)..... *M. circulotibialis* Li, Liu & Heng, 2015
- Hind tibia with subapical white macula shorter than half length of hind tibia..... 11
- 11 Abdominal tergum 1 entirely black, posterior margin without white macula; middle serrulae each with 1 or 2 proximal and 14 or 15 distal teeth, subbasal teeth small. China (Jilin) *M. changbaina* Li, Liu & Heng, 2015
- Posterior margin of abdominal tergum 1 with 2 small, distinct and white maculae; middle serrulae flat, middle serrulae each with 2 proximal and 15–18 distal teeth, subbasal teeth minute. China (Jilin, Ningxia)..... *M. curvatithea* Li, Liu & Heng, 2015
- 12 Punctures on head and mesepisternum clearly defined, equal in size, interspaces strongly shiny; punctures on metepimeronal appendage clearly separated; hind tibia with white macula as long as half length of hind tibia. Myanmar; China (Chongqing, Guizhou, Hubei, Shaanxi, Tibet) *M. postscutellaris* Malaise, 1945
- Punctures on mesepisternum smaller than punctures on head, punctures crowded on both, interspaces very fine, partly obscure, less shiny; punctures on metepimeronal appendage hardly separated; hind tibia with subapical white macula distinctly shorter than half length of hind tibia..... 13
- 13 Frons distinctly convex and extending above top of eyes; posterior 1/3 of abdominal tergum 1 with white bands across its full breadth. China (Sichuan) *M. kangdingensis* Wei & Li, 2012
- Frons flat and not extending above top of eyes; posterior margin of abdominal tergum 1 with very narrow white band, or with 2 small transverse white maculae..... 14
- 14 Posterior margin of pronotum white 15
- Pronotum entirely black 16
- 15 Setae on ovipositor sheath short and straight in dorsal view; posterior margin of metepimeronal appendage without glabrous patch; middle serrulae with 9 or 10 fine distal teeth; annular spine bands narrow and remaining distant from each other. China (Gansu, Guizhou, Hubei, Hunan, Shaanxi, Sichuan) *M. imitoides* Wei, 2007
- Setae on ovipositor sheath long and evenly curved in dorsal view; posterior margin of metepimeronal appendage with a distinct glabrous patch; middle serrulae with 5 or 6 fine distal teeth; annular spine bands broadly meeting each other. China (Gansu, Hubei, Ningxia, Shaanxi, Sichuan)..... *M. curvatisaeta* Wei & Li, 2011
- 16 Hind trochanter entirely black..... 17
- Ventral surface of hind trochanter with black macula..... 18
- 17 Postocellar area 1.7× broader than long; subapex in dorsal surface with a clear white macula; middle serrulae with 2 proximal and 5 or 6 distal teeth. Korea, Japan, Russia (East Siberia); China (Heilongjiang, Jilin, Liaoning)..... *M. imitator* Takeuchi, 1937
- Postocellar area twice broader than long (Figure 2B); hind tibia with subapical white macula on dorsal surface weak (Figure 2A); middle serrulae with 2 proximal and 7–10 distal teeth (Figure 2H). China (Yunnan) *M. nieshuaiguoi* Li, Liu & Wei, sp. nov.
- 18 Ventral surface of hind trochanter with a large, distinct black macula 19
- Ventral surface of hind trochanter with a small, weak black macula 20
- 19 Postocellar area 2.2× broader than long; white band at center of posterior margin of abdominal tergum 1 narrow; subapical white macula on dorsal surface of hind tibia indistinct; petiole of anal cell in fore wing slightly shorter than vein 1r-m, about half length of vein cu-a; middle serrulae of lancet each with 2 proximal and 7 or 8 distal teeth, cypsella between the 8th–9th serrulae slightly broader than length of the 9th serrula. China (Sichuan) *M. semipunctata* Li, Liu & Wei, 2018
- Postocellar area 2.5× broader than long; white band at center of posterior margin of abdominal tergum 1 broader than the former; subapical white macula on dorsal surface of hind tibia distinct and small, but oblique; petiole of anal cell in fore wing twice length of vein 1r-m, and about as long as vein cu-a; middle serrulae each with 2 proximal and 5–7

- distal teeth, cypsella between the 8th–9th serrulae as broad as length of the 9th serrula. China (Gansu, Ningxia, Shaanxi, Sichuan) *M. nigromaculata* Wei & Li, 2010
- 20 Anterior margin of clypeus incised to approximately 1/3 its length (Figure 1C); middle serrulae with 2 proximal and 8–11 distal teeth (Figure 1H); petiole of anal cell in hind wing as long as cross-vein cu-a (Figure 1A). China (Yunnan)...
..... *M. longlingensis* Li, Liu & Wei, sp. nov.
- Anterior margin of clypeus incised to approximately 1/5 its length; middle serrulae with 2 proximal and 5–7 distal teeth; petiole of anal cell in hind wing 0.5× longer than cross-vein cu-a. China (Hubei, Jilin, Shaanxi)
..... *M. jiaozhaoae* Wei & Zhao, 2011
- 21 Hairs on abdominal terga erect, approximately as long as diameter of middle ocellus; anterior margin of valviceps somewhat acute *M. weni* Wei, 1998
- Hairs on abdominal terga oblique, much shorter than diameter of middle ocellus; anterior margin of valviceps more or less evenly rounded 22
- 22 Hind tibia with a white macula extending over approximately half its length 23
- Hind tibia with a white macula clearly shorter than half its length 24
- 23 Hind tibia with a broad, white ring about its mid-length; all trochanters mostly black; white macula on posterior margin of pronotum broad; valviceps slightly narrowed toward apex, ergot long below *M. circulotibialis* Li, Liu & Heng, 2015
- Hind tibia with a white macula dorsally, but not forming; all trochanters entirely white; white macula on posterior margin of pronotum narrow; valviceps not narrowed toward apex, ergot short above *M. postscutellaris* Malaise, 1945
- 24 Fore and middle trochanters mostly to entirely black 25
- Fore and middle trochanters entirely white 29
- 25 Hind trochanter mostly to entirely black 26
- Hind trochanter entirely white 28
- 26 Hind trochanter entirely black; pronotum entirely black *M. bui* Wei & Li, 2012
- Hind trochanter mostly black, marginal parts white; posterior margin of pronotum with white band more or less 27
- 27 Posterior margin of pronotum with broad white band; hind tibia with a distinct dorsal white macula; ergot of penis valve long below *M. curvatithea* Li, Liu & Heng, 2015
- Posterior margin of pronotum with narrow white band; hind tibia with dorsal white macula weak or distinct; ergot of penis valve short above *M. nigromaculata* Wei & Li, 2010
- 28 White band in posterior margin of pronotum narrow but distinct; interspaces between punctures on vertex as broad as diameter of a puncture; valvula of penis valve not broadened toward apex *M. imitatoides* Wei, 2007
- Posterior margin of pronotum entirely black; interspaces between punctures on vertex narrower than diameter of a puncture; valvula of penis valve clearly broadened toward apex *M. imitator* Takeuchi, 1937
- 29 Labrum and clypeus entirely white 30
- Labrum largely black and clypeus entirely black 32
- 30 Punctures on vertex large; ventral surface of hind femur black, without white band; valviceps approximately 2.3× longer than broad *M. kangdingensis* Wei & Li, 2012
- Punctures on vertex minute; ventral surface of hind femur with distinct white band; valviceps clearly 1.4–1.7× longer than broad 31
- 31 White band on posterior margin of abdominal tergum 1 very narrow; entire posterior margin of pronotum with narrow white macula; sterna of abdomen entirely black *M. flactoserrula* Chen & Wei, 2002
- White band submedially on posterior margin of abdominal tergum 1 approximately 2/5 of its breadth clearly; posterior margin of pronotum with a distinct, broad white macula; sterna of abdomen largely white *M. funiushana* Wei, 1998
- 32 White band at posterior margin of pronotum distinct *M. curvatisaeta* Wei & Li, 2011
- White band at posterior margin of pronotum weak or indistinct *M. jiaozhaoae* Wei & Zhao, 2011

***Macrophya longlingensis* Li, Liu & Wei, sp. nov.**

<http://zoobank.org/6129209F-9628-4C4B-9CBC-F5B241B25A4F>

Figure 1

Diagnosis. The new species is morphologically similar to *M. parimitator* Wei, 1998 in body and legs mainly black; antennae rather robust, middle antennomeres not inflated; anterior margin shallowly incised to approximately 1/3 its length, lateral corners somewhat short and broad; malar space linear, approximately 0.5× as broad as diameter of middle ocellus; lancet narrow and long, with 20 serrulae; but differs from the latter in having vertex shiny; frontal area coarsely and densely punctured, with

smooth interspaces between punctures distinct; anterior 1/6 of katepimeron very smooth and shiny, without punctures or microsculpture, posterior 5/6 with some shallow large punctures, microsculpture indistinct; dorsal surface of middle tibia black, without white macula subapically; dorsal surface of hind tibia with a small, narrow white macula; cell 2Rs of fore wing clearly shorter than cell 1R₁, petiole of anal cell in hind wing as long as cross-vein cu-a; middle serrulae with 2 proximal and 8–11 distal teeth, subbasal teeth clear and small. The new species is also morphologically similar to *M. jiaozhaoae* Wei & Zhao, 2011 in body and legs mainly black; antennae

rather robust, middle antennomeres not inflated; ventral surface of hind trochanter with a small, weak black macula; pronotum entirely black; fronts flat and not extending above top of eyes; hind tibia with subapical white macula distinctly shorter than half length of hind tibia; ovipositor sheath clearly shorter than middle tibia; but differs from the latter in having anterior margin of clypeus incised to approximately 1/3 its length; middle serrulae with 2 proximal and 8–11 distal teeth; petiole of anal cell in hind wing as long as cross-vein cu-a.

Description. Holotype: female. Body length 7 mm. Body and legs black; following parts pale brown: palp mostly, a small triangular macula on apical margin of clypeus, ventral surface of fore tarsomere mostly; following parts white: basal half of mandibles, transverse macula submedially on posterior margin of abdominal tergum 1, apical margins of all coxae, apical margins of fore and middle trochanters, hind trochanter except for ventral surface with a small black macula, apex of fore and middle femora anteriorly, anterior surface of middle tibia, hind tibia with long, narrow subapical macula on dorsal surface. Body hairs short and dense, silver; setae on ovipositor sheath slightly long and curved, blackish brown. Wings hyaline, without smoky macula, pterostigma and veins mostly blackish brown (Figure 1A).

Vertex shiny; frontal area coarsely and densely punctured clearly, smooth interspaces distinct and smooth; interspaces of postocellar area with small areas and some large punctures, interspaces distinct and without microsculpture (Figure 1B); labrum and clypeus less shiny, punctures on labrum sparse, punctures on clypeus denser, microsculpture weak (Figure 1C). Mesonotum less shiny, punctures on mesonotum smaller and denser than punctures on head, interspaces distinct and smooth; center of mesoscutellum with some large punctures, interspaces broad, marginal area with denser punctures than center; mesoscutellar appendage mostly and metascutellum entirely smooth and shiny, but bottom of mesoscutellar appendage with weak microsculpture and without distinct punctures. Mesopleuron less shiny, mesepisternum with dense and coarse punctures, upper half with punctures large and interspaces broad, lower half with punctures small and interspaces narrow; anepimeron dull, with coarse wrinkles; anterior 1/6 of katepimeron very smooth and shiny, without punctures or microsculpture, posterior 5/6 of katepimeron with some shallow large punctures, dorsal half with some deep punctures; metepisternum dull, with minute punctures, microsculpture distinct; metepimeron less shiny, depressed area with some punctures and weak microsculpture; metepimeronal appendage platform-shaped, with some minute punctures (Figure 1E). All abdominal terga shiny, laterally abdominal tergum 1 with some shallow punctures, nearly smooth submedially; other abdominal terga less shiny, anterior 2/3 with some shallow punctures and weak microsculpture, posterior 1/3 smooth. Outer surface of hind coxa with somewhat

dense and coarse punctures, outer surface of hind femur with sparse shallow punctures and fine microsculpture. Surface of ovipositor sheath coriaceous, with indistinct punctures and fine microsculpture.

Labrum elevated medially, anterior margin slightly truncate; clypeus weakly elevated, base slightly broader than distance between lower inner orbits of eyes, lateral sides distinctly convergent apically, anterior margin shallowly incised to approximately 1/3 its length, lateral corners somewhat short and broad, lobe margin subtriangular (Figure 1C); malar space linear, approximately 0.5× as broad as diameter of middle ocellus; frontal area and face flat, slightly higher than top of eyes in lateral view; middle fovea weak, pot-shaped, lateral foveae clear, short furrow-like; interocellar furrow shallow, postocellar furrow weak; POL: OOL: OCL = 8: 12: 9; postocellar area weakly elevated, approximately 2.2× broader than long; lateral furrow somewhat broad and shallow, divergent posteriorly; head narrowed behind eyes in dorsal view, occipital carina complete. Antenna rather robust, approximately 1.1× longer than head and thorax together (16: 15), approximately as long as abdomen; antennomere 2 approximately 1.3× as long as breadth; antennomere 3 approximately 1.5× as long as antennomere 4 (43: 29), approximately 0.8× as long as antennomeres 4 and 5 together (43: 55), middle antennomeres not inflated, subapical antennomeres weakly compressed (Figure 1D). Mesoscutellum elevated, without median ridge or carina, as high as top of mesonotum in lateral view; mesoscutellar appendage with acute middle longitudinal carina; metascutellum with short and low carina; posterodorsal platform of mesepimeron as broad as diameter of middle ocellus; metepimeronal appendage small platform-shaped; distance between cenchri 2.5× breadth of a cenchrus; mesopleuron and metapleuron as shown in Figure 1E. Inner tibial spur of hind leg 0.6× length of metabasitarsus (20: 33); metabasitarsus slender, about 1.1× longer than following four tarsomeres together (11: 10); claw with inner tooth slightly shorter than outer tooth. Ovipositor sheath slightly shorter than metabasitarsus (10: 11), apical sheath longer than basal sheath (3: 2), setae on ovipositor sheath slightly curved and long in dorsal view, apical margin round in lateral view (Figure 1F). Fore wing with cross-vein cu-a joining cell 1M in basal 1/3, cross-vein 2r joining cell 2Rs in apical 1/5, cell 2Rs clearly shorter than cell 1R₁, petiole of anal cell twice longer than cross-vein 1r-m and as long as cross-vein cu-a; petiole of anal cell in hind wing as long as cross-vein cu-a. Lancet narrow and long, with 20 serrulae (Figure 1G), serrulae slightly protruding and oblique, middle serrulae with 2 proximal and 8–11 distal teeth, subbasal teeth distinct and small, annular spine bands somewhat broad, the 7th–9th serrulae as shown in Figure 1H.

Male. Unknown.

Type material. Holotype, ♀, China: Yunnan Province: Longling County, Mount Xiaohei, 24°41.713'N, 98°45.574'E, 2010 m, 2.vi.2009, leg. Zejian Li, ethylac-

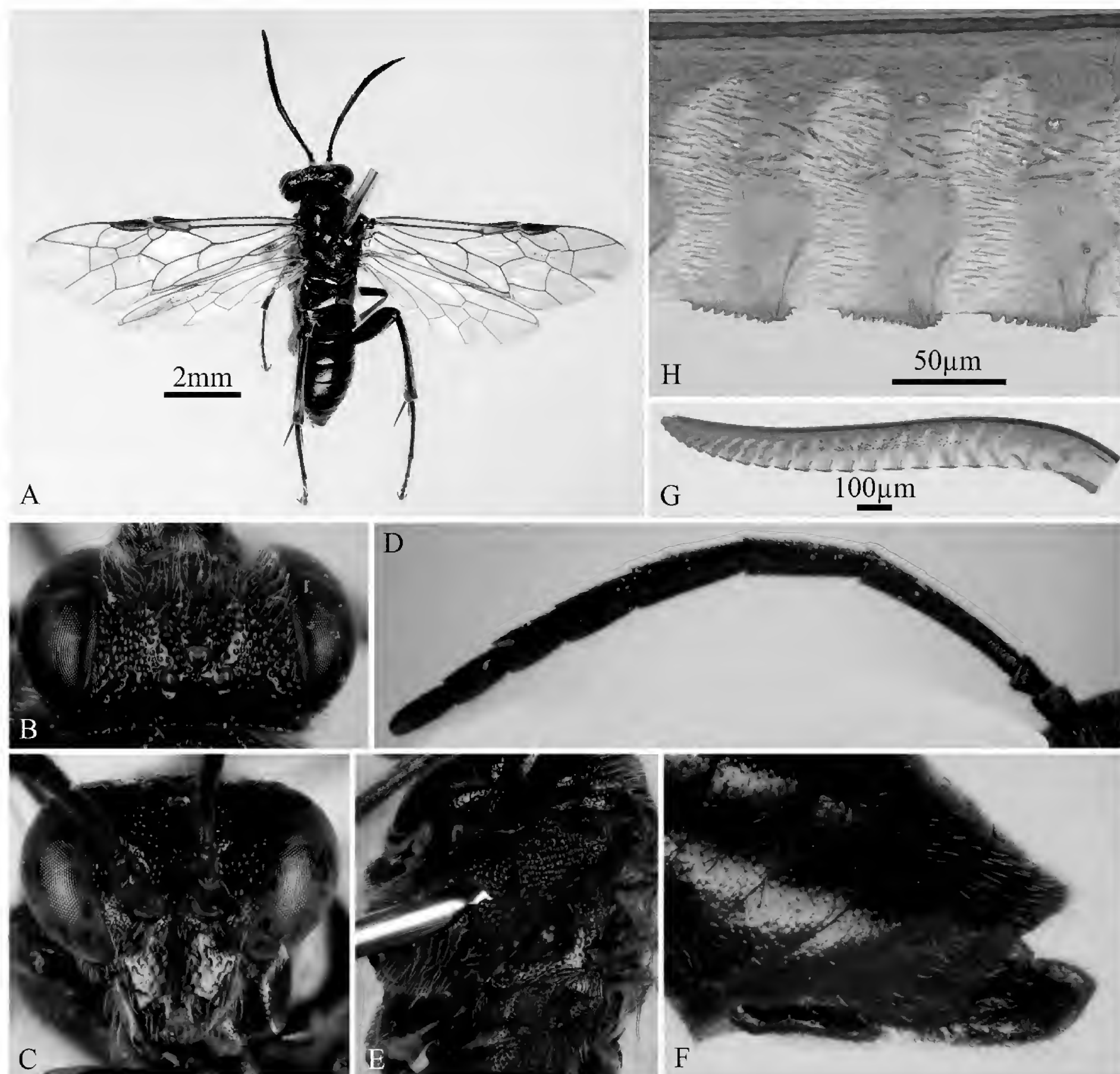


Figure 1. *Macrophya longlingensis* sp. nov., ♀, holotype. **A.** Female adult, dorsal view; **B.** Head of female, dorsal view; **C.** Head of female, frontal view; **D.** Antenna of female, lateral view; **E.** Mesopleuron and metapleuron of female; **F.** Ovipositor sheath, lateral view; **G.** Lancet; **H.** The 7th–9th serrulae. Scale bars: 2 mm (A); 100 µm (G); 50 µm (H).

etate. **Paratypes**, 1♀, same data, but leg. Gengyun Niu; 2♀, Yunnan Province: Longling County, Mount Gaoligong, 24°49.700'N, 98°46.062'E, 2145 m, 2.vi.2009, leg. Yihai Zhong, ethylacetate; 1♀, Yunnan Province: Yunlong County, Mount Daoren, 25°32.893'N, 99°11.267'E, 2265 m, 3.vi.2009, leg. Gengyun Niu, ethylacetate; 1♀, Yunnan Province: Lushui County, Yaojiaping, 25°9'75"N, 98°7'10"E, 2550 m, 3.vi.2009, leg. Wei Xiao, ethylacetate.

Host plants. Unknown.

Distribution. China (Yunnan).

Etymology. The specific name “*longlingensis*” is derived from Longling County (Yunnan Province) where the holotype was collected.

***Macrophya nieshuaigui* Li, Liu & Wei, sp. nov.**

<http://zoobank.org/DC7F944E-39C9-4E30-A022-F33927E38791>

Figure 2

Diagnosis. The new species is morphologically similar to *M. jiaozhaoae* Wei & Zhao, 2010 in body and legs mainly black; antennae rather robust, middle antennomeres not inflated; lancet narrow and long, serrulae slightly protruding and oblique; hind tibia with subapical white macula distinctly shorter than half length of hind tibia; ovipositor sheath clearly shorter than middle tibia; but differs from the latter in having vertex less shiny, interspaces of postocular area and postocellar area with some large punctures, interspaces between punctures distinct; anterior margin of clypeus deeply incised to approximately 2/5 its length; postocellar area about 1.6× broader than long; posterior margin

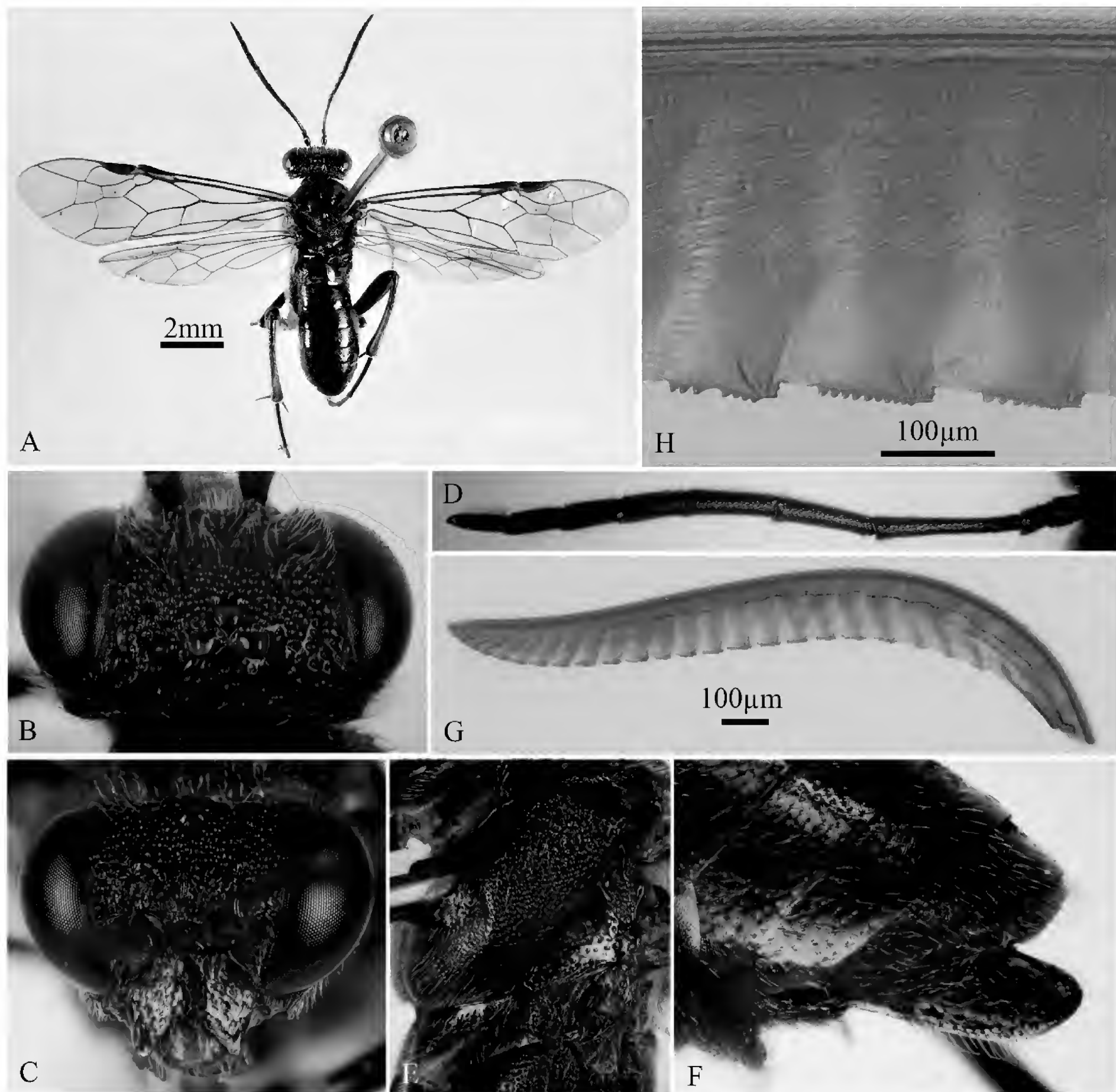


Figure 2. *Macrophya nieshuaiguoii* sp. nov., ♀, holotype. **A.** Female adult, dorsal view; **B.** Head of female, dorsal view; **C.** Head of female, frontal view; **D.** Antenna of female, lateral view; **E.** Mesopleuron and metapleuron of female; **F.** Ovipositor sheath, lateral view; **G.** Lancet; **H.** The 8th–10th serrulae. Scale bars: 2 mm (A); 100 µm (G, H).

of abdominal tergum 1 with broad white band; petiole of anal cell in fore wing shorter than cross-vein cu-a, petiole of anal cell in hind wing as long as cross-vein cu-a; setae on ovipositor sheath slightly curved and sparse in dorsal view; middle serrulae with 2 proximal and 7–10 distal teeth. The new species is also morphologically similar to *M. imitator* Takeuchi, 1937 in body and legs mainly black; antennae rather robust, middle antennomeres not inflated; pronotum and hind trochanter entirely black; but differs from the latter in having postocellar area twice broader than long; hind tibia with subapical white macula on dorsal surface weak; middle serrulae with 2 proximal and 7–10 distal teeth.

Description. Holotype: female. Body length 8 mm. Body and legs black; palp mostly blackish brown; a

small triangular macula on apical margin of clypeus pale brown; following parts white: basal half of mandibles, broad band on posterior margin of abdominal tergum 1 submedially, apical margins of fore and middle coxae, their outer surfaces with some longitudinal stripes, apical margin of hind coxa, fore and middle trochanters narrowly, hind trochanter entirely, anterior surface of fore and middle femora apically, anterior surface of fore tibia, hind tibia with small dorsal macula subapically; ventral surfaces of fore and middle tarsomeres mostly pale brown to pale blackish brown. Body hairs short and dense, silver; setae on ovipositor sheath slightly long and curved, blackish brown. Wings hyaline, without smoky macula, pterostigma and veins mostly blackish brown (Figure 2A).

Vertex less shiny; frontal area coarsely and densely punctured, interspaces smooth and narrow; interspaces of postocular area and postocellar area with sparse large punctures, interspaces between punctures distinct (Figure 2B); labrum and clypeus less shiny, labrum and clypeus with sparse shallow large punctures, microsculpture distinct; punctures on labrum shallow, punctures on clypeus denser toward apex (Figure 2C). Mesonotum less shiny, punctures smaller than those on head, interspaces smooth but indistinct and without microsculpture; center of mesoscutellum with sparse large punctures, interspaces broad, marginal area with dense punctures than center; mesoscutellar appendage somewhat shiny, with sparse minute punctures and weak microsculpture; metascutellum somewhat shiny, with punctures indistinct and microsculpture weak. Mesopleuron less shiny, mesepisternum with dense and coarse punctures, upper half with punctures large and interspaces broad, lower half with punctures small and interspaces narrow; anepimeron dull, with coarse wrinkles; anterior 1/5 of katepimeron very smooth and shiny, without punctures or microsculpture, posterior 4/5 of katepimeron with some large shallow punctures, dorsal half with sparse coarse punctures; metepisternum dull, with minute punctures, microsculpture clear; metepimeron less shiny, depressed area with sparse punctures and weak microsculpture; metepimeronal appendage platform-shaped, with sparse minute punctures (Figure 2E). All abdominal terga somewhat shiny, two lateral sides of abdominal tergum 1 with sparse shallow punctures, central parts with fine but distinct microsculpture; other abdominal terga less shiny, anterior 3/5 of abdominal terga 2–8 with sparse shallow punctures, posterior 2/5 of abdominal terga 2–8 with weak microsculpture. Outer surface of hind coxa with somewhat dense and coarse punctures, outer surface of hind femur with some shallow punctures and fine microsculpture. Surface of sheath coriaceous, with indistinct punctures and fine microsculpture.

Labrum elevated medially, anterior margin slightly truncate; clypeus weakly elevated, base slightly broader than distance between lower inner orbits of eyes, lateral sides distinctly convergent apically, anterior margin deeply incised to approximately half its length, lateral corners short and broad, lobe margin roundly subtriangular (Figure 2C); malar space linear, approximately 0.6× as broad as diameter of middle ocellus; frontal area and face flat, as high as top of eyes in lateral view; middle fovea weak, lateral foveae shallow, short furrow-like; interocellar furrow shallow, postocellar furrow weak; POL: OOL: OCL = 7: 20: 13; postocellar area weakly elevated, approximately twice as broad as long; lateral furrow somewhat narrow, divergent posteriorly; head narrowed behind eyes in dorsal view, occipital carina complete. Antenna rather robust, approximately 1.3× longer than head and thorax together (4: 3), approximately 1.2× longer than abdomen (20: 17); antennomere 2 approximately 1.2× as long as breadth; antennomere 3 approximately 1.4× as long as antennomere 4 (33: 23), approximately 0.75× as long as antennomeres 4 and 5 together (33: 44), middle antennomeres not inflated,

subapical antennomeres weakly compressed (Figure 2D). Mesoscutellum elevated roundly, without median ridge or carina, as high as top of mesonotum in lateral view; mesoscutellar appendage with slightly acute middle longitudinal carina; metascutellum with short and low carina; posterodorsal platform of mesepimeron as broad as diameter of middle ocellus; metepimeronal appendage small platform-shaped; distance between cenchri 2.2× breadth of a cenchrus; mesopleuron and metapleuron as shown in Figure 2E. Inner tibial spur of hind leg 0.6× length of metabasitarsus (3: 5); metabasitarsus slender, about 1.3× longer than following four tarsomeres together (5: 4); claw with inner tooth slightly shorter than outer tooth. Ovipositor sheath shorter than metabasitarsus (31: 45), apical sheath clearly longer than basal sheath (20: 11), setae on ovipositor sheath slightly curved in dorsal view, apical margin round in lateral view (Figure 2F). Fore wing with cross-vein cu-a joining cell 1M in basal 1/3, cross-vein 2r joining cell 2Rs in apical 1/3, cell 2Rs clearly slightly shorter than cell 1R₁, petiole of anal cell 1.5× longer than cross-vein 1r-m and slightly shorter than cross-vein cu-a; petiole of anal cell in hind wing as long as cross-vein cu-a. Lancet narrow and long, with 24 serrulae (Figure 2G), serrulae slightly protruding and oblique, middle serrulae with 2 proximal and 7–10 distal teeth, subbasal teeth distinct and small, annular spine bands somewhat narrow, the 8th–10th serrulae as shown in Figure 2H.

Male. Unknown.

Type material. Holotype, ♀, China: Yunnan Province: Liuku County, Pianma, Yakou, 25°58.21'N, 98°41.06'E, 3138 m, 19.vii. 2008, leg. Shuaiguo Nie, ethylacetate.

Host plants. Unknown.

Distribution. China (Yunnan).

Etymology. The specific name “*nieshuaiguo*” is derived from the name of Mr. Shuaiguo Nie for collecting the holotype of this new species.

***Macrophya zejiani* Liu & Wei, sp. nov.**

<http://zoobank.org/1528F16E-8F84-4FE3-9682-60D4733E2A20>

Figure 3

Diagnosis. The new species is morphologically similar to *M. weni* Wei, 1998 in body and legs mainly black; antennae rather robust, middle antennomeres not inflated; ovipositor sheath much longer than middle tibia; but differs from the latter in having postocellar area twice as broad as long; pronotum entirely black; distance between cenchri twice breadth of a cenchrus; middle serrulae with 2 or 3 proximal and 9 or 10 distal teeth; fore wing below pterostigma with slightly smoky and ill-defined maculae. The new species is also morphologically similar to *M. omeialpina* Li, Jiang & Wei, 2018 in body and legs mainly black; antennae rather robust, middle antennomeres

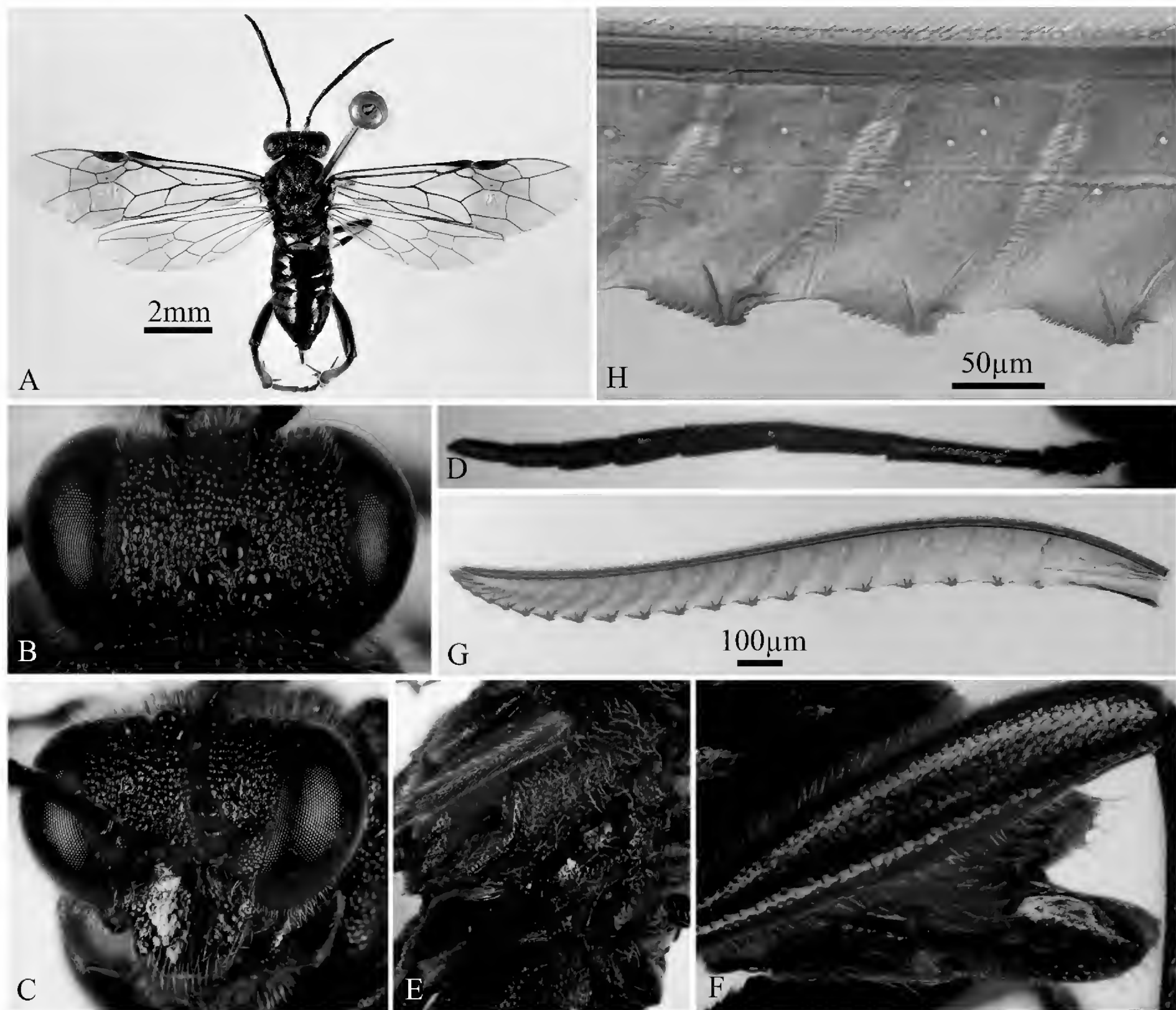


Figure 3. *Macrophya zejiani* sp. nov., ♀, holotype. **A.** Female adult, dorsal view; **B.** Head of female, dorsal view; **C.** Head of female, frontal view; **D.** Antenna of female, lateral view; **E.** Mesopleuron and metapleuron of female; **F.** Ovipositor sheath, lateral view; **G.** Lancet; **H.** The 8th–10th serrulae. Scale bars: 2 mm (A); 100 µm (G); 50 µm (H).

not inflated; pronotum entirely black; dorsal surface of hind tibia with a subapical white macula smaller than *M. weni*; but differs from the latter in having postocellar area 2.5× broader than long; POL: OOL: OCL = 4.5: 10: 5.5; antennomere 3 approximately 1.4× as long as antennomere 4 (13: 9); distance between cenchri twice breadth of a cenchrus; middle serrulae with 2 or 3 proximal and 9 or 10 distal teeth; cell 2Rs as long as cell 1R₁, petiole of anal cell in hind wing 0.6× as long as cross-vein cu-a.

Description. Holotype: female. Body length 7.5 mm. Body and legs black; a small triangular macula in anterior margin of clypeus pale brown; following parts white: basal half of mandibles, narrow band on posterior margin of abdominal tergum 1 submedially, apical margins of fore and middle coxae, apical half in anterior surface of fore femur, base mostly in anterior surface of fore tibia, hind trochanter entirely, hind tibia with small dorsal macula subapically. Body hairs short and dense, silvery; se-

tae on ovipositor sheath slightly curved, blackish brown. Wings hyaline, below pterostigma with pale smoky macula, boundary ill-defined, pterostigma and veins mostly blackish brown (Figure 3A).

Vertex less shiny; frontal area coarsely and densely punctured, interspaces smooth but weak; postocellar area mostly with sparse large punctures, interspaces narrow (Figure 3B); labrum and clypeus less shiny, punctures on labrum and clypeus sparse shallow and microsculpture fine (Figure 3C). Mesonotum less shiny, punctures smaller than those on head, interspaces smooth but indistinct and without microsculpture; center of mesoscutellum with sparse large punctures and fine microsculpture; basal half of mesoscutellar appendage rugose, apical half smooth, without distinct puncture; metascutellum somewhat shiny, punctures indistinct and microsculpture weak. Mesopleuron less shiny, mesepisternum with dense and coarse punctures, interspaces smooth but indistinct; anepimeron dull, with coarse wrinkles; anterior margin of katepimeron very

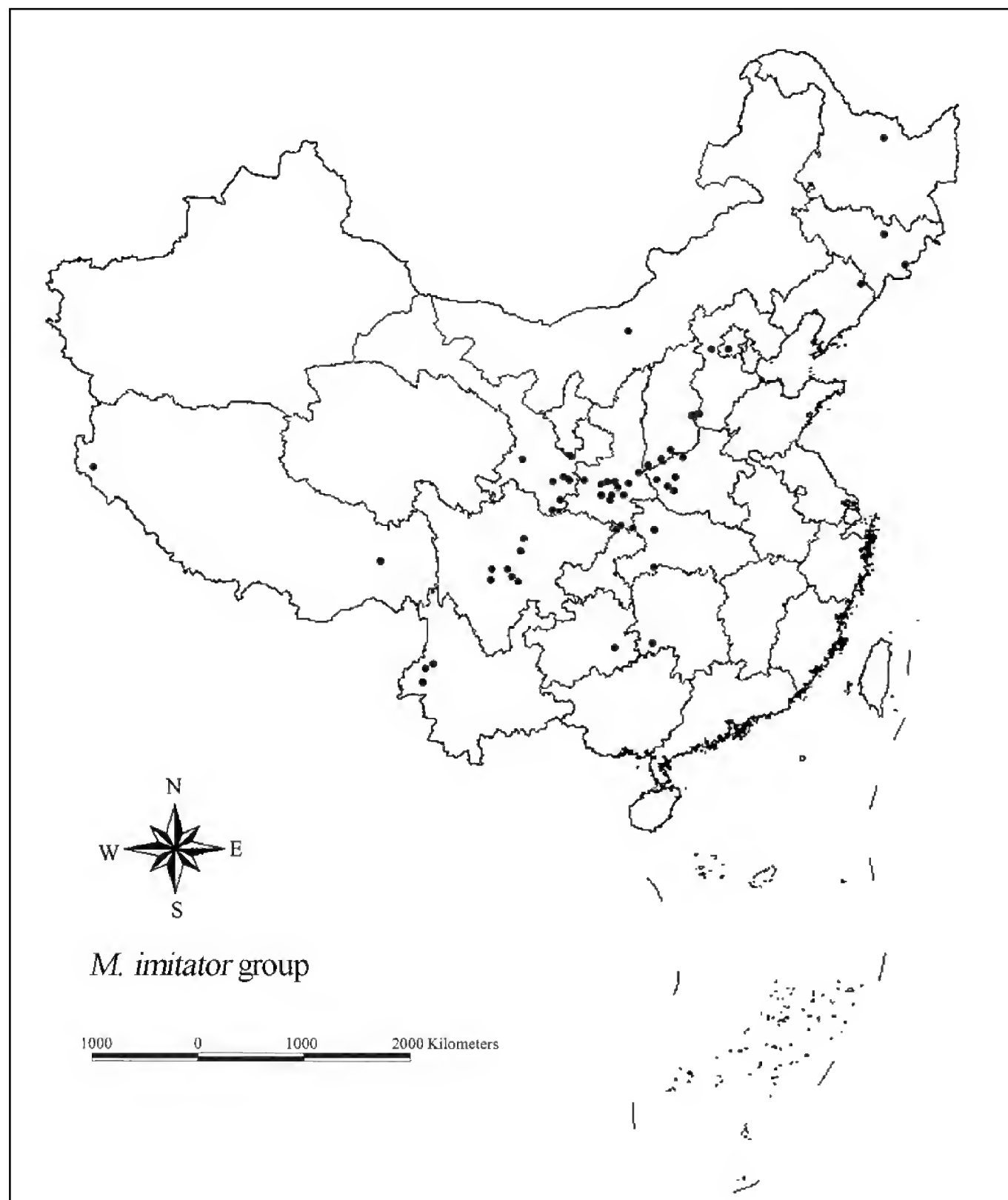


Figure 4. Geographical distribution map of *M. imitator* group in China.

smooth and shiny, without punctures or microsculpture, otherwise with sparse large shallow punctures, dorsal half with sparse coarse punctures; metepisternum dull, with minute punctures; metepimeron less shiny, most parts with sparse punctures and weak microsculpture; metepimeronal appendage platform-shaped, with some minute punctures (Figure 3E). All abdominal terga somewhat shiny, abdominal tergum 1 with sparse shallow punctures, with fine but distinct microsculpture submedially; other abdominal terga with minute and shallow punctures, microsculpture weak. Outer surface of hind coxa with somewhat dense and coarse punctures, ventral surface of hind coxa and outer surface of hind femur with sparse shallow punctures and fine microsculpture. Surface of ovipositor sheath coriaceous, with indistinct punctures and fine microsculpture.

Labrum elevated medially, anterior margin slightly truncate; clypeus weakly elevated, base slightly broader than distance between lower inner orbits of eyes, lateral sides distinctly convergent apically, anterior margin deeply incised to approximately 1/5 its length, lateral corners short and broad, lobe margin roundly subtriangular (Figure 3C); malar space linear, approximately 0.5× as

broad as diameter of middle ocellus; frontal area and face flat, slightly higher than top of eyes in lateral view; middle fovea weak, lateral foveae shallow, short furrow-like; interocellar furrow shallow, postocellar furrow weak; POL: OOL: OCL = 9: 20: 11; postocellar area weakly elevated, 2.5× broader than long; lateral furrow somewhat narrow, divergent posteriorly; head narrowed behind eyes in dorsal view, occipital carina complete. Antenna rather robust, approximately 1.2× longer than head and thorax together (17:14), approximately 1.1× longer than abdomen (17: 15); antennomere 2 approximately 1.2× as long as breadth; antennomere 3 approximately 1.4× as long as antennomere 4 (39: 27), approximately 0.8× as long as antennomeres 4 and 5 together (39: 51), middle antennomeres not inflated, subapical antennomeres weakly compressed (Figure 3D). Mesoscutellum roundly elevated, with weak middle ridge or carina, as high as top of mesonotum in lateral view; mesoscutellar appendage with lower middle longitudinal carina; metascutellum with short and lower carina; posterodorsal platform of mesepimeron as broad as diameter of middle ocellus; metepimeronal appendage small platform-shaped; distance be-

tween cenchri twice breadth of a cenchrus; mesopleuron and metapleuron as shown in Figure 3E. Inner tibial spur of hind leg $0.6\times$ length of metabasitarsus (5: 8); metabasitarsus slender, about $1.1\times$ longer than following four tarsomeres together (8: 7); claw with inner tooth slightly shorter than outer tooth. Ovipositor sheath clearly longer than metabasitarsus (5: 4), apical sheath as long as basal sheath, setae on ovipositor sheath slightly curved in dorsal view, apical margin round in lateral view (Figure 3F). Fore wing with cross-vein cu-a joining cell 1M in basal $1/4$, cross-vein 2r joining cell 2Rs in apical $1/4$, cell 2Rs as long as cell $1R_1$, petiole of anal cell slightly shorter than cross-vein 1r-m and petiole of anal cell in hind wing $0.6\times$ longer than cross-vein cu-a. Lancet narrow and long, with 21 serrulae (Figure 3G), serrulae clearly protruding and oblique platform-shaped, middle serrulae with 2 or 3 proximal and 9 or 10 distal teeth, subbasal teeth distinct and small, annular spine bands narrow, the 8th–10th serrulae as shown in Figure 3H.

Male. Unknown.

Type material. Holotype, ♀, China: Yunnan Province: Deqin County, Mount Meri, $28^{\circ}42'5''N$, $98^{\circ}80'5''E$, 2700 m, 20.vi.2009, leg. Yihai Zhong, ethylacetate.

Host plants. Unknown.

Distribution. China (Yunnan).

Etymology. The specific name “*zejiani*” is derived from the name of Dr. Zejian Li who has made great contributions to the study of *Macrophya* systematics.

Discussion

The *Macrophya imitator* group originally proposed by Liu et al. (2015) is the second largest of defined species group of *Macrophya* Dahlbom, 1835 in terms of known species. At present, there are 20 species belonging to this group in China, including the three new species described above: *M. bui* Wei & Li, 2012, *M. changbaina* Li, Liu & Heng, 2015, *M. circulotibialis* Li, Liu & Heng, 2015, *M. curvatisaeta* Wei & Li, 2010, *M. curvatithecata* Li, Liu & Heng, 2015, *M. flactoserrula* Chen & Wei, 2002, *M. funiushana* Wei, 1998, *M. imitatoides* Wei, 2007, *M. imitator* Takeuchi, 1937, *M. jiaozhaoae* Wei & Zhao, 2010, *M. kangdingensis* Wei & Li, 2012, *M. longlingensis* Li, Liu & Wei, sp. nov., *M. nishuaiguo* Li, Liu & Wei, sp. nov., *M. nigromaculata* Wei & Li, 2010, *M. omeialpina* Li, Jiang & Wei, 2018, *M. parimitator* Wei, 1998, *M. postscutellaris* Malaise, 1945, *M. semipunctata* Li, Liu & Wei, 2018, *M. weni* Wei, 1998 and *M. zejiani* Liu & Wei, sp. nov. The host plants of this group are unknown. The included

key and geographical distribution map of the *M. imitator* group should facilitate the recognition and identification of the Chinese species.

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Abstract

Fishes are a paraphyletic group composed by craniates except for the four-limbed clade Tetrapoda. This group was the only vertebrate representative until the Devonian but now comprises almost half of the vertebrate species, dominating nearly all aquatic environments. The fossil record is the key to understand the ancient paleobiodiversity and the patterns that lead the modern fish fauna, and paleontological collections play a fundamental role in providing accommodation, maintenance, and access to the specimens and their respective metadata. Here we present a systematic checklist of fossil fishes housed in the type collection of the Colección Nacional de Paleontología which is located at the Instituto de Geología of Universidad Nacional Autónoma de México. Currently housed in the type collection are 14 chondrichthyan specimens, belonging to two superorders, five orders, seven families, 10 genera, and five nominal species, and 361 osteichthyan specimens, belonging to eight orders, nine families, nine genera, and 26 nominal species. These fossils come from 32 localities and 15 geological units, which range temporally from the Jurassic to the Pleistocene. The paleoichthyofauna housed in the type collection of the Colección Nacional de Paleontología is remarkable for its singularity and reveals new insights about the origin and diversification of many groups of fishes. The recovery and curation of this fossil material indicates that knowledge of Mexican fossil fish diversity and its role in understanding lower vertebrate evolution are just emerging and reaffirms the importance of the biological and paleontological collections to the future biodiversity research.

Key Words

Collection, diversity, fishes, paleontology, taxonomy, Mexico

Introduction

Fishes are craniate animals that have gill arches and use fins for locomotion in aquatic environments (Berra 2007; Nelson et al. 2016; Clarke and Friedman 2018). Among vertebrates, fishes exhibit incomparable diversity in morphology, behavior, physiology, and distribution (Nelson et al. 2016). Currently, the extant fishes are classified in four distinct classes: Myxini (hagfishes), Petromyzontida (lampreys), Chondrichthyes (cartilaginous fishes, such as sharks and stingrays), and Osteichthyes. The last class is

divided into ray-finned (Actinopterygii) and lobe-finned fishes, Dipnoi and Actinistia, respectively (Helfman et al. 1997). Nevertheless, if we consider the extinct ichthyofauna, the number of classes at least doubles (see Nelson et al. 2016).

In the current understanding of vertebrate systematics, fishes constitute a paraphyletic group (Gill and Mooi 2002; Berra 2007) because it excludes the four-limbed osteichthyan clade Tetrapoda, which shares a common ancestor

with lobe-finned fishes (Zhu and Yu 2002). Nevertheless, with at least 32,000 species, fishes represent one-half of the world's living vertebrates and the study of fishes contributes to many subjects of scientific natural history knowledge, such as ontogeny, distribution, speciation, and diversification through space and time (Kornfield and Smith 2000; Peñáz 2001, Cavin et al. 2008; Nelson et al. 2016).

Fossils are physical evidence that helps in the recognition and interpretation of biological patterns and processes on Earth through time (Cavin et al. 2008). Nevertheless, by its composition, fossil material is so fragile that specific care is required for good long-term preservation, and museums and academic institutions are responsible for protecting and conserve this material (Allmon 1994, 2005; Llorente-Bousquets et al. 1994).

Paleontological collections not only have the responsibility of accommodating and storing the fossil record but also of providing the care and good conditions to use these materials for scientific research purposes and entertainment (Llorente-Bousquets et al. 1994; Cristín and Perrilliat 2011). Good practices in museum curation, such as the collection of specimens in appropriate spaces and conditions, the creation of systematic catalogues, and regulations for the proper use of fossils, are essential to generate and validate the information on which the advance of science is possible (Allmon 2005). Furthermore, paleontological collections have an important social and teaching role in spreading the scientific discoveries accessible to the public (Suarez and Tsutsui 2004).

The Colección Nacional de Paleontología of Universidad Nacional Autónoma de México (CNP-UNAM) is remarkable by its number of specimens collected in many regions of the country from various geological ages (e.g. Perrilliat 1993; Cristín and Perrilliat 2011; Perrilliat and Castañeda-Posadas 2013; Rojas-Zúñiga and Gio-Argáez 2016). Although the birth of CNP-UNAM was at the end of the 19th century, its formal consolidation inside the Institute of Geology occurred between 1978 and 1986. Only in 2004 did this collection become recognized as the National Collection of Paleontology and given the designation as the “Museum María del Carmen Perrilliat”. All fossils housed at the CNP-UNAM have the acronym (IGM) and began to be incorporated in 1978. Previous fossil records are in other institutions or are lost.

Today, the CNP-UNAM has five sections: geographic reference, foreign materials, Recent materials, molds, and the collection of types (Perrilliat et al. 1986; Carreño and Montellano-Ballesteros 2005). The type collection includes: 1) specimens belonging to type series and 2) voucher specimens, which are recorded in this collection as hypotypes. This section comprises about 10,000 specimens of microfossils, plants, invertebrates, and vertebrates, ranging from the end Precambrian to the Quaternary period of the Cenozoic (e.g. Perrilliat 1993; Perrilliat and Castañeda-Posadas 2013).

After 25 years since the last report about the fossil vertebrates housed in the type collection of CNP-UNAM (Perrilliat 1993), fossil fish specimens have been incre-

mentally added and many changes in fish taxonomy and classification have occurred. Therefore, following Article 72 of the International Code of Zoological Nomenclature, we present the systematic list of fishes currently housed in this collection and their respective localities. Furthermore, we provide information about the implications of these discoveries to understanding the taxonomy, biogeography, and early evolutionary history of some taxa and highlight the importance of biological collections to future research on paleodiversity in Mexico.

Methods

All fish fossils housed in the CNP-UNAM type collection were reviewed. Information on the taxonomy, age, and distribution are from both the collection database and the literature. For each species, we include the catalogue number (IGM), taxonomic classification, and respective distribution and age. Nomenclature on extinct Chondrichthyes follows Nelson et al. (2016) and Van de Laan (2018), while nomenclature on Recent Osteichthyes follows Betancur-R. et al. (2017) and Fricke et al. (2019). The nomenclature of extinct bony fishes follows Nelson et al. (2016), Van der Laan (2018), and original references. The maps were created with QGIS software version 2.18.19 (QGIS Development Team 2018) and the fossil fish localities were plotted using the software ArcView version 3.3 (Environmental Systems Research Institute, Inc., Redlands, California). Most of the taxonomic database used is available under open access at Unidad Informática para la Paleontología of UNAM (UNIPALEO; <http://www.unipaleo.unam.mx>).

Results

1. Systematic checklist list of CNP-UNAM fossil fishes

Subphylum Vertebrata Cuvier, 1812
 Infraphylum Gnathostomata Zittel, 1879
 Class Chondrichthyes Huxley, 1880
 Subclass Elasmobranchii Bonaparte, 1838
 Cohort Euselachii Hay, 1902
 Order †Hybodontiformes Maisey, 1975
 Superfamily †Hybodontoidae Owen, 1846
 Family †Hybodontidae Agassiz, 1843
 Genus †*Planohybodus* Rees & Underwood, 2008

†*Planohybodus* indet.

Referred specimen. IGM 9316, IGM 9317 (Alvarado-Ortega et al. 2014).

Locality and age. Llano Yosobé, Sabinal Formation, Tlaxiaco, Oaxaca; Jurassic (Kimmeridgian-Tithonian).

Subcohort Neoselachii Compagno, 1977
 Superorder Galeomorphii Compagno, 1973
 Order Carcharhiniformes Compagno, 1973

Carcharhiniformes indet.

Referred specimen. IGM 6990 (Ferrusquía-Villafranca et al. 1999).

Locality and age. Rancho el Jobo, San Juan Formation, Tuxtla Gutiérrez, Chiapas; Middle Eocene.

Family Carcharhinidae Jordan & Evermann, 1896
 Genus *Galeocerdo* Müller & Henle, 1837

†*Galeocerdo rosaliensis* Applegate, 1978

Referred specimen. IGM 5854 (holotype).

Locality and age. Tirabuzón Formation, Santa Rosalía, Baja California Sur; Pliocene.

Galeocerdo indet.

Referred specimen. IGM 6989 (Ferrusquía-Villafranca et al. 1999).

Locality and age. Rancho el Jobo, San Juan Formation, Tuxtla Gutiérrez, Chiapas; Middle Eocene.

Family Hemigaleidae Hasse, 1878
 Genus *Hemipristis* Agassiz, 1843

Hemipristis indet.

Referred specimen. IGM 6988 (Ferrusquía-Villafranca et al. 1999).

Locality and age. Rancho el Jobo, San Juan Formation, Tuxtla Gutiérrez, Chiapas; Middle Eocene.

Order Lamniformes Berg, 1958
 Family Lamnidae Bonaparte, 1835
 Genus *Carcharodon* Smith, 1938

†*Carcharodon auriculatus* Jordan, 1923

Referred specimen. IGM 6986 (Ferrusquía-Villafranca et al. 1999).

Locality and age. Rancho el Jobo, San Juan Formation, Tuxtla Gutiérrez, Chiapas; Middle Eocene.

Genus *Isurus* Rafinesque, 1810

†*Isurus* cf. *praecursor* Leriche, 1902

Referred specimen. IGM 6985 (Ferrusquía-Villafranca et al. 1999).

Locality and age. Rancho el Jobo, San Juan Formation, Tuxtla Gutiérrez, Chiapas; Middle Eocene.

Family Odontaspidae Müller & Henle, 1839
 Genus *Carcharias* Rafinesque, 1810

Carcharias indet.

Referred specimen. IGM 6983 (Ferrusquía-Villafranca et al. 1999).

Locality and age. Rancho el Jobo, San Juan Formation, Tuxtla Gutiérrez, Chiapas; Middle Eocene.

Genus *Odontaspis* Agassiz, 1838

Odontaspis indet.

Referred specimen. IGM 6984 (Ferrusquía-Villafranca et al. 1999).

Locality and age. Rancho el Jobo, San Juan Formation, Tuxtla Gutiérrez, Chiapas; Middle Eocene.

Genus †*Striatolamia* Glikman, 1964

†*Striatolamia macrota* (Agassiz, 1843)

Referred specimen. IGM 6982 (Ferrusquía-Villafranca et al. 1999).

Locality and age. Rancho el Jobo, San Juan Formation, Tuxtla Gutiérrez, Chiapas; Middle Eocene.

Family †*Otodontidae* Glikman, 1964

†*Otodontidae* indet.

Referred specimen. IGM 6987 (Ferrusquía-Villafranca et al. 1999).

Locality and age. Rancho el Jobo, San Juan Formation, Tuxtla Gutiérrez, Chiapas; Middle Eocene.

Order Orectolobiformes Compagno, 1973
 Suborder Orectoloboidei Regan, 1908
 Family Ginglymostomatidae Gill, 1862
 Genus *Nebrius* Rüppel, 1837

Nebrius indet.

Referred specimen. IGM 6981 (Ferrusquía-Villafranca et al. 1999).

Locality and age. Rancho el Jobo, San Juan Formation, Tuxtla Gutiérrez, Chiapas; Middle Eocene.

Superorder Batoidea Compagno, 1973
 Order Rhinopristiformes Last, Serét & Naylor, 2016

Family *incertae sedis*

Genus †*Tlalocbatos* Brito, Villalobos-Segura & Alvarado-Ortega, 2019

†*Tlalocbatos applegatei* Brito, Villalobos-Segura & Alvarado-Ortega, 2019

Referred specimens. IGM 5853 (holotype).

Locality and age. Tlayúa quarry, Tlayúa Formation, Tepexi de Rodríguez, Puebla; Cretaceous (Albian).

Megaclass Osteichthyes Huxley, 1880
 Class Actinopterygii Woodward, 1891
 Subclass Neopterygii Regan, 1923

Order *incertae sedis*

Family *incertae sedis*

Genus †*Cipactlichthys* Brito & Alvarado-Ortega, 2013

†*Cipactlichthys scutatus* Brito & Alvarado-Ortega, 2013

Referred specimens. IGM 6605 (holotype), IGM 6606 (paratype).

Locality and age. Tlayúa quarry, Tlayúa Formation, Tepexi de Rodríguez, Puebla; Cretaceous (Albian).

Order †Aspidorhynchiformes Bleeker, 1859
 Family †Aspidorhynchidae Bleeker, 1859
 Genus †*Vinctifer* Jordan, 1919

†*Vinctifer ferrusquiai* Cantalice, Alvarado-Ortega & Brito, 2018

Referred specimen. IGM 8873 (holotype).

Locality and age. Llano Yosobé, Sabinal Formation, Tlaxiaco, Oaxaca; Jurassic (Kimmeridgian-Tithonian).

Order †Pycnodontiformes Berg, 1937
 Suborder †Pycnodontoidei Nursall, 1966
 Family †Pycnodontidae Agassiz, 1833

†Pycnodontidae indet.

Referred specimen. IGM 3143 (Carranza-Castañeda and Applegate 1994).

Locality and age. Cerro los Mendoza, El Doctor Formation, Zimapán, Hidalgo; Cretaceous (Albian-Cenomanian).

Subfamily †Pycnodontinae (Agassiz, 1833)
 Genus †*Pycnodus* Agassiz, 1833

†*Pycnodus* indet.

Referred specimen. IGM 4551 (Alvarado-Ortega et al. 2015).

Locality and age. Belisario Domínguez quarry, Tenejapa-Lacandón geological unity; Salto de Agua, Chiapas; Paleocene (Danian).

Genus †*Tepexichthys* Applegate, 1992

†*Tepexichthys aranguthyrorum* Applegate, 1992

Referred specimens. IGM 3286 (holotype), IGM 3288-IGM 3289, IGM 3291-IGM 3300, IGM 3455, IGM 3513, IGM 3587, IGM 3689, IGM 3690, IGM 4052-IGM 4122 (paratypes).

Locality and age. Tlayúa quarry, Tlayúa Formation, Tepexi de Rodríguez, Puebla; Cretaceous (Albian).

Suborder †Gyrodontoidei Nursall, 1996
 Family †Gyrodontidae Berg, 1940
 Genus †*Gyrodus* Agassiz, 1833

†*Gyrodus* indet.

Referred specimens. IGM 9318, IGM 9319 (Alvarado-Ortega et al. 2014).

Locality and age. Llano Yosobé, Sabinal Formation, Tlaxiaco, Oaxaca; Jurassic (Kimmeridgian-Tithonian).

Infraclass Holostei Müller, 1845
 Division Ginglymodi Cope, 1871
 Order †Semionotiformes Arambourg & Bertini, 1958 (*sensu* López-Arbarello 2012)
 Family †Semionotidae Woodward, 1890
 Genus †*Tlayuamichin* López-Arbarello & Alvarado-Ortega, 2011

†*Tlayuamichin itzli* López-Arbarello & Alvarado-Ortega, 2011

Referred specimens. IGM 6716 (holotype), IGM 6717-IGM 6720 (paratypes).

Locality and age. Tlayúa quarry, Tlayúa Formation, Tepexi de Rodríguez, Puebla; Cretaceous (Albian).

Family †Macrosemiidae Wagner, 1860
 Genus †*Notagogus* Agassiz, 1843

†*Notagogus novomundi* González-Rodríguez & Reynoso, 2004

Referred specimen. IGM 8172 (holotype), IGM 8173-IGM 8181 (paratypes).

Locality and age. Tlayúa quarry, Tlayúa Formation, Tepexi de Rodríguez, Puebla; Cretaceous (Albian).

Genus †*Macrosemiocotzus* González-Rodríguez, Applegate & Espinosa-Arrubarrena, 2004

†*Macrosemiocotzus americanus* González-Rodríguez, Applegate & Espinosa-Arrubarrena, 2004

Referred specimens. IGM 8163 (holotype), IGM 8164-IGM 8171 (paratypes).

Locality and age. Tlayúa quarry, Tlayúa Formation, Tepexi de Rodríguez, Puebla; Cretaceous (Albian).

Order Lepisosteiformes Hay, 1929

Lepisosteiformes indet.

Referred specimens. IGM 9321, IGM 9322 (Alvarado-Ortega et al. 2014).

Locality and age. Llano Yosobé, Sabinal Formation, Tlaxiaco, Oaxaca; Jurassic (Kimmeridgian-Tithonian).

Family Lepidotidae Owen, 1860
 Genus *Scheenstia* López-Arbarello & Sferco, 2011

***Scheenstia* indet.**

Referred specimen. IGM 9320 (Alvarado-Ortega et al. 2014).

Locality and age. La Lobera, “Caliza con *Cidaris*”, Tlaxiaco, Oaxaca; Jurassic (Oxfordian-Early Kimmeridgian).

Superfamily Lepisosteoidea López-Arbarello, 2012

Family Lepisosteidae Agassiz, 1832

Lepisosteidae indet.

Referred specimens. IGM 7657-IGM 7662 (Rodríguez De la Rosa and Cevallos-Ferriz 1998).

Locality and age. El Pelillal, Cerro del Pueblo Formation, Coahuila; Cretaceous (Campanian).

Genus †*Nhanulepisosteus* Brito, Alvarado-Ortega & Meunier, 2017

†*Nhanulepisosteus mexicanus* Brito, Alvarado-Ortega & Meunier, 2017

Referred specimens. IGM 4898 (holotype), IGM 4899-IGM 4902 (paratypes).

Locality and age. Llano Yosobé, Sabinal Formation, Tlaxiaco, Oaxaca; Jurassic (Kimmeridgian-Tithonian).

Division Halecomorphi Cope, 1872

Order †Ionoscopiformes Grande & Bemis, 1998

Family †Ionoscopidae Lehman, 1966

Genus †*Quetzalichthys* Alvarado-Ortega & Espinosa-Arrubarrena, 2008

†*Quetzalichthys perrillatae* Alvarado-Ortega & Espinosa-Arrubarrena, 2008

Referred specimen. IGM 8592 (holotype), IGM 8593-IGM 8596 (paratypes).

Locality and age. Tlayúa quarry, Tlayúa Formation, Tepexi de Rodríguez, Puebla; Cretaceous (Albian).

Family †Ophiopsidae Bartram, 1975

Genus †*Teoichthys* Applegate, 1988

†*Teoichthys kallistos* Applegate, 1988

Referred specimen. IGM 3460 (holotype), IGM 4126 (paratype).

Locality and age. Tlayúa quarry, Tlayúa Formation, Tepexi de Rodríguez, Puebla; Cretaceous (Albian).

†*Teoichthys brevipina* Machado, Alvarado-Ortega, Machado & Brito, 2013

Referred specimens. IGM 6741 (holotype), IGM 6742 and IGM 6744 (paratypes), IGM 6604, IGM 6743, IGM 6745-IGM 6747 (Machado et al. 2013).

Locality and age. Tlayúa quarry, Tlayúa Formation, Tepexi de Rodríguez, Puebla; Cretaceous (Albian).

Order Amiiformes Hay, 1929

Family Amiidae Bonaparte, 1837

Subfamily †Vidalamiinae Grande & Bemis, 1998

Genus †*Pachyamia* Chalifa & Tchernov, 1982

†*Pachyamia mexicana* Grande & Bemis, 1998

Referred specimens. IGM 7379 (holotype), IGM 7380-IGM 7387 (paratypes).

Locality and age. Tlayúa quarry, Tlayúa Formation, Tepexi de Rodríguez, Puebla; Cretaceous (Albian).

Genus †*Melvius* Bryant, 1987

†*Melvius* indet.

Referred specimens. IGM 7663, IGM 7664 (Rodríguez De la Rosa and Cevallos-Ferriz 1998).

Locality and age. El Pelillal, Cerro del Pueblo Formation, Coahuila; Cretaceous (Campanian).

Infraclass Teleostei Müller, 1845

Order †Pholidophoriformes Wagner, 1860

Family †Pleuropholidae Saint-Seine, 1949

Genus †*Pleuropholis* Egerton, 1858

†*Pleuropholis cinerosorum* Alvarado-Ortega & Brito, 2016

Referred specimens. IGM 4733 (holotype), IGM 4734, IGM 4735, IGM 9323 (paratypes).

Locality and age. Llano Yosobé, Sabinal Formation, Tlaxiaco, Oaxaca; Jurassic (Kimmeridgian-Tithonian).

Order †Ichthyodectiformes Bardack & Sprinkle, 1969

†Ichthyodectiformes indet.

Referred specimen. IGM 9048 (Alvarado-Ortega et al. 2007).

Locality and age. Tlayúa quarry, Tlayúa Formation, Tepexi de Rodríguez, Puebla; Cretaceous (Albian).

Suborder †Ichthyodectoidei Maisey, 1991

Family †Ichthyodectidae Crook, 1892

Genus †*Unamichthys* Alvarado-Ortega, 2004

†*Unamichthys espinosai* Alvarado-Ortega, 2004

Referred specimens. IGM 8373 (holotype), IGM 8374-IGM 8376 (paratypes).

Locality and age. Tlayúa quarry, Tlayúa Formation, Tepexi de Rodríguez, Puebla; Cretaceous (Albian).

Megacohort Elopoccephalai Arratia, 1999

Cohort Elopomorpha Greenwood, Rosen, Weitzman & Myers, 1966

Order Anguilliformes Goodrich, 1909

Anguilliformes indet.

Referred specimen. IGM 4547 (Alvarado-Ortega et al. 2015).

Locality and age. Belisario Domínguez quarry, Tenejapa-Lacandón geological unity, Salto de Agua, Chiapas; Paleocene (Danian).

Megacohort Osteoglossocephalai Betancur-R., Broughton, Wiley, Carpenter, López, Holcroft, Arcila, Sanciangco, Cureton, Zhang, Borden, Rowley, Reneau, Hough, Lu, Grande, Arratia & Ortí, 2013 (=Osteoglossocephala *sensu* Arratia 1999)

Supercorhort Osteoglossomorpha Greenwood, Rosen, Weitzman & Myers, 1966

Order Osteoglossiformes Berg, 1940

Suborder Osteoglossoidei Regan, 1909

Family Osteoglossidae Bonaparte, 1832

Subfamily Osteoglossinae Nelson, 1968

Genus †*Phaerodus* Leidy, 1873

†*Phaerodus* indet.

Referred specimen. IGM 4549 (Alvarado-Ortega et al. 2015).

Locality and age. División del Norte quarry, Tenejapa-Lacandón geological unity, Palenque, Chiapas; Paleocene (Danian).

Supercohort Clupecocephala Patterson & Rosen, 1977

Order †Crossognathiformes Taverne, 1989

Suborder †Pachyrhizodontoidei Forey, 1977

†**Pachyrhizodontoidei indet.**

Referred specimen. IGM 9049 (Alvarado-Ortega et al. 2007).

Locality and age. Tlayúa quarry, Tlayúa Formation, Tepexi de Rodríguez, Puebla; Cretaceous (Albian).

Family *incertae sedis*

Genus †*Michin* Alvarado-Ortega, Mayrinck & Brito, 2008

†*Michin csernai* Alvarado-Ortega, Mayrinck & Brito, 2008

Referred specimens. IGM 9028 (holotype), IGM 9029-IGM 9033 (paratypes).

Locality and age. Tlayúa quarry, Tlayúa Formation, Tepexi de Rodríguez, Puebla; Cretaceous (Albian).

Cohort Otomorpha Wiley & Johnson, 2010

Subcohort Clupei Wiley & Johnson, 2010

Order †Ellimmichthyiformes Grande, 1982

Family †Paraclupeidae Chang & Chou, 1974

†*Paraclupea seilacheri* Alvarado-Ortega & Melgarejo-Damián, 2017

Referred specimens. IGM 4717 (holotype), IGM 4718-IGM 4723 (paratypes).

Locality and age. Tlayúa quarry, Tlayúa Formation, Tepexi de Rodríguez, Puebla; Cretaceous (Albian).

Order Clupeiformes Rafinesque, 1810

Suborder Clupeoidei Rafinesque, 1810

Family *incertae sedis*

†*Ranulfoichthys dorsonudum* Alvarado-Ortega, 2014

Referred specimens. IGM 9034 (holotype), IGM 9467, IGM 9468 (paratypes); IGM 9035-IGM 9047 (Alvarado-Ortega, 2014).

Locality and age. Tlayúa quarry, Tlayúa Formation, Tepexi de Rodríguez, Puebla; Cretaceous (Albian).

Family Clupeidae Cuvier, 1817

Clupeidae indet.

Referred specimen. IGM 4548 (Alvarado-Ortega et al. 2015).

Locality and age. División del Norte quarry, Tenejapa-Lacandón geological unity, Palenque, Chiapas; Paleocene (Danian).

Subcohort Ostariophysa Lord, 1922

Section Otophysa (=Series Otophysi sensu Rosen & Greenwood, 1970)

Superorder Cypriniphysae Fink & Fink, 1981

Order Cypriniformes Rafinesque, 1810

Superfamily Cobitoidea Swainson, 1839

Family Catostomidae Agassiz, 1850

Subfamily Ictiobinae Smith, 1992

Genus *Ictiobus* Rafinesque, 1820

†*Ictiobus aguilerai* Alvarado-Ortega, Carranza-Castañeda & Álvarez-Reyes, 2006

Referred specimens. IGM 8444 (holotype), IGM 8445-IGM 8591 (paratypes).

Locality and age. La Cementera, La Viga, Tecalco, and El Hoyo, Tarango Formation, Tula de Allende, Hidalgo; Pliocene.

Order Siluriformes Rafinesque, 1810

Suborder Siluroidei Rafinesque, 1810

Superfamily Bagroidea Bleeker, 1858

Family Ariidae Bleeker, 1858

Ariidae indet.

Referred specimen. IGM 5318, IGM 5319 (Hernández-Junquera 1977).

Locality and age. Laguna de la Media Luna, Río Verde, San Luis Potosí; Pleistocene.

Cohort Euteleosteomorpha Greenwood, Rosen, Weitzman & Myers, 1966

Subcohort Neoteleostei Nelson, 1969

Infracohort Eurypterygia Rosen, 1973

Section Ctenosquamata Rosen, 1973

Subsection Acanthomorphata Rosen, 1973

Division Acanthopterygii Rosen &

Patterson, 1969

Subdivision Percomorphaceae Betancur-R.,

Broughton, Wiley, Carpenter, López, Holcroft,

Arcila, Sanciangco, Cureton, Zhang, Borden, Rowley, Reneau, Hough, Lu, Grande, Arratia & Ortí, 2013 (=Percomorphacea sensu Wiley & Johnson, 2010)

Percomorphaceae indet.

Referred specimen. IGM 7968 (Cantalice and Alvarado-Ortega in press).

Locality and age. Ixtapa locality, Ixtapa Formation, Ixtapa, Chiapas; Miocene.

Genus †*Kelemejtubus* Cantalice & Alvarado-Ortega, 2017

†*Kelemejtubus castroi* Cantalice & Alvarado-Ortega, 2017

Referred specimens. IGM 4864 (holotype), IGM 4865-IGM 4867, IGM 4908, IGM 4909 (paratypes).

Locality and age. Belisario Domínguez and División del Norte quarries, Tenejapa-Lacandón geological unity, Salto de Agua and Palenque, Chiapas; Paleocene (Danian).

Series Syngnatharia Betancur-R., Wiley, Bailly, Miya, Lecointre et al., 2014

Order Syngnathiformes Berg, 1940

Suborder Syngnathoidei Regan, 1909

Superfamily Aulostomoidea Greenwood, Rosen, Weitzman & Myers, 1966

Family †Eekaulostomidae Cantalice & Alvarado-Ortega, 2016

Genus †*Eekaulostomus* Cantalice & Alvarado-Ortega, 2016

†*Eekaulostomus cuevasae* Cantalice & Alvarado-Ortega, 2016

Referred specimen. IGM 4716 (holotype).

Locality and age. Belisario Domínguez quarry, Tenejapa-Lacandón geological unity, Salto de Agua, Chiapas; Paleocene (Danian).

Series Carangaria Betancur-R., Broughton, Wiley, Carpenter, López, Holcroft, Arcila, Sanciangco, Cureton, Zhang, Borden, Rowley, Reneau, Hough, Lu, Grande, Arratia & Ortí, 2013(=Carangimorpha sensu Li et al. 2009)

Order Istiophoriformes Betancur-R., Broughton, Wiley, Carpenter, López, Holcroft,

Arcila, Sanciangco, Cureton, Zhang, Borden, Rowley, Reneau, Hough, Lu, Grande, Arratia & Ortí, 2013

Family Istiophoridae Rafinesque, 1815

Istiophoridae indet.

Referred specimens. IGM 7885-IGM 7887, IGM 7890-IGM 7892, IGM 7894 (Fierstine et al. 2001).

Locality and age. La Angostura and Rancho Algodones, Trinidad Formation, Baja California Sur; Upper Miocene.

Genus *Makaira* Lacépède, 1802

Makaira nigricans Lacépède, 1802

Referred specimens. IGM 7882-IGM 7884, IGM 7888, IGM 7889, IGM 7893 (Fierstine et al. 2001).

Locality and age. La Angostura, Los Dientes Grandes, Cañada de En medio, and Rancho Algodones, Trinidad Formation, Baja California Sur; Upper Miocene.

Series Ovalentaria Wainwright, Smith, Price, Tang, Sparks, Ferry, Kuhn, Eytan & Near, 2012
Superorder Atherinomorphae Betancur-R., Wiley, Arratia, Acero, Bailly, Miya, Lecointre & Ortí, 2017 (=Atherinomorpha sensu Greenwood et al. 1996)

Order Cyprinodontiformes Berg, 1940

Cyprinodontiformes indet. (sensu Espinosa-Perez et al. 1991)

Referred specimen. IGM 7967 (Cantalice and Alvarado-Ortega in press)

Locality and age. Los Ahuehuetes, Pie de vaca Formation, Tepexi de Rodríguez, Puebla; Oligocene.

Suborder Cyprinodontoidei Dyer & Chernoff, 1996

Family Goodeidae Jordan & Gilbert, 1883

Genus †*Tapatia* Álvarez & Arriola-Longoria, 1972

†*Tapatia occidentalis* Álvarez & Arriola-Longoria, 1972

Referred specimen. IGM 7966 (Cantalice and Alvarado-Ortega in press).

Locality and age. Barranca de Santa Rosa, Amatitán, Jalisco; Pliocene.

Series Eupercaria Sanciango, Carpenter & Betancur-R., 2016
 Order Perciformes Rafinesque, 1810
 Suborder Serranoidei Imamura & Yabe, 2002
 Family Serranidae Swainson, 1839
 Genus †*Paleoserranus* Cantalice, Alvarado-Ortega & Alaniz-Galvan, 2018

†*Paleoserranus lakamhae* Cantalice, Alvarado-Ortega & Alaniz-Galvan, 2018

Referred specimens. IGM 4550 (holotype), IGM 9469-IGM 9477 (paratypes).

Locality and age. Belisario Domínguez and División del Norte quarries, Tenejapa-Lacandón geological unit, Salto de Agua and Palenque, Chiapas; Paleocene (Danian).

2. CNP-UNAM fossil fish localities

The fossil fishes catalogued into the Type Collection of CNP-UNAM are from 32 paleontological localities belonging to four undefined geological units (Fig. 1; Suppl. material 1), seven marine formations, and five freshwater formations. The oldest strata found is from Oxfordian “Caliza con *Cidaris*” geological unit, Oaxaca, while the youngest fish fossil beds are from the Pleistocene of La-

guna de Media Luna (San Luis Potosí), the Tarango Formation, near Tula (Hidalgo), and Pie de Vaca, near Tepexi de Rodríguez (Puebla) (Fig. 2). This range represents approximately the last 150 million years of Earth’s history. Below are the main features of these Mexican lithostratigraphic units.

The Tirabuzón Formation

This geological unit was first known as the Gloria Formation and based on an outcrop exposed few kilometers away from Santa Rosalía town, Baja California Sur (Wilson 1948). Given that this last name was pre-occupied for a unit of Jurassic rocks from Coahuila (Imlay 1936), Applegate and Espinosa-Arrubarrena (1981) suggested the name of Cañada Gloria Formation for the rocks of Baja California Sur; however, the name of this geological unit changed to Tirabuzón Formation (Carreño 1981), based on Wilson (1948) and on nomenclatural incongruences present in the previous suggestions. The stratotype of the Tirabuzón Formation is inside the Bole Basin, at Santa Rosalía, Baja California Sur (Wilson 1948; Carreño 1981) and is a discontinuous basal conglomerate covered with potentially fossiliferous marine sandstone sediments that are overlaid with conglomerate strata containing a gradual lateral transition to littoral, deltaic, and nonmarine facies (Carreño 1981; Ortlieb and Colleta 1984; Carreño and Smith 2007). The abundant fossil content in this formation includes ichnofossils, foraminifers,

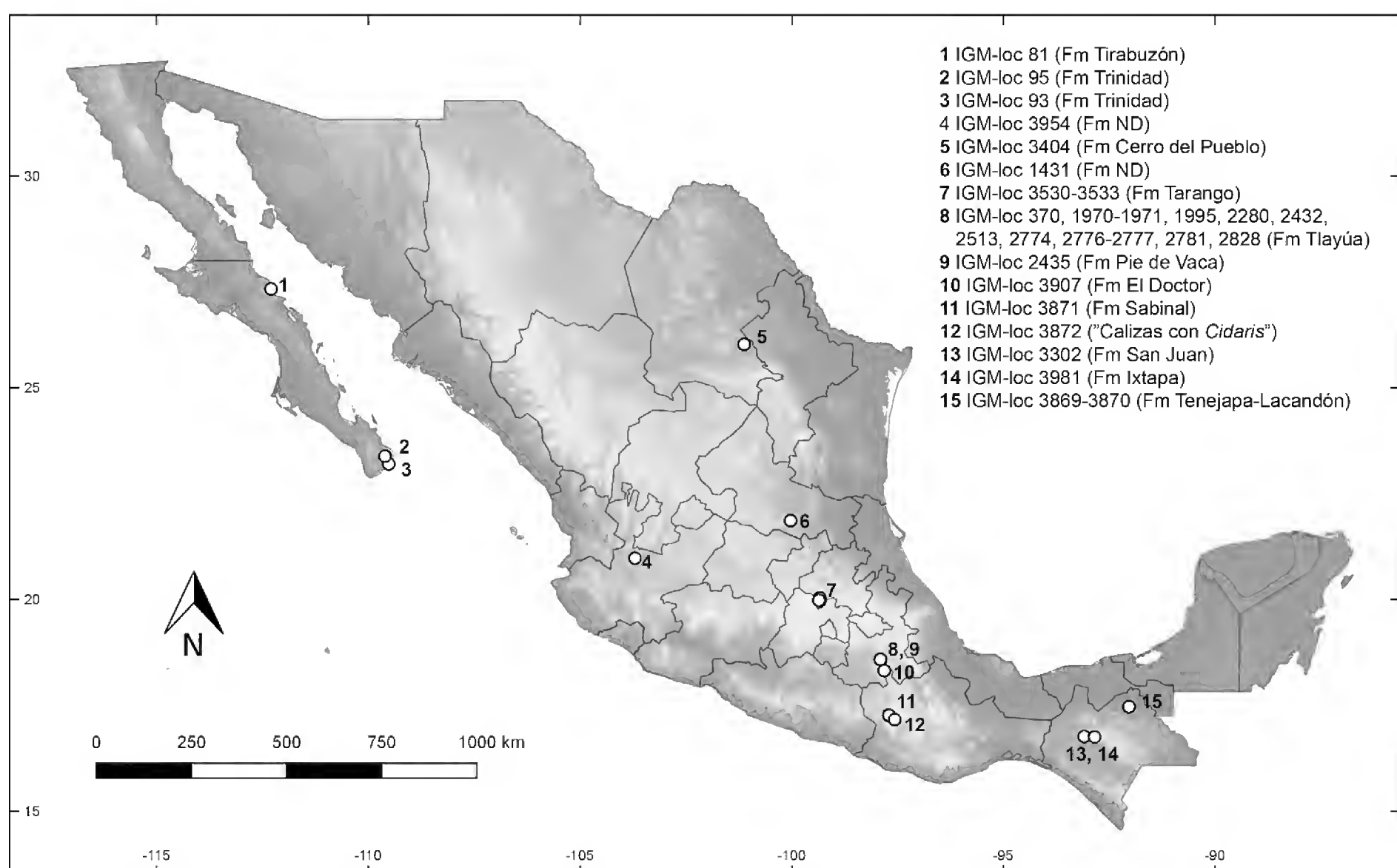


Figure 1. Map of Mexico, showing the localities currently catalogued at CNP-UNAM.

Cenozoic	Quaternary	Holocene		
		Pleistocene	Upper	Fm ND
			Middle	
			Calabrian	
	Neogene	Pliocene	Gelasian	
			Piacenzian	Fm Trinidad
		Miocene	Zanclean	Fm Tirabuzón, Fm Tarango
			Messinian	Fm ND
			Tortonian	
			Serravallian	Fm Ixtapa
			Langhian	
			Burdigalian	
			Aquitania	
			Paleogene	Oligocene
	Rupelian			
	Eocene	Priabonian		
		Bartonian		
		Lutetian		Fm San Juan
	Paleocene	Ypresian		
		Thanetian		
Mesozoic	Cretaceous	Selandian	Fm Tenejapa-Lacandón	
		Danian		
		Upper	Maastrichtian	Fm Cerro del Pueblo
			Campanian	
			Santonian	
			Coniacian	
	Lower	Turonian		
		Cenomanian	Fm El Doctor	
		Albian	Fm Tlayúa	
		Aptian		
		Barremian		
		Hauterivian		
		Valanginian		
		Berriasian		
Jurassic	Upper	Tithonian		
		Kimmeridgian	Fm Sabinal	
		Oxfordian	"Calizas con <i>Cidaris</i> "	
	Middle	Callovian		
		Bathonian		
		Bajocian		
		Aalenian		
	Lower	Toarcian		
		Pliensbachian		
		Sinemurian		
Hettangian				

Figure 2. Partial chronostratigraphic chart correlating each formation catalogued in CNP-UNAM that contains fossil fishes and its respective geological age.

mollusks, echinoderms and cetaceans (Wilson 1948; Applegate 1978; Carreño 1981; Ortlieb and Colleta 1984; Quiroz-Barroso and Perrilliat 1989; Barnes 1998; Carreño and Smith 2007; Shroat-Lewis 2007). The age of the unit is Late Miocene-Early Pliocene based on planktonic foraminifers (Carreño 1981), nannofossils (Ortlieb and Colleta 1984), and the shark fauna (Applegate 1978).

The Trinidad Formation

Pantoja-Alor and Carrillo-Bravo (1966) first described this unit which is also located in Baja California Sur. Its stratotype is near the intersection of the Coyote and La Trinidad Streams, in the western margin of the Coyote Stream;

however, these outcrops are from both San José del Cabo and Los Barriles Basins (Pantoja-Alor and Carrillo-Bravo 1966; Martínez-Gutiérrez and Sethi 1997; Schwennicke et al. 2017). The unit mainly has a fine-grained sandstone, siltstone, and mudstone but is also composed of gray-greenish, laminated, fine to medium marine sandstone, shale and siltstone, and some diatomite laminate toward the center of the San José del Cabo Basin (Martínez-Gutiérrez and Sethi 1997; Schwennicke et al. 2017). The age of the Trinidad formation range from the middle Miocene to upper Pliocene and its depositional environment has three distinct types of strata: 1) a basal nearshore-lagoon deposit; 2) a deep marine environment; 3) a high-energy, shallow marine waters, which they relate to inner shelf shoals and bars (Martínez-Gutiérrez and Sethi 1997; McCloy 1984; Carreño 1992; Fierstine et al. 2001; Schwennicke et al. 2017). The fossil record of the unit comprises nanoplanktons (Schwennicke et al. 2017), foraminifers and diatomite (McCloy 1984; Carreño 1992), mollusks (Martínez-Gutiérrez and Sethi 1997) fishes (Fierstine et al. 2001), and trace fossils (Schwennicke et al. 2017).

The Cerro del Pueblo Formation

Located in Coahuila state, this formation was described at the beginning 20th century (Imlay 1936); however, its formal description as Cerro del Pueblo Formation was later (Murray et al. 1962). Belonging to the Difunta Group (Eberth et al. 2004), its stratotype is northeast to Saltillo City, and its outcrops are in several localities in the Parras Basin (Murray et al. 1962). The lithology of the unit is mainly composed of mudstone and sandstone but also of lesser amounts of limonite, conglomerates, and limestone (McBride et al. 1974; Kirkland et al. 2000). The unit contains a vast fossil record, comprising plants (fruiting structures, palm fronds, conifer cones), rudists, bivalves, gastropods, cephalopods, elasmobranchs, bony fishes, dinosaurs, crocodiles, turtles (Kirkland et al. 2000), and insects (Cifuentes-Ruiz et al. 2006). There are seven distinct facies, and sediments were laid down in a low coastal plain and shallow marine conditions which were strongly influenced by frequent changes in the relative sea-level or coastal physical processes (Eberth et al. 2004). Hence, the paleoenvironment is a cyclic alternation of marine, estuarine, and freshwater environments (Cifuentes-Ruiz et al. 2006). The age of the formation ranges from uppermost late Campanian to Maastrichtian (Kirkland et al. 2000).

The Tarango Formation

This formation is in the Valley of Mexico (which includes the states of Ciudad de México, Estado de México, and Hidalgo) and was first proposed based on sediments exposed about 4 km southwest of Mixcoac, Mexico City (Bryan 1948; Ferrusquía-Villafranca et al. 2017). This geological unit is composed of sandstone and poorly cemented con-

glomerate, poorly cemented sandstone and interleaved clay, layers of clay, some layers of basalt interspersed with detrital units, lightly compacted conglomerate lenses, insulated limestone lenses, thin lenses of volcanic ash and tuff, and caliche nodules tuff, tuff-breccia, fluvial volcanic gravel, and thin pumice layers (Bryan 1948; Cervantes-Medel and Armienta 2004; Ferrusquía-Villafranca et al. 2017). The fossil record includes ostracods and diatoms (Ferrusquía-Villafranca et al. 2017), bony fishes (Alvarado-Ortega et al. 2006), and mammals of the genera *Equus* Linnaeus, 1758, *Cuvieronius* Osborn, 1923, *Mammuthus* Brookes, 1828, *Sylvilagus* Gray, 1867, *Canis* Linnaeus, 1758, and *Bison* Smith, 1827 (Castillo-Cerón et al. 1996). The depositional environment is a series of fluvial/lacustrine conditions with sandstone crossbedding which indicates deltaic conditions (Segerstrom 1962; Alvarado-Ortega et al. 2006; Ferrusquía-Villafranca et al. 2017). Based on the paleofauna, geochronology, and fault systems, the Tarango Formation is currently considered to present a Pliocene-Quaternary age (Castillo-Cerón et al. 1996; Suter et al. 2001).

The El Doctor Formation

The El Doctor Formation outcrops from the eastern portion of Queretaro state to the western edge of Hidalgo (Wilson et al. 1955). Its type locality is in the north flank, near El Doctor village in the Sierra Gorda, Queretaro, northeastern Peña de Bernal (Wilson et al. 1955; Segerstrom 1961; Aguirre-Díaz et al. 2013). This unit has a large limestone bank of varied textures with some chert lenses, dolomite interbeds, and shale partings (Segerstrom 1961). Based on lithology, there are four subunits: 1) La Negra, deposited in the deep of the neritic zone; 2) San Joaquín, with the same sediments of La Negra but deposited at a depth and under storm wave action; 3) Cerro Ladrón, a calcareous bank formed in shallow waters; and 4) Socavón, with clastic sediments deposited not far from the input origin (Wilson et al. 1955). The fossil record found in the El Doctor Formation includes rudists (Wilson et al. 1955), miliolids, corals, oysters, gastropods, ammonites, echinoids (Segerstrom 1962), planktic and benthic foraminifers, radiolarians (Bravo-Cuevas et al. 2009), crustaceans (Feldmann et al. 2007), and fishes (Carranza-Castañeda and Applegate 1994; Bravo-Cuevas et al. 2009). Its deposits originate on a platform shelf followed by a transitional marine system, including open sea to deep shelf margin, with alternation of neritic and open oceanic waters and, occasionally, influx of near-shore waters, probably during storms (Wilson et al. 1955; Carrillo-Martínez 1981; Bravo-Cuevas et al. 2009). The age of this formation is Albian-Cenomanian (Wilson et al. 1955; Bravo-Cuevas et al. 2009).

The Tlayúa Formation

The stratotype is a few kilometers north of Tepexi de Rodríguez town, Puebla state, eastern Mexico (Pantoja-Alor

1992). There is a subdivision of the Tlayúa Formation: 1) the Lower Member, formed by micritic limestones (mudstone to wackestone) with silica concretions and chert lenses; 2) the Middle Member, formed by red lithographic laminar limestone (mudstone) and chert lenses; and 3) the Upper Member, with layers of dolomite and dolomitic limestone (Pantoja-Alor 1992). The fossil record is preserved in the Middle Member and, by its abundance and exceptional quality of preservation, the Tlayúa Formation is currently considered the first fossil-*Lagerstätte* site found in Mexico (Alvarado-Ortega et al. 2007). The paleontological record are both marine and terrestrial fauna and flora, including rudists (Alencáster 1973), foraminifera, sponges, gorgonians, gastropods, ammonoids (Cantú-Chapa 1987), belemnoids (Seibertz and Buitrón 1987), bivalves, arthropods (Feldmann et al. 1998), asteroids (Buitrón-Sánchez et al. 2015), holothurians (Applegate et al. 1996), ophiuroids, fishes (Applegate 1987; Alvarado-Ortega 2004), lizards, crocodiles, turtles (Reynoso 1997, 2000), pterosaurs (Cabral-Perdomo and Applegate 1994), algae, and gymnosperms (Espinosa-Arrubarrena et al. 1996). The paleoenvironment is a double-enclosed shallow lagoon behind a barrier reef with stagnant, anaerobic, and hypersaline conditions and bounded by semi-arid land, on the other side, by a barrier bordering a deeper, well-oxygenated lagoon (Applegate 1987; Pantoja-Alor 1992; Espinosa-Arrubarrena and Applegate 1996). Nevertheless, some influences of an open sea have been proposed (Kashiyama et al. 2004). The age of Tlayúa quarry strata ranges between the Aptian and Albian stages in the Early Cretaceous between 125 and 100 Ma (Cantú-Chapa 1987; Seibertz and Buitrón 1987; Kashiyama et al. 2004).

The Pie de Vaca Formation

The outcrops of the Pie de Vaca Formation are in the southern portion of Puebla, a few kilometers northeast of Tepexi de Rodríguez town very close to the Tlayúa Formation (Pantoja-Alor 1992). The lithology of the formation consists of continental deposits of fluvial-lacustrine and alluvial environments formed by conglomerates, gravel, silt, clay, marl, limestone, travertine, and volcanic rocks (Pantoja-Alor 1992). These are followed by micritic sandstone with siliciclastic bands and intraclasts of flint, limestone, and volcanic rocks (Cabral-Perdomo et al. 2018). The fossil records of the unit are ichnites belonging to birds, camelids, felids, proboscideans, small artiodactyls (Cabral-Perdomo 1995, 2013), and bony fishes (González-Rodríguez et al. 2013; Guzmán 2015). Fungus, leaves, leaflets, wood, and fruits of angiosperms are also well conserved in this unit, as well as ostracods and stromatolites (Beraldi-Campesi et al. 2006). The paleoenvironmental condition is a tropical paleolake which evolved from a basin with alluvial conditions to shallow, alkaline, and evaporitic lacustrine circumstances, indicating the gradual desertification of the environment

(Beraldi-Campesi et al. 2006). Although the palynological record indicates an Eocene-Oligocene age for this formation (Martínez-Hernández and Ramírez-Arriaga 1999), the paleobotanical and ichnological record with associated mammals indicates with more robustness an Oligocene-Pleistocene age (Cabral-Perdomo 1995, 2013; Cabral-Perdomo et al. 2018; Ramírez and Cevallos-Ferri 2002).

The Sabinal Formation

The Sabinal Formation is in northeastern Oaxaca, with its outcrops (Yosobé and La Lobera) in the southern portion of Tlaxiaco Basin (López-Ticha 1985; Meneses-Rocha et al. 1994; Alvarado-Ortega et al. 2014). The lithology of the formation consists of a sequence of mudstone and wackestone clay, marl, and dark gray to black bituminous shale strata with abundant calcareous concretions arranged in thin laminar layers and showing abundant light oil impregnations (López-Ticha 1985; Felix 1891; Meneses-Rocha et al. 1994; Alvarado-Ortega et al. 2014). The fossil contents of the unit are microfossils (ostracods), plants, invertebrates (mostly ammonites), marine reptiles, and bony fishes (Alvarado-Ortega et al. 2014; Barrientos-Lara et al. 2015). The paleoenvironment is as a transitional environment under the marine influence (Alvarado-Ortega et al. 2014). A Kimmeridgian-Tithonian age is attributed to the Sabinal Formation based on the ammonite assemblage (Alvarado-Ortega et al. 2014).

The “Caliza con *Cidaris*” geological unit

This Jurassic geological unit was informally named because it carries numerous remains of urchins belonging to the genus *Cidaris* Leske, 1778. Main outcrops of this unit are present between Tlaxiaco and Mixtepec in Oaxaca State (Buitrón 1970). This includes the outcrops in “La Titana” hills, near Tlaxiaco, firstly reported by Felix (1891) (also see Alvarado-Ortega et al. 2014). The numerous marine invertebrates recovered in the gray marls and limestones interbedded with shales present in this site suggest that its age could extend from the Late Callovian to the Early Kimmeridgian (Buitrón 1970). Besides the first fossil fishes from the Lobera site reported by Alvarado-Ortega et al. (2014), where “Caliza con *Cidaris*” sediments outcrops; the fossils already documented in this geological unit include three bivalves, echinoids, calcareous sponges, gastropods, annelids, crinoids, a brachiopod (Buitrón 1970; Felix 1891).

The San Juan Formation

Located to the northwest of Tuxtla Gutiérrez in Chiapas state (Licari 1960; Allison 1967; Ferrusquía-Villafranca 1996), the San Juan Formation have light-brown shales and yellowish-brown fine-grained calcarenite, composed

of conglomerates, sandstone, siltstone, limestone, marl, and coquina (Ferrusquía-Villafranca 1996; Perrilliat et al. 2003). The fossil record in the unit contains foraminifers (Ferrusquía-Villafranca 1996; Perrilliat et al. 2003), calcareous algae, wood, bivalves, corals, annelids, gastropods, nautiloids, bivalves, echinoderms (Perrilliat et al. 2003), crustaceans, bony fishes (Vega et al. 2001), and sharks (Ferrusquía-Villafranca et al. 1999). The paleoenvironments are episodes of shallow, marine waters with high organic productivity and low terrigenous influence, combined with well-oxygenated shallow waters influenced by continental sedimentation and, probably, with marsh conditions from a deltaic lagoon system (Ferrusquía-Villafranca 1996; Perrilliat et al. 2003). Based on the foraminifer fossil record, the age assigned to the San Juan Formation is middle Eocene (Ferrusquía-Villafranca 1996; Perrilliat et al. 2003).

The Ixtapa Formation

Also located in Chiapas, the Ixtapa Formation is 28 km east from Tuxtla Gutiérrez City and its outcrops mainly at the east side of the Soyaló-Ixtapa highway (State Road 195) next to the bridge that crosses the Río Hondo 1 km north of Ixtapa Municipality (Langenheim and Frost 1963; Ferrusquía-Villafranca 1996). This unit has a sequence of pyroclastic materials interbedded with calcitic pebbly gravels and tuffs, which become more frequent towards the base of the unit forming part of interbedded layers of conglomerates, sandstones, and clays where crystalline and calcareous conglomerates are sporadically present (Langenheim and Frost 1963; Martínez-Hernández 1992). The fossil record in Ixtapa Formation is diverse and includes charophytes, foraminifers, mollusks (Daily and Durham 1966), palynomorph assemblages (e.g. dinoflagellates and mangrove pollen), proboscides, horses, rhinoceros (Langenheim and Frost 1963; Daily and Durham 1966), freshwater turtles (Ferrusquía-Villafranca 1996), and only one record of a bony fish (Cantalice and Alvarado-Ortega in press). The Ixtapa Formation was formed under a low-energy fluvial-lacustrine conditions over the Middle Miocene continental sandstones of the Coyolar Formation and is below the Pliocene-Pleistocene volcanic deposits of the Punta de Llano Formation (Ferrusquía-Villafranca 1996; Martínez-Amador et al. 2004; Hernández-Villalva et al. 2013). The paleoenvironment is a continental lacustrine or a brackish transitional environment near the coast (Daily and Durham 1966; Martínez-Hernández 1992). The age assigned to this Formation ranges from the Middle to Late Miocene (Ferrusquía-Villafranca 1996).

The Tenejapa-Lacandón geological unity

The Tenejapa-Lacandón geological unity was first mentioned by Islas-Tenorio et al. (2005). This layer represents the union of two contemporary and laterally continuous formations: Tenejapa, first described from outcrops of San Cristóbal de las Casas City (Quezada-Muñetón

1987), and Lacandón, primary known from Petén, Guatemala (Vinson 1962; Fourcade et al. 1999). Because it is not possible to determine the boundaries between the two Formations and the proper identity of each unit is poorly understood, here we interpret both formations as a single element, the Tenejapa-Lacandón geological unity (see Alvarado-Ortega et al. 2015). This layer outcrops in diverse portions of Chiapas state (Islas-Tenorio et al. 2004, 2005); however, the fossils housed in the CNP are from the División del Norte and Belisario Domínguez quarries. The first one is approximately 2 km southeast of the archeological site of Palenque City, while the last is 9.5 km from Palenque City. Both strata are limestone marls deposited in laminated and parallel strata, which show yellowish-creamy colors with some dark-grey silicified bands and nodules (Alvarado-Ortega et al. 2015; Cantalice et al. 2018a). The fossil specimens are many poor-preserved impressions of plant remains and a singular paleoichthyofauna (Alvarado-Ortega et al. 2015; Cantalice and Alvarado-Ortega 2016, 2017; Cantalice et al. 2018a). The number of well-preserved specimens (mostly on massive mortality) makes this geological unity a fossil-*Lagerstätte* site. The paleoenvironment of Tenejapa-Lacandón geological unity is a marine platform with influences of external conditions to the west, originating the Tenejapa Formation, and to the east, shallow waters influenced by primarily internal conditions composes the Lacandón Formation (Quezada-Muñetón 1987; Alvarado-Ortega et al. 2015). Studies based on stable strontium isotopes indicate a Paleocene (Danian) age for this geological unity (Alvarado-Ortega et al. 2015).

Discussion

Since the last systematic review of the vertebrates housed on the CNP-UNAM (Perrilliat 1993), the number of specimens of fossil fishes has increased from five to 375, and the number of valid species raised from two to 27, including 20 new to science. This means that the number of fossil fishes species housed in the collection is currently 11 times greater than previously, not considering, however, the fossils that were are not determinable to species, which represent almost one-half of the palaeoichthyological material currently housed in the type collection. These numbers show a great increment in the knowledge of Mexican fossil fishes over the last two decades.

Many of the species housed in CNP-UNAM are the oldest record of its respective group and the first report of the taxon in North America (Table 1). These represent not only an increase of the knowledge about the fish diversity but also constitute valuable tools to a new understanding of the historical biogeography of fishes. This is the case of †*Vinctifer ferrusquiai* (Fig. 3A), from Kimmeridgian-Tithonian marine deposits from Oaxaca, which is the oldest fossil record and the first report of a member of the genus †*Vinctifer* outside the Cretaceous Period (Cantalice et al. 2018b). Its age and distribution suggest that the family Aspidorhynchidae under went a

Table 1. Remarks of outstanding Mexican species housed at the CNP-UNAM. Abbreviation: A. America; L. last occurrence; N. North America; O. oldest occurrence. The asterisk means the oldest generic occurrence.

Taxon	Oldest or Last occurrence	First report	Apparent endemism
Class CHONDRICHTHYES			
Order †HYBODONTIFORMES			
Family †HYBODONTIDAE			
† <i>Planohybodus</i> indet.		N	
Order CARCHARHINIFORMES			
Family CARCHARHINIDAE			
† <i>Galeocerdo rosaliensis</i>			X
Order RHINOPRISTIFORMES			
Family <i>incertae sedis</i>			
† <i>Tlalocbatus applegatei</i>			X
Class ACTINOPTERYGII			
Order <i>incertae sedis</i>			
Family <i>incertae sedis</i>			
† <i>Cipactlichthys scutatus</i>			X
Order †ASPIDORHYNCHIFORMES			
Family †ASPIDORHYNCHIDAE			
† <i>Vinctifer ferrusquiai</i>	O*		X
Order †PYCNOdontIFORMES			
Family †PYCNOdontIDAE			
† <i>Pycnodus</i> sp.	O	A	
† <i>Tepeichthys aranguthyrum</i>			X
Division GINGLYMODI			
Order †SEMIONOTIFORMES			
Family †SEMIONOTIDAE			
† <i>Tlayuamichin itzli</i>			X
Family †MACROSEMIIDAE	L	A	
† <i>Notagogus novomundi</i>			X
† <i>Macrosemiocotzus americanus</i>			X
Order LEPISOSTEIFORMES			
Family LEPIDOTIDAE			
<i>Scheenstia</i> sp.		A	
Family LEPISOSTEIDAE	O	A	
† <i>Nhanulepisosteus mexicanus</i>			X
Division HALECOMORPHI			
Order †IONOSCOPIFORMES			
Family †IONOSCOPIIDAE	L	A	
† <i>Quetzalichthys perilliatæ</i>			X
Family †OPHIOPSIDAE	L	A	
† <i>Teoichthys kallistos</i>			X
† <i>Teoichthys brevipina</i>			X
Order AMIIFORMES			
Family AMIIDAE	O	A	
† <i>Pachyamia mexicana</i>	O*		X
Order †PHOLIDOPHORIFORMES			
Family †PLEUROPHOLIDAE			
† <i>Pleuropholis cinerosorum</i>		A	X
Order †ICHTHYODECTIFORMES			
Family †Ichthyodectyidae			
† <i>Unamichthys espinosai</i>			X
Order OSTEOGLOSSIFORMES			
Family OSTEOGLOSSIDAE			
† <i>Phaerodus</i> indet.	O*		
Order †CROSSOGNATHIFORMES			
Family <i>incertae sedis</i>			
† <i>Michin csernai</i>			X
Order †ELIMMICHTHYIFORMES			
Family †PARACLUPIDAE			
† <i>Paraclupea seilacheri</i>		A	
Order CLUPEIFORMES			
Family <i>incertae sedis</i>			
† <i>Ranulfoichthys dorsonudum</i>			X
Order CYPRINIFORMES			
Family CATOSTOMIDAE	O		
† <i>Ictiobus aguilerai</i>			X
Division ACANTHOPTERYGII			
Order <i>incertae sedis</i>			
Family <i>incertae sedis</i>			
† <i>Kelemejtubus castroi</i>			X
Order SYNGNATHIFORMES	O		
Family †EEKAUlostOMIDAE			
† <i>Eekaulostomus cuevasae</i>			X
Order CYPRINODONTIFORMES			
Family GOODEIDAE	O		
† <i>Tapatia occidentalis</i>			X
Order PERCIFORMES			
Family SERRANIDAE	O		
† <i>Paleoserranus lakamhae</i>			X

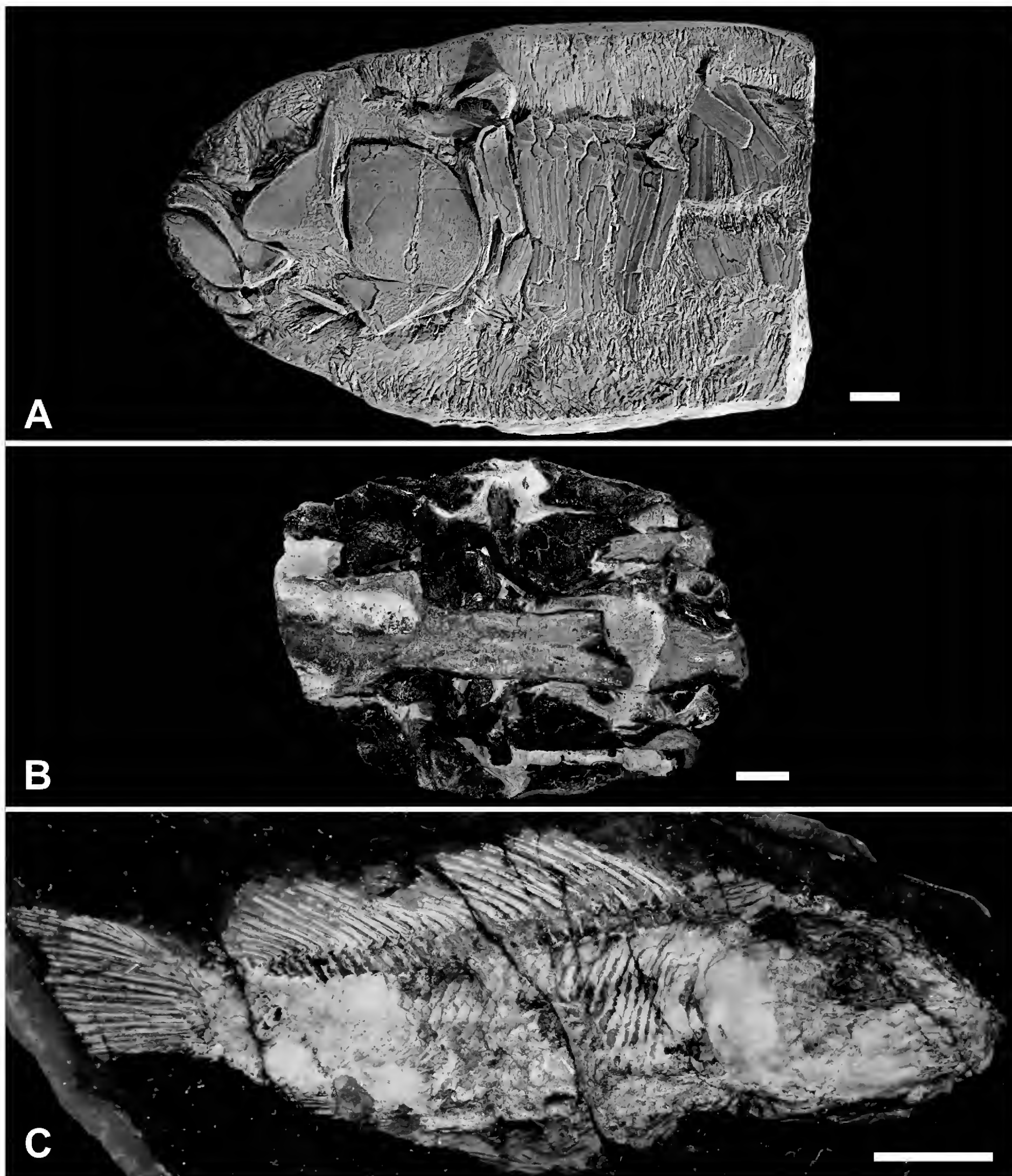


Figure 3. Some species housed in the CNP-UNAM type collection. **A.** †*Vinctifer ferrusquiai* Cantalice, Alvarado-Ortega & Brito, 2018; **B.** †*Nhanulepisosteus mexicanus* Brito, Alvarado-Ortega & Meunier, 2017; both being the most ancient species of their families to date; **C.** †*Macrosemiocotzus americanus* González-Rodríguez, Applegate & Espinosa-Arrubarrena, 2004, the first report of Macrosemiidae in North America. Scale bars: 10 mm.

rapid diversification and had a wide distribution during the Late Jurassic (Cantalice et al. 2018b). Another example is the earliest known lepisosteoid, †*Nhanulepisosteus mexicanus* (Fig. 3B), which raises the origin of modern gars to the Late Jurassic (Brito et al. 2017). Furthermore, the Paleocene fossil fishes from Chiapas (Fig. 4) push back the absolute age of origin of many acanthomorph

groups (e.g. seabasses and flutemouth fishes) to the early Cenozoic, just after the K/Pg boundary (Late Paleocene, 63 Ma). These finds reveal that the Caribbean Region is an important place for the origin and diversification of some modern ray-finned fish lineages (Alvarado-Ortega et al. 2015; Cantalice and Alvarado-Ortega 2016, 2017; Cantalice et al. 2018a).

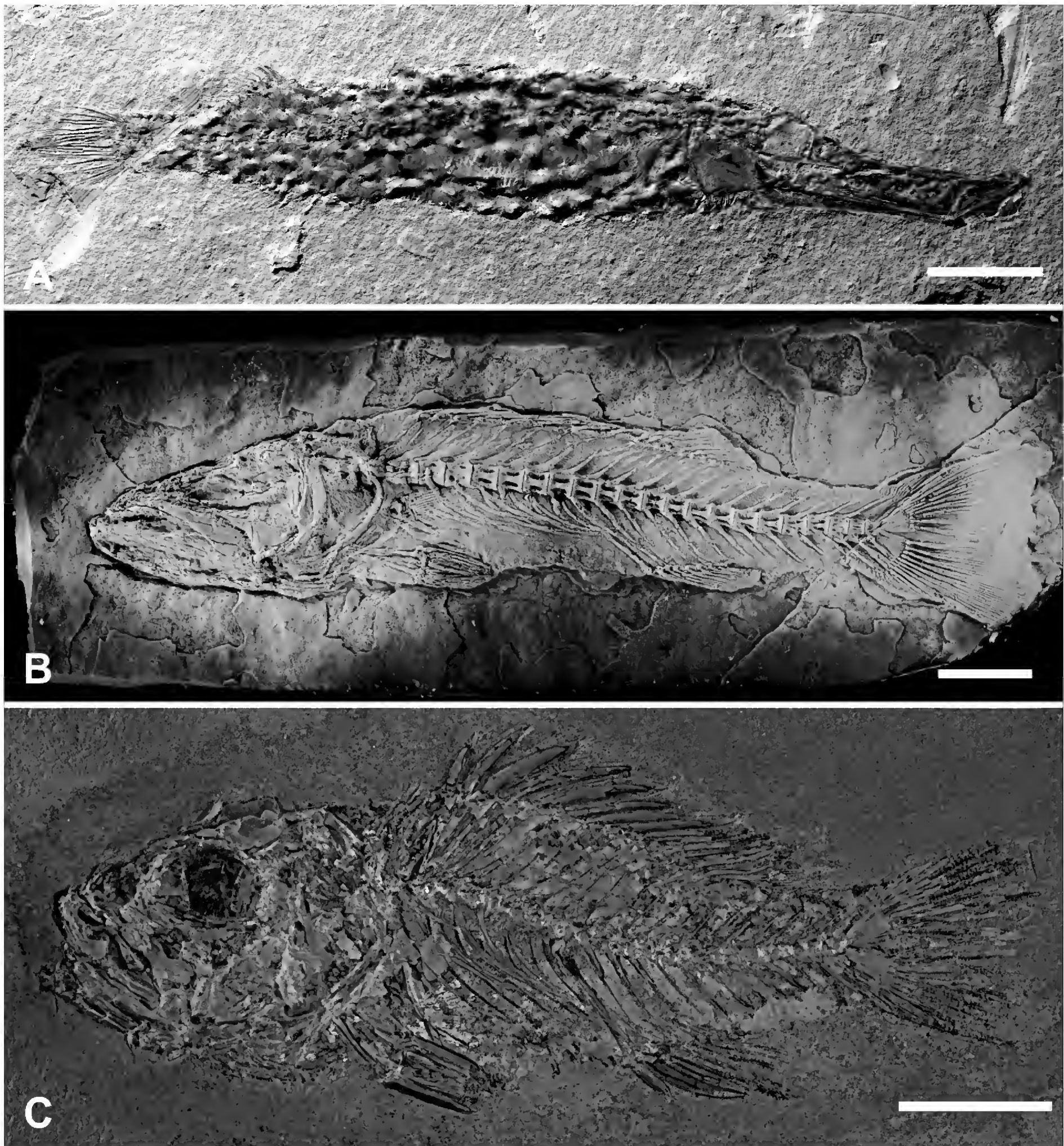


Figure 4. Paleocene fossil fishes found in marine outcrops of Chiapas housed in CNP-UNAM **A.** †*Eekaulostomus cuevasae* Cantalice & Alvarado-Ortega, 2016; **B.** †*Kelemejtubus castroi* Cantalice & Alvarado-Ortega, 2017; **C.** †*Paleoserranus lakamhae* Cantalice, Alvarado-Ortega & Alaniz-Galvan, 2018. Scale bars: 10 mm.

When included in a phylogenetic context, some species housed in CNP-UNAM offer valuable details that help understanding the morphological and ecological changes that occurred in some groups of fishes through time. One example is the aulostomoid †*Eekaulostomus cuevasae* (Fig. 4A), which is considered the stem group of Recent flutemouth fishes and reveals that reduction of body scutes size and enlargement of the snout, trunk, and fin rays are evolutionary trends of aulostomoids (Cantalice and Alvarado-Ortega 2017). These morphological modifications are possibly related to improvements in

predation in extant species (Cantalice and Alvarado-Ortega 2017). Moreover, including CNP-UNAM species in phylogenetic analyses also provide support to solve some incongruences on fish classification, such as †*Quetzalichthys* and †*Teoichthys* (Fig. 5), two genera collected in Tlayúa quarry (Puebla), which when included in the phylogeny of the order Ionoscopiformes proved the monophyly of the families Ophiopsidae and Ionoscopidae (Alvarado-Ortega and Espinosa-Arrubarrena 2008).

Mexico has been in the tropical region since the Jurassic, the period of the oldest fossil fish records report-

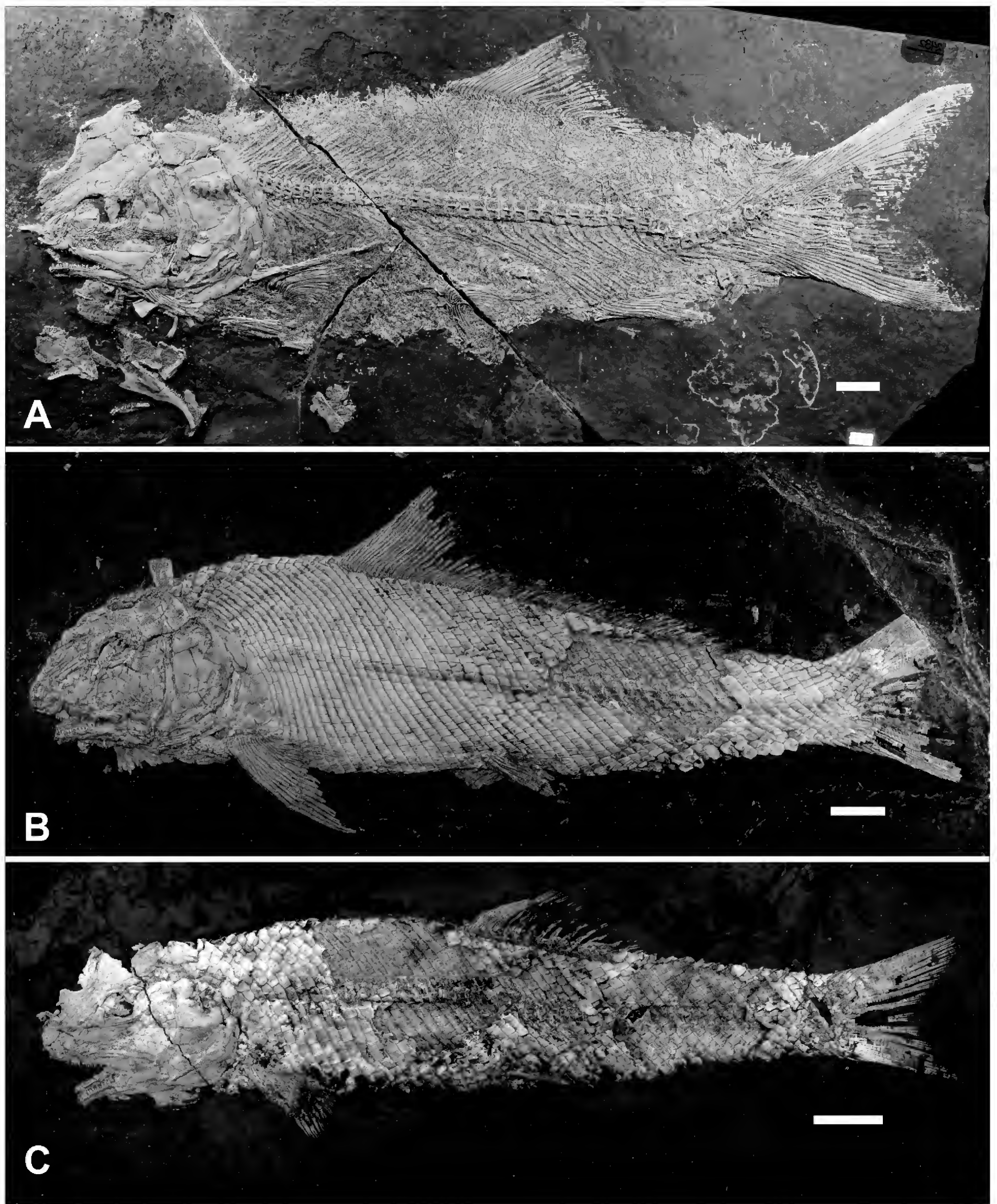


Figure 5. Cretaceous fossil fishes from Tlaúa quarry, Puebla, housed in CNP-UNAM **A.** †*Quetzalichthys perrillatae* Alvarado-Ortega & Espinosa-Arrubarrena, 2008; **B.** †*Teoichthys kallistos* Applegate, 1988; **C.** †*Teoichthys brevipina* Machado, Alvarado-Ortega, Machado & Brito, 2013. Scale bar: 10 mm.

ed at CNP to date (Scotese 2014). The 150 million years since the Jurassic to present day could explain the diversification of several groups of fishes and the richness of possible Mexican endemic fauna (Table 1). Therefore, the continual collection and increases in knowledge of

the paleoichthyofauna housed at CNP is fundamental to understand the patterns of fish diversity through the geological ages and highlights the Mexican fossil records as essential to understanding biogeographic patterns and current global fish diversity.

Conclusions

After 25 years since the last vertebrate catalogue (Perilliatt 1993), we present the first fossil fish catalogue of the species housed in the type collection of the Colección Nacional de Paleontología of Universidad Nacional Autónoma de México (CNP-UNAM). The increase of knowledge of fossil fish diversity, as its biological and biogeographical implications, are evidence that maintaining a proper collection of the Mexican fossil record is necessary for understanding the complex evolutionary history of fishes. The knowledge of the Mexican paleoichthyofauna is emerging. The formal description of many specimens housed in the geographic reference section is still necessary and increasing with periodic fieldwork. Palaeoichthyology is a promising research area in Mexican paleontology.

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Supplementary material 1

Supplementary Information

Authors: Kleyton Magno Cantalice, Alejandra Martínez-Melo, Violeta Amparo Romero-Mayén

Data type: locality data

Explanation note: Table with essential information about the distinct geological localities containing fishes catalogued in the CNP-UNAM.

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Taxonomic revision of the genus *Hyperaulax* Pilsbry, 1897 (Gastropoda, Stylommatophora, Odontostomidae)

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<http://zoobank.org/EE9B3C6B-D4AE-4508-BF0E-5CCEEB7F12EA>

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Abstract

The genus *Hyperaulax* Pilsbry, 1897 comprises two living species endemic to the oceanic Fernando de Noronha Archipelago, off north-eastern Brazil. They are currently allocated in two subgenera, *Hyperaulax* s. str. and *Bonnanius* Jousseume, 1900, belonging to the family Odontostomidae. Herein we present a taxonomic revision of these species, assessing their familiar allocation within Orthalicoidea, offering updated diagnoses and descriptions, figuring the type materials and further relevant specimens, and providing barcoding DNA sequences. We conclude that *Bonnanius* is a junior synonym of *Hyperaulax*, which is classified in Odontostomidae. The genus contains two valid species, *H. ridleyi* and *H. ramagei*, both endemic to Fernando de Noronha.

Key Words

Bonnanius, endemic species, Fernando de Noronha, island speciation, Orthalicoidea, Pulmonata

Introduction

The genus *Hyperaulax* Pilsbry, 1897 had a unique composition. It comprised two living species endemic to the oceanic Fernando de Noronha Archipelago off Brazil, *H. ridleyi* (Smith, 1890) and *H. ramagei* (Smith, 1890), and eight species from Tampa Silex beds (Oligocene) of Florida, USA: *H. americanus* (Heilprin, 1887), *H. ballistae* (Dall, 1915), *H. floridanus* (Conrad, 1846), *H. heilprinianus* (Dall, 1890), *H. remolinus* (Dall, 1915), *H. stearnsii* (Dall, 1890), *H. tampae* (Dall, 1915), and *H. tortilla* (Dall, 1915). Suspecting this could not reflect an actual relationship, the fossil species previously assigned to *Hyperaulax* were revised by Auffenberg et al. (2015). Those authors concluded that the fossils bore only a superficial similarity to *Hyperaulax* and erected the new genus *Tocobaga* Auffenberg et al., 2015 to house the North American fossil species, which they classified in the Bulimulidae rather than in Odontostomidae. Auffenberg et al. (2015) considered most of the fossil forms to be synonymous and rec-

ognized only three valid species: *Tocobaga americanus*, *T. floridanus* and *T. wakullae* Mansfield, 1937 (previously considered a subspecies of *T. americanus*).

The two Recent species are also not without problems, as two names are currently considered synonymous with *H. ramagei*; moreover, this species is included in the subgenus *Bonnanius* Jousseume, 1900, which can sometimes be recognized as a valid genus (e.g., Simone 2006). The peculiar morphological features of *Hyperaulax* also present some challenges, as it is reminiscent of several lineages of Orthalicoidea. The genus is usually placed in Odontostomidae, but it also bears resemblance to insular Bulimulidae from the Galapagos; furthermore, *Hyperaulax* had also been assigned to the extinct family Grangerellidae by Henderson (1935), although this author suggested this based on Oligocene material from Florida (now in *Tocobaga*), not the Recent Brazilian species (for a full discussion see Auffenberg et al. 2015).

Therefore, herein we conducted a taxonomic review of the two Recent species of *Hyperaulax*, assessing their

familiar allocation within Orthalicoidea and the validity of the subgenus *Bonnanius* and of the two species synonymized with *H. ramagei*. Furthermore, an updated diagnosis and description, alongside images of the type and additional materials, is provided here for each species.

Methods

Fernando de Noronha is an archipelago located ca 350 km off northeastern Brazil ($3^{\circ}50'–3^{\circ}52'S$, $32^{\circ}24'–32^{\circ}28'W$) originating from extinct volcanic structures estimated to be 1.8–12.4 Ma old. It comprises the main island of Fernando de Noronha (17 km²) and over 20 smaller islands and rocks (Fig. 1). The local climate is dry tropical with a mean annual rainfall of 1,300 mm and a mean annual temperature of 25.4 °C. It has strong oceanic influence, with two well-defined seasons: dry from August to January and rainy from February to July (Fávaro et al. 2006; Marques et al. 2007). The vegetation on the islands has close affinities with the Atlantic Rainforest, though only 5% of the original cover remains (Claudino-Sales 2019). Even so, the islands are rich in endemic species of plants and animals but have a low overall diversity compared to the mainland, which is especially true for terrestrial snails, of which there are three known endemic species (Lopes and Alvarenga 1955). The entire area totals

112.7 km² including land and sea; it was designated as an environmental protection area by the Brazil in 1989 and became a World Heritage Site in 2001. Nevertheless, the islands are populated and suffer the negative impacts of overtourism and pollution (Claudino-Sales 2019).

All the type specimens were analyzed and the main museum collections worldwide that could contain material of *Hyperaulax* were visited or contacted for loans or photographs and information of their specimens. The type materials are illustrated herein, alongside additional specimens to thoroughly show conchological variation. Shell measurements were taken with a digital caliper. SEM images of the protoconchs were obtained at the Staatliches Museum für Naturkunde Stuttgart (SMNS; Stuttgart, Germany).

The material studied in the present work is housed in the following collections: ANSP, Academy of Natural Sciences of Drexel University (Philadelphia, USA); MNHN, Muséum national d'Histoire naturelle (Paris, France); MNZ, Museum of New Zealand Te Papa Tongarewa (Wellington, New Zealand); MZSP, Museu de Zoologia da Universidade de São Paulo (São Paulo, Brazil); NHMUK, Natural History Museum (London, UK); USNM, Smithsonian Institution National Museum of Natural History (Washington, DC, USA); ZMB, Museum für Naturkunde, Leibniz Institute for Evolution and Bio-



Figure 1. Map showing the location of Fernando de Noronha, Brazil.

diversity Science (Berlin, Germany); ZSM, Zoologische Staatssammlung München (Munich, Germany).

The following abbreviations are used herein for shell dimensions: H, shell height (parallel to coiling axis); D, greatest shell width (perpendicular to H); h, aperture height (maximum length parallel to aperture plane); d, aperture width (maximum width parallel to aperture plane); W, number of whorls of shell (approximated to closest quarter); w = number of whorls of protoconch (approximated to closest quarter).

Two adult specimens of *H. ridleyi* from lot MZSP 89940 had a fraction of their foot clipped for molecular study. No specimen of *H. ramagei* with preserved soft parts is known. Given our suspected systematic affinity of *Hyperaulax*, we also sequenced a specimen of *Tomigerus corrugatus* Ihering, 1905 (lot MZSP 43077). DNA extraction was carried out with QIAGEN DNeasy Blood & Tissue Kit, standard protocol. We targeted the barcoding fragment of the mitochondrial COI gene (primers LCO and HCO of Folmer et al. 1994), with circa 650 bp. The PCR protocol was set as: (1) initial denaturation at 96 °C (2 minutes); (2) denaturation at 94 °C (30 seconds); (3) annealing at 48 °C (1 minute); (4) extension at 72 °C (2 minutes); (5) repeat steps (2) to (4) 34 times, for a total of 35 cycles; (6) final extension at 72 °C (5 minutes). PCR products were quantified via agarose gel electrophoresis, cleaned with ExoSAP-IT™ (Affymetrix Inc.), and Sanger sequenced. The sequences were assembled and quality-checked in Geneious Prime (version 2019.0.3, Biomatters Ltd), and uploaded to NCBI GenBank under the accession numbers MN175954 and MN175955 (*H. ridleyi*) and MN175956 (*T. corrugatus*).

Additional orthalicoid COI sequences were obtained from GenBank, originating from the work of Breure and Romero (2012; see Appendix 1 for accession numbers). We excluded some species from those authors' dataset, namely those with uncertain identification, incomplete sequences, and the basal-most taxa (e.g., Bothriembryontidae, Megaspiridae), which could bring too much noise to the analysis. We used one Planorbidae as outgroup (sequence from GenBank, see Appendix 1). A total of 35 species were used from that work; sequences were 654 bp long, with the exception of the outgroup, with 669 bp due to an indel.

All sequences were aligned in Geneious Prime with the MUSCLE plugin (Edgar 2004; default settings, accuracy-optimized) and further proofed manually. A tree was built in Geneious Prime by Bayesian Inference (MrBayes plugin; Huelsenbeck and Ronquist 2001; Ronquist and Huelsenbeck 2003); settings: HKY85 substitution model, 200,000 burn-in length, 1,100,000 iterations.

Systematics

Superfamily Orthalicoidea

Family Odontostomidae Pilsbry & Vanatta, 1898

Genus *Hyperaulax* Pilsbry, 1897

Bulimulus (*Hyperaulax*) Pilsbry 1897a: 10; Pilsbry 1897b: 82.

Bonnanius Jousseaume 1900: 39; Schileyko 1999: 337.

Hyperaulax: Pilsbry 1901: 102; Wenz 1923: 729; Thiele 1931: 660; Henderson 1935: 145; Morretes 1949: 153; Oliveira et al. 1981: 350; Parkinson et al. 1987: 29; Schileyko 1999: 320; Salgado and Coelho 2003: 165; Simone 2006: 178; Salvador 2019: 87.

Hyperaulax (*Bonnanius*): Pilsbry 1901: 103; Thiele 1931: 661; Morretes 1949: 153; Zilch 1960: 505; Breure 1974: 52; Oliveira et al. 1981: 350.

Hyperaulax (*Hyperaulax*): Thiele 1931: 661; Morretes 1949: 153; Zilch 1960: 505; Breure 1974: 109.

Tomigerus (*Bonnanius*): Parodiz 1962: 453.

Bonnarius [sic]: Simone 2006: 178.

Type species. *Bulimus* (*Bulimulus*) *ridleyi* Smith, 1890, by original designation.

Included species. *Hyperaulax ridleyi* (Smith, 1890) and *H. ramagei* (Smith, 1890).

Diagnosis. Shell bulimoid. Protoconch sculptured by sinuous axial riblets, which can anastomose and fade on abapical region. Umbilicus surrounded by a periumbilical spiral angulation.

Description. Shell small to medium-sized, bulimoid, with ca 4–5 convex whorls; ground color cream, ochre or brown, with 1–4 lighter-colored spiral bands on lateral portion of whorls; periumbilical region completely or marginally discolored, whitish; apex (especially protoconch) usually of lighter color. Suture well-marked. Protoconch sculptured by numerous fine sinuous axial riblets, transition unclear. Teleoconch overall smooth except for axial growth lines. Aperture ovoid; peristome white, reflected, thickened, and continuous, with 0–4 apertural teeth. Umbilicus perforate, well marked.

Remarks. After Auffenberg et al. (2015) removed all fossil taxa from *Hyperaulax*, the genus was left only with two living species, *Hyperaulax ridleyi* (Fig. 2) and *H. ramagei* (Figs 3, 4), with the latter classified in the subgenus or full genus *Bonnanius*. Both species are known only from Fernando de Noronha Archipelago off north-eastern Brazil.

The genus *Bonnanius* is considered here synonymous with *Hyperaulax* as there are no diagnostic characters allowing its clear separation other than its larger shell size. The presence of teeth in the aperture of *H. ramagei* (previously classified in *Bonnanius*) could be used as a diagnostic genus-level character; however,

it is well known that odontostomid genera show great inter- and intraspecific variation in the presence and strength of apertural teeth. Moreover, some specimens of *H. ridleyi* do show a palatal tooth (Fig. 2A) similar in position and length to that of *H. ramagei*. Furthermore, for a genus with only two species, keeping them separated into two distinct subgenera is excessively zealous taxonomy. As for the other conchological characters, *Bonnanius* share all of them with *Hyperaulax*, as discussed below.

The protoconch sculpture has always been deemed a good character to define genera in Orthalicoidea and has more recently received large support from molecular studies (Breure and Romero 2012). The protoconchs of *Hyperaulax* and *Bonnanius* are very similar and indicate a close affinity between the two forms: same number of whorls (ca 1 $\frac{3}{4}$); same sculpture pattern (sinuous axial riblets, more clearly separate on adapical area of whorl, but anastomosing on abapical area and sometimes fading into scattered dots). There are also some differences on the protoconch, but nothing that would suggest two distinct genera (many genera of Orthalicoidea bear some minor differences in their protoconchs, which helps with species diagnosis; e.g., Salvador and Cavallari 2013; Salvador and Simone 2016). The main difference is that the protoconch of *H. ramagei* is more flattened and rounded, which makes the riblets a little more spaced; this can be attributed to its shell being larger and wider overall. Furthermore, the protoconch of *H. ridleyi* has a raised ridge on its middle region. Finally, the protoconch sculpture of museum specimens of *H. ramagei* is often faded or eroded, which has led to claims of a smooth protoconch in the literature (e.g., Parodiz 1962; Abbott 1989).

Other conchological characters are very similar in both *H. ridleyi* and *H. ramagei*: the roughly pentagonal shape of the aperture and its positioning in relation to the body whorl, the long palatal tooth (absent in most *H. ridleyi* specimens), the shape of the umbilicus and the periumbilical spiral angulation, the unsculptured teleoconch (except for growth striations), and the periostracum color (brown with at least one white spiral band).

The classification of *Hyperaulax* in Odontostomidae has been well supported in the literature, with just a few different classification schemes. For instance, Schileyko (1999) argued in favor of Bulimulidae because *H. ridleyi* has no teeth; however, not all odontostomids actually have teeth and some specimens of *H. ridleyi* do show a faint palatal tooth, as discussed above and already remarked by Pilsbry (1901). Moreover, *H. ridleyi* has the typical channel-like structure on the junction of the parietal and palatal regions of the peristome. Schileyko (1999), however, maintained *Bonnanius* (and hence *H. ramagei*) in Odontostomidae.

In any event, there are other conchological characters favoring an allocation within Odontostomidae, such as the elevated embryonic whorls (Auffenberg et al. 2015) and the protoconch sculpture (wavy riblets, similar to *Plagiodontes* Doering, 1876; Pizá and Cazzaniga 2016). The overall

shell shape of *Hyperaulax* is very similar to *Tomigerus* Spix, 1827 and *Biotocus* Salgado & Leme, 1990, but with a different position of the aperture in relation to the body whorl and a different structure of the umbilical region; also, the protoconch of *Tomigerus* is smooth. The periostracum color is also similar to what is seen in *Tomigerus* (e.g., *T. clausus* Spix, 1827, *T. matthewsi* Salgado & Leme, 1991, and *T. rochai* Ihering, 1905), but a striped pattern can also be found in species of *Moricandia* Pilsbry & Vanatta, 1898 and even *Anostoma* Waldheim, 1807. The dentition of *Hyperaulax* (mainly of *H. ramagei*) is similar to that of *Burringtonia* Parodiz, 1944 and also *Anctus angiosomus* (Wagner, 1827). Finally, the channel-like structure on the junction of the parietal and palatal regions of the peristome is virtually identical to what is observed in some species of *Cyclodontina* Beck, 1837, *Spixia* Pilsbry & Vanatta, 1898, and *Anostoma* Waldheim, 1807.

Our analysis of interspecific affinities using the barcoding region of the COI marker has grouped *Hyperaulax* (*H. ridleyi* only) with *Tomigerus*, as expected by our morphological analysis, with a posterior probability of 0.997. However, these two species were grouped with *Simpulopsis* Beck, 1837 (family Simpulopsidae) in our Bayesian tree, instead of being grouped with other odontostomids. This is likely due to the fact that COI alone is not sufficient to solve family-level relationships among stylommatophoran snails (Breure and Romero 2012), despite being sufficient to capture the relationship of close species-level taxa. Based on morphological data, we retain *Hyperaulax* (and *Tomigerus*) in the family Odontostomidae.

It is curious that another orthalicoid lineage, from the other side of South America, evolved an uncannily similar shell shape to *Hyperaulax*: *Naesiotus wolffi* (Reibisch, 1892), from the Galapagos (lectotype ZMB 47.950, paralectotype NHMUK 1894.6.8.7). Furthermore, *N. wolffi* is within the size range of *Hyperaulax*, and has a similar color pattern to *H. ridleyi*, including the median white spiral band. The protoconch, naturally, is different (*Naesiotus* Albers, 1850 has very fine and well-defined axial striae), alongside other more general shell features: higher spire, different proportion of body whorl to spire, and a larger number of whorls (ca 6 $\frac{1}{2}$). In any event, this is a remarkable case of convergent evolution on islands and deserves further investigation.

Hyperaulax ridleyi (Smith, 1890)

Fig. 2

Bulimus (*Bulimulus*) *Ridleyi* E.A. Smith 1890: 501, pl. 30, fig. 9; Dall 1896: 415.

Bulimulus (*Hyperaulax*) *ridleyi*: Pilsbry 1897a: 10; Pilsbry 1897b: 82, pl. 14, figs 11–13.

Buliminus ridleyi: Möllendorff 1901: 126.

Hyperaulax ridleyi: Pilsbry 1901: 103; Ihering 1923: 191; Wenz, 1923: 729; Schileyko 1999: 321, fig. 396; Salgado and Coelho 2003: 165; Simone 2006: 178, fig. 637; Breure and Ablett 2012: 36, figs 20C, D, 20ii; Salvador 2019: 87.

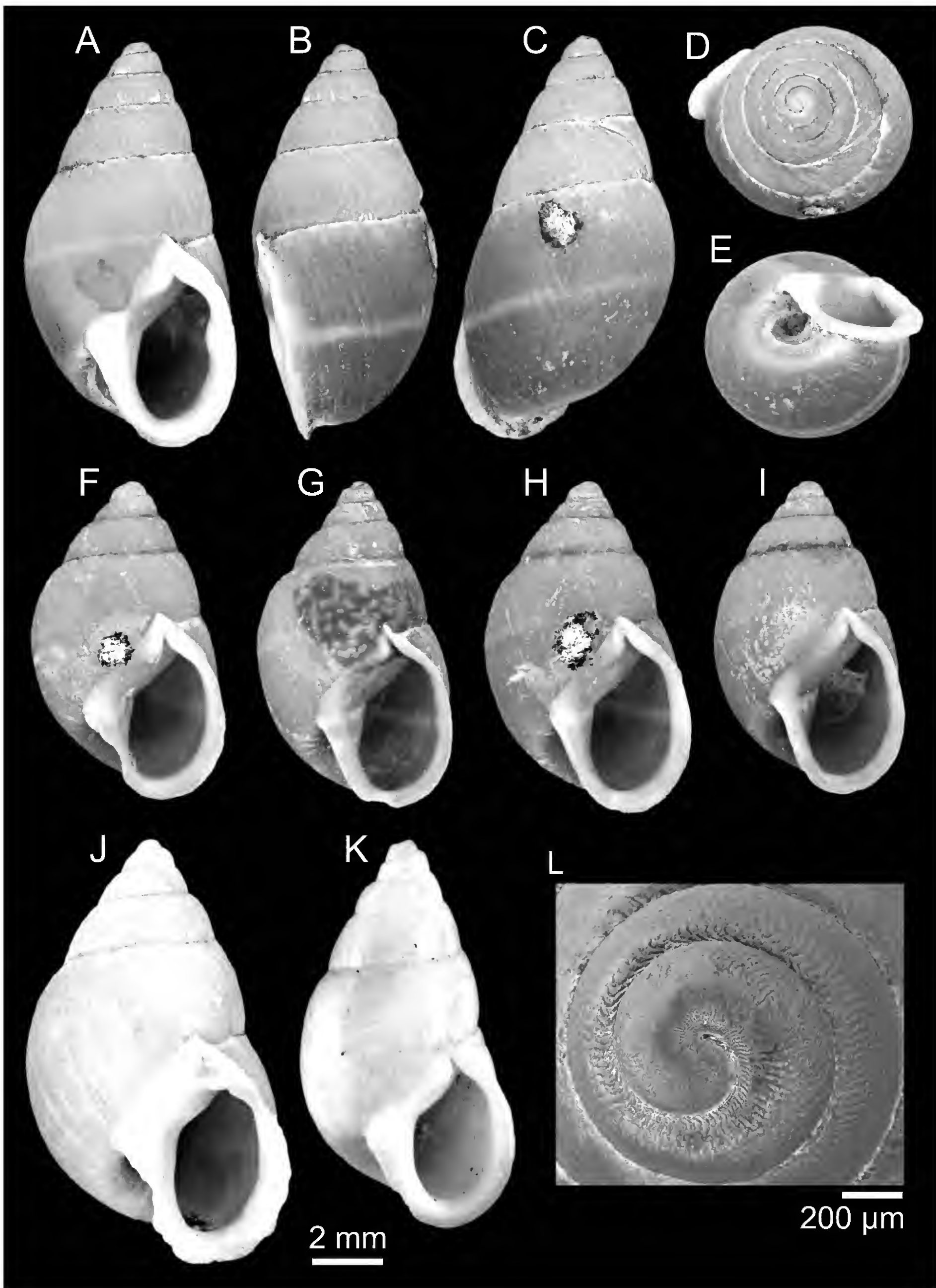


Figure 2. *Hyperaulax ridleyi*. **A–E.** Lectotype, NHMUK 1888.6.27.106. **F–I.** Paralectotypes #1 to #4 (in order), NHMUK 1888.6.27.107-110. **J.** Extreme form, large and with thick callus, NHMUK 1888.6.27.88-94. **K.** Weathered specimen, ZMS unnumbered (ex Heimburg colln.). **L.** Protoconch detail (same specimen from K).

Hyperaulax (Hyperaulax) ridleyi: Thiele 1931: 661; Morretes 1949: 153; Zilch 1960: 505, fig. 1771; Breure 1974: 51; Breure and Schouten 1985: 4.

Hyperaulax (s. str.) *ridleyi*: Lopes and Alvarenga 1955: 181.

Bulimus (Bulimulus) ridleyi: Oliveira and Oliveira 1984: 19.

Type locality. Fernando de Noronha Archipelago, Fernando de Noronha Island and Rata Island. Original (Smith 1890: 501): "Living under bark of Mango-trees in the garden and on north side of island; also at base of the Peak, north side, under stones, and on Rat Island."

Distribution. Known only from Fernando de Noronha Archipelago.

Type material. Lectotype NHMUK 1888.6.27.106 (designation by Breure and Ablett 2012). Paralectotypes: NHMUK 1888.6.27.107-110, 4 shells.

Material examined. Types. **BRAZIL:** Fernando de Noronha: ANSP 71271, 7 shells, H.H. Smith leg., 1896; MNZ 205835, 4 shells, ex Suter coll. 5637; ANSP 81426, 1 shell; ANSP 100530, 4 shells, H.v. Ihering leg., 1910; ANSP 220399, 2 shells, ex B.R. Bales coll., J.S. Schwengel leg., 1958; MNZ 205835, 4 shells, ex Suter coll. 5637; MZSP 501, 14 shells, 1900; MZSP 7752, 20 shells. MZSP 30134, 10 shells, dunes of Praia das Caieiras, E.F. Nonato leg., 25/vii/1955; MZSP 30135, 8 shells, de Fiore leg., 1983; MZSP 31064, 1 shell, Praia do Meio, L.R.L. Simone & Souza leg., 22/vii/1999; MZSP 31305, 30 specimens, between Baía dos Porcos and Baía do Sancho, L.R.L. Simone leg., 21/vii/1999; MZSP 31676, 14 shells, Praia das Caieiras, L.R.L. Simone et al. leg., 23/vii/1999; MZSP 31681, 15 specimens, mangrove on Praia do Sudeste, C.M. Martins leg., 20/vii/1999; MZSP 31686, 50 specimens, Praia do Meio, C.M. Martins leg., 17-23/vii/1999; MZSP 48824, 1 shell, Praia do Porto, 3°50'05"S, 32°24'04"W, L.R.L. Simone leg., 30/iv/2005; MZSP 48990, 9 shells, Praia das Caieiras, 3°50'19"S, 32°24'00"W, L.R.L. Simone leg., 3/v/2006; MZSP 49001, 11 shells, mangrove on Praia do Sudeste, 3°51'58"S, 32°25'35"W, L.R.L. Simone leg., 4/v/1005; MZSP 49089, 39 shells, in front of Morro Dois Irmãos and Cacimba do Padre, L.R.L. Simone leg., 3/v/2005; MZSP 86542, 13 shells; Praia do Porto, 3°50'11"S, 32°24'04"W, L.R.L. Simone et al. leg., 28/x/2007; MZSP 89929, >50 shells, 3°50'00"S, 32°24'05"W, L.R.L. Simone & C.M. Cunha leg., iii/2009; MZSP 89933, 17 shells, L.R.L. Simone & C.M. Cunha leg., 11/iii/2009; MZSP 89939, 2 specimens; 3°50'21"S, 32°24'10"W, L.R.L. Simone & C.M. Cunha leg., 12/iii/2009; MZSP 89940, 5 specimens, Mirante, L.R.L. Simone & C.M. Cunha leg., 11/iii/2009; MZSP 89993, 1 shell, Praia do Sudeste, 3°52'06"S, 32°25'32"W, L.R.L. Simone & C.M. Cunha leg., 9/iii/2009; MZSP 97854, 3 shells, ex J. Vaz coll., A. Nüssenbaum leg., viii/1973; MZSP 97878, 3 shells, ex J. Vaz coll., Praia das Caieiras, C. Bardelli leg., vi/1994; MZSP 119089, 23 shells, Cacimba do Pa-

dre, 3°50'36"S, 32°25'14"W, L.R.L. Simone et al. leg., 8/v/2013; MZSP 119090, 29 shells, Cacimba do Padre, 3°50'36"S, 32°25'14"W, L.R.L. Simone et al. leg., 7/v/2013; NHMUK 1888.6.27.88-94, 7 shells; NHMUK 1888.6.27.95-100, 6 shells, Rata Island; NHMUK 1888.6.27.101-105, 5 shells; NHMUK 20170270, 4 shells, H.E.J. Biggs coll., H. Fiedrick leg.; USNM 134849, 1 shell, H.A. Pilsbry leg.; USNM 214401, 1 shell, H.A. Pilsbry leg.; USNM 307580, 2 shells, Henderson coll., H. Clapp leg.; USNM 518214, 3 shells, W. Williamson leg.; ZSM no nr., 2 shells, Blume coll. 4003; ZSM no nr., 4 shells, H.H. Smith coll.

Diagnosis. The shell is smaller overall and has a more elongated and slender profile. The protoconch has a more raised ridge and its sculpture consists largely of more anastomosed riblets. Typically, there is no apertural dentition.

Description. Shell small, bulimoid, slender; spire tall; $W \sim 4\frac{3}{4}$ –5. Shell color ochre to brown; body whorl sometimes darker than rest; fine white spiral band on middle portion of whorl; periumbilical spiral angulation discolored, whitish; peristome white. Protoconch ($w \sim 1\frac{3}{4}$) rounded, with raised ridge that becomes a faint sub-sutural ridge on teleoconch; sculptured by fine sinuous axial riblets, which sometimes anastomose (especially on abapical area of whorl); transition to teleoconch unclear. Teleoconch smooth (except for growth lines). Suture well marked, but not deep. Aperture ovoid, elongated. Peristome reflected and slightly thickened; presence of small channel-like structure on division between parietal and palatal regions of aperture; parietal callus might be present in older specimens. Apertural teeth usually absent, but faint elongated tooth on middle portion of palatal region may be present (Fig. 2A). Umbilicus narrow, deep, surrounded by a periumbilical spiral angulation.

Dimensions. Lectotype: $H = 11.4$ mm, $D = 5.9$ mm, $h = 4.8$ mm, $d = 3.0$, $W = 5\frac{1}{4}$, $w = 1\frac{3}{4}$. Paralectotype #1: $H = 9.5$ mm, $D = 5.3$ mm, $h = 4.4$ mm, $d = 3.0$ mm, $W = 4\frac{1}{2}$, $w = 1\frac{1}{2}$. Paralectotype #2: $H = 9.1$ mm, $D = 5.3$ mm, $h = 4.3$ mm, $d = 2.9$ mm, $W = 4\frac{1}{2}$, $w = 1\frac{3}{4}$. Paralectotype #3: $H = 8.9$ mm, $D = 5.2$ mm, $h = 4.3$ mm, $d = 2.9$ mm, $W = 4\frac{1}{2}$, $w = 1\frac{3}{4}$. Paralectotype #4: $H = 8.9$ mm, $D = 5.2$ mm, $h = 4.2$ mm, $d = 2.8$ mm, $W = 4\frac{1}{2}$, $w = 1\frac{3}{4}$. Average ($n = 63$, except for w , where $n = 10$): $H = 10.2 \pm 1.00$ mm (min = 7.8 mm, max = 12.7 mm), $D = 5.7 \pm 0.51$ mm, $h = 4.9 \pm 0.45$ mm, $d = 3.5 \pm 0.34$ mm, $W = 4\frac{3}{4}$ to 5 (min = 4 $\frac{1}{4}$, max = 5 $\frac{1}{2}$), $w = 1\frac{3}{4}$ (occasionally 1 $\frac{1}{2}$).

Remarks. Other than showing a reasonable variation in shell size, the species displays little conchological variation (Fig. 2). Rare specimens, however, do deviate from the typical form, for instance by having broader shells with shorter spires (Fig. 2F–I) or by having a palatal tooth (Fig. 2A, lectotype). The color might vary from more ochre tones to more reddish-brown ones, but the single white spiral band on the mid-section of the whorl is always pres-

ent. *Hyperaulax ridleyi* can be easily distinguished from its only congener, *H. ramagei*, by its smaller shell (with a single spiral white band) and more elongated and slender shell profile. Moreover, its protoconch has a more raised ridge and the riblets of its sculpture are much more anastomosed. Finally, *H. ridleyi* typically bears no apertural dentition (although a weak palatal tooth might be present; Fig. 2A).

Unfortunately, not much can be found in the literature about this species' habitat or habits, but the museum labels point to a variety of collection locales, albeit more usually referring to dead shells only. In any event, this species has been reported alive from forested areas, mangrove, beaches, dunes, and gardens.

Hyperaulax ramagei (Smith, 1890)

Figs 3, 4

“Turbine, in cui la prima voluta è (...)” Buonanni 1681: 185, fig. Turbine #44.

Bulimus (Tomigerus) Ramagei E.A. Smith 1890: 500, pl. 30, fig. 8.

Bulimus (Tomigerus?) Ramagei: Dall 1896: 415.

Bonnanius bouvieri Jousseume 1900: 39, pl. 1, fig. 19.

Bonnanius bonnanius Jousseume 1900: 41.

Hyperaulax (Bonnanius) ramagei: Pilsbry 1901: 103, pl. 11, figs 60–62; Thiele 1931: 611; Morretes 1949: 153; Lopes and Alvarenga 1955: 181; Zilch 1960: 505, fig. 1772; Breure 1974: 52; Breure 1975: 1158; Oliveira et al. 1981: 350; Parkinson et al. 1987: 29; Abbott 1989: 106, text fig.

Tomigerus (Bonnanius) ramagei: Parodiz 1962: 453.

Bulimus (Tomigerus) ramagei: Oliveira and Oliveira 1984: 19.

Bonnanius ramagei: Schileyko 1999: 339, fig. 419; Breure and Ablett 2012: 34, figs 20A, B, 20i.

Hyperaulax ramagei: Salgado and Coelho 2003: 165; Salvador 2019: 87.

Bonnanius [sic] *ramagei*: Simone 2006: 178, fig. 638.

Type locality. Fernando de Noronha Archipelago, Fernando de Noronha Island, Ponta do Tabaco. Original (Smith 1890: 500): “imbedded in sandy mud on a raised reef at Tobacco Point (G.A. Ramage leg.)”.

Distribution. Known only from Fernando de Noronha Archipelago.

Type material. Lectotype NHMUK 1888.6.27.163 (designation by Breure and Ablett 2012). Paralectotypes: NHMUK 1888.6.27.164–170, 7 shells.

Material examined. Types. **BRAZIL:** Fernando de Noronha: ANSP 100531, 4 shells, H.v. Ihering leg., 1910; MNZ 205835, 4 shells, ex Suter coll. 5637; MNHN-IM-2000-28020 syntype of *Bonnanius bouvieri*, Jousseume coll.; MNZ 205822, 5 shells, ex Suter coll. 5639; MZSP 7738, 14 shells; MZSP 97933, 3 shells, ex J. Vaz coll., A. Nüssenbaum leg., viii/1973; NHMUK 1902.10.16.4, 1 shell; MZSP 131996, 3 shells, Ponta das Caracas, 3°52'28"S, 32°25'24"W, F. Schunck leg., 27/ix/2013; NHMUK 20170271, 13 shells, from sand

on north end of island, 16/vi/1887; USNM 518215, >30 shells, W. Williamson leg.; USNM 709805, >30 shells, dunes in Porto Santo Antônio, L. Storrs et al. leg., vii–viii/1973; USNM 709806, >30 shells, Porto Santo Antônio, L. Storrs et al. leg.; ZSM 7861, 1 shell, 1940; ZSM no nr., 3 shells.

Diagnosis. The shell is larger overall and has a broader profile. The riblets on the second part of the protoconch are more defined. The peristome is strongly thickened and displays marked apertural teeth.

Description. Shell medium-sized, bulimoid, rounded; W ~ 4½. Shell color chestnut brown; spire apex light brown to cream-colored; up to four equidistant white spiral bands might be present on lateral portion of whorls (but entirely brown morphs also occur); periumbilical region usually discolored, whitish; peristome and apertural teeth white. Protoconch (w ~ 1¾) rounded; first ½ whorl presenting undefined anastomosing sculpture; remainder sculptured by fine sinuous axial usually well-defined riblets (but sometimes anastomosed in some areas) that become less pronounced towards teleoconch; transition to teleoconch unclear (but sometimes with thickening of the last riblet). Teleoconch smooth (except for growth lines, which become more marked towards aperture). Suture well-marked, but not deep. Aperture roughly ovoid, but angulate. Peristome reflected and strongly thickened; some older specimens show continuous thickening of the peristome; parietal callus might be present in older specimens. Apertural teeth present: two knob-like parietal teeth positioned slightly towards the interior of shell (not always present); long palatal tooth in the middle portion of palatal region (its surface goes from smooth to serrated, with up to three distinct points); columellar tooth elongated, with smooth surface. Both columellar and palatal tooth produce a marked depression on outer wall of shell. Umbilicus slit-like.

Dimensions. Lectotype: H = 17.3 mm, D = 12.3 mm, h = 8.8 mm, d = 6.6, W = 4, w = 2. Paralectotype #1: H = 22.3, D = 15.6 mm, h = 10.9 mm, d = 7.7 mm, W = 4¾. Paralectotype #2: H = 23.5 mm, D = 16.0 mm, h = 11.2 mm, d = 8.7 mm, W = 5. Paralectotype #3: H = 19.5 mm, D = 14.6 mm, h = 10 mm, d = 7.2 mm, W = 4½, w = 1¾. Paralectotype #4: H = 19.6 mm, D = 13.7 mm, h = 8.8 mm, d = 6.7 mm, W = 4½. Paralectotype #5: H = 20.3 mm, D = 13.2 mm, h = 9.8 mm, d = 7.4 mm, W = 4¾, w = 1¾. Syntype of *Bonnanius bouvieri*: H = 22.5 mm, D = 15.4 mm (Breure, 1975). Average (n = 34, except for w, where n = 10): H = 17.9 ± 1.56 mm (min = 16.1 mm, max = 22.0 mm), D = 12.9 ± 0.96 mm, h = 9.7 ± 0.71 mm, d = 7.6 ± 0.63 mm, W = 4½ (min = 4¼, max = 5), w = 1¾ (occasionally 2).

Remarks. The names *H. bouvieri* and *H. bonnanius* were synonymized with *H. ramagei* by Pilsbry (1901); this decision is followed here. The syntype of *H. bouvieri* (Fig.

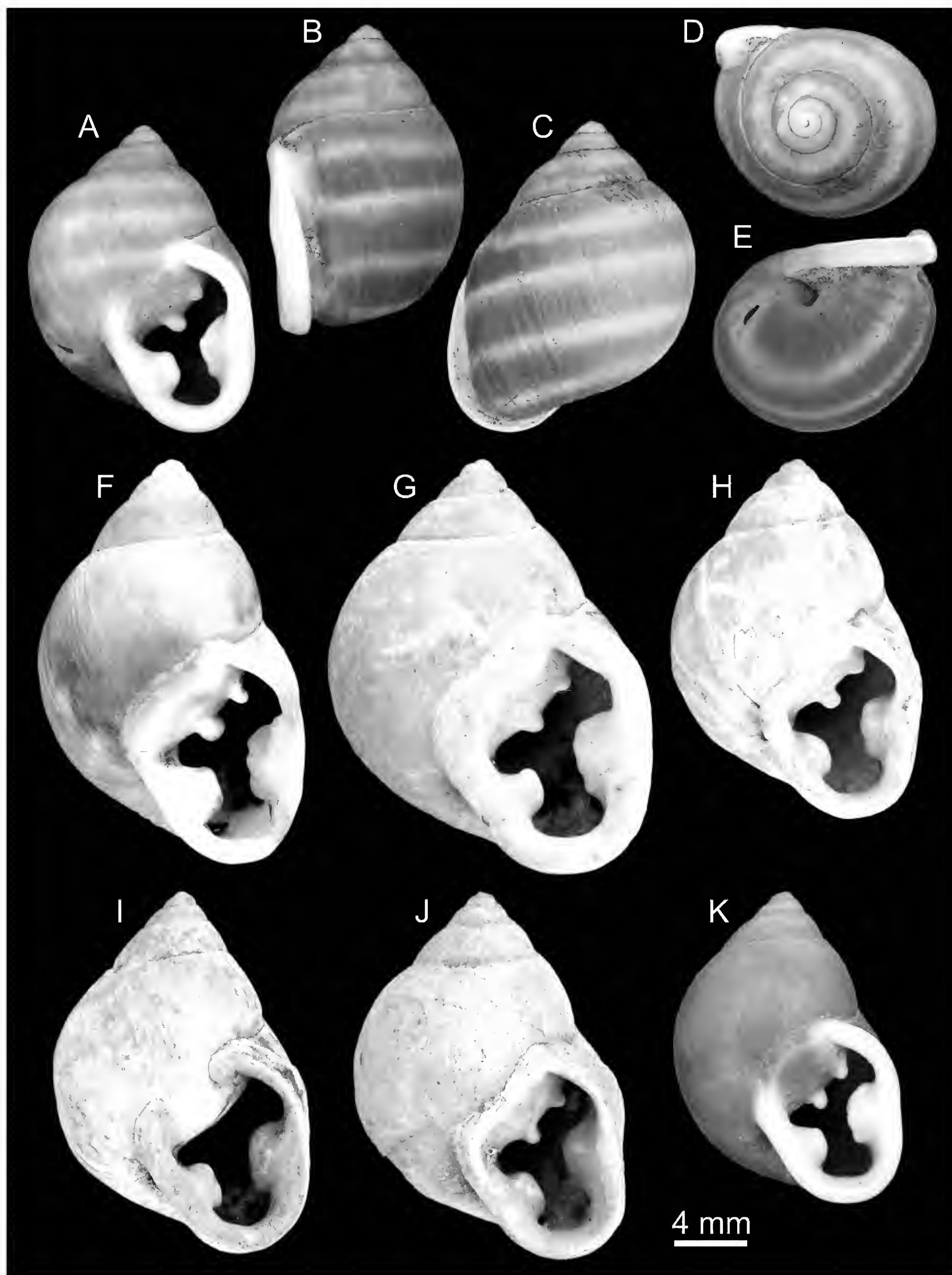


Figure 3. *Hyperaulax ramagei*. A–E. Lectotype, NHMUK 1988.6.24.163. F–J. Paralectotypes #1 to #5 (in order), including large forms in apparent sub-fossil state, NHMUK 1988.6.24.164-170. K. Specimen without the white spiral bands, NHMUK 1902.10.16.4.

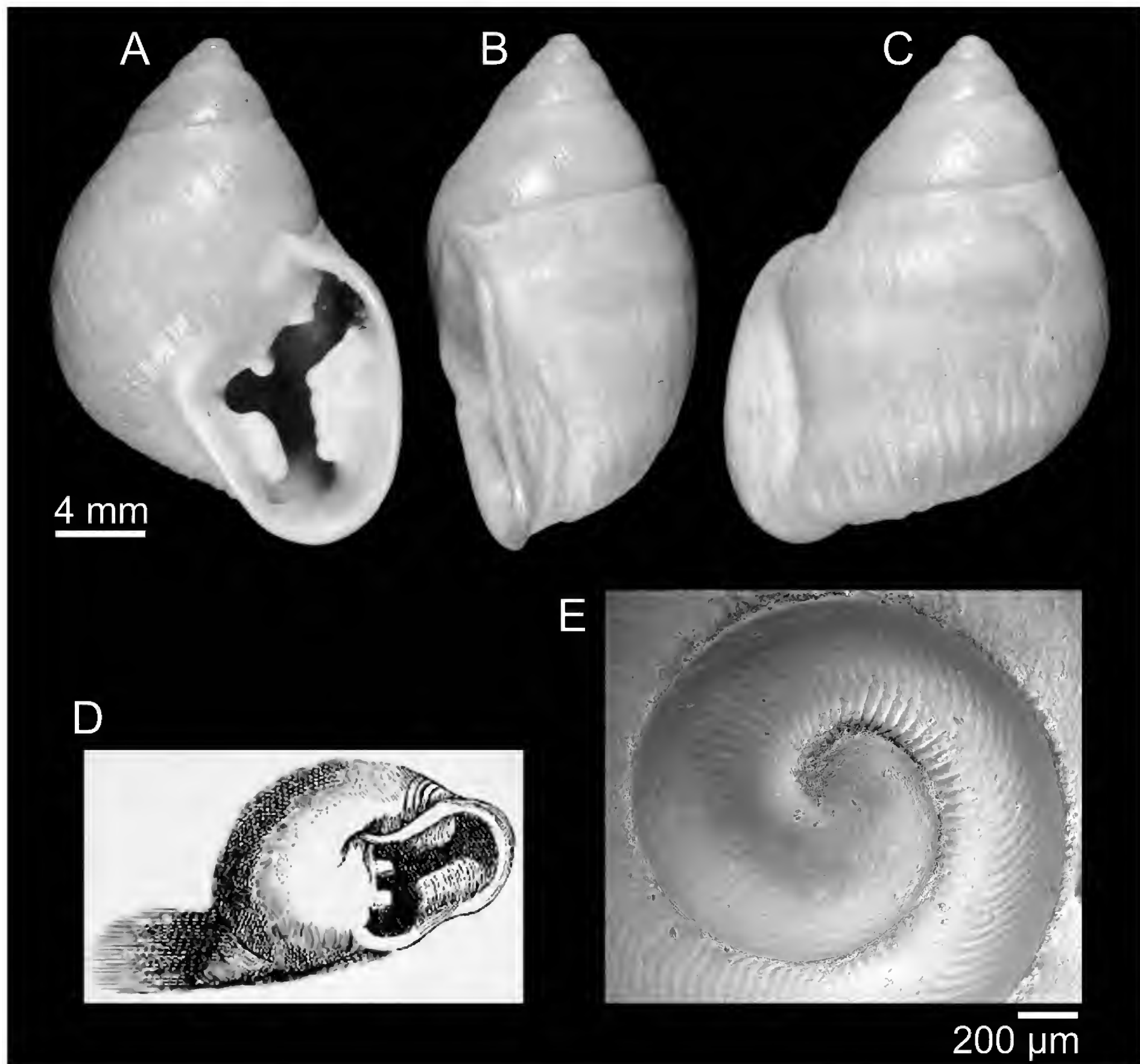


Figure 4. *Hyperaulax ramagei*. A–C. Syntype of *Bonnanus bouvieri*, MNHN-IM-2000-28020 (MNHN). D. Reproduction of ‘‘Turbine #44’’ of Buonanni (1861), the holotype of *Bonnanus bonnanius*. E. Protoconch detail, NHMUK 1902.10.16.4.

4A–C) is indistinguishable from *H. ramagei*, but the discussion regarding *H. bonnanius* is slightly more colorful and it is worthwhile to recapitulate it here. Its original description (Jousseume 1900) was based upon the work of the Jesuit scholar Filippo Buonanni (1638–1723), who compiled the first conchology manual (Buonanni 1681) and is thus considered the Father of Conchology (Leonhard 2007). As Pilsbry (1901) argued, Buonanni’s (1681) description of his Turbine #44 and its illustration (allowing for some distortion in the drawing) are vastly consistent with *H. ramagei*. Despite later authors such as Linnaeus having relied on Buonanni’s work, this particular species was overlooked until Jousseume (1900) published it as *Bonnanus Bonnanius*, misspelling the Jesuit’s name and likely without knowing the work of Smith (1890).

The shell features of *H. ramagei* display some morphological variation: (1) shell size, from some rather

small specimens to very large ones ($H_{\min} = 16$ mm and $H_{\max} = 22$ mm); (2) shell color can go from entirely brown to marked with four white spiral bands; (3) aperture size, relative to remainder of the shell; (4) shell shape, with some specimens having a much shorter spire (Fig. 3A–C, lectotype); (5) two parietal teeth might be absent (Fig. 3I); (6) the surface of the palatal tooth goes from nearly smooth (Fig. 3I, J) to serrated (Fig. 3F, G), with up to three distinct points (Fig. 3A), reminiscent of the carnassial tooth of Carnivora (apparently this is not related to the age of the individual or to the freshness of the specimen when collected). The syntype of *H. bouvieri* show a four-pronged palatal tooth, which is also unusually large, and a three-pronged parietal tooth (Fig. 4A–C); this could be seen as morphological variation, but, as this specimen bears a mark of breakage near the aperture and further growth (Fig. 4C), it could be simply post-trauma anom-

alous growth. For a comparison with its single congener, *H. ridleyi*, see the Discussion section of that species.

Some of the specimens available (including some paralectotypes) appear to be of a sub-fossil state, as already noted by Smith (1890). These appear to be larger than the fresh specimens, but this could be due to collection bias towards larger specimens; at present, there is not enough sub-fossil material for a statistically meaningful assessment.

Conclusions

Hyperaulax is here classified in the Odontostomidae and presently contains two species, *H. ridleyi* and *H. ramagei*, both endemic to Fernando de Noronha Archipelago. This genus seems to be more closely related to *Tomigerus* than to other odontostomids.

According to recent collection events on Fernando de Noronha, *H. ramagei* cannot be found alive in spite of meaningful search efforts (L.R.L. Simone personal communication). In fact, museum specimens of *H. ramagei* still bearing the periostracum typically date back to the first half of the 20th century. It is a troubling possibility that presently this species has a much-reduced range or is altogether extinct. Future collection efforts should focus on this species to properly define its status according to current guidelines for conservation (IUCN 2012).

Finally, another curious aspect of the fauna of Fernando de Noronha deserving further study is *Amphisbaena ridleyi* Boulenger, 1890, an amphisbaenid (worm lizard) endemic to the archipelago that possesses adaptations for a durophagous diet including a large proportion of land snails (Pregill 1984). In the original report, the author could not indicate which species of terrestrial gastropods were part of the lizard's diet and a study involving this species and possible defensive adaptations of the snails would be very welcome.

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Appendix 1

Below are listed the COI sequences of other Orthalicoidea species, obtained from the work of Breure and Romero (2012), used to ascertain the classification of the species studied herein. The list is organized by family and species (in alphabetical order), followed by the respective GenBank accession number. Bulimulidae: *Bostryx agueroi* JF514623; *Bostryx bilineatus* JF514637; *Bostryx edmundi* JF514622; *Bostryx longispira* JF514624; *Bostryx strobili* JF514636; *Bostryx superbus* JF514621; *Bulimulus diaphanus* JF514633; *Bulimulus guadalupensis* JF514630; *Bulimulus hummelincki* JF514629; *Bulimulus sporadicus* JF514632; *Bulimulus tenuissimus* JF514631; *Drymaeus inusitatus* JF514648; *Drymaeus laticinctus* JF514646; *Drymaeus multifasciatus* JF514647; *Drymaeus serratus* JF514649; *Drymaeus vexillum* JF514625; *Naesiotus quitensis* JF514635; *Naesiotus stenogyroides* JF514650; *Neopetraeus tessellatus* JF514627; *Rabdotus alternatus* JF514638; *Scutalus chiletensis* JF514628. Odontostomidae: *Clessinia cordovana cordovana* JF514618; *Clessinia cordovana stelzneri* JF514617; *Clessinia pagoda* JF514613; *Cyclodontina guarani* JF514619; *Plagiodontes multiplicatus* JF514620; *Spixia pervarians* JF514614; *Spixia philippii* JF514612; *Spixia popana* JF514616; *Spixia tucumanensis* JF514615. Simpulopsidae: *Leiostracus perlucidus* JF514640; *Simpulopsis decussata* JF514639.

The sequence of the outgroup taxon was obtained from GenBank: *Planorbis planorbis* EF012175 (Planorbidae).

Contributions to the taxonomy of the long-jawed orb-weaving spider genus *Tetragnatha* (Araneae, Tetragnathidae) in the Neotropical region, with comments on the morphology of the chelicerae

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Abstract

We newly diagnose, illustrate, and clarify the distribution ranges of six of the most common and broadly distributed species of *Tetragnatha* Latreille, 1804 found in the Neotropical region. Twenty new junior synonyms from around the world are included, nine for *T. bogotensis* Keyserling, 1865, four for *T. mandibulata* Walckenaer, 1841, three for *T. keyserlingi* Simon, 1890, three for *T. nitens* (Audouin, 1826), and one for *T. elongata* Walckenaer, 1841. *Tetragnatha vermiformis* Emerton, 1884 is newly recorded from South America. The Argentine *T. major* Holmberg, 1876 and *T. riparia* Holmberg, 1876 are considered nomina dubia. Finally, we discuss the terminology of the structures of the chelicerae to establish a coherent nomenclature for teeth and fang cusps.

Key Words

Biodiversity, Araneoidea, Systematics, Tetragnathinae

Introduction

The long-jawed spider genus *Tetragnatha* Latreille, 1804 (family Tetragnathidae) comprises 349 species, 67 of which restricted to the Neotropics (World Spider Catalog 2019). All species share spiny and elongate chelicerae, elongate and dorsally flattened carapace, parallel eye rows, and female genital openings located at the posterior end of the procurved epigastric furrow (Levi 1981; Gillespie 1992a, b; Barrion et al. 2011). Nonetheless, many species are poorly diagnosed at the taxonomic level and their geographic ranges are imperfectly known.

Although no complete revision is available for *Tetragnatha*, species redescriptions and local revisions are frequent. The first revisionary papers on the genus addressed species from North America (Seeley 1928) and Europe (Lendl 1886; Wiehle 1939, 1963). Chickering (1957a)

reviewed the Central American and Mexican species, followed by those from Jamaica (Chickering 1957b); Panama (Chickering 1957c); United States and Canada (Levi 1981); Australasia (Okuma 1987), Asia (Okuma 1988a, b), Mexico, and part of the Neotropical region (Okuma 1992), Hawaii (Gillespie (1992a, b, 2003a); Marquesas Islands (Gillespie 2003b); and Society Islands (Gillespie (2003c)).

In this paper, we analyse most of the widespread species of *Tetragnatha* in the Neotropical region. We propose 20 new synonymies for five of them and include new records from South America for one species previously known from Asia and introduced in North and Central America. We also provide new diagnoses, illustrations, and many new distribution records. Furthermore, we consider two species from Argentina as nomina dubia.

Methods

The taxonomic summary for all species is abbreviated to save space, including only the information we consider most relevant. See the World Spider Catalog (2019) for a complete list of synonymies. Terminology for chelicerae follows Okuma (1987, 1992) and Gillespie (1992a, 1992b). For the male palp, see Levi (1981), and for the female genitalia, see Álvarez-Padilla and Hormiga (2011). Colour patterns were described based on specimens preserved in 75% ethanol.

Structures were cleaned using a Cristofoli Ultrasonic Cleaner and positioned in 70% ethanol gel or glass spheres for automontage photographs and measurements. Images were taken with a Leica DFC450 camera mounted on a Leica M205C stereoscope microscope (Leica Camera AG, Wetzlar, Germany) at the Laboratório de Entomologia, Universidade do Brasil/Universidade Federal do Rio de Janeiro. All images were edited with Adobe Photoshop CS5.1 and figures were prepared using Adobe Illustrator CS5.1 (Adobe Inc., San Jose, California, USA). Measurements are given in millimeters. The position of teeth and fang cusps (upward, downward, distalward, and basalward) was noted when the chelicerae were attached to the body. The genital fold length was measured from the inner angle of book-lung plates to the posterior rim of the fold. The genital fold proportion is the comparison of its length versus the span between the outer angle of posterior rim of one book-lung plate to the outer angle of the other. Males were matched with conspecific females by cheliceral morphology and collection sites.

For scanning electron microscopy (**SEM**), samples were critically point dried, mounted on adhesive copper tape (Electron Microscopy Sciences, EMS 77802), affixed to a stub and sputter-coated with Au-Pd for examination under high vacuum with a JEOL JSM-6510 microscope at Laboratório de Imagens, Instituto de Biologia, Universidade Federal do Rio de Janeiro; a Philips XL 30 Field Emission ESEM at the Centro de Microscopia e Microanálises, Pontifícia Universidade Católica do Rio Grande do Sul, and a JEOL JSM-6390LV at Centro de Microscopia, Fundação Oswaldo Cruz.

To clear female genitalia, we used a borax solution (Álvarez-Padilla and Hormiga 2008) and digestive enzyme tablets of “Orthoplex D.E.F” (Bioconcepts Pty Ltd, Banyo, Queensland, Australia). We noted that sometimes the internal genitalia may appear darker or lighter, after clearing, usually related to the time spent in the solution. For example, the spermathecae and central membranous sac may appear dark, roundish, and well defined (Fig. 2H) or pale and partially collapsed (Fig. 2I).

Maps were produced using QGIS v. 2.14 software and geographic coordinates were extracted from original labels. When no coordinates was available, the closest nearby area coordinates were obtained from Global Gazetteer v. 2.3 (<http://www.fallingrain.com/world/index.html>) or Google Earth v. 9.1.39.1 (<https://earth.google.com/web/>).

Cited institutions and their acronyms are:

AMNH	American Museum of Natural History, USA (curator: L. Prendini);
CAS	California Academy of Sciences, USA (L. Esposito);
IBSP	Instituto Butantan, Brazil (A. Brescovit);
MACN	Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Argentina (M. Ramírez);
MCTP	Museu de Ciência e Tecnologia da Pontifícia Universidade Católica do Rio Grande do Sul, Brazil (R. Teixeira);
MCZ	Museum of Comparative Zoology, Harvard University, USA (G. Giribet);
MIZ	Muzeum i Instytut Zoologii Polskiej Akademii Nauk, Poland (W. Wawer);
MLP	Museo de La Plata, Argentina (L. Pereira);
MLPC	Mello-Leitão’s private collection, now at Museu Nacional, Universidade do Brasil/Universidade Federal do Rio de Janeiro, Brazil (A. Kury);
MNHN	Musée National d’Histoire Naturelle, France (C. Rollard);
MNRJ	Museu Nacional, Universidade do Brasil/Universidade Federal do Rio de Janeiro, Brazil (A. Kury);
MPEG	Museu Paraense Emilio Goeldi, Brazil (A. Bonaldo);
MRAC	Royal Museum for Central Africa, Belgium (D. Van den Spiegel);
MZUF	Università di Firenze, Museo Zoologico “La Specola”, Italy (L. Bartolozzi);
MZUSP	Museu de Zoologia da Universidade de São Paulo, Brazil (R. Pinto-da-Rocha);
NHM	Natural History Museum, United Kingdom (J. Beccaloni);
NHMW	Naturhistorisches Museum Wien, Austria (C. Hörweg);
NHRS	Naturhistoriska Riksmuseet (Swedish Museum of Natural History), Sweden (J. Stigenberg);
NMB	Naturhistorisches Museum Basel, Switzerland (A. Haenggi);
NMV	Museums Victoria, Australia (K. Walker);
OUMNH	Oxford University Museum of Natural History, United Kingdom (Z. Simmons);
SMF	Senckenberg Museum Frankfurt, Germany (P. Jäger);
UFRJ	Laboratório de Diversidade de Aracnídeos, Universidade Federal do Rio de Janeiro, Brazil (R. Baptista);
USNM	Smithsonian National Museum of Natural History, USA (J. Coddington);
ZMB	Museum für Naturkunde, Humboldt-Universität, Germany (J. Dunlop);
ZMH	Zoologisches Museum Hamburg, Germany (D. Harms).

Abbreviations used below for the chelicera:

- a** male dorsal apophysis, used to lock the fangs of females during copulation.
- AXI** auxiliary guide tooth of the lower row, present in some species.
- AXu** auxiliary guide tooth of the upper row, above Gu, present in some species.
- BC** basal cusp on the cheliceral fang of females (new terminology). Okuma applied different names to this structure: excrescence (1987) and posterior cusp (1992).
- CB** cheliceral bulge, a protruding area between the two rows of teeth, near the base of the fang (new terminology).
- CRu** cheliceral crest, a protruding marked area on the upper row of teeth (new terminology).
- CRI** cheliceral crest, a protruding marked area on the lower row of teeth (new terminology).
- Gu** guide tooth of the upper (or dorsal) row (follows Okuma 1983, 1987, 1992).
- Gl** guide tooth of the lower (or ventral) row (follows Okuma (1983, 1987, 1992).
- IC** inner cusp of fang (follows Okuma 1987, 1992) (new abbreviation).
- L2-n** teeth on the lower row numbered from the distal end after Gl.
- OC** outer cusp of fang (present in some species) (new terminology).
- rsu** remaining proximal teeth on the upper row of males after T (Okuma 1987; Gillespie 1992a, 1992b).
- rsl** remaining proximal teeth on the lower row of males and females after the last specialized tooth (Okuma 1987).
- sl** first major tooth after Gu in the upper row of males (absent in some species).
- T** elongated tooth in the upper row of some males (Okuma 1983, 1987, 1992).
- t** a tooth or prominence found in males of some species.
- U2-n** teeth on the upper row numbered from the distal end after Gu.

Abbreviations for male and female genitalia, male palps:

- E** embolus;
- C** conductor;
- Y** cymbium;
- P** paracymbium
- K** knob at the ectal side of paracymbium (new terminology),
- L** translucent lobe at the mesal side of paracymbium,
- N** notch at the apex of paracymbium.

Female genitalia:

- GF** genital fold;
- Sp** spermatheca;
- CS** central membranous sac.

Results

Order Araneae Clerck, 1757

Family Tetragnathidae Menge, 1866

Genus *Tetragnatha* Latreille, 1804*Tetragnatha bogotensis* Keyserling, 1865

Figs 1–4, 20A, 21A–G, 22A

Tetragnatha bogotensis Keyserling 1865: 854, pl. 21, fig. 5 (♀).*Tetragnatha andina* Taczanowski 1878: 144, pl. 1, fig. 2 (♀); Levi 1981: 291 (removed from syn. with *T. nitens*) syn. nov.*Tetragnatha boydi* O. Pickard-Cambridge 1898: 389, pl. 31, fig. 4 (♀) syn. nov.*Tetragnatha peninsulana* Banks 1898: 246, pl. 15, fig. 12 (♂ ♀); Levi (1981): 291 (removed from syn. with *T. nitens*) syn. nov.*Tetragnatha praedator* Tullgren 1910: 147, pl. 3, fig. 69 (♂)*Tetragnatha mandibulata bidentata* Gravely 1921: 442, fig. 3c, f (♂ ♀).*Tetragnatha eremita* Chamberlin 1924: 645, figs 89, 90 (♂); Levi 1981: 292 (removed from syn. with *T. nitens*) syn. nov.*Tetragnatha nitens* Lawrence 1927: 27, pl. 3, fig. 61, pl. 4, fig. 77 (♂ ♀ misidentified).*Tetragnatha bemalcuei* Mello-Leitão 1939: 67, figs 42–44 (♀) syn. nov.*Tetragnatha ramboi* Mello-Leitão 1943: 193, fig. 24, 24a, b (♂) syn. nov.*Tetragnatha haitiensis* Bryant 1945: 408, fig. 37 (♀); Levi 1981: 292 (removed from syn. with *T. nitens*) syn. nov.*Tetragnatha nitens kullmanni* Wiehle 1962: 379, figs 1–5, 6b, 9–11, 14, 15 (♂ ♀); Wunderlich 1992: 365 (removed from syn. with *T. nitens*) syn. nov.*Tetragnatha infuscata* Benoit 1978: 667, fig. 2D, E (♂); Saaristo 2003: 23, figs 21A, B, 25 (syn. with *T. boydi* rejected, see *T. mandibulata*).*Tetragnatha boydi praedator* Schmidt and Krause 1993: 6, fig. 5 (♂ ♀) syn. nov.

Type material. *Tetragnatha bogotensis*: COLOMBIA: ♀♀ syntypes, “Nova Granada” [surely Bogotá], 1859–1863? Alexander Lindig leg., not located, probably lost. *Tetragnatha andina*: PERU: ♂♂, ♀♀ syntypes, “Amable Maria” [surely province of Tarma, region of Junín] (38 syntypes, Coll. K. Jelski, MIZ 225346-225446), examined (photos). *Tetragnatha boydi*: YEMEN: ♀ syntype, Socotra, not located. *Tetragnatha peninsulana*: MEXICO: ♂♂ (CAS), ♀♀ (MCZ 22587) syntypes: San José del Cabo, Baja California Sur, females examined (photos), males destroyed (Levi 1981). *Tetragnatha praedator*: KENYA: 4♂, syntypes (NHRS JUST000000671-672), Kilimandjaro and Meru, examined (photos). *Tetragnatha eremita*: MEXICO: ♂ holotype, Baja California, Puerto Escondido, Arroyo de Escondido (Coll. J. C. Chamberlin, 14.vi.1921, male pedipalp in MCZ 15283, labeled RVC 1111; whole specimen in CAS 1430), examined (photos of CAS 1430); ♀ paratype, same data as holotype (MCZ 25228), examined (photos). *Tetragnatha bemalcuei*: PARAGUAY: ♀ holotype, Asunción (Coll. C. Ternetz, 1895, NMB-ARAN 01092a), examined (photos). *Tetragnatha ramboi*: BRAZIL: ♂, lectotype, Rio Grande do Sul (Coll. Father Balduino Rambo, MNRJ 42467), examined. *Tetragnatha haitiensis*: HAITI: ♀ holotype, “Hispanio-

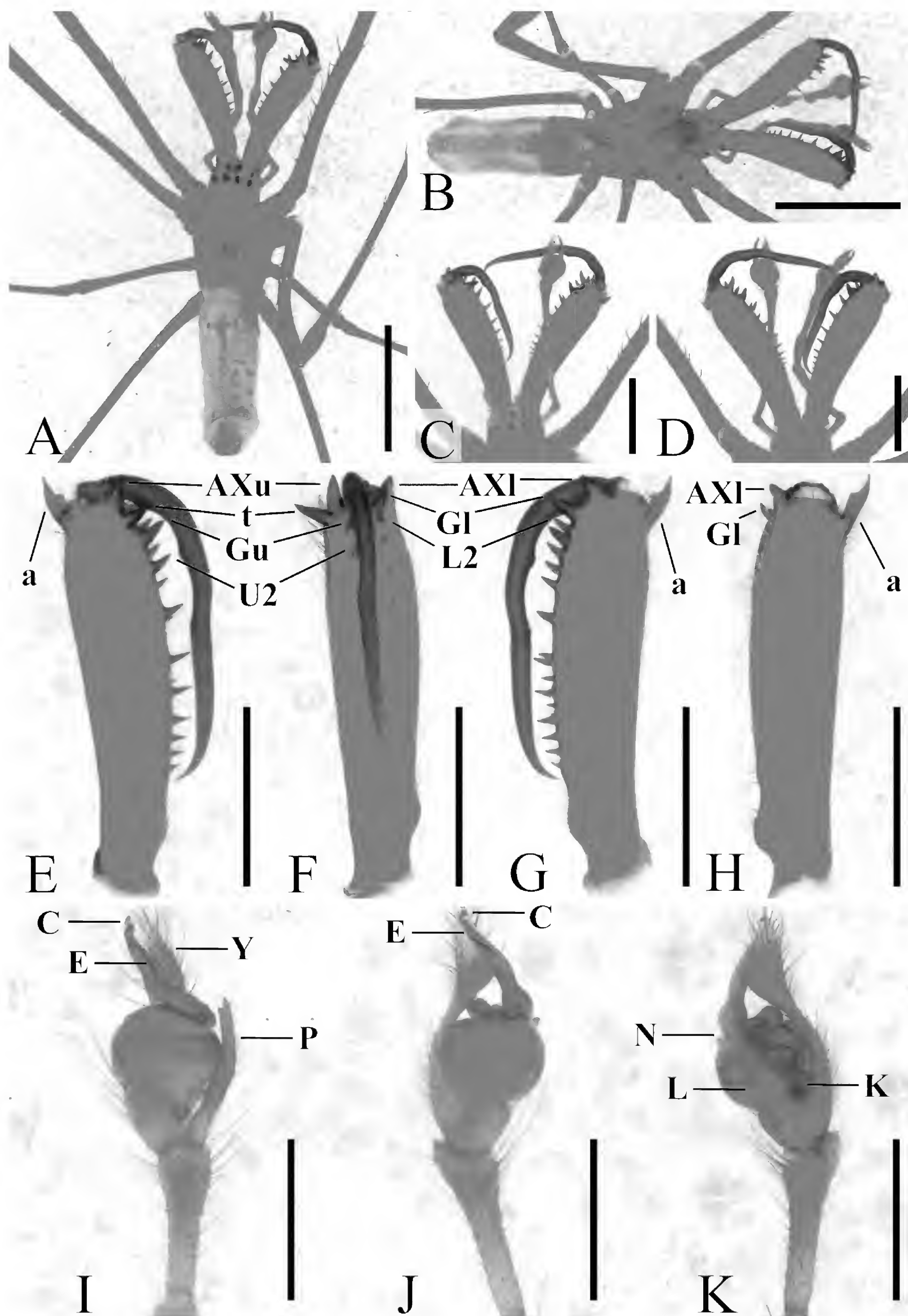


Figure 1. *Tetragnatha bogotensis* Keyserling, 1865, male (UFRJ 0035). **A.** Dorsal habitus; **B.** Ventral habitus; **C.** Chelicerae upper row and eyes; **D.** Chelicerae lower row and maxilla; **E–H.** Left chelicera: **E.** Upper view; **F.** Inner view; **G.** Lower view; **H.** Outer view; **I–K.** Left male palp: **I.** Mesal view; **J.** Dorsal view; **K.** Ventral view (paracymbium). Scale bars: 2 mm (**A, B**); 1 mm (**C, D, E, F, G, H**); 0.5 mm (**I, J, K**).

la” [Ennery] (Coll. P. J. Darlington Jr., 07.vii.1934, MCZ 21516), examined (photos). *Tetragnatha nitens kullmanni*: ITALY: ♂, holotype (SMF 12741), 2♀, 1 immature, paratypes (SMF 12742), Sardinia, Oliena (E. Kullmann leg.), not examined.

Extended diagnosis. Males of *T. bogotensis* are similar to *T. nitens* (Audouin, 1826) and share chelicerae with an elongated ‘a’, and AXu and ‘t’ extremely elongated and distally bent. AXu and ‘t’ differ as follows: thick and triangular in *T. bogotensis* (Figs 1C, E, F, 3B), but thinner and ‘t’ sickle-like in *T. nitens* (Figs 14C, D, F, 16A). Gu longer, sharper, straight and larger than U2 in *T. bogotensis* (Figs 1C, E, F, 3B) while it is shorter than U2 and slightly curved downward in *T. nitens* (Figs 14C, D, 16A). Palps share medium-sized conductors without pleats (Figs 1I, 3A, 14G, 15D, E). *Tetragnatha bogotensis* palps differ by shorter tibiae (ca 3× longer than wide) (Figs 1I–K, 3A), conductors not twisted at their distal halves, with completely folded apices enclosing the emboli tips (Figs 1I, J; 3A, E; 20A) and longer paracymbia, overreaching the upper border of teguli, each bearing deeper notch, resulting in an elongated tip of the paracymbium proper, and thinner and relatively narrow translucent lobe (Figs 1I, K; 3D). In *T. nitens*, palps have longer and thinner tibiae (almost 4× longer than wide) (Figs 14G–I, 16E), conductors twisted in distal half with their apices rounded and excavated, exposing the emboli tips (Figs 14G, H, 16D–F, 20E) and shorter paracymbia that do not reach the upper border of teguli, with expanded and very wide translucent lobes (Figs 14I, J, 16F). The epiandrous field is straight, with 19 fusules, in *T. bogotensis* (Fig. 3F) but arched and smaller, with only 15 fusules, in *T. nitens* (Fig. 16C).

Females are similar to *T. nitens* and also *T. mandibulata* Walckenaer, 1841, sharing: bulky body, wide and pointed at the terminal end (Figs 2A, B, 12A–C, 15A, B), and elongate genital fold (Figs 2G, 12H, 15J). Their chelicerae also bear an evident basal cusp (BC) in the fang (Figs 2D, E, 12D–G, 13C, D, 15D, F–I, 16B), Gu elongated and not contiguous to U2 (Figs 2C, D, 12D, E, 13C, 15C, E, F, 16B); Gl large and pointed distalward, followed by smaller L2 and L3 (Figs 2D, E, 3C, 12E, F, 13D, 15D, F, H, 16B). *T. bogotensis* and *T. mandibulata* differ from *T. nitens* by distinct bulky AXI, which are elongated, pointed and with large bases, clearly visible and overreaching the claws even in upper view (Figs 2C–F, 3C, 12D–G, 13C, D), while in *T. nitens* it is short and not pointed (Figs 15F–H, 16B). *T. bogotensis* and *T. mandibulata* also differ by the conspicuous bulge (CB) in the area between both rows (Figs 2C, E, 3C, 12D, F, 13C, D), which is absent in *T. nitens*. *Tetragnatha bogotensis* chelicerae can be distinguished from *T. mandibulata* by the following characters: more robust basal cusp (BC), placed at the middle line of the lower side of the claw, compared to a smaller BC, displaced towards the outer face of the claw (Figs 2D, E, 3C–F, 12D–G, 13C, D); Gu straight with a large basis, being separated from U2 by a wide and deep furrow, versus both teeth not quite spaced (Figs 2C, D, 3C, 12D, E, 13C); AXI bulkier, with much

larger basis, compared to a thinner and shorter tooth (Figs 2C–F, 3C, 12D–G, 13C, D); Gl shorter, straight and pointed, with wider basis, and much smaller than AXI, versus a longer and slanted Gl, regularly tapered and just a bit smaller than AXI (Figs 2D, E, 12E, F, 13D); and CB rounded and wide, extending from a bit above L2 to L3, and placed in the middle line between both rows of teeth, contrasting to a smaller and lower CB, extending from the basis of Gl to the middle of the gap between L2 and L3, and adjoined to the basis of L2 (Figs 2C, E, 3C, 12D, F, 13C, D). In *T. nitens*, BC is placed at a similar position to *T. bogotensis*, but is larger (Figs 15D, F–I, 16B) and Gu is connected to U2 by a thin and dark ridge, with a gap of similar size to *T. bogotensis* (Figs 15C, E, F, 16B). The genital fold (Figs 2G, 12H, 15J) is similar in all three species but shorter in *T. nitens* (genital fold length around 0.6× the width), intermediate in *T. bogotensis* (0.8×) and longer in *T. mandibulata* (1.1×). The internal genitalia of *T. bogotensis* is more similar to *T. mandibulata*, with medium-sized spermathecae and a sclerotized and rounded fundus (Figs 2H, I, 12I), in contrast to wider spermathecae without a well-defined fundus in *T. nitens* (Fig. 15K, L). The central membranous sac (CS) of *T. bogotensis* is medium-sized, with almost the same size of the spermathecae, and placed at the same level of their bases (Fig. 2H, I), while in *T. mandibulata* it is massive, longer, and placed at the same level as the spermathecae (Fig. 12I). In *T. nitens*, the CS is about the same size as in *T. bogotensis*, but with a stalk of variable size, sometimes longer than the spermathecae, placing the apical portion of the CS at the same level or anteriorly to the spermathecae (Fig. 15K, L).

Synonymy and notes. Keyserling (1865) described this species based on female specimens from “Nova Granada”, which encompasses a large area ranging from Panama to Ecuador, and which were collected by Alexander Lindig, who gathered many animals and plants in Bogotá (Colombia) from 1859 to 1863 (Meagher 2012). Therefore, the type specimens were most likely collected, at least partially, in this city, as indicated by the name *T. bogotensis*. The drawing of one female by Keyserling (1865: pl. 21, fig. 5) allows the recognition of the species by showing the long and robust AXI placed near to a smaller and traverse Gl of the right chelicera. In the original description, Keyserling wrote that he had “many copies in my collection”, without citation of any males (Keyserling 1865: 855).

The first author of this paper visited three collections with type material by Keyserling: MIZ; NHM (Beccaloni 2012), and ZMB (Kretschmann 2006), and we also contacted curators of NHMW and USNM. Possible well-preserved type specimens were found in two vials at only the NHM. In the first vial (Fig. 4A), there were three females labeled “type” and originated from “Taquara” (originally “Taquara do Mundo Novo”, state of Rio Grande do Sul, Brazil). In the second vial (Fig. 4B), there were two females and one male labeled “Bogotá”, but with no clear indication as type. All five females from both vials are *T. bogotensis* but the male from Bogotá belongs to *T. nitens*.

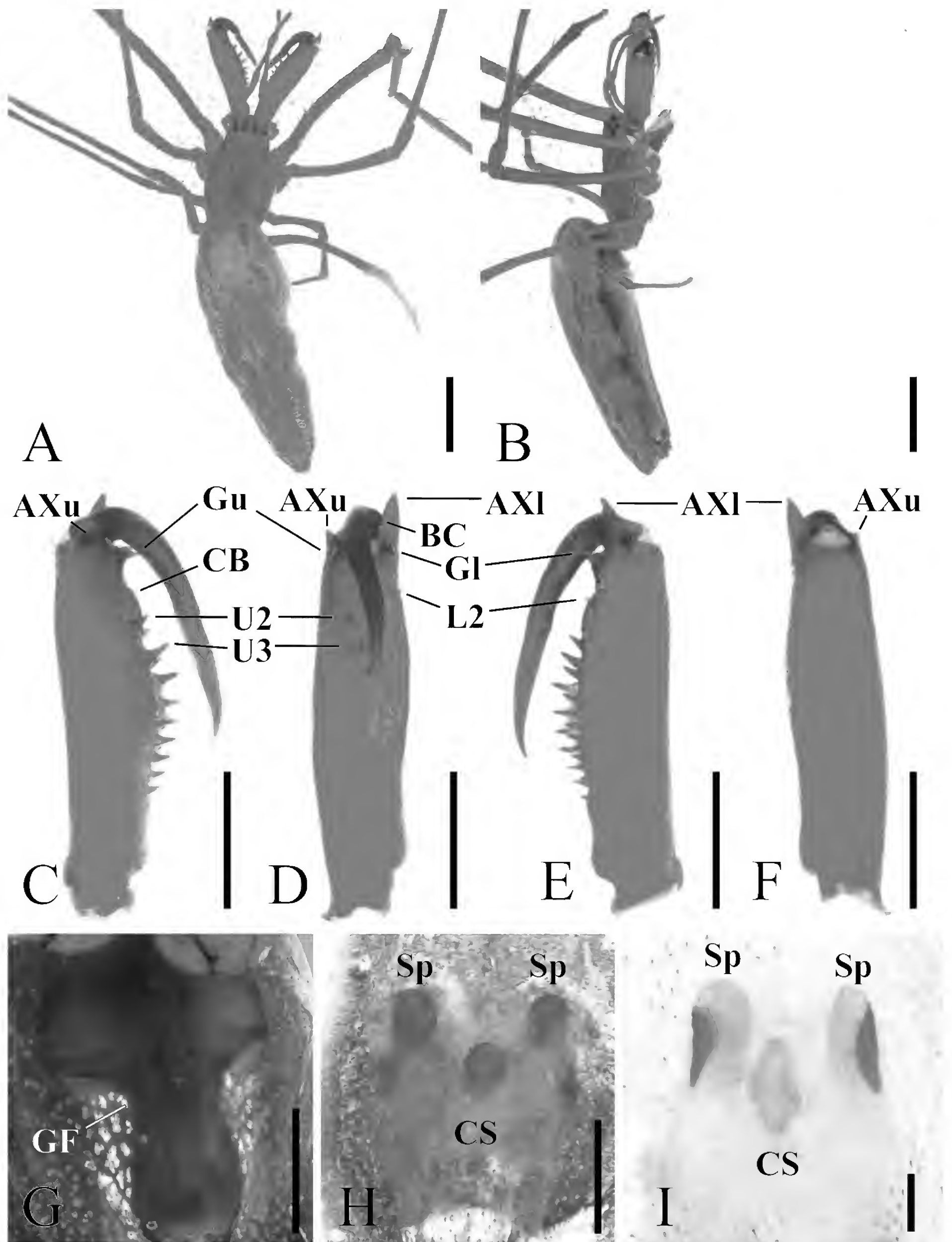


Figure 2. *Tetragnatha bogotensis* Keyserling, 1865, female. **A.** Dorsal habitus (UFRJ 1314); **B.** Lateral habitus (UFRJ 1314); **C–F.** Left chelicera (UFRJ 1314): **C.** Upper view; **D.** Inner view; **E.** Lower view; **F.** Outer view; **G–I.** Genital area: **G.** Genital fold, ventral view (MCTP 3381); **H.** Internal genitalia, cleared, ventral view (UFRJ 1314); **I.** Internal genitalia, cleared, ventral view (MCTP 13581). Scale bars: 2 mm (**A, B**); 1 mm (**C, D, E, F, G**); 0.2 mm (**H**); 0.1 mm (**I**).

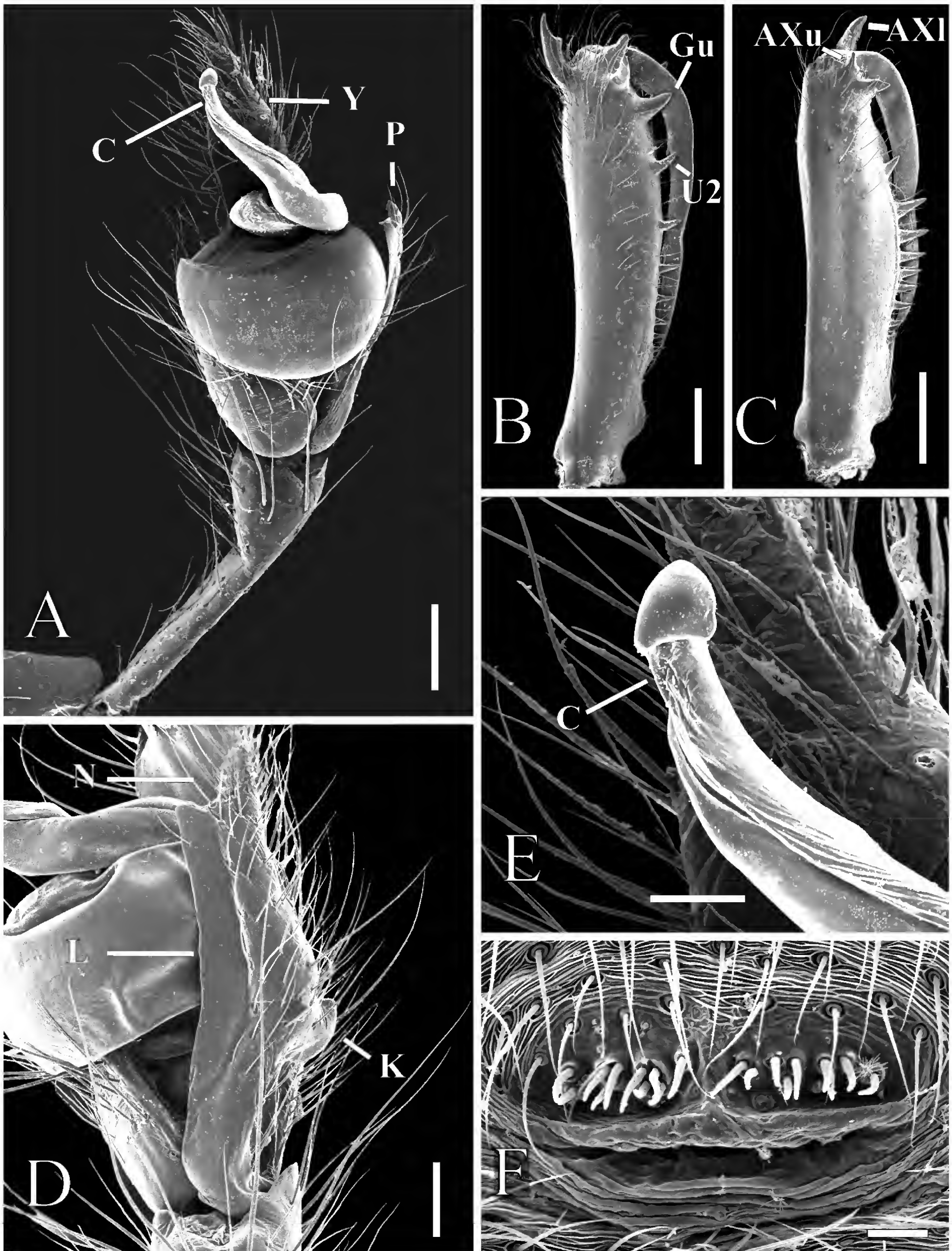


Figure 3. *Tetragnatha bogotensis* Keyserling, 1865, SEM photos. **A.** Left male palp, mesal view (MCTP 4299); **B.** Left male chelicera, upper view (MCTP 4299); **C.** Left female chelicera, upper view (MCTP 4299); **D.** Left male palp paracymbium, ventral view (UFRJ 0044); **E.** Left palp conductor detail, mesal view (MCTP 4299); **F.** Epiandrous field, ventral view (UFRJ 0044). Scale bars: 0.2 mm (**A**), 0.5 mm (**B**, **C**), 0.1 mm (**D**), 0.05 mm (**E**), 0.02 mm (**F**).

We consider Keyserling's syntypes to be lost, as there is no clear indication that the specimens above were used to describe the species: females from Taquara are not syntypes because Keyserling had not cited any specimens from that Brazilian locality, and females from Bogotá are also not syntypes as they were not labeled as type or "N. Granada" and are kept in the same vial as the additional male. Therefore, the confirmation of the identity of Keyserling's species relies on the illustration in the original description and the fact that specimens collected in Bogotá and other cities from Colombia clearly display the key cheliceral teeth characters that allow the diagnosis of *T. bogotensis*.

Tetragnatha boydi has been redescribed and illustrated many times (see World Spider Catalog 2019). Pickard-Cambridge (1898) described this species based on a female from Socotra (Yemen), giving detailed illustrations of the lower and inner views of the chelicerae (Pickard-Cambridge 1898: fig. 4a, b). Males were first described as *T. praedator* Tullgren, 1910 from Kenya, a species considered junior synonym afterwards (see below). Unfortunately, the female type material was not located at NHM or in OUMNH, institutions where O. Pickard-Cambridge normally deposited his specimens, and remains lost. Lawrence (1927) (sub *T. nitens*) and Okuma (1983) were the first authors to correctly match both sexes in their papers. Lawrence (1927) gave very detailed illustrations of the male left palp and chelicera, clearly showing the diagnostic characters of this species. On the other hand, the females were not illustrated, but his description points to the "inferior margin with a large apical tooth" (Lawrence 1927: 28), thereby rejecting the identification as *T. nitens*. Okuma (1983) also correctly matched the couples, gave very detailed drawings of chelicerae and genitalia, synonymised *T. mandibulata bidentata* and *T. nitens kullmanni* with *T. boydi*, and gave the first records for Brazil. Later, Okuma (1992) also provided new drawings of the species. After examining illustrations by Keyserling (1865: pl. 21, fig. 5), the NHM specimens of *T. bogotensis* from the type locality (Bogotá), and making comparisons with O. Pickard-Cambridge's (1898) illustrations and the later illustrations by Tullgren (1910), Lawrence (1927), and Okuma (1983, 1992), we conclude that all specimens belong to the same common species and establish that *T. boydi* is a junior synonym of *T. bogotensis*.

Tetragnatha praedator Tullgren (1910: fig. 69a, b) was described from four male specimens from Kilimandjaro and Meru (Kenya). Lessert (1915) also cited males of *T. praedator*, and the species was later synonymised with *T. boydi* by Roewer (1942). Finally, it was treated as a subspecies of *T. boydi* by Schmidt and Krause (1993), who also described females from Comoros Island, forming the combination *T. boydi praedator* Tullgren, 1910. After comparing Tullgren's (1910) illustrations and photos of the syntypes we received (Fig. 21C) with the specimens we identified as *T. bogotensis*, we observed that they clearly match. Thus, *T. boydi praedator* is synonymised here with *T. bogotensis*. On the other hand, the females assigned to *T. boydi praedator* by Schmidt and Krause (1993: fig. 5) probably belong to a different species judg-

ing by their illustrations, which are, however, too poor to allow a proper evaluation.

Tetragnatha bemalcuei was described by Mello-Leitão (1939: 68, figs 42–44), who mentioned on the original description "a robust conical frontward apophysis" (AXI) on the lower row of the chelicerae. We examined detailed images of the holotype (NMB) that show the characters of *T. bogotensis* (Figs 4D, 21E) and establish *T. bemalcuei* as a junior synonym of *T. bogotensis* Keyserling, 1865.

Mello-Leitão (1943) described *T. ramboi* based on males and females from Rio Grande do Sul, south Brazil. He indicated the vial MNRJ 42467 as "tipo" (type in Portuguese) in the description, but did not label it as "typus", in contrast to his common practice (Fig. 4C). We examined the type series (one male, two females, and one immature specimen) and agree with Silva-Moreira et al. (2010) that the whole series of specimens should be treated as syntypes. In the original description, the male was cited first and its diagnostic chelicerae and palps were illustrated (Mello-Leitão 1943: fig. 24a, b), whereas only the habitus of the female was illustrated (Mello-Leitão 1943: fig. 24). Under the rule of the "First Reviser" (ICZN 1999, article 24), we consider the sequence of descriptions and the presence of diagnostic illustrations in establishing the male as the lectotype of the species. This male clearly belongs to *T. bogotensis* according to the chelicerae and palp diagnostic characters (Figs 1C, E, J, 3A, B, E, 20A, 21F; Mello-Leitão 1943: fig. 24b) and must be newly synonymised with this species. Finally, we consider the female and juveniles of the type series of *T. ramboi* as misidentified specimens of *T. argentinensis* Mello-Leitão, 1931 which were erroneously attributed to *T. ramboi*.

We also note that several species previously considered junior synonyms of *T. nitens* should be newly synonymised with *T. bogotensis*. For example, Levi (1981: 291, 292) established 13 junior synonyms of *T. nitens*. Indeed, most of those species are correctly junior synonyms of it, but at least four should now be regarded as junior synonyms of *T. bogotensis* (see *T. nitens* below). It also seems that Levi (1981: figs 23–29) matched males of *T. nitens* with at least some females of *T. bogotensis*, as it is evident by the female illustrations he gave. These clearly depict the large AXI of *T. bogotensis* (Levi 1981: figs 23–25) and similar genitalia (Levi 1981: figs 27–29), with a pattern very different from *T. nitens* (Fig. 15K, L, Zhu and Zhang 2011: fig. 125G). In the "Variation" and "Diagnosis" sections of his paper, Levi (1981: 292) pointed out "On Panamanian specimens the diagnostic tooth at the posterior base of the fang is as long as the chelicerae are wide, and is sometimes smaller than illustrated on the most northern specimens" and "The female chelicerae have a large posterior lateral tooth at the insertion of the fang". Unfortunately, he did not provide the collection site for the female specimen he illustrated, and although there is no formal record for *T. bogotensis* or any of its synonyms from the United States, at least some of the females from the southern USA cited as *T. nitens* may belong to that species instead.

Levi (1981: 291, 292) synonymised *T. andina* Taczanowski, 1878 with *T. nitens* based on multiple male

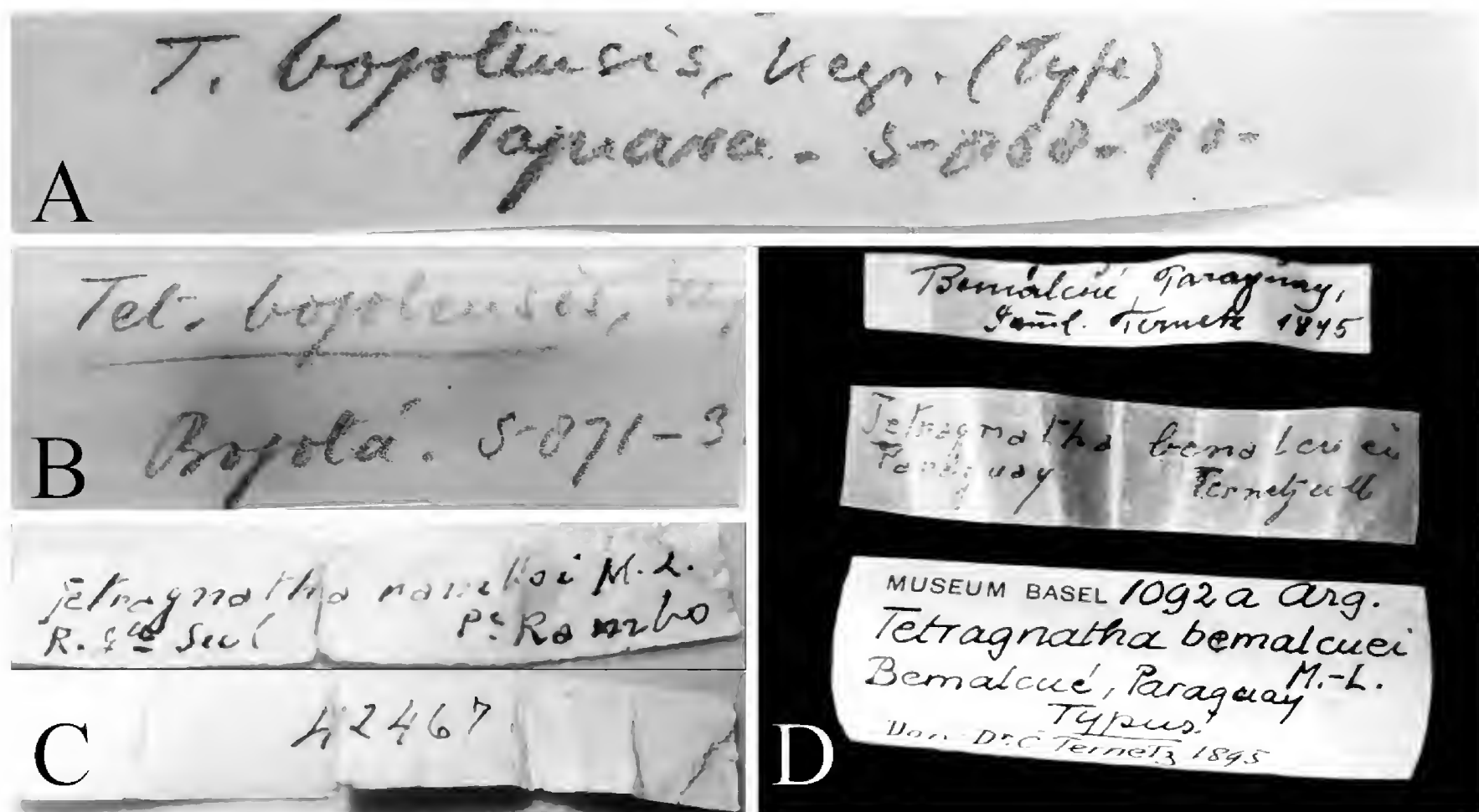


Figure 4. *Tetragnatha bogotensis* Keyserling, 1865 labels. **A.** *T. bogotensis* from Taquara, Brazil (NHM); **B.** *T. bogotensis* from Bogotá, Colombia (NHM); **C.** *T. ramboi* syntype from Rio Grande do Sul, Brazil (MNRJ 42467); **D.** *T. bemalcei* holotype from Paraguay (NMB).

and female syntypes from Amable Maria, Peru, however, Taczanowski’s (1878: fig. 2) poor illustration of the female chelicerae allows its recognition as *T. bogotensis*, as verified in the photos we received from MIZ (Fig. 21A). Thus, *T. andina* is here removed from the synonymy of *T. nitens* and newly synonymised with *T. bogotensis*.

Banks (1898) described *T. peninsulana* from two males and “several females” from San José del Cabo, Baja California Sur, Mexico. Photos of females provided by the MCZ (Fig. 21B) include three specimens of *T. bogotensis* and one of *T. nitens*, which we consider a misidentification. Additionally, according to Levi (1981), the male syntypes were destroyed. Based on the elongated AXI (Fig. 21B), this species must also be removed from the synonymy of *T. nitens* and be newly synonymised with *T. bogotensis*.

Tetragnatha eremita Chamberlin, 1924 was based on a male holotype from Baja California, Mexico. Chamberlin (1924: figs 89, 90) provided a short description and two good illustrations that clearly show the characteristic shape and teeth formula of *T. bogotensis*, besides citing a female paratype collected at the same time. The male holotype is represented by the right pedipalp in the MCZ (MCZ 15283, RVC 1111), and by the whole specimen in CAS 1430. We were able to examine the holotype’s chelicerae through photos (Fig. 21D), and thus confirmed its identity, removing *T. eremita* from the synonymy with *T. nitens* and newly synonymising it with *T. bogotensis*.

Furthermore, Levi (1981: 292) followed Chickering (1957b: 2) in the synonymization of *T. haitiensis* Bryant, 1945, which was based on a female from Haiti, with *T. nitens*. Bryant (1945: fig. 37) illustrated the huge AXI tooth typical of *T. bogotensis*, which we also observed in the photos we received from MCZ (Fig. 21G). Therefore, *T. haitiensis* Bryant, 1945 is also removed from the synonymy of *T. nitens* and newly synonymised with *T. bogotensis*.

Wunderlich (1992: 365) also mistook *T. bogotensis* as *T. nitens*, removing *T. nitens kullmanni* from its proper synonymy with *T. boydi* (Okuma 1983: 70). We agree with Okuma (1983) that this species is “undoubtedly identical with *T. boydi*”, as both males and females of *T. nitens kullmanni* bear the same diagnostic characters of *T. bogotensis* in comparison with *T. nitens*: male chelicerae with Gu longer than U2 (Figs 1E, 3B; Wiehle 1962: fig. 9) and female chelicerae with a long AXI (Figs 2D–F, 3C; Wiehle 1962: fig. 15). Therefore, the synonymy with *T. nitens* is rejected and *T. nitens kullmanni* is a junior synonym of *T. bogotensis*.

Variation. Males ($n = 18$): total length, 7.36–11.60; females ($n = 17$): total length, 7.52–11.76. The gap between Gu and U2 is variable in males of this species and can have almost the double of the length of the specimen illustrated.

Distribution. This species is widespread in the Neotropics and Mexico, but potentially north into the southern United States; it also occurs in the Old World, with records from Africa, Yemen, India, Nepal, and China (Fig. 22A).

***Tetragnatha elongata* Walckenaer, 1841**

Figs 5–7, 20B, 22B

Tetragnatha elongata Walckenaer 1841: 211 (♂ ♀).

Tetragnatha tropica O. Pickard-Cambridge 1889: 11, pl. 2, fig. 3 (♀); F. O. Pickard-Cambridge 1903: 431, pl. 40, figs 10, 11 (♂ ♀) syn. nov.

Type material. *Tetragnatha elongata*: GUADELOUPE: ♂ ♀ syntypes, lost; UNITED STATES OF AMERICA: ♂ neotype, Raleigh, North Carolina (Coll. C. S. Brimley, 21–31.viii.1944, MCZ 21192), not examined. *Tetragna-*

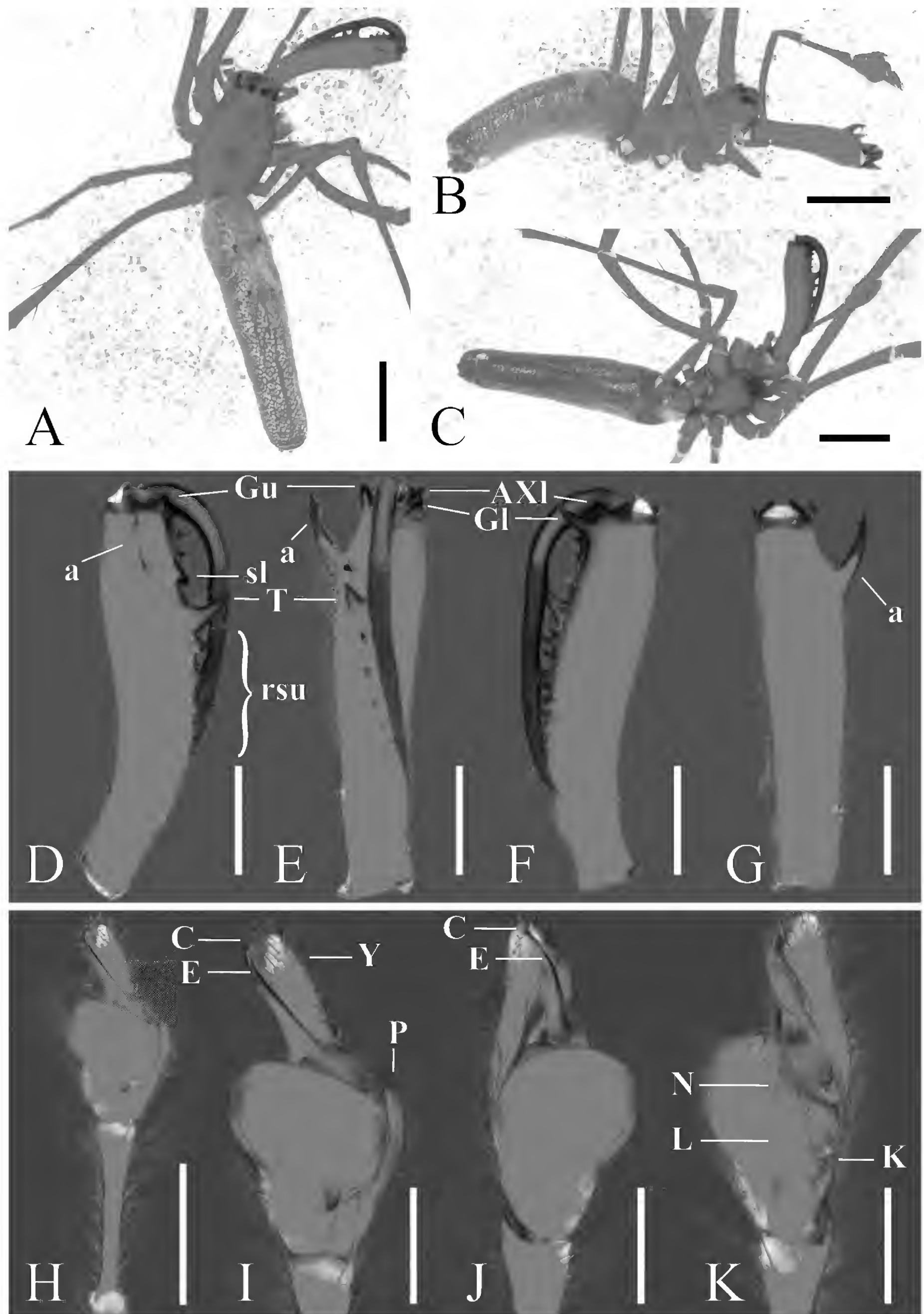


Figure 5. *Tetragnatha elongata* Walckenaer, 1841, male (MCTP 28045). **A.** Dorsal habitus; **B.** Lateral habitus; **C.** Ventral habitus; **D–G.** Left chelicera: **D.** Upper view; **E.** Inner view; **F.** Lower view; **G.** Outer view; **H–K.** Left male palp: **H.** Mesal view with tibia; **I.** Mesal view detail; **J.** Dorsal view; **K.** Ventral view (paracymbium). Scale bars: 2 mm (A, B, C); 1 mm (D, E, F, G, H); 0.5 mm (I, J, K).

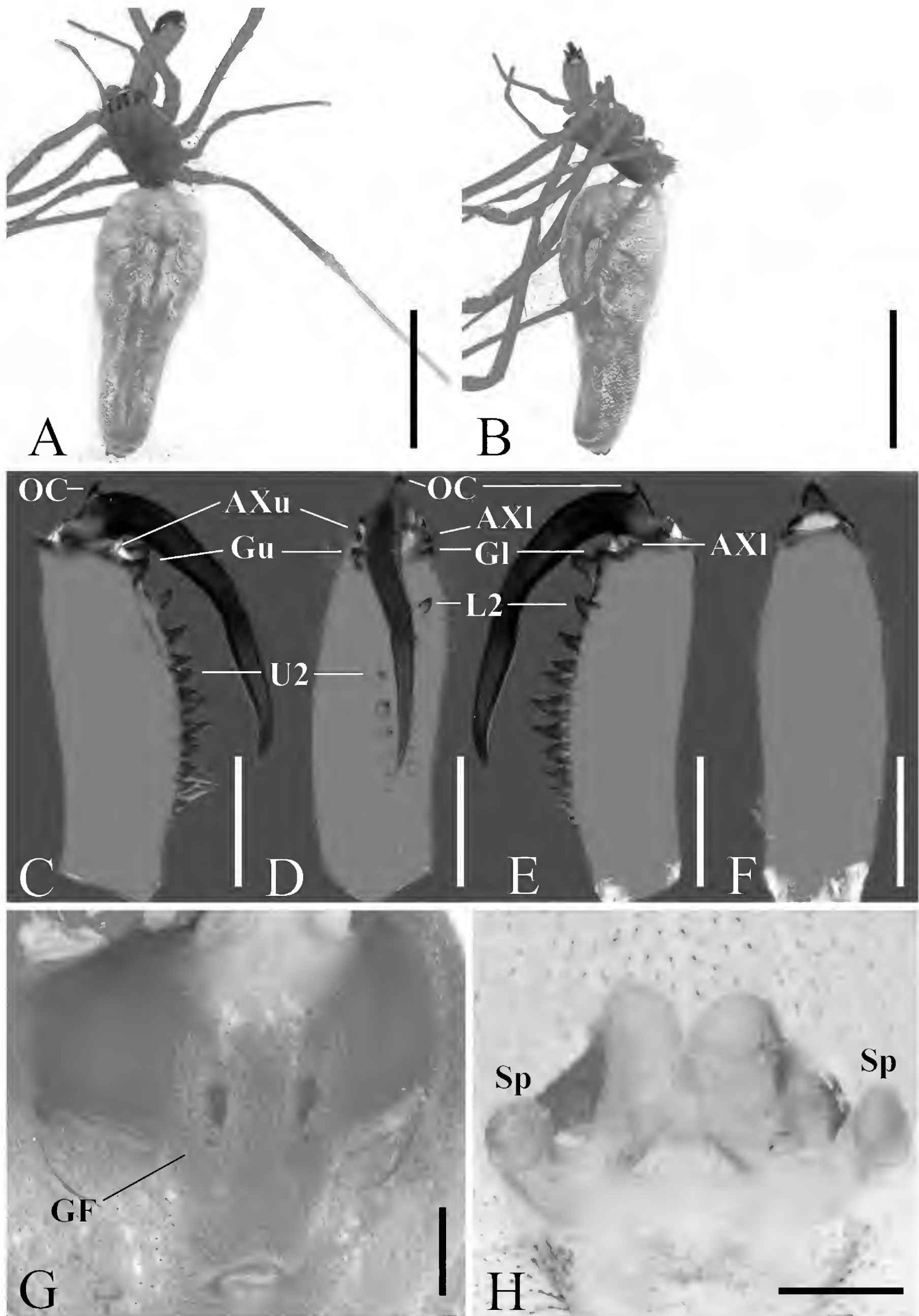


Figure 6. *Tetragnatha elongata* Walckenaer, 1841, female. **A.** Dorsal habitus (MCTP 28045); **B.** Lateral habitus (MCTP 28045); **C–F.** Left chelicera (MCTP 28045): **C.** Upper view; **D.** Inner view; **E.** Lower view; **F.** Outer view; **G, H.** Genital area: **G.** Genital fold, ventral view (MCTP 28045); **H.** Internal genitalia, cleared, ventral view (MCTP 28306). Scale bars: 5 mm (**A, B**); 1 mm (**C, D, E, F**); 0.5 mm (**G**); 0.2 mm (**H**).

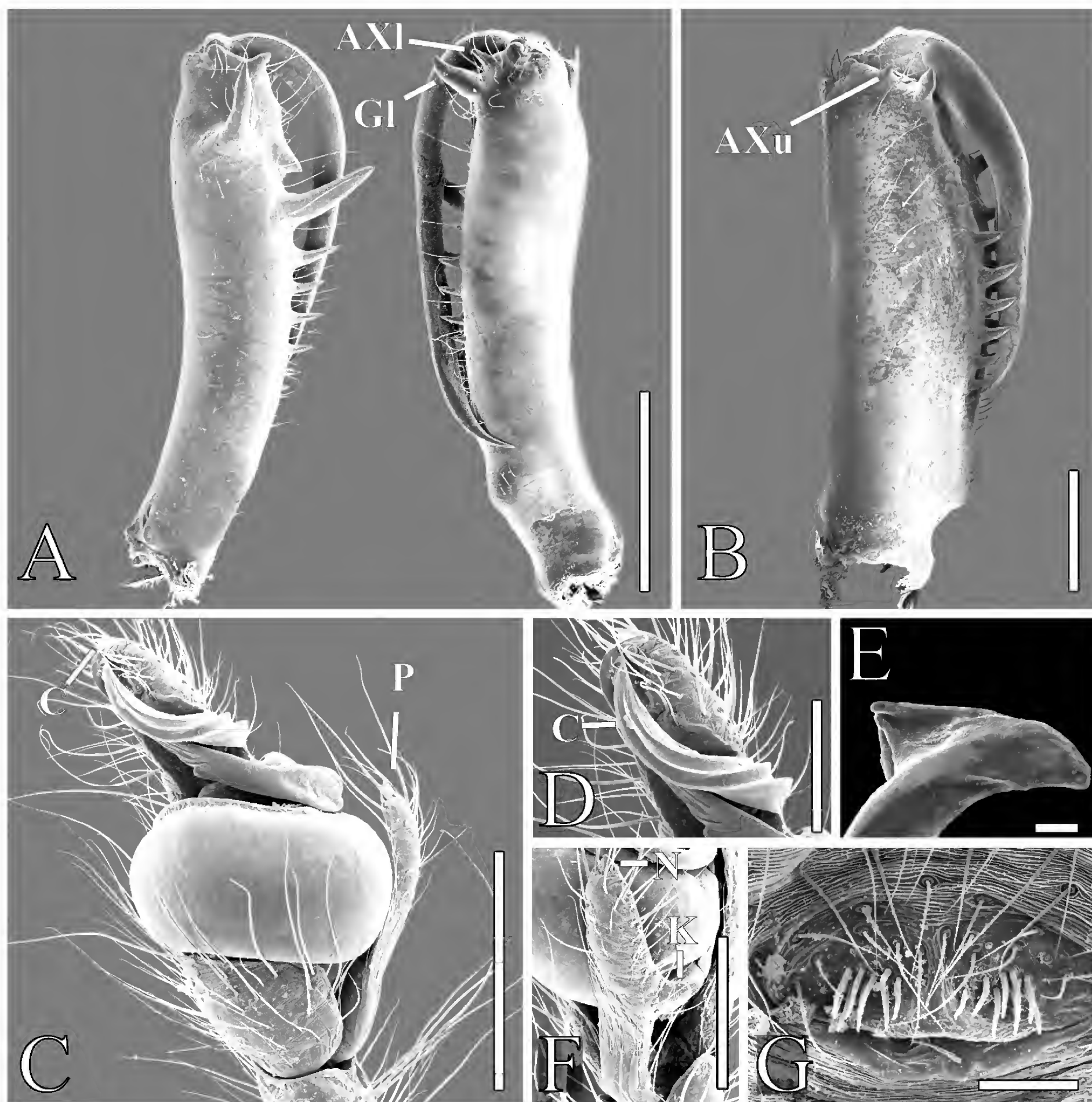


Figure 7. *Tetragnatha elongata* Walckenaer, 1841, SEM photos. **A.** Left male chelicera, upper and lower views (MCTP 0229); **B.** Left female chelicera, upper view (MCTP 43306 ex 0370); **C.** Left male palp, mesal view (MCTP 0229); **D.** Left male palp conductor detail and pleats, mesal view (MCTP 0229); **E.** Tip of conductor detail, dorsal view (MCTP 43306 ex 0370); **F.** Left male palp paracymbium, ventral view (MCTP 0229); **G.** Epiandrous field, ventral view (MCTP 43306 ex 0370). Scale bars: 1 mm (**A**); 0.5 mm (**B**, **C**); 0.2 mm (**D**); 0.01 mm (**E**); 0.3 mm (**F**); 0.05 mm (**G**).

tha tropica: GUATEMALA: ♀ holotype, Menché, Godman and Salvin, not located.

Extended diagnosis. Females of *T. elongata* can be distinguished from all other Neotropical species by their elongated body, abdomen anteriorly enlarged and much narrower posteriorly, large chelicerae with an outer cusp (OC), and a short genital fold (Figs 6A–G, 7B). The unique internal genitalia has large spermathecae with two thick tubular lobes connected mid-way, forming a kidney-shaped structure, with the median lobe more than twice as long as

its width and parallel to each other and to the longitudinal axis of the abdomen (Fig. 6H). The lateral lobe is smaller and thinner than the median lobe and may vary in position, with the fundus directed dorsally (Fig. 6H) or laterally (Levi 1981: fig. 76). Central membranous sac (CS) is small and poorly sclerotized (Fig. 6H; Levi 1981: fig. 76).

Male chelicerae of *T. elongata* are similar to those of *T. laboriosa* Hentz, 1850, insofar as sharing elongated apophyses with excavated tips, elongated and robust ‘T’, and long GI, the last as the longest teeth of both lower rows (Figs 5D–G; Okuma 1992: fig. 11A–C). *Tetragna-*

tha elongata differs from *T. laboriosa* by its longer and narrower chelicerae (4.4× vs 3.5× longer than wide), ‘sl’ shorter, ‘T’ with larger basis, more elongated and distalward projected, a higher number of ‘rsu’ teeth (Figs 5D, 7A; Okuma 1992: 231, fig. 11A), AXI stouter, slender and distalward projected and GI pointed and much more elongated, both arising from a common base and displaced to a lower position than the remaining lower teeth (Figs 5D–F, 7A; Okuma 1992: 231, fig. 11A, B). Males can also be distinguished from congeners by the palps with conductors having triple pleats, enclosing the long filiform emboli, which bear small bird-head tips that are projected in small tails (Figs 5H–J, 7C–E, 20B), and by short and thick paracymbia that are perpendicular to the palps axes and with undivided notches, narrow, thin translucent lobes, and thumb-like projecting knobs (Figs 5K, 7C, F). The epiandrous field has a large depressed lateral area at both sides of the spigots (Fig. 7G).

Synonymy and notes. *Tetragnatha tropica* was described from a single female from Guatemala (Menché, currently Atxchilan, near the Mexican border), not located in NHM or OUMNH collections. Thus, we rely on the original illustrations and subsequent descriptions of both sexes to diagnose this species (O. Pickard-Cambridge 1889: pl. 2, fig. 3; F. O. Pickard-Cambridge 1903: pl. 40, figs 10, 11; Chickering 1957c: figs 97–102). We compared these illustrations with our specimens and the drawings of both sexes and SEM images of the conductor tip of *T. elongata* by Levi (1981), who proposed a neotype for this species (MCZ 21192) and identified many specimens from northern Mexico, and with Okuma (1992), who identified specimens from Mexico, Costa Rica, and Panama. Based on our investigations, *T. tropica* can be diagnosed as a junior synonym of *T. elongata* because the morphology of male palps and the chelicerae of both sexes perfectly match.

We also highlight that Mello-Leitão (1943, 1945, 1947, 1949) repeatedly recorded *T. elongata* from Brazil and Argentina, but all his specimens we analysed belong to other common species, especially *T. bogotensis* and *T. nitens*. However, after analyzing many other specimens, we were able to confidently record this species for these two countries.

Variation. Males ($n = 8$): total length, 7.20–13.45; females ($n = 15$): total length, 8.88–13.90.

Distribution. *Tetragnatha elongata* is a very common species in the Nearctic and Neotropical regions, recorded from Canada (Dondale et al. 2003) to Misiones, north-eastern Argentina (Fig. 22B).

Tetragnatha keyserlingi Simon, 1890

Figs 8–10, 20C, 21H, I, L, M, O, 22C

Tetragnatha mandibulata: Keyserling 1865: 848, pl. 21, figs 6–9 (♂ ♀ misidentified).

Tetragnatha mandibulata?: L. Koch 1872: 194, pl. 17, figs 2a, b, 3a, b (♂ ♀ misidentified).

Tetragnatha keyserlingi Simon 1890: 134 (♂ ♀).

Tetragnatha mandibulata: Thorell 1890: 221 (♀ misidentified)

Tetragnatha maxillosa Thorell 1895: 139 (♂ ♀) syn. nov.

Tetragnatha kochi Thorell 1895: 140 (♂ ♀) syn. nov.

Tetragnatha japonica Bösenberg and Strand 1906: 177, pl. 15, fig. 409a–d (♂ ♀).

Tetragnatha conformans Chamberlin 1924: 9, pl. 2, figs 13–15 (♂ ♀).

Tetragnatha propioides Schenkel 1936: 89, fig. 31 (♂ ♀).

Tetragnatha ethodon Chamberlin and Ivie 1936: 64, pl. 17, figs 144–146 (♂ ♀) syn. nov.

Type material. *Tetragnatha keyserlingi*: COLOMBIA [Neu Granada]: ♂ ♀ syntypes, not located. *Tetragnatha maxillosa*: INDONESIA: ♀ syntype, Java, not located; SINGAPORE: ♂ ♀ syntypes (Coll. Workman), not located. *Tetragnatha kochi*: ♂ ♀ syntypes, FIJI (Ovalau), not located; TONGA, not located; SAMOA (Upolu) [2♀ sub *T. mandibulata*, Mus. Godeffroy collection, 1869 (NHRS-GULI000069809)], examined (photos). *Tetragnatha japonica*: JAPAN: 10♂, 5♀ syntypes, Saga (Yunohama Mountain) (Coll. W. Dönitz, 25.v.1881, SMF 4212–121), not examined; 3♀ syntypes, 2♂ (misidentified), Osaka (ZMH), examined (photos). *Tetragnatha conformans*: CHINA: ♀ holotype, ♂ paratype, Suzhou [Soochow] on the labels, Kuliang on the publication (Coll. N. Gist Gee, USNM 865), examined (photos). *Tetragnatha propioides*: CHINA: ♂ ♀ syntypes, Sichuan, not located. *Tetragnatha ethodon*: PANAMA: ♂ holotype, Barro Colorado Island (AMNH), not examined.

Extended diagnosis. Males of *T. keyserlingi* are similar to *T. elongata*. Both species have a long body, a very long paturon, AXI and GI placed on a common base and displaced to a lower position than the remaining lower teeth, and conductor tips not extended in tail-like projections (Figs 5A–J, 7A, C–E, 8A–I, 10A, C, D, 20B, C; Levi 1981: pls 5g, i, 6h, i; Okuma 1992 sub *T. maxillosa*: fig. 11A–D, F). *Tetragnatha keyserlingi* may be distinguished from *T. elongata* by having pairs of black dots on the postero-dorsal region of the abdomen, ‘a’ placed closer to the external border of the paturon and directed upwards and outwards, ‘t’ present, ‘sl’ absent, a crest filling the gap from Gu to ‘T’, a large gap between ‘T’ and ‘rsu’, lower teeth onwards from L3 placed in a shallow concave row (Figs 5A–E, 7A, 8A–E, 10A). Palps of both species are also similar, but those of *T. keyserlingi* have shorter and wider tibiae (2.3× vs 4.7×), conductors with one pleat that only partially enfold the ribbon-like and twisted emboli, and paracymbia that are elongated, boomerang-shaped with slanted, basally projecting knobs and clearly visible translucent lobes (Figs 8H–J, 10C–E, 20C). The epiandrous field has a spinning area which is not as high and without the depressed lateral areas found in *T. elongata* (Figs 7G, 10F).

Female chelicerae have elongated Gu, U2, and U3, where Gu is set apart from U2 by a very large gap and is lo-

cated on an upper crest (CRu) (Figs 9D, E, 10B). U2 and remaining upper side teeth form a row displaced to lower side of paturon, following the slanted fangs closing (Figs 9D, E, 10B). AXI very small and located near G1 base and lower row with first three teeth on a lower crest (CRI); G1 straight, elongated, bulky, pointed, its base large, and projected slightly upwards (Fig. 9E, F). Cheliceral fang enlarged in middle portion and apical third slanted and tapering to the acute tip, also harboring a narrow ridge (Figs 9D, E, 10B). Internal genitalia unique, with two rounded spermathecae linked by two thick tubes to a median, slender and very elongated stalk, which places CS at a far anterior position (Fig. 9I; Zhu and Zhang 2011, sub *T. maxillosa*: fig. 123G).

Synonymy and notes. This species is widespread in the Old World tropics and has been cited and illustrated many times under *T. maxillosa* (World Spider Catalog 2019), especially by Okuma (1983, 1987) and Zhu and Zhang (2011).

Tetragnatha keyserlingi was named by Simon (1890: 134) for the specimens described and illustrated as *T. mandibulata* by Keyserling (1865: 848, pl. 21, figs 6–9) from “Neu Granada” (currently Colombia) and *T. mandibulata?* by L. Koch (1872: 194, pl. 17, figs 2, 3) from Fiji (Ovalau), Samoa (Upolu), and Tonga in the Pacific. The illustrations by Keyserling (1865) and L. Koch (1872) already clearly show, for example, the large ‘T’ and small ‘t’ in male chelicerae and the characteristic Gu and G1 of the female chelicerae of *T. keyserlingi* (Figs 8D, E, G, 9D–F, 10A, B).

Tetragnatha keyserlingi was also recorded from Java (Indonesia) (Thorell 1890: 221) and in his paper on Burmese spiders, Thorell (1895: 139) newly named this species as *T. maxillosa*, based on the female from Java he described in 1890 and on males and females from Singapore collected by Cel. Workman; he pointed out that he considered *T. maxillosa* to be distinct from *T. keyserlingi*. One page later, he (Thorell 1895: 140) named the specimens reported by L. Koch (1872) from the Pacific islands as another new species: *T. kochi*, heavily relying on geographical distributions to separate the specimens from South America, Southeast Asia, and the Pacific Islands. The only morphological differences mentioned in his paper (Thorell 1895: 139–140) are minor details in eye position and cheliceral teeth arrangement in females; no male characters were mentioned. In particular for *T. maxillosa* and *T. keyserlingi*, he compared the position of the second tooth on upper row of female chelicerae (U2 in our terminology) in relation to teeth of the lower row. According to Thorell, U2 of *T. maxillosa* would face the 6th or 7th tooth of the lower row, while in *T. keyserlingi* it would face the 4th or 5th tooth. However, the apparent position of teeth of one row in relation to the teeth of the opposite row is not easy to evaluate, as small changes on chelicerae inclination may change the apparent alignment. In addition, small changes in the relative position of teeth of the upper and lower rows are very common in this and other species.

We agree with Simon (1890) that the detailed illustrations given by Keyserling (1865) from “Neu Granada”,

and L. Koch (1872), from Pacific Islands (Fig. 21H), allow the clear recognition of just one species, despite the great distances between localities. Moreover, the specimens from Southeast Asia that Thorell (1895) named *T. maxillosa* also belong to the same widespread species. As Simon (1890) and Thorell (1895) had never seen the specimens they named as new species, no type specimens have ever been designated. No type or non-type material from the type localities of *T. keyserlingi* or *T. maxillosa* could be located in NHM, NMV, and ZMH. However, we received photos of two females from Upolu, collected in 1869 and deposited at NHRS, both identified as *T. mandibulata* (labeled Museum Godeffroy, NHRS-GU-LI000069809). These specimens are surely part of the material which L. Koch (1872) designated and illustrated as “*T. mandibulata?*” (Fig. 21H) and Thorell (1895) afterwards named *T. kochi*. Thus, these specimens represent part of the type series of *T. kochi*. As *T. keyserlingi* Simon, 1890 was proposed five years before both Thorell’s names (1895), it is senior synonym of *T. maxillosa* and *T. kochi*.

Bösenberg and Strand (1906: 177, pl. 15, fig. 409a–d) provided comprehensive illustrations of male and female chelicerae and genitalia of *T. japonica*. Based on photos of the chelicerae of syntypes of both sexes from Osaka (Japan) deposited at ZMH (Fig. 21I–K), we confirm that the female is *T. keyserlingi* (Fig. 21I) and that the male actually belongs to *T. nigrita* Lendl, 1866 (Fig. 21J, K). Nonetheless, the illustrations of the male by Bösenberg and Strand (1906: fig. 409c, d) are like *T. keyserlingi*, with a laterally directed apophysis, large Gu, absent or not noticeable ‘t’, and apical portion of embolus and conductor curved in a gentle slope. Thus, we consider that at least the originally illustrated male syntype belongs to *T. keyserlingi* and that it may be deposited in SMF instead. The female specimen of *T. japonica* should be considered as name bearing, as it was described, measured, and illustrated first by Bösenberg and Strand (1906: fig. 409a, b). We agree here with Okuma’s synonymy (1983) of *T. japonica* with *T. maxillosa* (= *T. keyserlingi*) and consider the male syntype from Hamburg and any other possible similar male syntype as misidentified specimens of *T. nigrita*. Unfortunately, we were not able to examine the syntypes from Saga deposited in SMF.

Chamberlin (1924: 12, pl. 3, figs 21–23) described *T. conformans* (Fig. 21L, M) and *T. cliens* Chamberlin, 1924 (Fig. 21N–Q), each based on a couple from Suzhou [Soochow on the labels (Fig. 21P, Q), but Kuliang (Fuzhou) in the original paper], China. Later, Schenkel (1936: 89–91, fig. 31) described *T. propioides* based on a couple from Sichuan, also in China. All were separately synonymised with *T. keyserlingi* (under *T. maxillosa* or its junior synonyms): Zhu (1983) for *T. conformans* (sub *T. japonica*) and Okuma (1983: 72, 73) for *T. japonica*, *T. cliens*, and *T. propioides*.

Another mismatching of *T. keyserlingi* and *T. nigrita* occurred with the type series of *T. cliens*, as observed by Song (1988: 127), who removed *T. cliens* from the synonymy with *T. maxillosa*. The male holotype of *T. cliens*

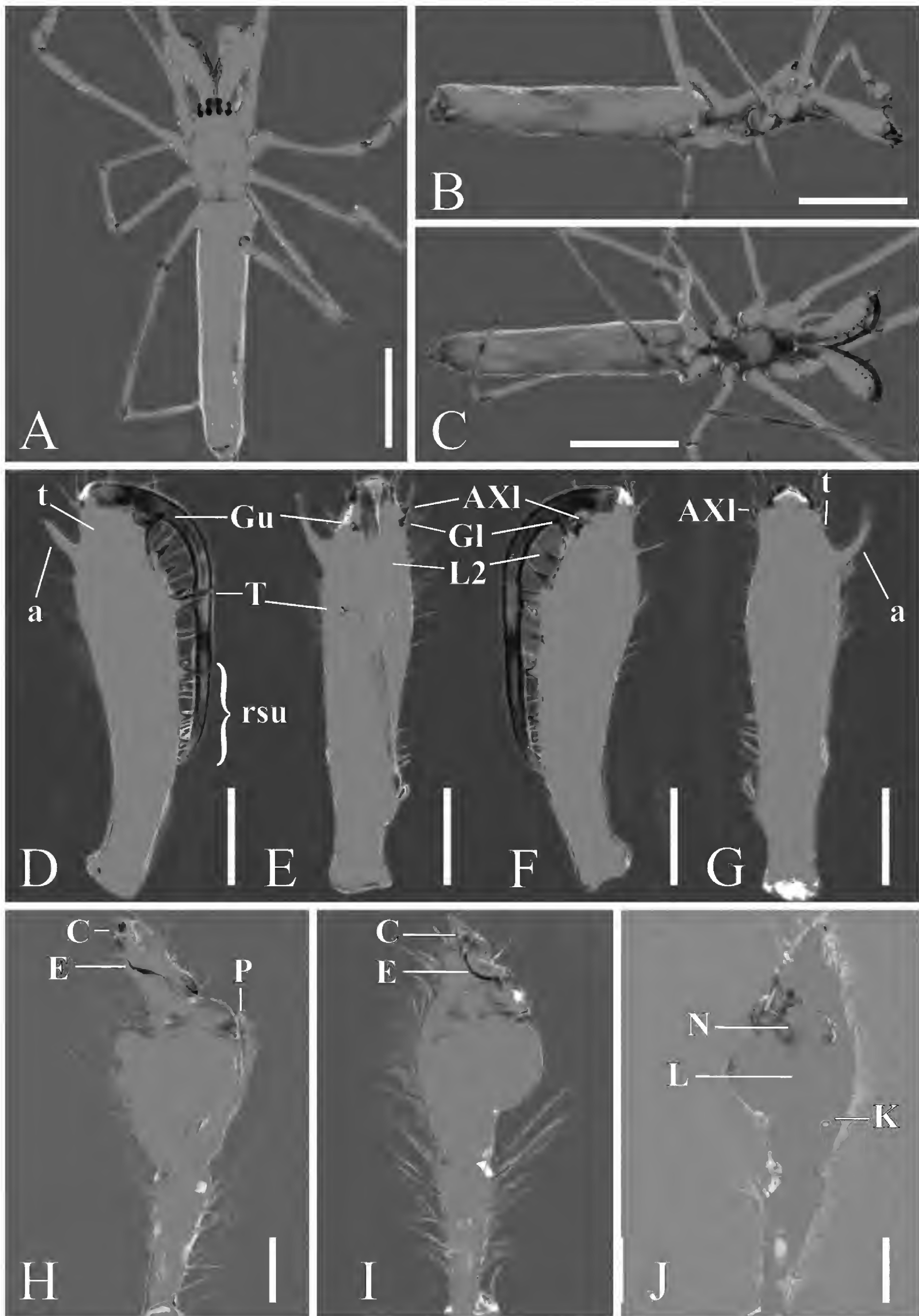


Figure 8. *Tetragnatha keyserlingi* Simon, 1890, male (UFRJ 1553). **A.** Dorsal habitus; **B.** Lateral habitus; **C.** Ventral habitus; **D–G.** Left chelicera: **D.** Upper view; **E.** Inner view; **F.** Lower view; **G.** Outer view; **H–J.** Left male palp: **H.** Mesal view; **I.** Dorsal view; **J.** Ventral view (paracymbium). Scale bars: 2 mm (A, B, C); 0.5 mm (D, E, F, G); 0.2 mm (H, I, J).

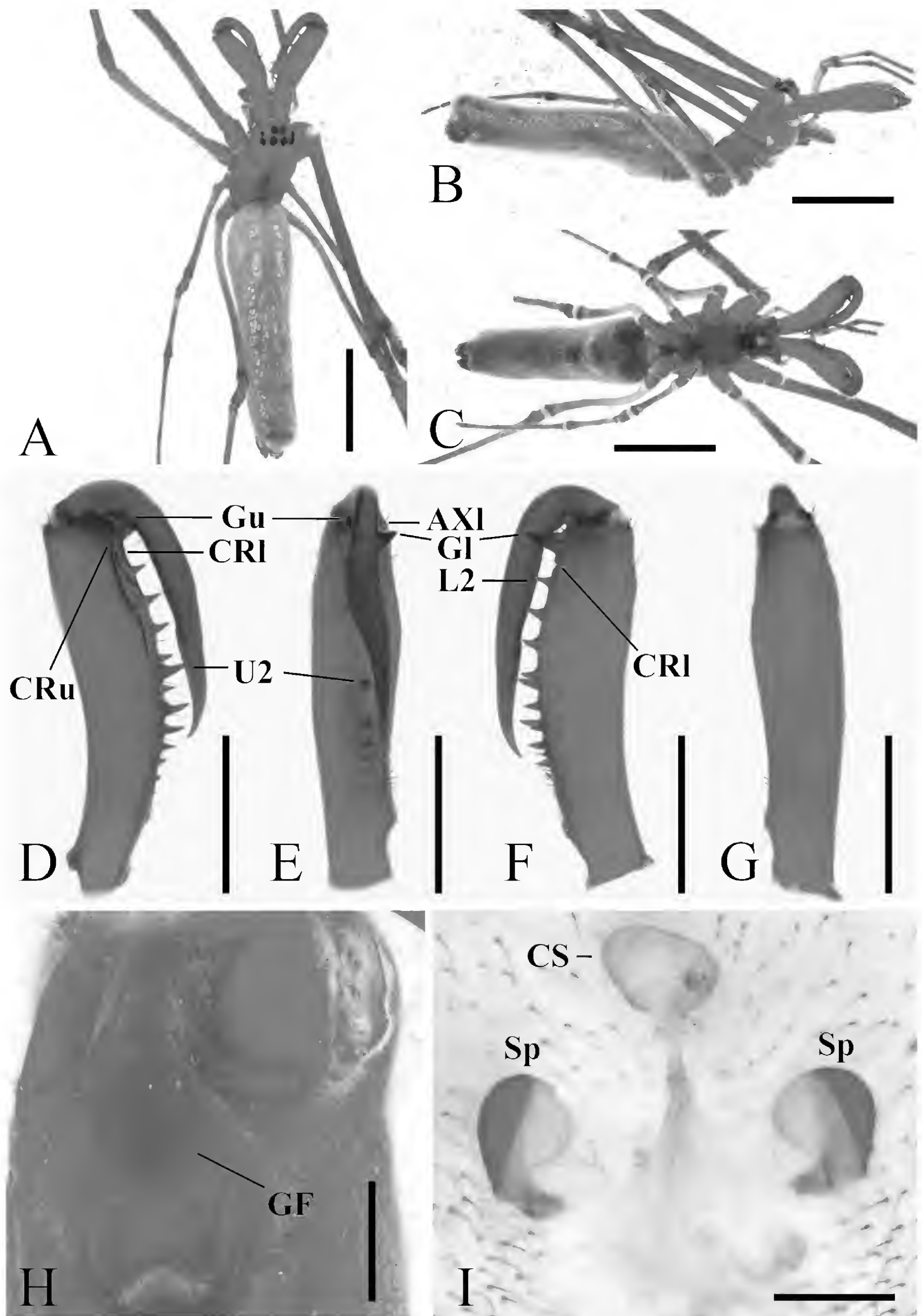


Figure 9. *Tetragnatha keyserlingi* Simon, 1890, female. **A.** Dorsal habitus (UFRJ 1351); **B.** Lateral habitus (UFRJ 1351); **C.** Ventral habitus (UFRJ 1351); **D–G.** Left chelicera (MCTP 14749): **D.** Upper view; **E.** Inner view; **F.** Lower view; **G.** Outer view; **H, I.** Genital area: **H.** Genital fold, ventral view (MCTP 14749); **I.** Internal genitalia, cleared, ventral view (UFRJ 1504). Scale bars: 2 mm (A, B, C); 1 mm (D, E, F, G); 0.5 mm (H); 0.1 mm (I).

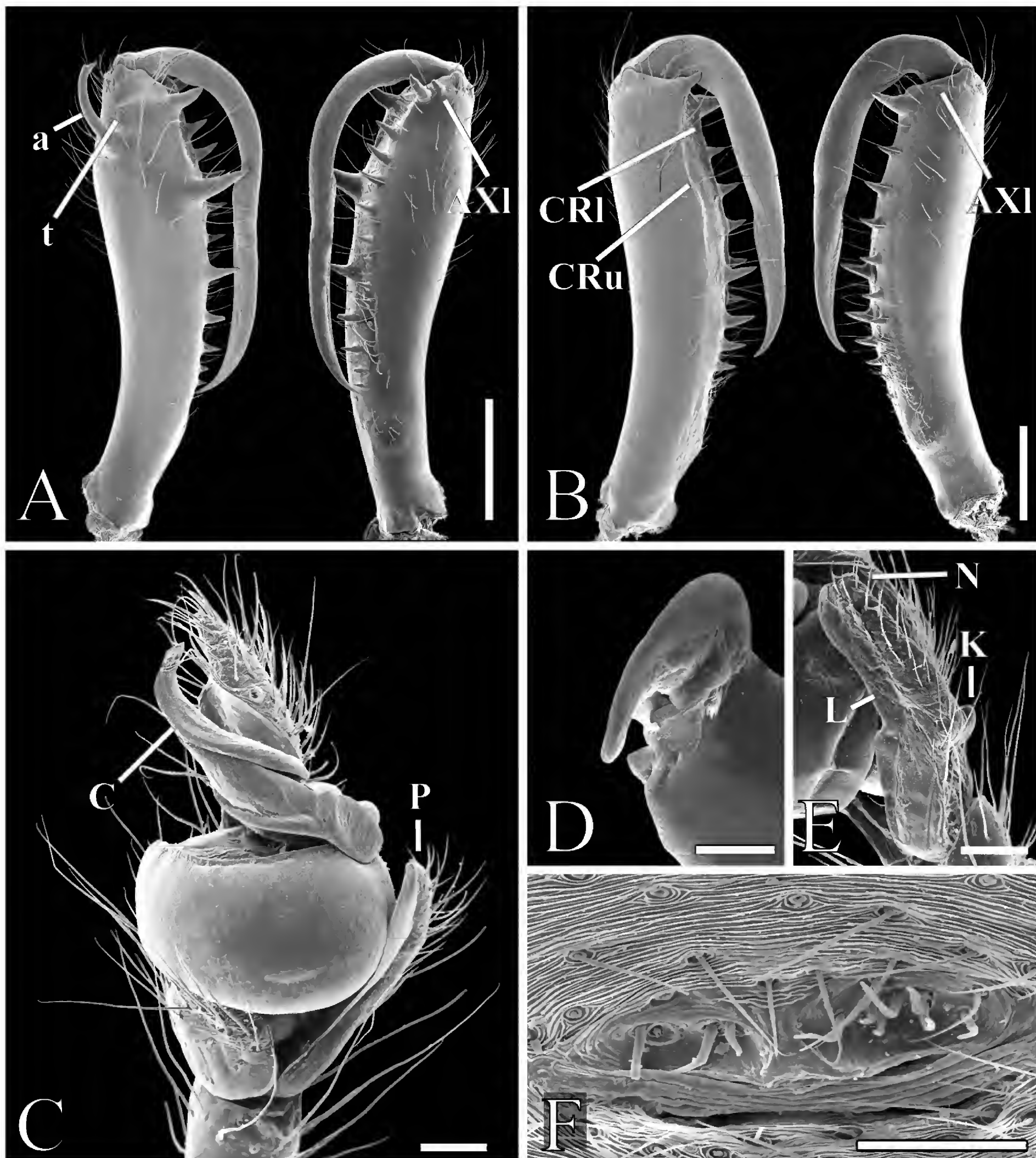


Figure 10. *Tetragnatha keyserlingi* Simon, 1890, SEM photos. **A.** Left male chelicera, upper and lower views (MCTP 43319 ex 6944); **B.** Left female chelicera, upper and lower view (MCTP 14749); **C.** Left male palp, mesal view (MCTP 43319 ex 6944); **D.** Left palp conductor tip, mesal view (UFRJ 1552); **E.** Left male palp paracymbium, ventral view (UFRJ 1552); **F.** Epiandrous field, ventral view (MCTP 43319 ex 6944). Scale bars: 0.5 mm (**A, B**); 0.1 mm (**C, E**); 0.02 mm (**D**); 0.05 mm (**F**).

is clearly *T. nigrita* and was wrongly coupled with the female, which belongs to *T. keyserlingi* (Fig. 21N, O). Song (1988) noted that the male was labeled as “type” and the female as “paratype” in the original vials in USNM (Fig. 21P, Q). Like Song (1988), we were also able to analyse the type material and agree with the synonymy. Nonetheless, this mismatching was not noticed by Oku-

ma (1983), who probably did not analyse the type material and, years before Song, wrongly synonymised *T. cliens* with *T. maxillosa*, surely based on the order of description and illustrations of the original paper. Summing up, we agree with the synonymies for *T. conformans* (Fig. 21L, M), *T. japonica* (Fig. 21I) and *T. cliens* (Fig. 21N, P), according to original descriptions and illustrations and

type photos we received. Additionally, we also confirm the synonymy of *T. propioides* (see Schenkel 1936: fig. 31), but its syntypes were not located.

Finally, *T. ethodon* was described by Chamberlin and Ivie (1936: pl. 17, figs 144–146) based on specimens from both sexes collected in Panama. This species was redescribed by Chickering (1957c: 316, figs 27–31) who transferred Chamberlin and Ivie's females to *T. tenuissima* O. Pickard-Cambridge, 1889 and pointed out that the rather damaged male holotype was the only known specimen of the species from Panama. Okuma (1992: 228, fig. 7) also redescribed and illustrated *T. ethodon*, expanding its distribution to Puerto Rico and Barbados and adding a new description for females. She pointed out that this species was very similar to *T. maxillosa* (= *T. keyserlingi*) and separated both species by its wider genital fold. Comparing our specimens with previous illustrations under *T. maxillosa*, we consider the differences pointed out by Okuma (1992) to fall within the observed intraspecific variations, and hereby synonymise *T. ethodon* with *T. keyserlingi*.

Variation. Males ($n = 11$): total length, 5.29–7.28; females ($n = 14$): total length, 6.59–9.03. In Okuma (1968 sub *T. japonica*, 1983, 1992 under *T. ethodon*) and Bösenberg and Strand (1906 under *T. japonica*: fig. 409a), there is no visible upper crest (CRu) or lower crest (CRL). In fact, female syntypes of *T. kochi* (Fig. 21K), the paratype of *T. cliens* and holotype of *T. conformans* (Fig. 21M, O) do not have crests on the paturon. In contrast, other publications (e.g. Okuma 1987, 1988b, Zhu and Zhang 2011), the female syntype of *T. japonica* from Osaka (Fig. 21I), and all female specimens we examined from South America clearly possess CRu and CRL. So far, we cannot disregard the possibility that the absence of crests in some of the illustrated specimens is real or simply an artefact of poor illustration.

Distribution. Pantropical, including Africa, Asia, Polynesia, Central America, and Brazil (Fig. 22C).

Tetragnatha mandibulata Walckenaer, 1841

Figs 11–13, 20D, 21R–X, 22D

Tetragnatha mandibulata Walckenaer 1841: 211 (♂ ♀).

Tetragnatha confraterna Banks 1909: 207, pl. 6, fig. 34 (♂ ♀) syn. nov.

Tetragnatha necatoria Tullgren 1910: 149, pl. 3, fig. 72 (♂) syn. nov.

Tetragnatha petrunkevitchi Caporiacco 1947: 24 (♂ ♀) syn. nov.

Tetragnatha petrunkevitchi: Caporiacco 1948: 646 (♂)

Tetragnatha infuscata Benoit 1978: 667, fig. 2D, E (♂); Saaristo 2003:

23, figs 21A, B, 25 (removed from syn. with *T. boydi*) syn. nov.

Type material. *Tetragnatha mandibulata*: GUAM: ♂♀ syntypes, Mariana Archipelago, not located. *Tetragnatha confraterna*: COSTA RICA: ♂♀ syntypes, Machuca (Coll. P. Biolley); Escazii (Coll. J. F. Tristan); 3♂ 1♀ 1 immature, Tiribi (Coll. J. F. Tristan, MCZ 79139) and 2♂, Esparte (Coll.

P. Biolley, MCZ 20875), examined (photos). *Tetragnatha necatoria*: TANZANIA: ♂ holotype, Pare (Coll. Kimela, NHRS-GULI0000069808), examined (photos). *Tetragnatha petrunkevitchi*: GUYANA: 2♂, 5♀, 6j syntypes, Konawaruk (“Conwarook”), Potaro-Siparuni (18.iii.1937, MZUF 527), examined; 1♂ syntype, Hyde Park, Georgetown, Demerara-Mahaica (18.iv.1936, MZUF 528), examined; 1♂, 2♀, 1j syntypes (1♂, 1♀, 3j in the museum's catalog), Garraway Landing, Potaro-Siparuni (30.vi.1936, MZUF 529), examined. *Tetragnatha infuscata*: SEYCHELLES: ♂, holotype, Mahé (Coll. P. L. G. Benoit & J. J. Van Mol, 24.vi.1972, MRAC 143319), examined (photos).

Diagnosis. For females, see the extended diagnosis of *T. bogotensis*. Males can be distinguished by the elongated body (Fig. 11A–C), chelicerae with pointed undivided apophyses (Figs 11D–G, 13A), Gu extremely distinctive, thick, bulky and distally projected, followed by a tiny U2, contiguous to Gu (Figs 11D, E, 13A), two very small and almost connected AXI and GI (Figs 11E, F, 13B) and palps with shorter tibiae (ca 3× longer than large); conductor tips projected, large, flattened and winglet-shaped (Figs 11H–J, 13E, F, 20D) and paracymbia with divided notches and large membranous translucent lobes that constitute the mesal halves of the notches, as in *T. bogotensis* and *T. nitens* (Figs 1K, 3D, 11K, 13E, G, 14I, J, 16D–F). Differing from *T. bogotensis*, the translucent lobes of the other two species fill more than half of the total width of the paracymbia (Figs 1K, 3D, 11K, 13G, 14I, J, 16F). Finally, *T. mandibulata* can be distinguished from *T. nitens* by the narrower lobes (Figs 11K, 13G, 14I, J, 16F).

Synonymy and notes. We identified many specimens of *T. mandibulata* from northern to southeastern Brazil. Unfortunately we were not able to study the type material of this species from Guam. It was not available at the MNHN and NHM and is likely lost. However, this well-known and widely distributed species has been repeatedly redescribed and illustrated in many papers (e.g. Simon 1900; Gravely 1921; Okuma 1983, 1987).

After comparing our specimens with illustrations from redescrptions, we noticed close similarities between *T. mandibulata* and *T. confraterna* (Fig. 21R–V; Chickering 1957c: 312, figs 19–26; Okuma 1992: 223, fig. 4), similar to Okuma (1983), who pointed out that both species might be synonyms. Banks (1909) described *T. confraterna* from Costa Rica and published a simple illustration of the male chelicerae. Later on, Chickering (1957c) and Okuma (1992) provided better illustrations of chelicerae and genitalia of specimens from Panama and Costa Rica, respectively. Okuma (1992) also redescribed *T. confraterna* based on many specimens from various localities in Costa Rica and reaffirmed its relationship with *T. mandibulata*, acknowledging that *T. confraterna* “may be barely distinguished from the latter by the female cheliceral fang” (Okuma 1992: 225). We received photos of five males and one

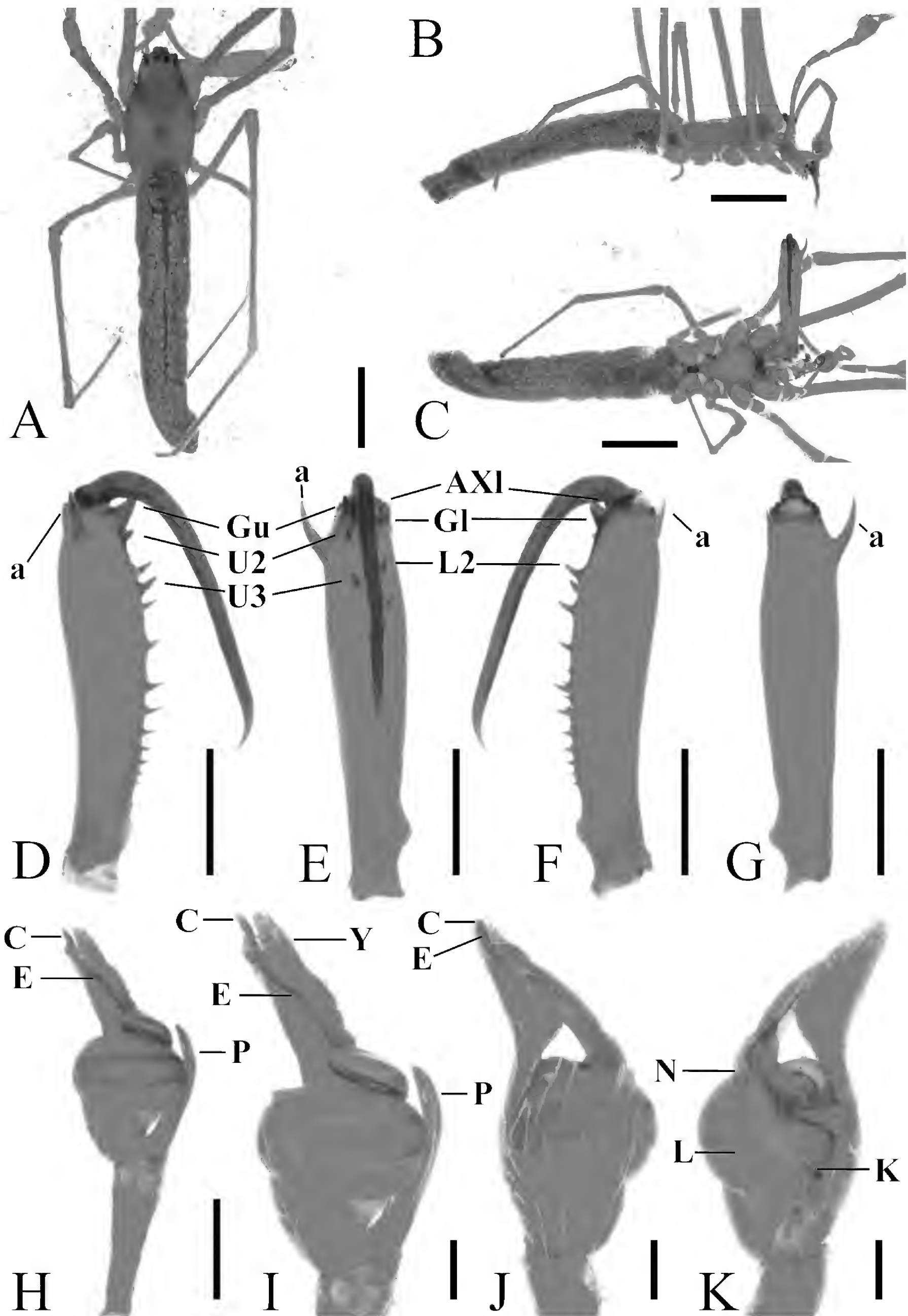


Figure 11. *Tetragnatha mandibulata* Walckenaer, 1841, male (UFRJ 1356). **A.** Dorsal habitus; **B.** Lateral habitus; **C.** Ventral habitus; **D–G.** Left chelicera: **D.** Upper view; **E.** Inner view; **F.** Lower view; **G.** Outer view; **H–K.** Left male palp: **H.** Mesal view with tibia; **I.** Mesal view detail; **J.** Dorsal view; **K.** Ventral view (paracymbium). Scale bars: 2 mm (**A, B, C**); 1 mm (**D, E, F, G**); 0.5 mm (**H**); 0.2 mm (**I, J, K**).

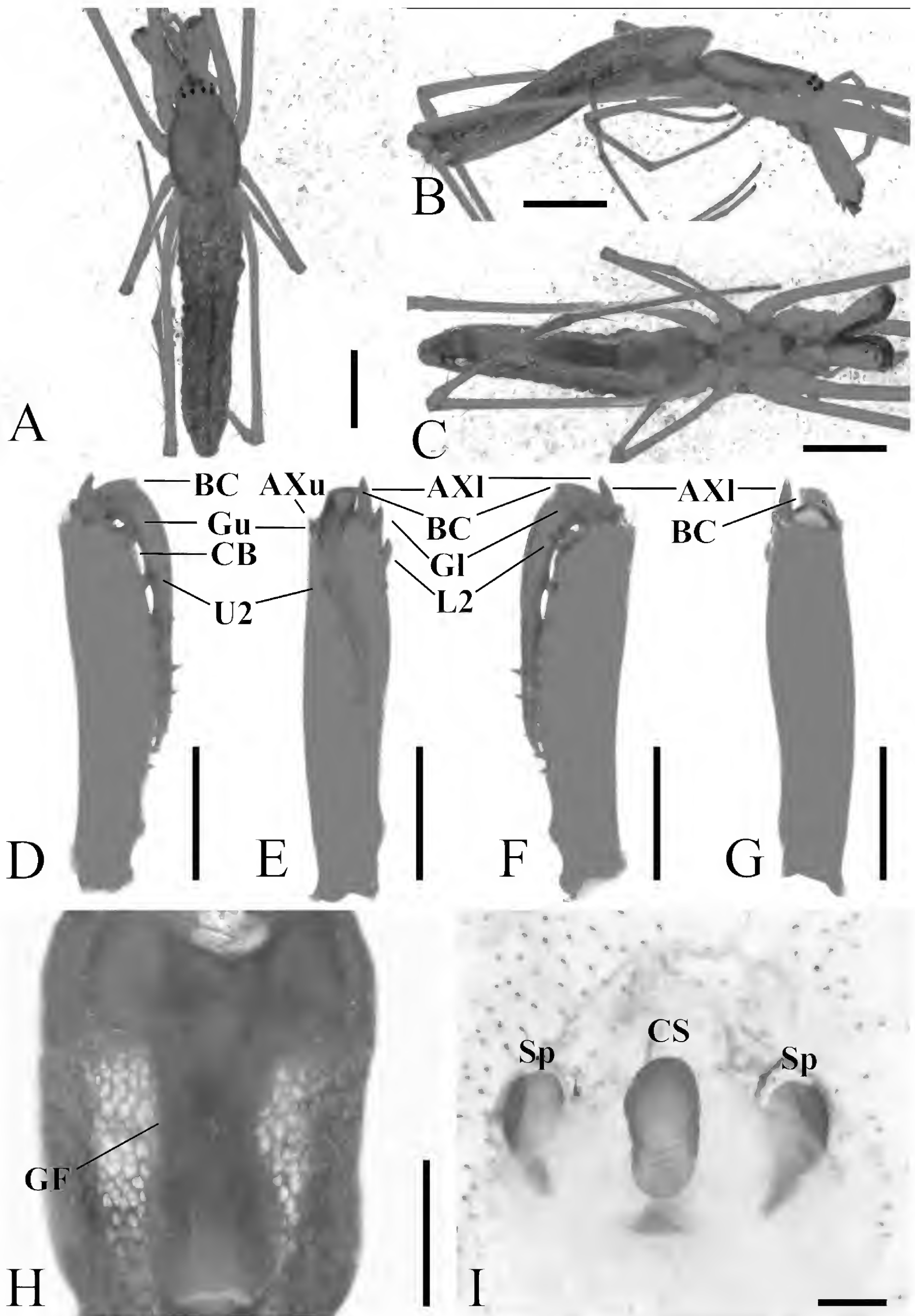


Figure 12. *Tetragnatha mandibulata* Walckenaer, 1841, female. **A.** Dorsal habitus (UFRJ 1552); **B.** Lateral habitus (UFRJ 1552); **C.** Ventral habitus (UFRJ 1552); **D–G.** Left chelicera (UFRJ 1552): **D.** Upper view; **E.** Inner view. **F.** Lower view; **G.** Outer view; **H, I.** Genital area: **H.** Genital fold, ventral view (UFRJ 1552); **I.** Internal genitalia, cleared, ventral view (UFRJ 1124). Scale bars: 2 mm (A, B, C); 1 mm (D, E, F, G, H); 0.1 mm (I).

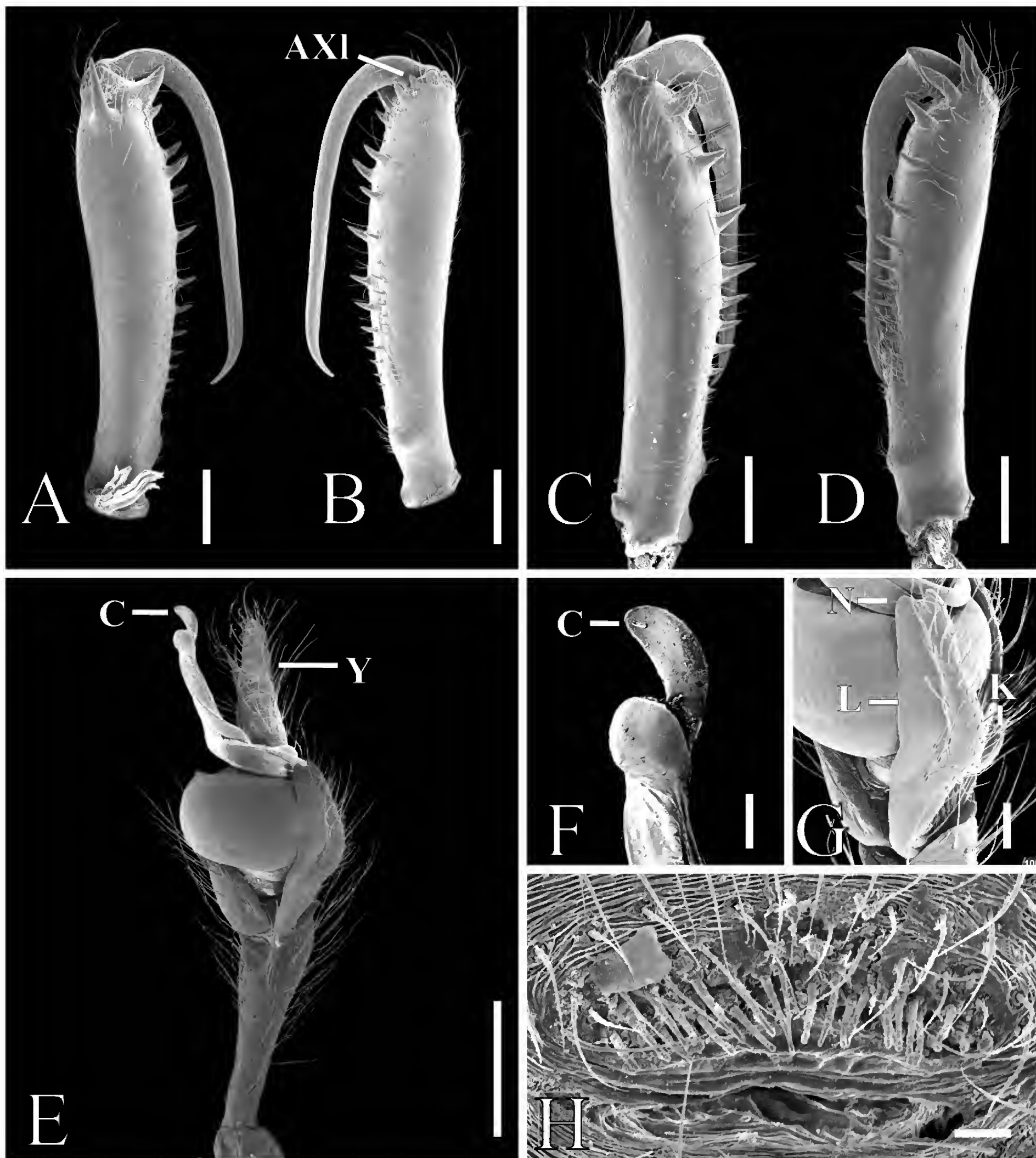


Figure 13. *Tetragnatha mandibulata* Walckenaer, 1841, SEM photos. **A.** Left male chelicera, upper view (UFRJ 1356); **B.** Left male chelicera, lower view (UFRJ 1356); **C.** Left female chelicera, upper view (UFRJ 1552); **D.** Left female chelicera, lower view (UFRJ 1552); **E.** Left male palp, mesal view (UFRJ 1356); **F.** Left male palp conductor detail, mesal view (UFRJ 1356); **G.** Left male palp paracymbium, ventral view (UFRJ 1356); **H.** Epiandrous field, ventral view (UFRJ 1356). Scale bars: 0.5 mm (**A, B, C, D, E**); 0.05 mm (**F**); 0.1 mm (**G**); 0.02 mm (**H**).

female syntypes from two different vials, all bearing the diagnostic characters of *T. mandibulata* (Fig. 21R–V). Based on the characteristic morphology of males and females of *T. mandibulata*, we consider the small differences pointed out in Okuma (1992) as representing intraspecific variation, and we propose that *T. confraterna* is a junior synonym of *T. mandibulata*.

Tetragnatha necatoria Tullgren, 1910 was based on a male specimen from the Pare Mountains in Tanzania. After studying one photo of the upper row of teeth of this male holotype and the original illustration of the distal part of the left chelicera of this species (Fig. 21W; Tullgren 1910: fig. 72), we noticed the large Gu had the U2 adjoined, which is typical of *T.*

mandibulata. So, *T. necatoria* is a junior synonym of *T. mandibulata*.

We received photos of one of the many specimens of *T. petrunkevitchi* Caporiacco, 1947 from Potaro and Georgetown, Guyana. This female (MZUF 529) clearly belongs to *T. nitens*, but there are also four specimens of *T. mandibulata* in the same vial. Additionally, all specimens in vials MZUF 527 and MZUF 528 are *T. mandibulata*, but the male and only adult specimen (amongst 25 immatures) in the vial MZUF 530 also belong to *T. nitens*. As the illustrations of chelicerae by Caporiacco (1948: figs 51, 52) of male and female specimens that he had preliminarily described in 1947 also match well with *T. mandibulata*, we conclude this species is another junior synonym of *T. mandibulata*.

Finally, based on photos of the male holotype of *T. infuscata* from the Seychelles (MRAC 143319), we observed that it also has the diagnostic characters of *T. mandibulata* (Fig. 21X). Saaristo (2003: figs 21A, B, 25; 2010: figs 27, 31) illustrated the genitalia of one male and one female from the same locality and placed this species in the synonymy of *T. boydi* (= *T. bogotensis*), but without any evidence for his claim. Ironically, Saaristo (1978: 121, figs 224–231) was the first to correctly identify *T. mandibulata* from the Seychelles and gave reliable illustrations of the typical female chelicerae and much elongated genital fold. However, Saaristo (2003, 2010) unexplicably considered his former identification as erroneous and attributed it to *T. boydi* instead. Hence, we correct this misidentification, removing *T. infuscata* from the synonymy with *T. boydi*, and consider it to be a junior synonym of *T. mandibulata*.

Variation. Males ($n = 6$): total length, 7.12–11.89; females ($n = 20$): total length, 7.54–11.63.

Distribution. Known from Africa, Asia, Australia, Central America, the Caribbean, and South America (Brazil and Guyana) (Fig. 22D).

Tetragnatha nitens (Audouin, 1826)

Figs 14–16, 20E, 22E

Eugnatha nitens Audouin 1826: 118, pl. 2, fig. 2 (♀).

Eugnatha pelusia Audouin 1826: 119, pl. 2, fig. 3 (♂ ♀).

Tetragnatha nitens Walckenaer 1841: 209.

Tetragnatha peruviana Taczanowski 1878: 142, pl. 1, fig. 1a–c (♂ ♀)
syn. nov.

Tetragnatha andina Taczanowski 1878: 144, pl. 1, fig. 2 (♀); Levi 1981: 291 (syn. rejected, see *T. bogotensis*).

Tetragnatha peninsulana Banks 1898: 246, pl. 15, fig. 12 (♂ ♀); Levi 1981: 291 (syn. rejected, see *T. bogotensis*).

Tetragnatha eremita Chamberlin 1924: 645, fig. 89, 90 (♂); Levi 1981: 292 (syn. rejected, see *T. bogotensis*).

Tetragnatha decipiens Badcock 1932: 13, fig. 9 (♀) syn. nov.

Tetragnatha haitiensis Bryant 1945: 408, fig. 37 (♀); Levi 1981: 292 (syn. rejected, see *T. bogotensis*).

Tetragnatha tullgreni Caporiacco 1947: 24 (♀ preoccupied by *T. tullgreni* Lessert, 1915)

Tetragnatha caporiaccoi Platnick 1993: 381 (replacement name of *T. tullgreni*) syn. nov.

Tetragnatha nitens kullmanni Wiehle 1962: 379, figs 1–5, 6b, 9–11, 14, 15 (♂ ♀); Wunderlich 1992: 365 (syn. rejected, see *T. bogotensis*).

Type material. *Tetragnatha nitens*: EGYPT: ♂ ♀ syntype, Rosetta, Markaz Rasheed, lost (Levi 1981). *Tetragnatha peruviana*: PERU: ♂♂, ♀♀, syntypes: Lima, El Callao and Pacasmayo (191 syntypes, Coll. K. Jelski and J. Sztolerman, MIZ 225658–225682), examined (photos). *Tetragnatha decipiens*: PARAGUAY: 1 ♀ holotype, “Nanahua”, probably Nanawa, Presidente Hayes, 05.ii.1927 [Coll. G. S. Carter and L. C. Beadle] (NHM), examined. *Tetragnatha caporiaccoi*: GUYANA: ♀ holotype, Alto Demerara-Berbice, xii.1931 (MZUF 532), examined.

Diagnosis. See the extended diagnosis under *T. bogotensis* for the diagnostic characters of *T. nitens*.

Synonymy and notes. *Tetragnatha nitens* was first described from Egypt, but its syntypes are lost according to Levi (1981). This common species has been diagnosed and redescribed many times, with plentiful illustrations of its body, chelicerae and genital morphology (e.g. L. Koch 1872; O. Pickard-Cambridge 1872; Simon 1898; F. O. Pickard-Cambridge 1903; Chickering 1957c; Okuma 1983, 1987, 1988b, 1992). Furthermore, it is a senior synonym for 17 species or subspecies according to the World Spider Catalog (2019). As it is easily mistaken for other large-bodied species, misidentified specimens are commonly found in museum collections.

Levi (1981: 291, 292), for example, listed 13 synonyms of *T. nitens*, of which 11 were new. We highlight that *T. festina* Bryant, 1945 was listed as a new synonym by Levi (1981) but was previously synonymised by Chickering (1957b: 2), *T. aptans* Chamberlin, 1920 was a new synonym but not listed as such, and *T. eremita* Chamberlin, 1924 was not included in the synonymic list of the World Spider Catalog (2019). Indeed, Levi (1981: figs 23–29) clearly misidentified at least some of the females he ascribed to *T. nitens*, whose illustrations belong to *T. bogotensis* instead (see above Synonymy and notes for *T. bogotensis*). Based on the original illustrations, we are able to confirm the synonymy of the following taxa: *T. pelusia* Audouin, 1826, *T. antillana* Simon, 1897, *T. vicina* Simon, 1897, *T. galapagoensis* Banks, 1902, *T. aptans* Chamberlin, 1920, *T. seminola* Gertsch, 1936, *T. steckleri* Gertsch & Ivie, 1936, *T. elmora* Chamberlin & Ivie, 1942, and *T. festina* Bryant, 1945. On the other hand, four species are in turn synonyms of *T. bogotensis* (see Synonymy and notes for that species).

Another lapsus occurred with *T. nitens kullmanni* from Sardinia, Italy (Wiehle 1962: 379, figs 1–5, 6b, 9–11, 14, 15). It was first synonymised with *T. nitens* by Wunder-

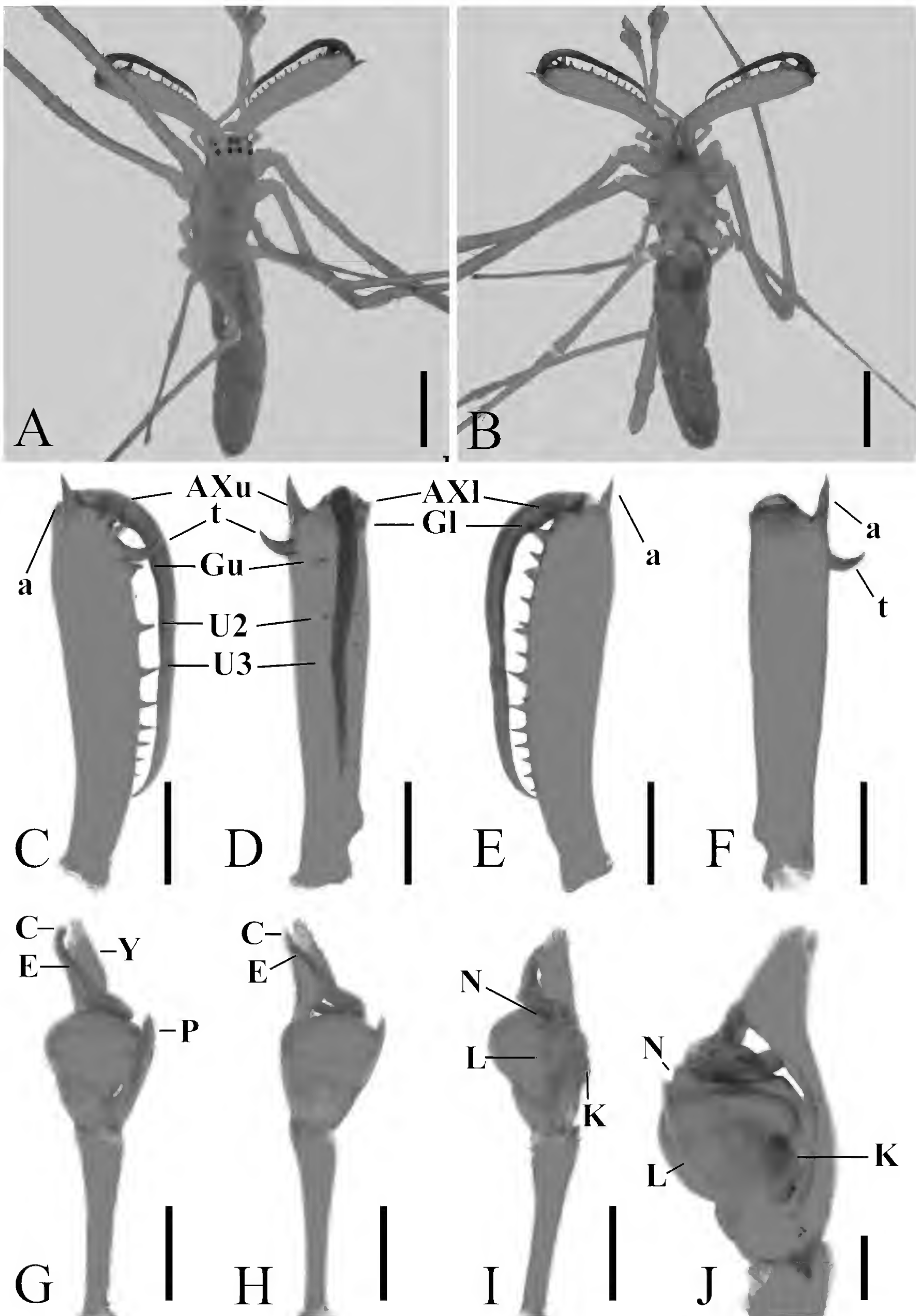


Figure 14. *Tetragnatha nitens* (Audouin, 1826), male (MCTP 1426). **A.** Dorsal habitus; **B.** Ventral habitus; **C–F.** Left chelicera: **C.** Upper view; **D.** Inner view; **E.** Lower view; **F.** Outer view; **G–J.** Left male palp: **G.** Mesal view. **H.** Dorsal view; **I.** Ventral view (paracymbium); **J.** Paracymbium detail, ventral view. Scale bars, 2 mm (**A, B**); 1 mm (**C, D, E, F**); 0.5 mm (**G, H, I**); 0.2 mm (**J**).

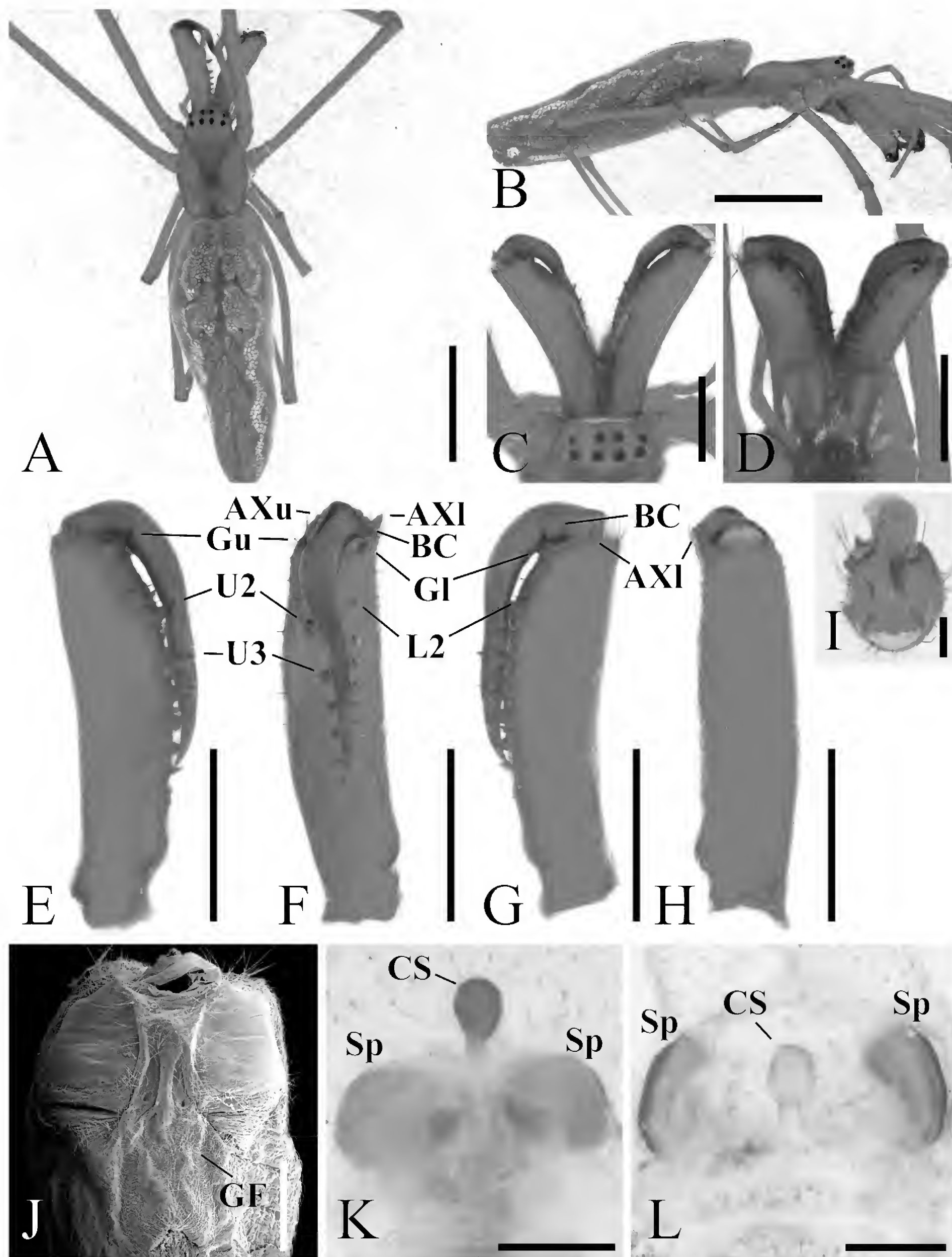


Figure 15. *Tetragnatha nitens* (Audouin, 1826), female. **A.** Dorsal habitus (UFRJ 1528); **B.** lateral habitus (UFRJ 1528); **C.** Chelicerae upper row and eyes (UFRJ 1528); **D.** Chelicerae lower row and maxilla (UFRJ 1528); **E–I.** Left chelicera (UFRJ 1528): **E.** Upper view. **F.** Inner view. **G.** Lower view. **H.** Outer view. **I.** Basal cusp detail, distal view; **J–L.** Genital area: **J.** SEM of genital fold, ventral view (MCTP 11555); **K.** Internal genitalia, cleared, ventral view (MCTP 43323 ex 7313); **L.** Internal genitalia variation, cleared, ventral view (UFRJ 1528). Scale bars: 2 mm (**A, B**); 1 mm (**C, D, E, F, G, H, J**); 0.2 mm (**I, K, L**).

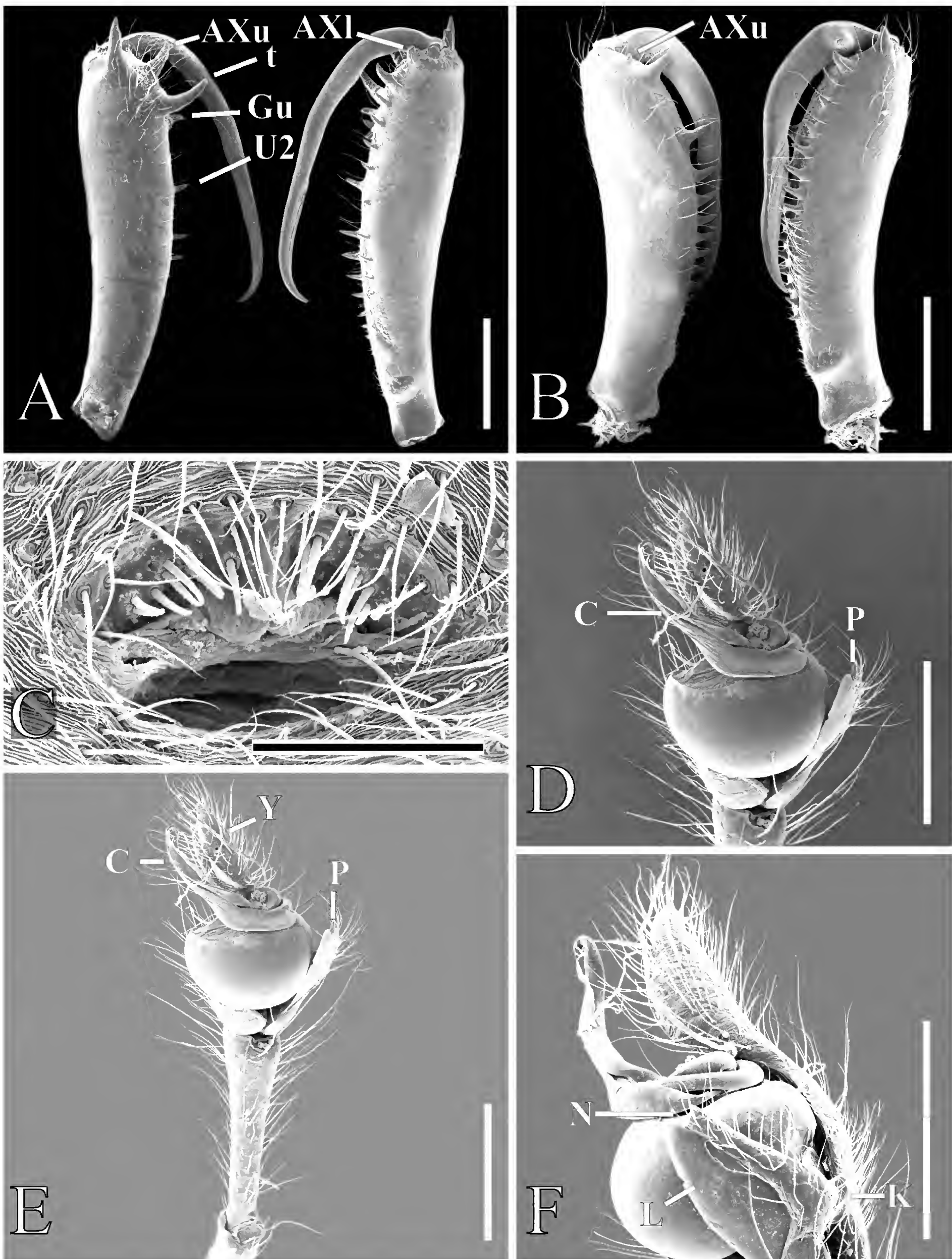


Figure 16. *Tetragnatha nitens* (Audouin, 1826), SEM photos. **A.** Left male chelicera, upper and lower views (MCTP 1618). **B.** Left female chelicera, upper and lower views (MCTP 11555). **C.** Epiandrous field, ventral view (MCTP 1618). **D.** Left male palp, bulb detail, mesal view (MCTP 5985). **E.** Left male palp, mesal view (MCTP 5985); **F.** Left male palp paracymbium, ventral view (MCTP 5985). Scale bars: 1 mm (**A, B**); 0.1 mm (**C**); 0.5 mm (**D, E, F**).

lich (1992: 365), but we disagree with this synonymy and consider *T. nitens kullmanni* as a synonym of *T. bogotensis* (see Synonymy and notes for that species).

Mainly based on our observations of the morphology of the chelicerae, we propose three new synonymies for *T. nitens*: *T. peruviana* from Peru, *T. decipiens* from Paraguay, and *T. caporiacoi* from Guyana. The type materials of all species were studied; for *T. peruviana* images from MIZ were examined, and for *T. decipiens* and *T. caporiacoi* specimens were studied on visits to NHM and MZUF, respectively.

Tetragnatha decipiens and *T. caporiacoi* were described only from females, while descriptions of *T. peruviana* were based on males and females, with males described first, even though only females were illustrated. Females of the three species and males of *T. peruviana* clearly show the diagnostic characters of *T. nitens* (see Diagnosis above).

Variation. Males ($n = 23$): total length, 7.22–9.04; females ($n = 30$): total length, 7.42–11.44. The internal genitalia of females is also variable, with CS stalk shorter or longer than CS head, which places this structure at the same level or anterior to the spermathecae, which also vary in size (Fig. 15K, L; Zhu and Zhang 2011: fig. 125G).

Distribution. This species was first described from Africa (Egypt), but it has a cosmopolitan distribution, with many new records from the Neotropics (Fig. 22E).

Tetragnatha vermiformis Emerton, 1884

Figs 17–19, 20F, 22F

Type material. UNITED STATES OF AMERICA: ♂ lectotype, ♀ paralectotype (Levi 1981). ♀ lectotype, 3♀ paralectotypes in MCZ database, Beverly, Essex, Massachusetts (Coll. J. H. Emerton, 15.xiii.18xx), not examined.

Extended diagnosis. Males and females of *T. vermiformis* are most similar to *T. pallescens* F. O. Pickard-Cambridge, 1903. Males have similar length and width of chelicerae (Figs 17D–G, 19A, Banks 1892: 51, pl. 5, fig. 88 as *T. pallida*; Okuma 1992: 236, fig. 16A–E); ‘T’ and ‘rsu’ very alike, sclerotized and pointed; Gl very sclerotized, thick and pointed, with a very large base, remaining teeth set apart by similar gaps. They also share similar elongated paracymbia, with finger-like notches and straight lateral knobs (Figs 17J, 19E; Okuma 1992: 236, fig. 16D). The epiandrous field sets this species apart as it is flat and wide, with 20 fuscules in two bands (Fig. 19F).

Females of both species have similar small, rounded and laterally bulging chelicerae (Figs 18D–G, 19B; Okuma 1992: 236, fig. 16F, G); Gu isolated from U2; Gl from L2 by large gaps, with all teeth very pointed; and similar short genital folds (Fig. 18H; Okuma 1992: 236, fig.

16J). Nonetheless, males and females of *T. vermiformis* differ from *T. pallescens* in having eyes much smaller and delicate and abdomen not as long and projecting (Figs 17A–C, 18A–C; Okuma 1992: 236, fig. 16H, I). Males differ by the following characters: absence of ‘sl’ (Figs 17D–F, 19A); ‘a’ bending downward and closer to fang base (Figs 17D–G, 19A); Gu not so close to fang base, larger and with thicker base (Figs 17D, E, 19A); Gu and ‘T’ placed apart from the row proper, towards lower side and following fang’s closing (Figs 17D, E, 19A); Gl with wider basis and close to AXI and fang basis (Figs 17E, F, 19A); presence of an inner cusp on fang (Figs 17D, F, 19A) and more elongated conductors, with thicker projected tips completely enfolding the emboli, not ending in long tails (Figs 17H–J, 19C, D, 20F). Females differ in lacking both AXu and AXI and having smaller and triangular Gu, longer and wider U2, and lack of a small denticle and groove near the base of L2 (Figs 18D–F, 19B; Okuma 1992: 236, fig. 16G). Females of *T. vermiformis* and *T. pallescens* have similar internal genitalia, with two curved kidney-shaped spermathecae on edge of plate, lacking central membranous sacs (Fig. 18I; Levi 1981: 311, fig. 131). However, *T. vermiformis* has longer spermathecae, without a median membranous area (Fig. 18I).

Variation. Males ($n = 4$): total length, 6.29–7.29; females ($n = 7$): total length, 6.99–10.98. The spermathecal lobes are variable in size and form. Both lobes may be more regularly cylindrical and the external lobe may be much smaller than the inner one (Levi 1981: figs 178–180) or both lobes may be curved and about the same size (Fig. 18I; Zhu and Zhang 2011: fig. 133H).

Distribution. Temperate and tropical Asia, North and Central America, newly recorded from South America (Brazil) (Fig. 22F).

Tetragnatha major Holmberg, 1876 and *Tetragnatha riparia* Holmberg, 1876

Remarks. *Tetragnatha major* and *T. riparia* were described by Holmberg (1876), but the original descriptions are very short, without any suitable characters to correctly diagnose the species. There is a lack of illustrations and no type materials are specified because Holmberg did not collect the specimens he described. No specimens labeled as types of either species were found in MACN during our visit to that collection; Galiano and Maury (1979) had previously determined this. Despite the lack of information on these two species, both were subsequently reported from many localities from Argentina (e.g. Mello-Leitão 1941, 1942). However, we re-examined many of these specimens at the MACN and MNRJ and they belong to either *T. argentinensis* or *T. nitens*. Therefore, we treat both species as nomina dubia.

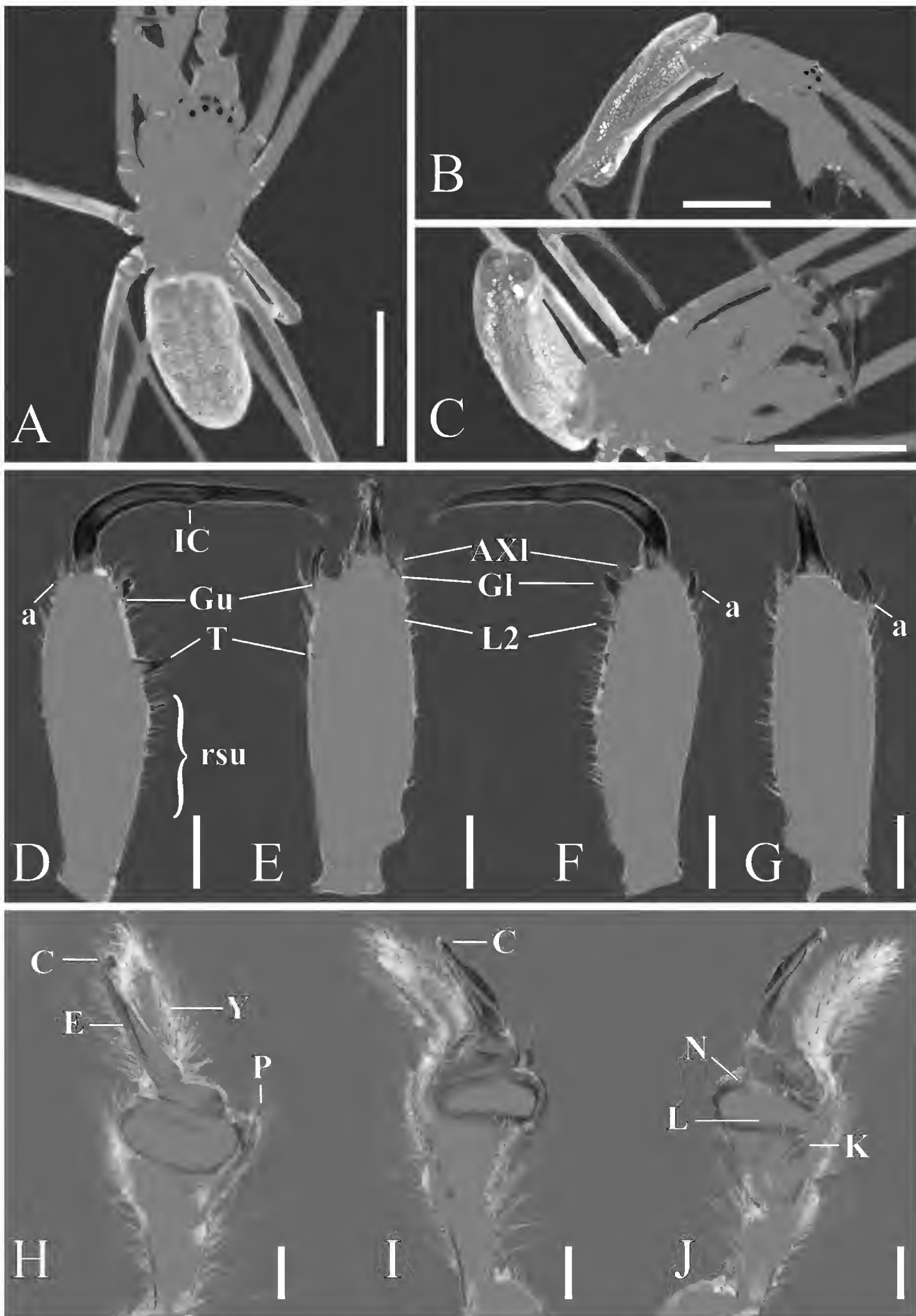


Figure 17. *Tetragnatha vermiformis* Emerton, 1884, male (UFRJ 1556). **A.** Dorsal habitus. **B.** Lateral habitus. **C.** Ventral habitus; **D–G.** Left chelicera: **D.** Upper view; **E.** Inner view; **F.** Lower view; **G.** Outer view; **H–J.** Left male palp: **H.** Mesal view; **I.** Dorsal view; **J.** Ventral view (paracymbium). Scale bars, 2 mm (**A, B, C**); 0.5 mm (**D, E, F, G**); 0.2 mm (**H, I, J**).

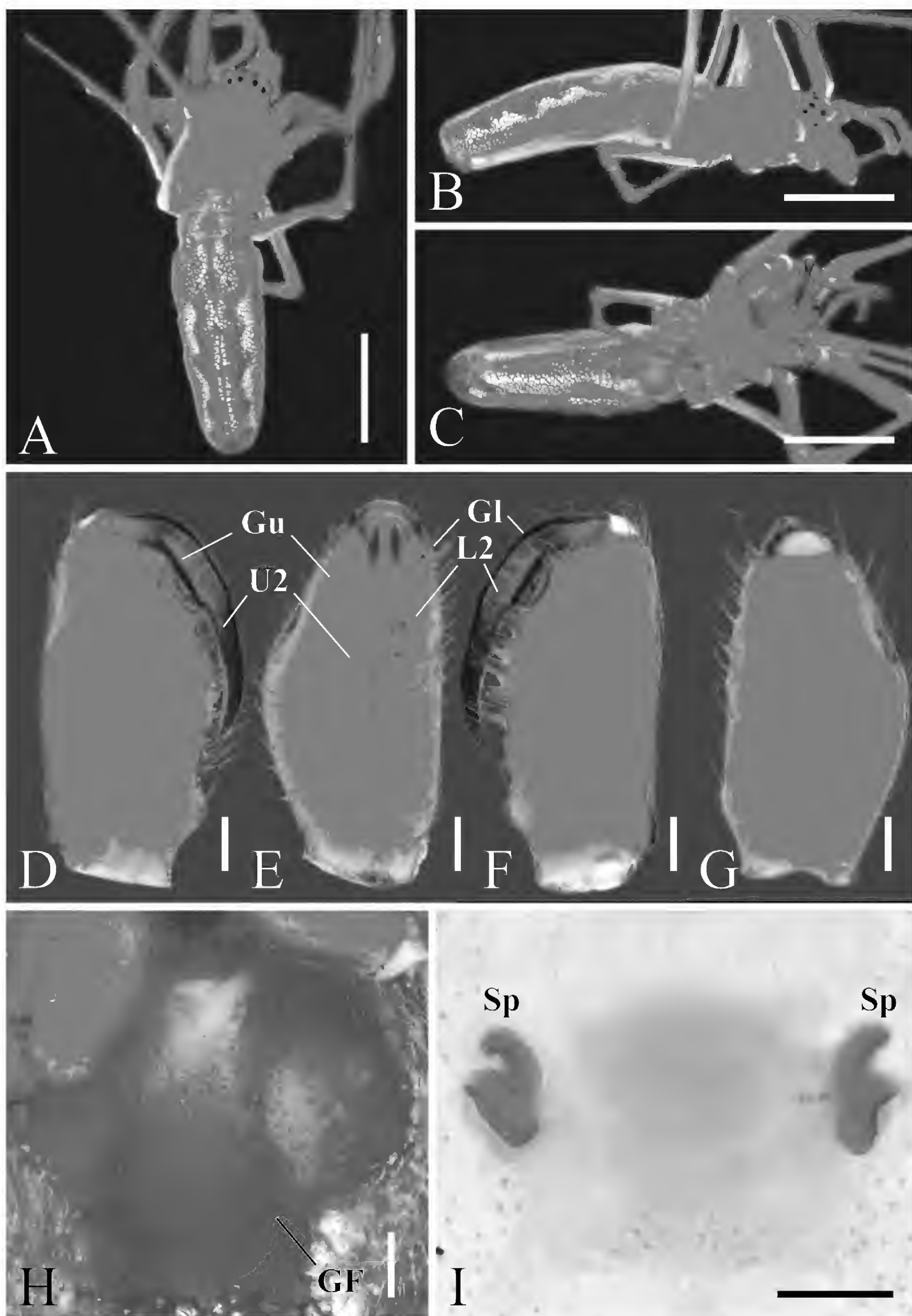


Figure 18. *Tetragnatha vermiformis* Emerton, 1884, female. **A.** Dorsal habitus (UFRJ 1556); **B.** Lateral habitus (UFRJ 1556); **C.** Ventral habitus (UFRJ 1556); **D–G.** Left chelicera (UFRJ 1556): **D.** Upper view; **E.** Inner view; **F.** Lower view; **G.** Outer view; **H, I.** Genital area: **H.** Genital fold, ventral view (UFRJ 1556); **I.** Internal genitalia, cleared, ventral view (MCTP 43339 ex 11333). Scale bars: 2 mm (A, B, C); 0.2 mm (D, E, F, G, H, I).

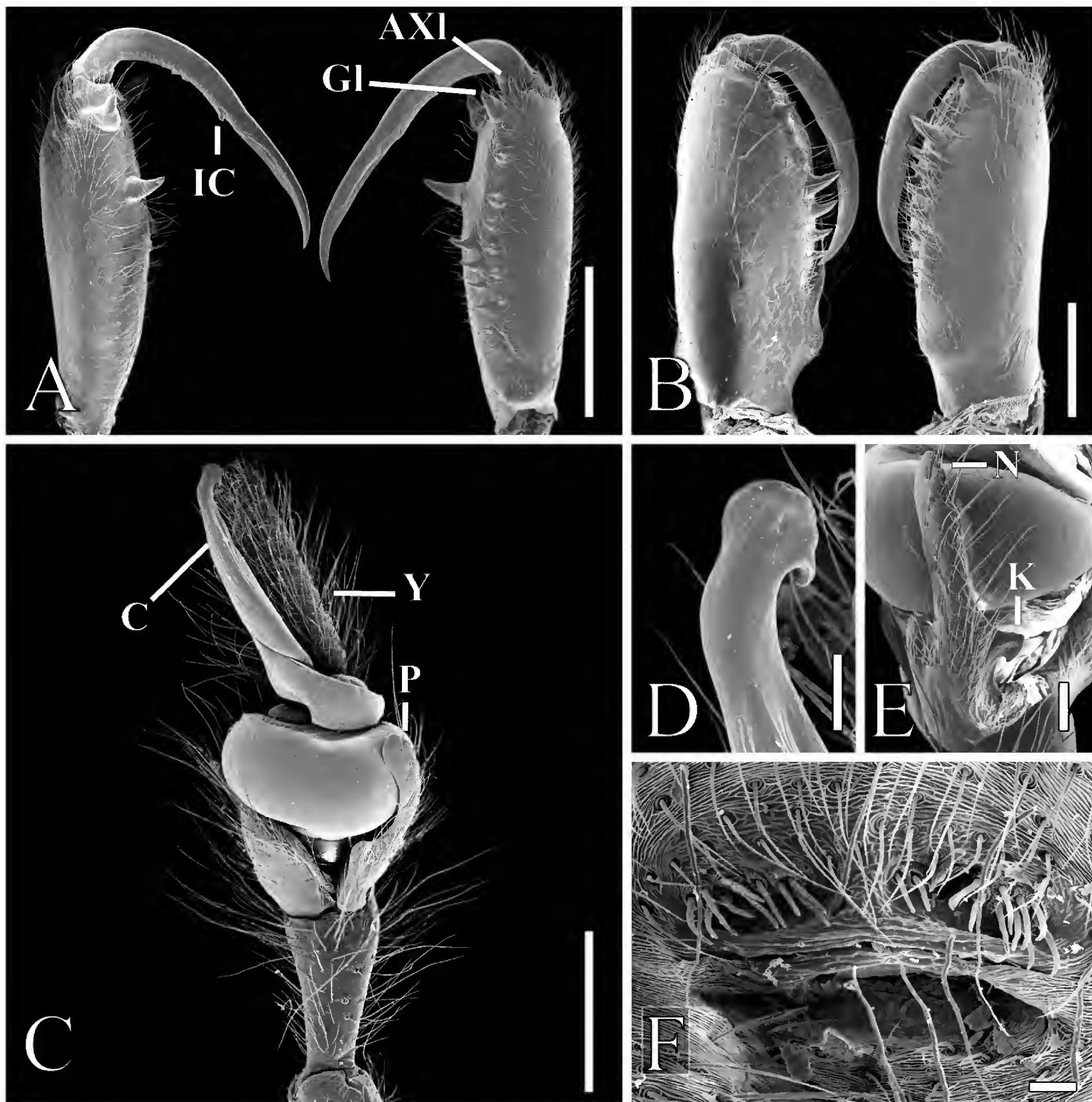


Figure 19. *Tetragnatha vermiformis* Emerton, 1884, SEM photos (MCTP 43339 ex 11333). **A.** Left male chelicera, upper and lower views; **B.** Left female chelicera, upper and lower views; **C.** Left male palp, mesal view; **D.** Left palp conductor detail, mesal view; **E.** Male palp paracymbium, ventral view; **F.** Epiandrous field, ventral view. Scale bars: 0.5 mm (**A, B, C**); 0.05 mm (**D**); 0.1 mm (**E**); 0.02 mm (**F**).

Discussion

In the literature the importance of the chelicerae for correctly diagnosing species has often been ignored. Old publications (e.g. Audouin 1826; Walckenaer 1841; Emerton 1884) usually had short descriptions, basically describing the body size, shape of abdomen, and eye length. On the other hand, some later authors like F. O. Pickard-Cambridge (1903), Chickering (1957c), Levi (1981), Okuma (1983, 1987, 1988a, 1988b, 1992) and Gillespie (1992a, 1992b), paid attention to chelicerae morphology and also genitalic features. Levi (1981),

for example, based most of his determinations only on genital morphology, because he believed intraspecific variation on chelicerae was too high to allow clearcut species separation. In contrast, Okuma (1983, 1987, 1988a, 1988b, 1992) based her determinations mostly on chelicerae morphology, with additional drawings of male palps and genital folds. Gillespie (1992a, 1992b) followed Okuma, but also paid attention to leg spines on some *Tetragnatha*. In the same way, we also heavily rely on cheliceral features for species diagnoses, but add genitalic and other somatic characters whenever possible. In our opinion, taxonomy in *Tetragnatha* cannot

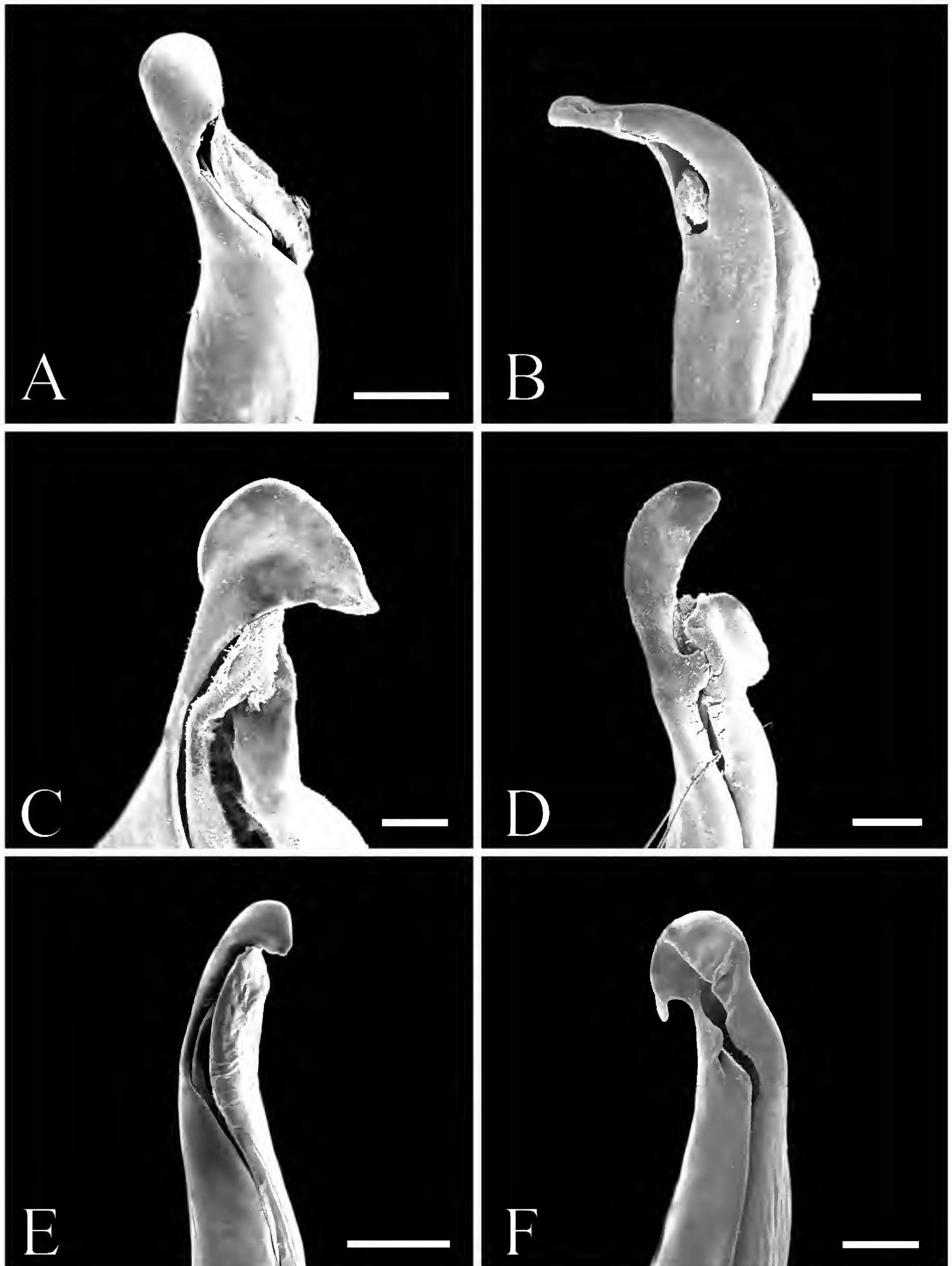


Figure 20. Embolus and conductor tip detail, dorsal view, SEM photos. **A.** *T. bogotensis* (MCTP 4299); **B.** *T. elongata* (MCTP 43306 ex 0370); **C.** *T. keyserlingi* (MCTP 43319 ex 6944); **D.** *T. mandibulata* (UFRJ 1356); **E.** *T. nitens* (MACN 2252); **F.** *T. vermiformis* (MCTP 43339 ex 1133). Scale bars: 0.05 mm (**A, B, C, E, F**); 0.02 mm (**D**).

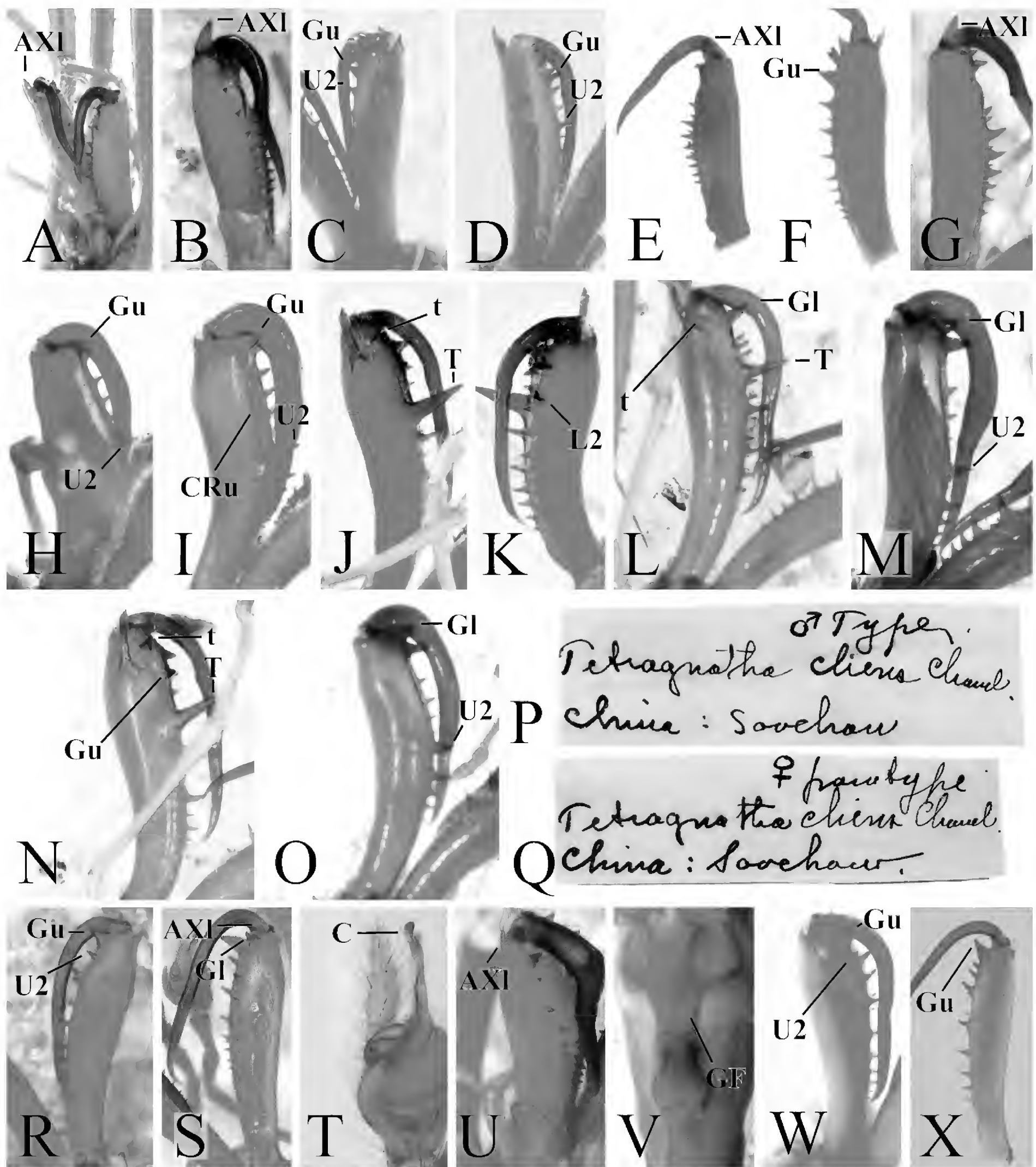


Figure 21. Junior synonyms mentioned on the manuscript. **A–G.** *T. bogotensis* synonyms chelicerae, ♂ upper view, ♀ lower view: **A.** *T. andina*, ♀ syntype; **B.** *T. peninsulana*, ♀ syntype; **C.** *T. boydi praedator*, ♂ syntype; **D.** *T. eremita*, ♂ holotype; **E.** *T. bemalcuei*, ♀ holotype; **F.** *T. ramboi*, ♂ lectotype; **G.** *T. haitiensis*, ♀ holotype; **H–M.** *T. keyserlingi* synonyms, left chelicerae: **H.** *T. kochi*, ♀ syntype upper view; **I–K.** *T. japonica* (ZMH): **I.** ♀ syntype upper view; **J, K.** ♂ *T. nigrita* (misidentification): **J.** Upper view; **K.** Lower view; **L, M.** *T. conformans* upper view: **L.** ♂ paratype; **M.** ♀ holotype; **N, O.** *T. nigrita* sub *T. cliens*, left chelicerae upper view: **N.** ♂ holotype; **O.** ♀ paratype (misidentification); **P, Q.** Labels of *T. cliens*: **P.** ♂ holotype; **Q.** ♀ paratype. **R–X.** *T. mandibulata* synonyms: **R–V.** *T. confraterna*: **R.** ♂ syntype right chelicera, upper view; **S.** ♂ syntype left chelicera, lower view; **T.** ♂ syntype right palp, mesal-ventral view; **U.** ♀ syntype right chelicera, lower view; **V.** ♀ syntype genital fold, ventral view; **W.** *T. necatoria*, ♂ holotype left chelicera, upper view; **X.** *T. infuscata*, ♂ holotype right chelicera, upper view.

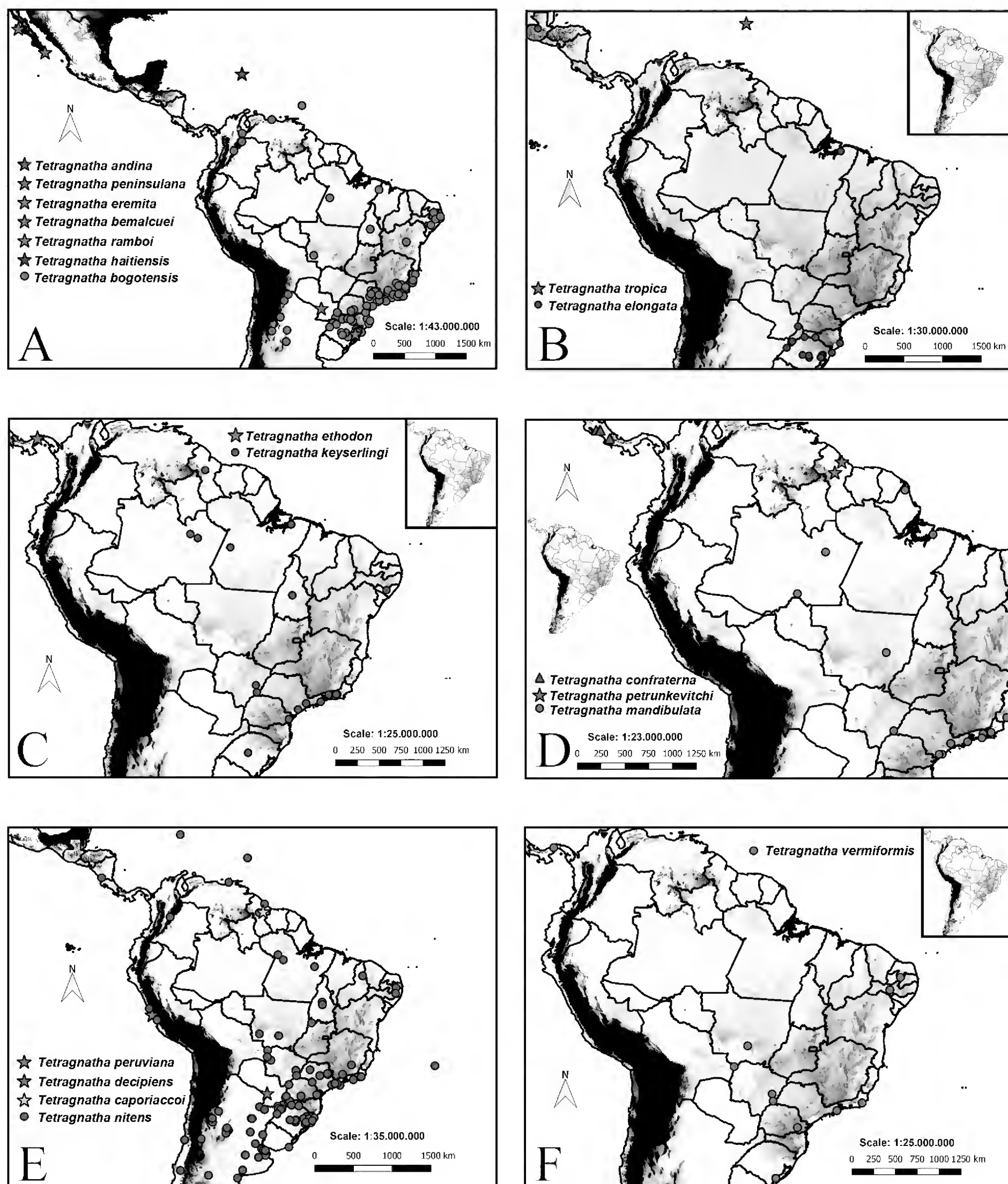


Figure 22. Records of the material we analysed (circles), including the type localities of Neotropical junior synonyms cited in the text (stars and triangles). **A.** *Tetragnatha bogotensis*; **B.** *Tetragnatha elongata*; **C.** *Tetragnatha keyserlingi* (excluding Haiti); **D.** *Tetragnatha mandibulata*; **E.** *Tetragnatha nitens*; **F.** *Tetragnatha vermiformis*.

only be based on genital morphology because there are many cryptic species with identical genitalia.

Unfortunately, Okuma and Gillespie lacked consistency on their nomenclature. For example, Okuma called “U2” the more elongated tooth on the upper row (Okuma 1987: figs 1A, 2A), instead of “T” (Okuma 1992: figs 6A,

21A) and variously named fang cusps as excrescence (Okuma 1987) or posterior cusps (Okuma 1992). Besides, Gillespie (1992a) ignored Gu and Gl on females, renaming these structures U1 and L1, respectively.

The inconsistent terminology for chelicerae in *Tetragnatha* has hampered the recognition of homologies be-

tween species, shown by the lack of such characters in family phylogenies including morphological data (Álvarez-Padilla et al. 2009; Álvarez-Padilla and Hormiga 2011). Besides the lack of a straightforward set of homologies based on comprehensive phylogenies at the subfamily and genus levels, we believe that a practical system for naming chelicerae teeth and fang details in adult *Tetragnatha* is valuable for taxonomic purposes. Although some teeth may slightly vary in shape and size, teeth position in the groove row is less prone to variation. In that way, Okuma's terms are a good basis for a classification system, despite the observed inconsistencies.

In *Tetragnatha*, adults normally bear guide teeth on upper (Gu) and lower rows (Gl). It is the usually robust first tooth on each margin (e.g. Figs 1E–G, 2E, 3B, C, 5D–F, 6C–E) which receives and guides the folding of the fang. Adjoined to the guide teeth, but not placed on the furrow, we can find additional teeth of variable size near the fang basis, from a small AXu (Figs 15E, F, 16B) or AXl (Figs 8E, F, 9E, F, 10A, B) to an extremely elongated AXu (Figs 14C, D, 16A) or a bulky and elongated AXl (Figs 2C, D, 12E, F, 13D). Okuma (1987) named 'rsu' "the upper row of small teeth". As this is not very consistent, we kept the name, with some minor changes. In the same paper, she named 'rsl' "the lower row of small teeth" after Gl or L2 (Okuma 1987: 38). In both sexes 'rsu' and 'rsl' refer to the teeth after the last specialized tooth, commonly of the same size, or uniformly decreasing towards paturon basis.

Males usually have specialized teeth, longer, more conspicuous, and more numerous than in females. There is an apophysis (spur) on the upper surface, which varies in shape and position, from the middle portion on distal part of paturon (Figs 5A, 7A) to its outer margin (Figs 8D, 10A). In some species, there is an additional 't', a unique tooth near the apophysis basis, sometimes reduced to a nub (Figs 8D, E, 10A) or in other species elongated (Figs 1C, E, F, 3B, 14C, D, 16A). Considering the row itself, some males also bear a conspicuous and much more elongated tooth on the upper row, named 'T', which replaces U2 or U3 (Figs 5D, E, 7A, 8D, E, 10A, 17D, E, 19A), and it can sometimes be slightly displaced from the furrow (Figs 17D, E, 19A). Okuma (1987, e.g. fig. 5F) also named 'T' in some females. We think the use of 'T' for females is inconsistent, as sometimes it is not the most elongated tooth, but just larger than 'rsu'. Moreover, we can find 'sl', a tooth on the upper row of males of some species with an elongated 'T'. It is always the last tooth before 'T', normally basally projected (Figs 5A, B, 7A). Again, Okuma (1987, e.g. fig. 5F) considered it to be present in females, named as 'e'. As we do not use 'T' in females, 'e' is deemed to be just a regular tooth. Therefore, in males with a 'T', we consider all remaining teeth after this elongated tooth to be 'rsu' (Figs 5D, 8D).

In relation to fangs, we call the massive pointed projection placed at lower side and near fang basis the basal cusp (BC) (Figs 2D, E, 12D–G, 13C, D, 15D, F–I, 16B) and the spiky projection placed at outer side, varying in

distance from fang basis, the outer cusp (OC) (Figs 6C–F, 7B; Okuma 1988b: fig. 1A–C; 1992: fig. 21E, F). The projection placed near or on the inner face of fang is named the inner cusp (IC) (Figs 17D, F, 19A; Okuma 1992: fig. 3A, C). Finally, we name very robust forking projection at the upper side and near the middle of fang the median cusp (MC) (e.g. Zhu et al. 2003: fig. 59C–E; Mello-Leitão 1931: fig. 1).

We also introduce new terminology for modifications of the paturon. Some have a rounded elevated cheliceral bulge (CB) in the area between both rows of teeth (Figs 2C, E, 3C, 12D, E, 13C) or bear well-marked crests or thick keels on gaps alongside the teeth. There may be an upper crest (CRu) departing from Gu (Figs 9D, 10B; Okuma 1992: fig. 21E) or a lower crest (Crl) occupying the total length of furrow (Figs 9F, 10B). Nonetheless, those crests and bulges may not always be illustrated or simply do not occur in some specimens (see Variation in *T. keyserlingi*).

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Appendix

Material examined

Tetragnatha bogotensis

ARGENTINA: 3♀, Córdoba: Córdoba, Barrio Arguello, -31.416667, -64.183333, xii.1944, De Carlo leg. (MACN 1957); 1♀, Jujuy: Parque Nacional Calilegua, -23.638889, -64.571389, 23–24.ix.1995, M. Ramirez, P. Goloboff and C. Szumik leg. (MACN 24513); 2♀, La Rioja:

drelétrica Santa Catarina, -25.6477777778, -51.9536111111, 2005, J. Ricetti leg. (IBSP 143567); 1♀, Tijucas do Sul, Serra do Cabral, Lagoa, -25.927778, -49.198889, J. Ricetti leg. (IBSP 39272); 1♂, same locality, 29.v.2000, J. Ricetti leg. (IBSP 39082); Pernambuco: 1♀, Araçoiaba, Centro de Instrução Marechal Newton Cavalcanti, -7.79, -35.090833, 16.vi.2009, A. Costa leg. (IBSP 143819); 1♀, Moreno, Bonança (Tapeira), -8.118611, -35.092222, B. Pickel leg. (MNRJ 42574); 1♀, Rio Pojuca, -8.3016931, -36.0058392, O. Leonardos leg. (MNRJ 41844); 1♂, Piauí: Brasileira e Piracuruca, Parque Nacional de Sete Cidades, -41.005280, -41.715056, 29.vi.2007, L. S. Carvalho leg. (MPEG 031353); Rio de Janeiro state: 1♀, Angra dos Reis, Ilha Grande, Dois Rios, -23.140556, -44.247222, 8–11.viii.2008, R. Baptista leg. (UFRJ 0650); 1♂, Bom Jesus de Itabapoana, -21.133889, -41.68, iv.1985, R. Baptista leg. (MNRJ 1573); 1♂, 3♀, Cachoeiras de Macacu, Reserva Ecológica de Guapiaçu, -22.462778, -42.652778, 08.vii.2016, R. Baptista leg. (UFRJ 1225); 1♀, same locality, 08.viii.2016, R. Baptista leg. (UFRJ 1314); 1♂, 1♀, same locality, 24–26.v.2017, R. Baptista leg. (UFRJ 1348); 5♂, 3♀, 5j, same locality, 29.vi.2017, P. Castanheira leg. (UFRJ 1355); 2♂, 1♀, Casemiro de Abreu, -22.480833, -42.203889, 27.xii.2002, E.H. Wienskoski leg. (MZSP 62310); 1♂, Guapimirim, Segredo, Sítio Sonho Meu, -22.543525, -42.967035, 25–26.vi.2016, R. Baptista leg. (UFRJ 1223); 1♂, Magé, Citrolândia, brejo da pedreira, -22.652778, -43.040833, 23.vi.2017, P. Castanheira and N. Ferreira Júnior leg. (UFRJ 1352); 1♂, 1♀, same locality, córrego do Sertão, 22.vi.2017, B. R. Soares and L. F. Botelho leg. (UFRJ 1354); 1♂, same locality, 23.vi.2017, H. Schinelli and L. F. Botelho leg. (UFRJ 1357); 1♂, Maricá, Rio Ubatiba, -22.918889, -42.818889, 23.i.1999, Laboratório de Entomologia UFRJ leg. (UFRJ 0035); 1♀, Mendes, -22.526944, -43.732778, 551 m a.s.l., Mello-Leitão leg. (MNRJ 00406 ex MLPC 579); 1♂, same locality, Centro Marista São José das Paineiras (Sede), 29.iv.2011, R. Baptista leg. (UFRJ 1546); 2♂, 1♀, same locality, 27.iv.2011, R. Baptista leg. (UFRJ 1547); 1♂, same locality, 15.v.2012, R. Baptista leg. (UFRJ 1548); 1♂, 1j, Nova Friburgo, Lumar, Córrego da Pedra Vermelha, -22.281944, -42.530833, 14.xi.2008, Laboratório de Entomologia UFRJ leg. (UFRJ 0044); 1♀, Petrópolis, -22.499475, -43.175572, Mello-Leitão leg. (MNRJ 00402 ex MLPC 973); 1♂, 1♀, Pinheiral, Pinheiro, -22.512778, -44.000833, Mello-Leitão leg. (MNRJ 00401 ex MLPC 577); 3♀, same locality and collector (MNRJ 00415 ex MLPC 578); 1♂, same locality and collector (MNRJ 00416 ex MLPC 576); 2♀, same locality and collector (MNRJ 02604 ex 00408 ex MLPC 573); 1♂, 2j, Rio Bonito, Lavras, Estrada Velha de Lavras, tanques de piscicultura, -22.707778, -42.625833, 69 m a.s.l., 23.x.2017, J. F. Barbosa, A. F. Antunes, L. L. Dumas and J. L. Nessimian leg. (UFRJ 1487); 2♀, 3j, Rio de Janeiro, -22.902778, -43.207778, Mello-Leitão leg. (MNRJ 00409 ex MLPC 574); 2♀, same locality and collector (MNRJ 00413 ex MLPC 575); 1♂, São Pedro da Aldeia, -22.827679, -42.076422, xi.1963, S. Machado leg. (IBSP 4799); 1♀, Teresópolis, Serra do Subaio, -22.411944, -42.965833, 20–22.iv.1995, R. Baptista and M. Landim leg. (MNRJ 60014 ex MNRJ 1568); 1♀, Rio Grande do Sul: A. Rego leg. (MNRJ 41484); 1♀, 1j, Cachoeira do Sul, Cordilheira, -30.038889, -52.893889, 04.x.1992, R. G. Buss leg. (MCTP 3381); 9♂, 5♀, Capão da Canoa, Capão Novo, -29.664374, -49.972625, 17–18.v.1993, A. A. Lise leg. (MCTP 3161); 1♂, Caxias do Sul, Fazenda Souza, -29.121444, -51.018557, 11–12.x.1995, Eq. Lab Aracnologia PUCRS leg. (MCTP 43305 ex 7313); 2♀, Cerro Largo, -28.148008, -54.738189, 06.i.1965, C. Valle leg. (MZSP 4683); 1♀, Dois Irmãos, -29.58, -51.085, 20.iv.1965, C. Valle leg. (MZSP 6982); 1♂, EnCRuzilhada do Sul, -30.545548, -52.525733, 09.ix.1994, Luciane P. Koch leg. (MCTP 43303 ex 5063); 9♀, 3j, Estância Velha, -29.647778, -51.173889, 08.v.1967, P. Biasi leg. (MZUSP 8504); 1♀, Machadinho, -27.566944, -51.667778, ix.1988 (MCTP 0852); 1♀, Novos Cabrais, Parque Witeck, -29.735, -52.947778, 20.xi.2007, R. G. Buss leg. (MCTP 20278); 2♀, same locality, 02.xii.2007, R. G. Buss leg. (MCTP 28445); 3♀, Santa Maria, -29.683889, -53.806944, 26.iii.1990, D. Linck leg. (MCTP 43304 ex 5973); 6♂, 3♀, same locality, 16.iii.1990, D. Linck leg. (MCTP 5977); 1♂, São Borja, Rio Uruguai, -28.660833, -56.003889, 30.vi.1989, Garabi leg. (MCTP 0844); 1♀, São Francisco de Paula, Potreiro Velho, -29.447778, -50.583889, 24–25.iv.2005, Guilherme M. Peterson leg. (MCTP 017086); 2♂, 4♀, 1j, São Sepé, -30.164110, -53.571805, 18.vii.1994, E. C. Costa leg. (MCTP 40635); 1♀, same locality, 18.xii.1993, E. C. Costa leg. (MCTP 40638); 1♂, 1♀, same locality, 18.i.1994, E. C. Costa leg. (MCTP 40645); 3♀, Taquara, -29.650833, -50.780833, no further data (NHM S-068-70); 1♂, Viamão, Est. Exp. Fitotécnica, -30.072391, -51.097196, 25.viii.1995, A. A. Lise et al. leg. (MCTP 7578); Santa Catarina: 1♀, Rio Uruguai, -27.1751176, -53.555255, ix.2010, J. Cabra leg. (MCTP 41818 ex 34356); 2♂, 1♀, same locality, 02.ix.2010, Rafael C. Francisco leg. (MCTP 41824 ex 34382); 1♂, 1♀, Brusque, -27.097778, -48.917778, i.1965, A. Caolore leg. (MZSP 4819); 1♀, Chapecó, Quebra-Queixo, -27.104722, -52.614167, 26–27.ii.2002, Marcelo Kammers leg. (MCTP 12891); 1♂, 1♀, Concórdia, Estrada Joaçaba, -27.233889, -52.027778, 15.v.1967, P. Biasi leg. (MZSP 6225); 1♂, 2♀, Garopaba, -28.022778, -48.612778, 22.x.1993, M. P. Barros leg. (MCTP 4299); 3♀, same locality, Praia do Siritu, 28.viii.1994, Gilson Rey leg. (MCTP 4780); São Paulo state: 1♀, Araraquara, -21.783374, -48.179309, 04.vii.2009, Prefeitura Municipal de Araraquara leg. (IBSP 137683); 6♀, 4j, Botucatu, -22.885833, -48.445, 20.iv.1952, W. Bokermann leg. (MZSP 14742 ex 2033); 1♀, same locality, Fazenda Paulina, i.2002, E.H. Wienskoski leg. (MZUSP 74661 ex 62395); 1♀, Descalvado, Córrego Areia Branca, -21.903889, -47.618889, 11.viii.1950, Schubart leg. (MCTP 6400); 1♂, Engenheiro Marsilac, -23.8709642, -46.7731813, 30.xii.1966, P. Biasi leg. (MZSP 5150); 1♂, Ilha Bela, Ilha de São Se-

bastião, -23.815, -45.370556, 23.iii.1951, H. Urban leg. (MZUSP 14748); 1♂, Juquitiba, -23.934257, -47.070184, xii.1983, E. da S. Mattos leg. (IBSP 4352); 1♀, Pariqueira-Açu, -24.715, -47.880833, no further data (MZUSP 62113); 1♂, Pirassununga, Emas, -21.995833, -47.425833, 26.x.1951 (MZUSP 74662 ex 4972); 1♀, Santo André, Alto da Serra, -23.663889, -46.537778, v.1923, B. Spitz leg. (MZSP 5801); 1♂, 8♀, São Paulo, -23.6130474, -46.6065779, xi.1963, W. Fernandes leg. (IBSP 1860); 7♀, same locality, Sacomã, 29.iii.1942 (MZSP 4912); 6♂, same locality (MZUSP 4914); 1♂, Serra Negra, -22.611944, -46.700833, 16.viii.1965, P. Biasi leg. (MZSP 4476); 1♂, Torrinha, -22.425833, -48.168889, 16.ii.1945, A. Zamith leg. (IBSP 137935); **COLOMBIA**: 1♀, Boyacám La Uvita, 6.316111, -72.56, N. Maria leg. (MNRJ 01273); 2♀, Cundinamarca: Bogotá, 4.598056, -74.075833, no further data (NHM S-071-3); 1♂, 2♀, Norte de Santander: Cúcuta, 7.894167, -72.503889, N. Maria leg. (MNRJ 00767); **SAINT VINCENT AND THE GRENADINES**: 2♂, 2♀, 13.160833, -61.226111, E. Simon leg. (MNHN 18964). **VENEZUELA**: 1♂, 3♀, Distrito Capital: Caracas, 10.493333, -66.922778, 1883–1885, Chaper leg. (MNHN).

Tetragnatha elongata

ARGENTINA: Misiones: 1♀, 1j, „Puerto Yatay“, -25.985922, -54.4420392, viii.1959, Nuñez leg. (MACN 39602 ex 24424); 1♀, Parque Nacional Iguazú, Sendero Macuco y picadas aledañas, -25.683611, -54.453889, 18–21.i.2005, C. Grismado, L. Lopardo, L. Piacentini, A. Quaglino and G. Rubio leg. (MACN 31765); 1♂, San Javier, Arroyo Guerreiro, -27.7929567, -55.2352337, 11–21.iv.1989 (MCTP 43307 ex 0839); 4♀, 1j, Santa Maria, -27.934526, -55.407083, x.1956, Viana leg. (MACN 39616 ex 24423); 2♂, same locality, x.1953, De Carlo, Schiapelli, Vianna and Galiano leg. (MACN 3947); **BRAZIL**: 1♂, Pará: Belém, Fazenda Velha, -1.455833, -48.503889, 26.vii.1975, P. Waldir leg. (MPEG 003339); Rio Grande do Sul: 1♀, Cachoeira do Sul, Capão Grande, -30.038889, -52.893889, 10.x.1992, R. G. Buss leg. (MCTP 3387); 1♂, 2j, same locality, Porteira Sete, 31.x.1992, R. G. Buss leg. (MCTP 41482 ex 3386); 1♀, Eldorado do Sul, -29.997905, -51.308515, 28.iii.1993, M. Silveira leg. (MCTP 3105); 1♂, Novo Hamburgo, -29.677778, -51.130833, 17.vi.1988, C. J. Becker leg. (MCTP 0229); 1♂, 2♀, Novos Cabrais, Parque Witeck, -29.735, -52.947778, 19.x.2001, R. G. Buss leg. (MCTP 13054); 1♂, 3♀, same locality, 03.i.2008, R. G. Buss leg. (MCTP 20275); 1♀, same locality, 20.xi.2007, R. G. Buss leg. (MCTP 20276); 2♂, 4♀, same locality, 01.xi.2008, R. G. Buss leg. (MCTP 27955); 2♂, 6♀, same locality, 09.x.2008, R. G. Buss leg. (MCTP 28045); 3♂, same locality, 15.iv.2008, R. G. Buss leg. (MCTP 28131); 1♂, same locality, 18.vii.2008, R. G. Buss leg. (MCTP 28171); 1♂, 2♀, same locality, 08.iv.2008, R. G. Buss leg. (MCTP 28208); 1♀, same locality, 25.iii.2008, R. G. Buss leg. (MCTP 28238); 1♂, 1♀, same locality, 15.v.2008, R. G. Buss

leg. (MCTP 28257); 2♂, 4♀, same locality, 18.ii.2008, R. G. Buss leg. (MCTP 28306); 4♂, 1♀, same locality, 21.i.2008, R. G. Buss leg. (MCTP 28388); 3♂, 3♀, same locality, 21.i.2008, R. G. Buss leg. (MCTP 28389); 1♂, Santa Maria, -29.665521, -53.806318, 15.x.1998, C. B. Kotzian and L. Indrusiak leg. (MCTP 43309 ex 40632); 2♂, 3♀, São Borja, Reserva Biológica São Donato, -28.660833, -56.003889, 18.i.2012, M. Machado leg. (MCTP 34774); 1♂, São Leopoldo, -29.756345, -51.156759, 01.ix.1986, C. J. Becker leg. (MCTP 0332); 1♂, 1♀, same locality, 28.ix.1987, C. J. Becker leg. (MCTP 43306 ex 0370); 1♂, Sapiranga, Arroio Feitoris, -29.637187, -51.007799, 28.xii.2008, E. L. C. Silva leg. (MCTP 28557); 1♀, Torres, -29.338290, -49.728079, 26.iii.2006, E. L. C. da Silva leg. (MCTP 43308 ex 1426); Santa Catarina, 3♂, 4♀, Rio Uruguai, -27.1751176, -53.555255, ix.2010, J. Cabra leg. (MCTP 41825 ex 34356); 12♂, 13♀, 3j, same locality, 02.ix.2010, R. C. Francisco leg. (MCTP 34382); 1♀, Concórdia, Rio Jacutinga, BR-283, -27.233889, -52.027778, ii.1989 (MCTP 0856); 1♀, Garopaba, Praia do Siriu, -28.022778, -48.612778, 28.viii.1994, G. Rey leg. (MCTP 43310 ex 4780).

Tetragnatha keyserlingi

BRAZIL: 1♀, Alagoas: Quebrangulo, Reserva Biológica Pedra Talhada, -9.2591114, -36.4196054, 04.vii.2018, C. F. B. Floriano, J. F. Barbosa and J. M. S. Rodrigues leg. (UFRJ 1555); Amazonas: 1♂, Manaus, -3.121564, -60.024862, 01.ix.1962, K. Lenko leg. (MZUSP 11764); 1♀, Novo Airão-Moura, Parque Nacional do Jaú, -2.620833, -60.943889, vi.2000, E. M. Venticinque (IBSP 37751); Pará: 1♂, Belém, -1.455833, -48.503889, 09.v.1975, R. F. da Silva leg. (MPEG 011124); 1♂, same locality, Jardim Botânico Rodrigues Alves, -1.431777, -48.457088, Equipe curso biologia de aranhas leg. (MPEG 031359); 1♀, Itaituba, Comunidade Santo Antônio, -4.267837, -55.995863, 09.vii.2003, J. G. da Frota leg. (MCTP 14749); 1♂, Paraná: Morretes, Serra da Graciosa, -25.506135, -48.755088, 09–20.i.1995 (MCTP 43319 ex 6944); Rio de Janeiro state: 2♀, Barra do Pirai, Ipiabas, Fazenda Floresta, Açude Superior, -22.4792161, -43.8300607, 695 m a.s.l., 10.iv.2018, J. F. Barbosa, A. L. M. Oliveira, L. L. Dumas, J. L. Nessimian leg. (UFRJ 1504); 1♀, same data (UFRJ 1526 ex UFRJ 1504); 3♂, Cachoeiras de Macacu, Reserva Ecológica de Guapiaçu, -22.452931, -42.770474, 24–26.v.2017, R. Baptista leg. (UFRJ 1349); 2♀, 1j, same data (UFRJ 1351); 1♂, same locality, 15–22.v.2017, H. Schinelli leg. (UFRJ 1485); 5♂, 5♀, 3j, Magé, Citrolândia, brejo da pedreira, -22.660213, -43.034424, 23.vi.2017, P. Castanheira and N. Ferreira-Júnior leg. (UFRJ 1353); 1♂, 1♀, 1j, same locality, Córrego do Sertão, 23.vi.2017, H. Schinelli and L. F. Botelho leg. (UFRJ 1358); 1♂, Rio Bonito, Lavras, Estrada Velha de Lavras, açude, -21.3293582, -44.9689685, 88 m a.s.l., 23.x.2017, J. F. Barbosa, A. F. Antunes, L. L. Dumas and J. L. Nessimian leg. (UFRJ 1486); 1♀, Teresópolis, Serra do Subaio, -22.453124, -42.913033, 20–22.iv.1995,

R. Baptista and M. Landim leg. (MNRJ 60015 MNRJ 1568); 1♂, 2j, same data (MNRJ 1569); 1♀, Rio Grande do Sul: Santa Maria, -29.665521, -53.806318, 24.ii.2005, D. Linck leg. (MCTP 43318 ex 40256); São Paulo state: 1♂, Juquiá, -24.317808, -47.635463, 19.i.1950, F. Lane leg. (MZUSP 11248); 1♂, Ubatuba, Parque Estadual da Serra do Mar, Núcleo Picinguaba, Praia da Fazenda, -23.364470, -44.824987, 01.x.2009, A. Hoffmann leg. (UFRJ 1553); 1♀, same locality, 26–30.v.2010, A. Hoffmann leg. (UFRJ 1554); 1♀, Tocantins: Palmas, -10.184444, -48.333611, 2002, I. Knysak & R. Martins leg. (IBSP 214856); **GUYANA**: 1♀, Potaro-Siparuni, Tumatumari, 5.2615047, -59.1659206, 19.ix.1936 (MZUF); **HAITI**: 1♀, Ouest, Port-au-Prince, 18.5790242, -72.3545005, 1961, Duret leg. (MACN 39718 ex 26769).

Tetragnatha mandibulata

BRAZIL: 1♂, 1♀, Amapá: Uaçá [Uassa, ex French Guyana], 3.534001, -51.524370, K. Jelski leg. (MIZ 225530-225531, mixed with samples of *Tetragnatha filiformata* Roewer, 1942); Amazonas: 1♂, 1♀, Humaitá, -7.532108, -63.021515, i.1975, A. Scivittaro leg. (MZUSP 11247); 1♀, Manaus, -3.121564, -60.024862, 26.vii.1962, K. Lenko leg. (MZUSP 11765); 1♂, 3♀, Espírito Santo: Anchieta, CSV Pasto, -20.800352, -40.644682, 20.viii.2008, R. Baptista, A. Pérez-González and A. Alves leg. (UFRJ 1549); 1♀, Mato Grosso: foz do Rio Koluene [Rio Culuene], -13.824893, -53.525047, J. C. de M. Carvalho leg. (MNRJ 60007 ex MNRJ 02597); 1♀, Pará: Cotijuba, -1.216842, -48.533279, 01–02.IV.2006, N. Abraham leg. (MPEG 031361); Rio de Janeiro state: 2♀, Cachoeiras de Macacu, Reserva Ecológica de Guapiaçu, -22.452931, -42.770474, 24–26.v.2017, R. Baptista leg. (UFRJ 1350); 1♂, 1♀, same locality, 29.vi.2017, P. Castanheira leg. (UFRJ 1356); 2♀, Guapimirim, Segredo, Sítio Sonho Meu, -22.536428, -42.992255, 25–26.vi.2016, R. Baptista leg. (UFRJ 1224); 1♀, 1j, Nova Friburgo, Lumiar, -22.350749, -42.326073, 2012, D. T. Castro leg. (UFRJ 1163); 1♀, Petrópolis, -22.512286, -43.181206, Mello-Leitão leg. (MNRJ 60004 ex MNRJ 00402 ex MLPC 973); 1♂, 1♀, Rio de Janeiro, Parque Estadual da Pedra Branca, Represa do Cigano, -22.9527582, -43.3082834, 23.v.1974, Jandir and Argentino leg. (MNRJ 06600); São Paulo state: 3♀, Iguape, -24.703607, -47.551302, O. Leonardos leg. (MNRJ 02602 ex 41891); 1♀, Pariqueira-Açu, -24.715, -47.880833, no further data (MZUSP 74667 ex 62113); 1♂, Pirassununga, Emas, -23.550278, -46.633889, 26.x.1951 (MZUSP 74666 ex 4972); 1♀, Ubatuba, Parque Estadual Serra do Mar, Núcleo Picinguaba, Praia da Fazenda, -23.364470, -44.824987, 18.v.2007, R. Baptista leg. (UFRJ 1550); 3♂, 11♀, same locality, 26–30.v.2010, A. Hoffmann leg. (UFRJ 1551).

Tetragnatha nitens

ARGENTINA: Buenos Aires province: 1♂, 1♀, 1j, xii.1955, Chapadmalal and A. Bachmann leg. (MACN 24405); 1♀, 4j, Adela, -35.683889, -57.954083, vii.1972, Cesari leg. (MACN 24236); 1♂, Buenos Aires, 06.iv.1903

(MACN 24464); 1♀, same locality, Palermo, -34.599722, -58.381944, 16.iii.1954, J. A. de Carlo leg. (MACN 3953); 1♀, Carlos Casares, -35.616667, -61.366667, 04.xi.1978 (MACN 24527); 1♂, 2♀, Delta de Tigre, Arroyo Caraguatá, -34.425833, -58.596667, i.1969, A. Bachmann leg. (MACN 39604 ex 24500); 3♀, El Palomar, -34.616667, -58.583333, 19.ii.1951, A. Bachmann leg. (MACN 3230); 1♂, 1♀, 1j, Pedro Luro, -39.5, -62.683300, 12.ii.1973 (MACN 24565); 4♂, Punta Lara, -34.816667, -57.966667, A. Bachmann leg. (MACN 24574); 1♀, San Pedro, -33.679444, -59.666944, xii.1913, A. G. Fress leg. (MACN 24572); 5♀, 4j, Catamarca: El Rodeo, -28.216667, -65.866667, 16–23.i.1977 (MACN 24498); 1♀, Chaco: Resiste de la Serna, -27.451389, -58.986667, x.1975 (MACN 24433); Córdoba province: 3♂, 2♀, 28–29.i.1990, A. Peretti leg. (MACN 24567); 1♂, 1♀, Cabana, -31.236100, -64.328100, 08.v.1947, Max Birabén leg. (NHM); 1♀, Calamuchita, -31.916670, -64.633330, iii.1962, Viana leg. (MACN 24426); 1♀, Córdoba, Arguello, -31.416667, -64.183333, xii.1944, De Carlo leg. (MACN 39600 ex 1957); 1♂, 1♀, 1j, Villa Giardino, -31.033333, -64.483333, i.1990, T. Devoto leg. (MACN 24582); 13♂, 24♀, Corrientes: Manantiales, -27.9249206, -58.1102847, ix.1960, Apóstol leg. (MACN 5265); 1♀, same data (MACN 39611 ex 5266); Entre Ríos: 1♀, Paraná, Canal 6, -31.733333, -60.533333, ii.1963, A. Bachmann leg. (MACN 24425); 1♂, Villa Elisa, Balneario, -32.166667, -58.4, i.1989, A. Olive leg. (MACN 22252); 1♀, La Pampa: Combello, -36.620556, -64.3075, ii.1940, H. Hopper leg. (MACN 24451); La Rioja: 1♂, 1♀, x.1965, Mauny leg. (MACN 24406); 1♀, Patquía, Guayapa, -30.05, -66.883, x.1963, M. E. Galiano leg. (MACN 24460); 1♂, 3♀, Rioja: Iliar, -29.4142786, -66.9258173, 1940, Prof. P. Gomez leg. (MACN 24475); 1♀, Mendoza: -32.883333, -68.816667, iv.1970, Willian leg. (MACN 24471); Misiones: 1♂, “Misiones/ Corrientes”, 03–12.i.1989 (MCTP 0836); 2♂, 1♀, 7j, “Puerto Yatay?”, -25.985922, -54.4420392, viii.1959, Nuñez leg. (MACN 24424); 1♀, Cataratas del Iguazú, -25.683611, -54.453889, xi.54, B. C. Schiapelli leg. (MACN 24526); 3♀, Posadas, -27.361667, -55.900278, xi.1947, De Carlo and D’Amico leg. (MACN 2435); 1♀, San José, Pindapoy, -27.57185, -55.8405244, xii.1941, Max Birabén leg. (MLP 16425 wrongly mixed with a male syntype of *Tetragnatha longidens* Mello-Leitão, 1945); 1♀, same data (MNRJ 60016 ex MNRJ 2308 wrongly mixed with a male syntype of *Tetragnatha longidens* Mello-Leitão, 1945); 2♀, Santa Maria: -27.934526, -55.407083, x.1956, Viana leg. (MACN 39615 ex 24423); 1♀, Tobuna, -26.47, -53.891389, ii.1952, W. Partridge leg. (MACN 39610 ex MACN 4078); 2♂, 29♀, Río Negro: General Roca, Balsa, -39.033333, -67.583333, i.1962, A. Bachmann leg. (MACN 5480); 4♂, 4♀, 1j, Santa Fé: xi.1969, Arce leg. (MACN 24544); 1♂, 1j, Estancia Las Gamas, 20 Km W of Vera, -29.4265464, -60.3702699, 300 m a.s.l., 30.x.1994, M. Ramírez and J. Faibovich leg. (MACN 24543); 1♀, same locality, 20–24.iii.2014, M. Ramírez, C. Grismado, L. Piacentini and M. González Marquez leg. (MACN

31323); 1♂, same data (MACN 31341); 2♂, 2♀, same data (MACN 31612); 4♂, 4♀, same data (MACN 31613); **BRAZIL**: 6♂, 2♀ 1j, Espírito Santo: Ilha de Trindade -20.524722, -29.324722, no further data (MNRJ 02601); 1♀, same locality (MNRJ 02608); 1♂, same locality (MNRJ 04361); 17♂, 23♀ 7j, same locality, 17.viii.1957, Wolfgang (Exp. Inst. Butantan) leg. (IBSP 1323, 1328, 1329, 1330, 1334, 1368); 2♂, 2♀, 4j, Goiás: São Miguel do Araguaia, -13.275, -50.162778, 04.ix.2002, José Alexandre Barrigossi leg. (MCTP 19598); 2♂, 1♀, Mato Grosso: Chapada dos Guimarães, -15.460833, -55.75, 20–29.vii.2000, C. Strüssman leg. (MCTP 11314); 1♀, same data (MCTP 11555); 2♂, 1♀, same locality, 23–30.viii.2000, C. Strüssman leg. (MCTP 11333); 2♀, same locality, 20–30.ix.2000, C. Strüssman leg. (MCTP 11534); 1♂, 1♀, Pontes e Lacerda, Usina Hidrelétrica de Guaporé, -15.1353576, -58.9889658, 01–14.x.2002, Operação Coatá leg. (MCTP 43320 ex 13581); Mato Grosso do Sul: 4♂, 2♀, 5j, Anaurilândia, -22.187778, -52.717778, 05–11.iii.2001, F. S. Cunha & J. P. L. Guadanucci leg. (IBSP 39358); 1♂, 2♀, same locality, Usina Hidrelétrica Engenheiro Sérgio Motta, 12–19.iii.2001, F. S. Cunha & C. A. R. Souza leg. (IBSP 39500); 1♂, Corumbá, -19.008889, -57.652778, 1994, J. Raizer leg. (IBSP 6479); 1♀, Passo do Lontra, Base de Estudos do Pantanan (UFMS), -19.5750615, -57.0381845, 22.v.1993, J. Raizer leg. (IBSP 20548); 5♂, 9♀, 1j, Santa Rita do Rio Pardo, -21.302778, -52.830833, 27.iv.2001, R. Bertani & E. K. Kashimata leg. (IBSP 39482); 2♀, Parque Nacional de Ilha Grande, -23.7099638, -54.0012853, 12.viii.1963, M. P. Bueno leg. (IBSP 2685); Minas Gerais: 4♂, Caxambu, -21.976944, -44.932778, Mello-Leitão leg. (MNRJ 00412); 1♀, Mariana, Camargos, -20.377778, -43.415833, 25.x.1992, R. Baptista leg. (MNRJ 1575); Pará: 1♂, 1♀, Belterra, Praia São Domingos, FLONA Tapajós, -2.635833, -54.936944, 23.ix.2018, A. D. Brescovit and G. Puerto (IBSP 226621); 1♀, Oriximiná, Lago Iripixi, -1.765833, -55.865833, 19.vi.2011, E. L. C. Silva leg. (MCTP 31948); 1♂, 4j, Parauapebas, FLONA Carajás, -60.67778, -49.901944, 7.ix.2006, Entomologia UFRJ leg. (UFRJ 0049); 1♂, 2♀, same locality, N. Ferreira Jr. and V. Alecrim leg. (UFRJ 0080); 1♀, Tucuruí, -3.767778, -49.672778, viii.1984, Equipe IBSP leg. (IBSP 5415); Paraíba: 1♀, R. von Ihering leg. (MNRJ 41995); 133♂, 188♀, 79j, Juazeirinho, Serra da Borborema, -70.677780, -36.577778, 570 m a.s.l., ix.1956 (MNRJ 4259); 3♂, Queimadas, -7.357778, -35.897778, R. von Ihering leg. (MNRJ 60017 ex MNRJ 41826); 6♀, same data (MNRJ 41827); Paraná: 1♀, Curitiba, -25.429722, -49.271944, Z. Rohr leg. (MNRJ 14141); 2♀, same locality, 21.i.1965, C. Valle leg. (MZUSP 4328); 1♀, Santo Antônio de Platina, -23.283333, -50.066667, 10.vii.1965, Exp. Dpto. Zoologia USP leg. (MZUSP 11961); Pernambuco: 1♂, Caruaru, -8.282778, -35.975833, R. von Ihering leg. (MNRJ 41843); 1♂, Piauí: Castelo do Piauí, -5.321944, -41.552778, 13.vii.2008, L. S. Carvalho leg. (MPEG 031352); 1♂, same locality, ECB Rochas Ornamentais LTDA, Casa do Pesquisador, 03.v.2006, F. M. Oliveira-Neto leg. (MPEG 031354); Rio de Janeiro: 2♂, 3♀, Macaé, Lagoa de Imboassica, -22.370833, -41.786944, x.1986 (MNRJ 1567); 1♀, same locality, Ilha do Santana, iv.1985, R. Baptista leg. (MNRJ 1583); 1♂, Niterói, -22.882778, -43.103889, Mello-Leitão leg. (MNRJ 00407 ex MLPC 866); Rio Grande do Sul: 1♀, Pe. Balduino Rambo leg. (MNRJ 42104); 2j, same data (MNRJ 42107); 1♂, 1♀, Rio Uruguai, -27.1751176, -53.555255, 11–21.v.1989 (MCTP 0840); 1♂, Alvorada, -29.99, -51.083889, 17.v.1992, M. Cunha leg. (MCTP 1540); 1♀, Barra do Ribeiro, -30.290833, -51.300833, 20.x.2002, G. M. Petersen leg. (MCTP 016672); 1♂, Cachoeira do Sul, Porteira Sete, -30.038889, -52.893889, 31.x.1992, R. G. Buss leg. (MCTP 41820 ex 3386); 1♀, same locality, Cordilheira, 04.x.1992, R. G. Buss leg. (MCTP 41823 ex MCTP 3381); 1♀, Candelária, -29.668889, -52.788889, 14.x.2017, F. Biondo leg. (MCTP 41584); 1♂, Capão da Canoa, Arroio Teixeira, -29.6458034, -49.9478308, 24.x.1984, F. C. Quadros leg. (MCTP 1393); 1♀, Caxias do Sul, Fazenda Souza, -29.121444, -51.018557, 11–12.x.1995, Eq. Lab Aracnologia PUCRS leg. (MCTP 43323 ex 7313); 1♂, Cidreira, -30.160833, -50.233889, 26.v.1992, F. Donadel leg. (MCTP 1500); 1♂, Nova Santa Rita, -29.856944, -51.273889, 23.v.2009, A. Oliveira leg. (MCTP 37269); 3♂, Novos Cabrais, Parque Witeck, -29.735, -52.947778, 01.xi.2008, R. G. Buss leg. (MCTP 27956); 1♂, 3♀, same data (MCTP 28014); 1♂, same locality, 09.x.2008, R. G. Buss leg. (MCTP 41819 ex 28045); 2♀, 1j, same locality, 25.x.2007, R. G. Buss leg. (MCTP 28416); 1♂, Salvador do Sul, -29.437778, -51.510833, 27.xi.1964, C. Valle leg. (MZUSP 74668 ex 4412); 1♂, Santa Maria, -29.683889, -53.806944, 16.iv.2005, D. Linck leg. (MCTP 43321 ex 19627); 5♂, 7♀, 1j, same locality, 24.ii.2005, D. Linck leg. (MCTP 40256); 6♂, 8♀, same locality, 15.ii.2011, D. Linck leg. (MCTP 40287); 1♂, 2♀, same locality, 15.x.1998, C. B. Kotzian and L. Indrusiak leg. (MCTP 43322 ex 40632); 1♂, same locality, v.1988, Eq. Def. Fitos leg. (MCTP 4882); 4♀, same locality, v.1988, Eq. Def. Fitos leg. (MCTP 4883); 2♂, 2♀, 1j, same locality, 18.v.1990, Eq. Def. Fitos leg. (MCTP 4884); 1♂, 5♀, same locality, 26.iii.1990, D. Linck leg. (MCTP 5971); 1♀, same locality, 30.i.1990, D. Linck leg. (MCTP 5972); 1♂, 1♀, same locality, 26.iii.1990, D. Linck leg. (MCTP 5973); 4♂, 1♀, same locality, 28.ii.1990, D. Linck leg. (MCTP 5980); 1♂, 2♀, same locality, 28.ii.1990, D. Linck leg. (MCTP 5985); 3♂, 2♀, same locality, 28.ii.1990, D. Linck leg. (MCTP 5987); 1♀, São Borja, Rio Uruguai, -28.660833, -56.003889, 03–12.i.1989 (MCTP 0833); 1♂, same locality, Reserva Biológica São Donato, 10–25.v.2012, Miguel Machado leg. (MCTP 36184); 1♀, São Francisco de Paula, -29.447778, -50.583889, 09–12.i.1997, A. A. Lise et al. leg. (MCTP 10845); 1♂, Torres, -29.335, -49.726944, 26.iii.2006, E. L. C. da Silva leg. (MCTP 1426); 1♂, same locality, Colônia São Pedro, 07–09.iv.1992, A. Braul leg. (MCTP 1618); 1♀, Viamão, -30.072391, -51.097196, 07.xi.1995, A. A. Lise et al. leg. (MCTP 43325 ex 7807); 1♀, same locality, Est. Exp. Fiotécnica, 25.viii.1995, A. A. Lise et al. leg. (MCTP 43324 ex 7578); 1♂, Xangrilá, -29.800833, -50.043889, 05.

ii.1991, A. A. Lise leg. (MCTP 0476); 1♀, Santa Catarina: Itá, Rio Uruguai, -27.290833, -52.322778, ix.1988 (MCTP 0585); São Paulo state: 1♂, Araçatuba, -21.208889, -50.432778, 10.iii.1964, Vizotto leg. (MZUSP 3469); 1♀, Boracéia/Salesópolis, -22.192778, -48.778889, 16.viii.1964, P. Biasi leg. (MZUSP 70905); 1♂, Ilha Bela, Ilha de São Sebastião, -23.815, -45.370556, ix.1925, H. Luederwaldt leg. (MZUSP 11139); 1♀, Pirassununga, Cachoeira, -21.995833, -47.425833, 10.ii.1940 (MZUSP 6372); 1♂, 1♀, same locality, Emas, 26.x.1951 (MZUSP 4972); 1♀, 1j, Porto Ferreira, Lagoa São Vicente, -21.853889, -47.478889, 15.xii.1948, Schubart leg. (MZUSP 7112); 2♀, São Bernardo do Campo, -23.693889 -46.565, iii.1926, Spitz leg. (MZUSP 11129); 4♂, 2♀, 1j, Ubatuba, Parque Estadual da Serra do Mar, Núcleo Picinguaba, Praia da Fazenda, -23.433889, -45.070833, 26–30.v.2010, A. Hoffmann leg. (UFRJ 1527); 1♀, same data (UFRJ 1528); 1♀, Tocantins: Miracema do Tocantins, Usina Hidrelétrica Luis Eduardo Magalhães, -9.7557469, -48.3753172, 01-11.x.2001, E. K. Kashimata and C. Y. Fukami leg. (IBSP 31572); 1♂, Palmas, Taquaralto, Jardim Taquari, -10.184444, -48.333611, 04–10.xi.2002, I. Kny-sak & R. Martins leg. (IBSP 219579); 1♂, same locality, Margem direita do Rio Tocantins, i.2002, D. M. Cândido & M. Costa leg. (IBSP 40486); **CHILE**: 1♀, Malleco, Victoria, Fundo Maria Ester, -38.216667, -72.333333, 14.i.1989, M. Ramírez leg. (MACN 39805 ex 24533); 2♀, Valparaíso, Valparaíso, -33.05, -71.616667, x.1970, M. Fritz leg. (MACN 24656); **COLOMBIA**: 1♂, Cundinamarca, Bogotá, 4.598056, -74.075833, no further data [sub *T. bogotensis*, misidentified] (NHM S-071-73); **GUYANA**: 1♂, 25j, Demerara-Mahaica: Georgetown, Cummings Lodge, Espandaur, 6.814501, -58.111694, 09.viii.1936, Romiti leg. [sub syntypes of *T. petrunkevitchi*, 1♂, 2♀, 23j on Museum's catalog] (MZUF 530); 1♀, Potaro-Siparuni: Garraway Landing, 5.343960, -59.014512, 30.vi.1936 [misidentified syntype of *T.*

petrunkevitchi] (MZUF); **HAITI**: 1♂, Ouest, Porto Príncipe, 18.542500, -72.338611, 1961, Duret leg. (MACN 26769); **MARTINIQUE**: Carrere, 14.5906297, -60.99105, 08–21.vi.2013, A. Sánchez leg. (IBSP 169868); **NICARAGUA**: 1♂, Rivas, Sapoá, Rio Sapoá, 11.2475686, -85.6350908, 09.viii.1962, Duret leg. (MACN 24641); **PERU**: 7 ♀, 4j, Lima, Lima, -12.035, -77.018611, no further data (MNRJ 01350); 2j, same location (MNRJ 01291); **URUGUAY**: 1♀, 1j, Lavalleja, Ciudad de Minas, Parque de Vocaciones, -34.4246864, -55.1943214, xii.2005, E. H. Wienskosi leg. (MNRJ 60012 ex MNRJ 06920); **VENEZUELA**: 1 ♀, Sucre, Cumaná, 10.456389, -64.167500, 04.vii.1964, Ronderos leg. (MACN 24569).

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PANAMA: 1♂, 1j, Isla Barro Colorado, 9.152364, -79.846957, i.1958, A. M. Chickering leg. (MNHN); **BRAZIL**: 1♂, 1♀, Mato Grosso: Chapada dos Guimarães, -15.355152, -55.872669, 23–30.viii.2000, C. Strüssman leg. (MCTP 43339 ex 11333); Mato Grosso do Sul: 1♂, Pantanal, Serra do Amolar, -17.9161335, -57.5294296, 2010, L. S. M. Sugai leg. (IBSP 170045); 1♂, Paraíba: Juazeirinho, Serra da Borborema, -9.431399, -40.508095, 570m a.s.l., ix.1956 (MNRJ 60018 ex MNRJ 4259); 3♀, 2j, Paraná, São Luiz do Purunã, -25.461614, -49.710482, 27.iv.1967, P. Biasi leg. (MZUSP 7025); 1♂, 1j, Pernambuco: Moreno, Bonança (ex Tapera), -8.438258, -38.272535, B. Pickel leg. (MNRJ 42570); 1♂, Rio de Janeiro state: Macaé, Ilha do Santana, -22.416227, -41.704189, ix.1985, R. L. C. Baptista leg. (MNRJ 1584); 2♀, Rio Grande do Sul: Pelotas, Rodovia BR-116, -31.733448, -52.393171, 10.v.1967, P. Biasi leg. (MZUSP 7571); 1♂, 1♀, São Paulo state: Ubatuba, Parque Estadual Serra do Mar, Núcleo Picinguaba, Praia da Fazenda, -23.364470, -44.824987, 26–30.v.2010, A. Hoffmann leg. (UFRJ 1556).

A new species of *Aphyocharax* Günther, 1868 (Characiformes, Characidae) from the Maracaçumé river basin, eastern Amazon

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Abstract

A new species of *Aphyocharax* is described from the Maracaçumé river basin, eastern Amazon, based on morphological and molecular data. The new species differs from all its congeners, mainly by possessing the upper caudal-fin lobe longer than the lower one in mature males, and other characters related to teeth counts, colour pattern, and body depth at dorsal-fin origin. In addition, the new species is corroborated by a haplotype phylogenetic analyses based on the Cytochrome B (Cytb) mitochondrial gene, where its haplotypes are grouped into an exclusive lineage, supported by maximum posterior probability value, a species delimitation method termed the Wiens and Penkrot analysis (WP).

Key Words

Freshwater, integrative taxonomy, Neotropical ichthyology, sexual dimorphism

Introduction

The Neotropical fish genus *Aphyocharax* Günther, 1868 is distributed along the river basins of the Orinoco, Amazon, and La Plata systems, as well as in the river systems draining the Guiana Shield (Géry 1977; Taphorn and Thomerson 1991; Tagliacollo et al. 2012; Brito et al. 2018; Fricke et al. 2019), with highest diversity in the Amazon basin (Fricke et al. 2019). According to Brito

et al. (2018), the genus comprises 11 valid species: *Aphyocharax agassizii* (Steindachner, 1882), *A. anisitsi* Eigenmann & Kennedy, 1903, *A. avary* Fowler, 1913, *A. colifax* Taphorn & Thomerson, 1991, *A. dentatus* Eigenmann & Kennedy, 1903, *A. erythrurus* Eigenmann, 1912, *A. gracilis* Fowler, 1940, *A. nattereri* (Steindachner, 1882), *A. pusillus* Günther, 1868, *A. rathbuni* Eigenmann, 1907,

and *A. yekwanae* Willink, Chernoff & Machado-Allison, 2003. However, there are at least four undescribed species (Souza-Lima 2007).

Tagliacollo et al. (2012) included seven valid species of *Aphyocharax* in their phylogenetics analysis, and provided a hypothesis of interspecific relationships based on both molecular and morphological datasets. Their parsimony-based total evidence analysis (TE) indicates that *Aphyocharax* and *Prionobrama* Fowler, 1913 form a clade supported by three morphological synapomorphies: (1) interrupted lateral line with a single perforated scale on the posterior region of caudal peduncle; (2) absence or reduction of the fourth infraorbital bone canal; and (3) presence of a single large cusp on anterior maxillary teeth. In addition, three morphological synapomorphies have been proposed for *Aphyocharax*: (1) narrow trigemino-facialis foramen like a cleft with sphenotic almost excluded from its margin; (2) dorsal projection of maxilla overlapping the second infraorbital; and (3) dorsal margin of third postcleithrum not projecting dorsally to posterior region of scapula (Mirande 2010; Tagliacollo et al. 2012). However, several other morphological features have been commonly used to characterize *Aphyocharax* species, such as the red caudal-fin colouration, moderately elongated body, single series of tricuspid teeth on the premaxilla and mandible, and maxilla with teeth on up to two-thirds of its ventral margin (Taphorn and Thomerson 1991; Willink et al. 2003; Tagliacollo et al. 2012; Brito et al. 2018).

During recent fieldwork at the Maracaçumé river basin, eastern Amazon, specimens of an additional undescribed species of *Aphyocharax* were collected and is herein described, based on both morphological and molecular evidence, in accordance to an integrative taxonomy perspective.

Methods

Taxa sampling, specimens collection, and preservation

Individuals collected for this study were euthanized with a buffered solution of Tricaine methanesulfonate MS-222 at a concentration of 250 mg/L for a period of 10 min or more until opercular movements completely ceased. Specimens selected for morphological analysis were fixed in 10% formalin and left for 10 days, after which they were preserved in 70% ethanol and specimens selected for molecular analysis were fixed, and preserved in absolute ethanol.

Specimens for morphological analysis are listed in type and comparative material lists. Specimens for molecular analysis are listed in Table 1. We also retrieved sequences from other species of *Aphyocharax* and allied genera for a comparative analysis from the National Center for Biotechnology Information (NCBI) databases (Table 1).

Morphological analysis

Measurements and counts were made according to Fink and Weitzman (1974) and Brito et al. (2018), except for the count of scale rows below lateral line, which were counted to the insertion of pelvic-fin. Vertical scale rows between the dorsal-fin origin and lateral line do not include the scale of the median predorsal series situated just anterior to the first dorsal-fin ray. Counts of supraneurals, vertebrae, procurent caudal-fin rays, unbranched dorsal and anal-fin rays, branchiostegal rays, gill-rakers, and teeth were taken only from cleared and stained paratypes (C&S), prepared according to Taylor and Van Dyke (1985). The four modified vertebrae that constitute the Weberian apparatus were not included in the vertebrae counts and the fused PU1 + U1 was considered as a single element. Osteological nomenclature follows Weitzman (1962). Institutional abbreviations are: **ANSP** Academy of Natural Sciences, Philadelphia, Pennsylvania, USA; **BMNH** Natural History Museum, London, UK; **CAS** California Academy of Sciences, San Francisco, California, USA; **CICCAA** Coleção Ictiológica do Centro de Ciências Agrárias Ambientais, Universidade Federal do Maranhão, Chapadinha, Brazil; **FMNH** Division of Fishes, Department of Zoology, Field Museum of Natural History, Chicago, Illinois, USA; **LBP** Laboratório de Biologia e Genética de Peixes, Departamento de Morfologia, Instituto de Biociências, Universidade Estadual Paulista “Júlio de Mesquita Filho”, Campus de Botucatu, São Paulo, Brazil; **MNRJ** Museu Nacional, Departamento de Vertebrados, Setor de Ictiologia, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil; **UFRJ** Coleção Ictiológica do Instituto de Biologia, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil; **UFRO** Universidade Federal de Rondônia, Porto Velho, Brazil.

DNA extraction, amplification, and sequencing

DNA extraction was carried out with the Wizard Genomic DNA Purification kit (Promega) following manufacturer's protocol. DNA quality was evaluated by 0.8% agarose gel electrophoresis stained with GelRed (Biotium). DNA was stored in -20°C until further procedures. Samples (Table 1) were amplified using standard PCR (Polymerase Chain Reaction) for partial Cytochrome B gene (CytB), using primers developed by Ward et al. (2005) (CytB2F 5' - GTG ACT TGA AAA ACC ACC GTT G-3' and CytB2R 5' - AAT AGG AAG TAT CAT TCG GGT TTG ATG-3').

Amplification reactions were performed in a total volume of 15 μl comprising 1 \times buffer, 1.5 mM MgCl_2 , 400 μM dNTP, 0.2 μM of each primer, 1 U of Taq Polymerase (Invitrogen), 100 ng of DNA template, and ultrapure water. The amplification program consisted of a denaturation of 94°C for 3 min, followed by 35 cycles

Table 1. List of species, specimens and their respective GenBank sequence accession numbers. Sequences made available by this study in bold.

Species	Catalog number	Genbank accession
<i>Aphyocharacidium bolivianum</i>	LBP9055-42219	HQ289710
<i>Aphyocharax anisitsi</i>	LBP 25524	JQ820081
<i>Aphyocharax anisitsi</i>	LBP3764-22190	HQ289581
<i>Aphyocharax avary</i>	CICCAA2344-1	MK409660
<i>Aphyocharax avary</i>	CICCAA2344-3	MK409661
<i>Aphyocharax brevicaudatus</i> sp. nov. (female)	CICCAA02306	MK409668
<i>Aphyocharax brevicaudatus</i> sp. nov. (male)	CICCAA02308	MK409669
<i>Aphyocharax brevicaudatus</i> sp. nov. (male)	CICCAA02310	MK409670
<i>Aphyocharax dentatus</i>	LBP 26163	JQ820082
<i>Aphyocharax dentatus</i>	LBP 3604	JQ820083
<i>Aphyocharax</i> cf. <i>erythrurus</i>	LBP 15819	JQ820076
<i>Aphyocharax</i> cf. <i>erythrurus</i>	LBP 15820	JQ820077
<i>Aphyocharax nattereri</i>	LBP 22345	JQ820070
<i>Aphyocharax nattereri</i>	LBP 22132	JQ820071
<i>Aphyocharax pusillus</i>	LBP 23546	JQ820078
<i>Aphyocharax pusillus</i>	LBP4046-22920	HQ289590
<i>Aphyocharax rathbuni</i>	LBP 36496	JQ820079
<i>Aphyocharax rathbuni</i>	LBP 40434	JQ820080
<i>Aphyocharax</i> sp.	LBP1587-11774	HQ289533
<i>Aphyocharax</i> sp.	LBP 16349	JQ820084
<i>Prionobrama paraguayensis</i>	LBP 19465	JQ820073
<i>Prionobrama paraguayensis</i>	LBP 19468	JQ820072
<i>Prionobrama filigera</i>	LBP 23664	JQ820075
<i>Prionobrama filigera</i>	LBP 23663	JQ820074
<i>Leptagoniates steindachneri</i>	LBP 4137-23661	HQ289600
<i>Paragoniates alburnus</i>	LBP9208-43156	HQ289712
<i>Phenagoniates macrolepis</i>	LBP6105-35623	HQ289678
<i>Xenagoniates bondi</i>	LBP3074-19694	HQ289563

of 94 °C for 30 s, 46–48 °C for 45 s, and 72 °C for 80 s, and an extension phase of 5 min at 72 °C. Amplicons were visualised in 1% agarose gel electrophoresis stained with GelRed (Biotium) and purified with Illustra GFX PCR DNA and Gel Purification Kit (GE Healthcare). Samples were sequenced using both forward and reverse primers and BigDye Terminator 3.1 Cycle Sequencing kit in ABI 3730 DNA Analyser (Thermo Fisher Scientific).

Data partition, evolution models, and alignment

The dataset included the partial Cytochrome B (CytB) mitochondrial gene (754bp). Sequences were aligned using ClustalW (Chenna et al. 2003), and were translated into amino acids residues to test for the absence of premature stop codons or indels using the program MEGA 7 (Kumar et al. 2016). Substitution Saturation tests were performed in DAMBE5 (Xia 2013) according to the algorithm proposed by Xia et al. (2003). The best-fit evolutionary model (GTR+G) was selected using Akaike Information Criterion (AIC) by jModelTest 2.1.7 (Darriba et al. 2012).

Phylogenetic analysis

A Bayesian inference-based phylogenetic (BI) tree was estimated in MrBayes (Huelsenbeck and Ronquist 2001) plugin in Geneious 9.0.5 to reconstruct the evolutionary relationships among terminals using General Time Reversible (GTR+G) as evolutionary model; and following parameters: two Markov chain Monte Carlo (MCMC) runs of four chains each for 3 million generations and sampling frequency of 1,000. We used sequences of *Aphyocharacidium bolivianum* Géry, 1973, *Leptagoniates steindachneri* Boulenger, 1887, *Paragoniates alburnus* Steindachner, 1876, *Phenagoniates macrolepis* (Meek & Hildebrand, 1913), *Prionobrama filigera* (Cope, 1870), *Prionobrama paraguayensis* (Eigenmann, 1914), and *Xenagoniates bondi* Myers, 1942 as outgroups.

Species concept, species delimitation, and diagnoses

The unified species concept is herein adopted by expressing the conceptual definition shared by all traditional species concepts, “species are (segments of) separately evolving metapopulation lineages”, disentangling opera-

tional criterion elements to delimit taxa from species concepts (de Queiroz 2005, 2007). According to this concept, species are treated as hypothetical units and could be tested by the application of distinct criteria (species delimitation methods) (de Queiroz 2005, 2007). It allows for any criterion to separately provide evidence about species limits and identities, independently from other criteria (de Queiroz 2005, 2007). However, evidence corroborated from multiple operational criteria is considered to produce stronger support for hypotheses of lineage separation (de Queiroz 2007; Goldstein and Desalle 2010), a practice called “integrative taxonomy” (Dayrat 2005; Goldstein and Desalle 2010; Padial et al. 2010).

Two distinct and independent operational criteria for species delimitation, based on morphological and molecular data, were implemented here: the population aggregation analysis (Davis and Nixon 1992) (hereafter PAA); and a tree-based method as proposed by Wiens and Penkrot (2002) (hereafter WP, following Sites and Marshall 2003).

Population aggregation analysis (PAA)

The PAA (Davis and Nixon 1992) is a character-based method, in which species are delimited by unique combination of morphological character states occurring in one or more populations (Costa et al. 2014). The morphological data was based on both examined material and literature (e.g. Günther 1869; Cope 1870; Eigenmann and Kennedy 1903; Eigenmann and Ogle 1907; Fowler 1913; Eigenmann 1915; Fowler 1940; Géry 1977; Taphorn and Thomerson 1991; Britski et al. 1999; Souza-Lima 2003a, 2003b; Willink et al. 2003; Gonçalves et al. 2005; Tagliacollo et al. 2012; Brito et al. 2018).

Wiens and Penkrot analysis (WP)

The WP analysis was based on CytB haplotypes, supported on the direct inspection of the haplotype tree generated by the phylogenetic analysis having as terminals at least two individuals (haplotypes) of each focal species. In this method, the term ‘exclusive’ is used instead of monophyletic, as the term monophyly is considered inapplicable below the species level (Wiens and Penkrot 2002). Clustered haplotypes with concordant geographic distribution forming mutual and well supported clades (exclusive lineages) are considered strong evidence for species discrimination (absence of gene flow with other lineages). When haplotypes from the same locality fail to cluster together, there is potential evidence of gene flow with other populations (Wiens and Penkrot 2002). Statistical support for clades is assessed by the posterior probability, considered as significant values about 0.95 or higher (Alfaro and Holder 2006). When only one haplotype (specimen) from one putative population was available, the species delimitation was based on the exclusivity of the sister clade of this single haplotype,

supported by significant values, allowing us to perform the test in populations with only one haplotype (Wiens and Penkrot 2002). In addition, the method allows recognition of non-exclusive lineages as species if their sister clade is exclusive and supported by significant values (Wiens and Penkrot 2002).

Results

Aphyocharax brevicaudatus sp. nov.

<http://zoobank.org/C5D86CB2-B51B-4B45-AFF7-6E483533B680>

Figs 1, 2

Holotype. CICCAA 02293, (male) 35.9 mm SL, Brazil, Maranhão state, Maracaçumé municipality, Maracaçumé River, 2°3'14"S, 45°57'16"W; 29 Jun 2018, E.C. Guimarães and P.S. Brito.

Paratypes. All from Brazil, Maranhão state: CICCAA 02294, 1 (female), 32.4 mm SL, CICCAA 02295, 35 (males), 20.9–31.7 mm SL, CICCAA 02296, 94 (females), 21–32.1 mm SL, CICCAA 02297, 30 (females) C&S, 22.2–30.8 mm SL, CICCAA 02312, 2 (males) C&S, 28.3–32.1 mm SL, UFRJ 11746, 10 (female), 24.2–30.2 mm SL; all collected with holotype.

Diagnosis (PAA). *Aphyocharax brevicaudatus* sp. nov. differs from all its congeners by possessing the upper lobe of the caudal fin longer than the lower lobe in mature males (vs upper and lower lobes similar in length, see Figs 1, 2; Tagliacollo et al. 2012: fig. 4). Additionally, the new species is distinguished from *Aphyocharax avary* and *A. pusillus* by having hyaline middle caudal-fin rays (vs black or dark brown middle caudal-fin rays, Brito et al. 2018: fig. 3); from *Aphyocharax colifax*, *A. yekwanae*, and *A. rathbuni* by having caudal-fin light red colouration never surpassing the vertical line of the adipose-fin (vs red colouration extending to the lateral midline of body, Willink et al. 2003: fig. 1); from *A. gracilis* by having a larger body depth at dorsal-fin origin (body depth), 24.5–29.2% SL (vs 20.1–20.6% SL); and from *A. pusillus* by having teeth along 2/3 of the maxillary extension (vs along proximal half of the bone, Brito et al. 2018: fig. 4).

Description. Morphometric data is presented in Table 2. Body shape is generally fusiform, slightly elongate, greatest body depth slightly anterior to dorsal-fin base; dorsal body profile straight or slightly convex from snout to vertical through anterior nostrils; straight or slightly convex from posterior nostrils to tip of supraoccipital bone; straight or slightly convex from this point to dorsal-fin origin; slightly convex along dorsal-fin base; postdorsal profile straight from base of last dorsal-fin ray to adipose-fin origin; slightly concave from adipose-fin to end of caudal peduncle; ventral profile convex from snout to pelvic-fin insertion; straight or slightly convex from this point to anal-fin origin; straight along anal-fin

Table 2. Morphometric data ($N = 141$) of the holotype and paratypes of *Aphyocharax brevicaudatus* sp. nov. from the Maracaçumé river basin. SD: Standard deviation.

	Holotype (Male)	Paratypes (Male) N = 35	Mean	SD	Paratypes (Female) N = 105	Mean	SD
Standard length (mm)	35.9	20.9–35.9	26.6	–	21.0–32.4	28.0	–
Percentages of standard length							
Depth at dorsal-fin origin (body depth)	25.4	24.5–28.7	25.9	1.0	25.6–29.1	26.3	0.8
Snout to dorsal-fin origin	53.1	51.9–55.6	52.6	1.1	51.8–54.5	52.1	0.7
Snout to pectoral-fin origin	23.2	23.0–27.7	23.9	0.9	22.6–25.2	23.5	0.6
Snout to pelvic-fin origin	46.3	45.1–49.4	45.2	0.6	44.2–47.1	44.6	0.9
Snout to anal-fin origin	67.4	63.9–68.6	64.4	0.9	64.0–68.5	64.2	0.7
Caudal peduncle depth	10.8	10.1–12.5	11.3	0.5	10.9–12.2	11.3	0.3
Caudal peduncle length	13.2	12.2–17.2	14.0	1.2	12.2–14.9	13.1	0.7
Pectoral-fin length	20.4	17.9–22.5	19.7	0.3	18.6–21.1	19.3	0.6
Pelvic-fin length	15.9	14.6–20.6	15.6	0.5	14.0–17.1	15.3	0.7
Dorsal-fin base length	11.6	9.5–13.4	11.3	0.5	10.8–13.0	11.8	0.5
Dorsal-fin height	23.1	21.2–24.8	22.4	0.5	20.8–24.0	22.3	0.7
Anal-fin base length	18.9	16.7–21.1	18.1	0.4	16.8–20.7	18.3	1.0
Eye to dorsal-fin origin	42.6	40.6–54.6	42.1	0.6	41.4–52.4	41.8	1.9
Dorsal-fin origin to caudal-fin base	47.6	46.5–49.5	46.5	0.7	46.4–49.4	46.5	0.7
Head length	24.0	22.3–26.6	24.0	1.7	22.3–24.9	23.1	0.6
Percentages of head length							
Horizontal eye diameter	30.2	28.7–36.0	31.4	1.5	29.5–34.8	31.6	1.4
Snout length	24.2	19.7–28.8	23.5	0.6	22.8–29.3	25.4	1.2
Least interorbital width	36.8	32.7–38.9	34.1	0.1	32.9–37.0	11.1	1.1
Upper jaw length	34.2	31.9–37.3	33.4	0.2	32.7–39.9	33.9	1.4

**Figure 1.** *Aphyocharax brevicaudatus* sp. nov. **a.** CICCAA 02293, holotype (male), 35.9 mm SL; **b.** CICCAA 02294, paratype (female), 32.4 mm SL, Brazil: Maranhão state: Maracaçumé river basin. (Photographed by Erick Guimarães).

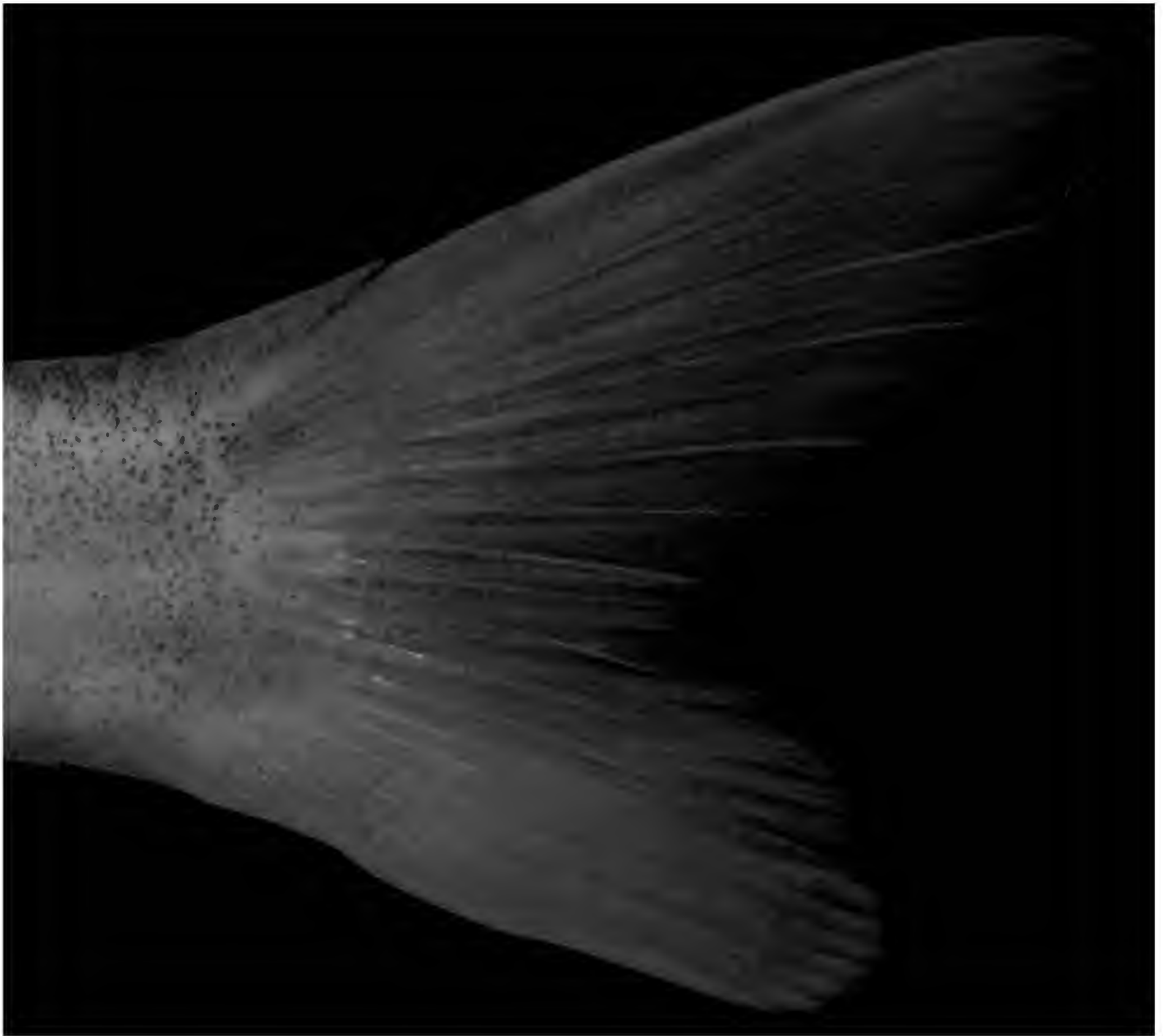


Figure 2. Caudal-fin of *Aphyocharax brevicaudatus*, holotype, CICCAA 02293, (male).

base; long snout, with its length larger than orbital diameter; five infraorbital bones; fourth infraorbital absent and sixth infraorbital reduced; posterior border of maxilla rounded, extending vertically through anterior margin of orbit, not reaching third infraorbital.

All teeth unicuspid or tricuspid and lateral cusps, when present, much smaller; premaxillary teeth in one rows with 6(9), 7(23) tricuspid teeth; maxilla with 11(3), 12(12), 13(14), or 14(3) unicuspid teeth; dentary with 6(2) or 7(30) larger tricuspid teeth followed by 6(26) or 7(6) smaller tricuspid teeth.

Scales cycloid and same size over entire body generally. Predorsal scales mostly regular, but sometimes irregular just posterior to supraoccipital and/or slightly anterior to dorsal-fin. Scales covering anterior third of caudal-fin, with up to two, three, or four scales beyond posterior margin of hypural plate. Lateral line interrupted; last scale on caudal-fin base, with 9+1(12), 10+1(74), 11+1(50), or 12+1(5). Longitudinal scales series including lateral-line scales 35(3), 36(3), 37(56), 38(49), or 39(30). Longitudinal scales

rows between dorsal-fin origin and lateral line 5(1), 6(93) or 7(47). Horizontal scale rows between lateral line and pelvic-fin origin 4(141), Axillary scale present. Scales in median series between tip of supraoccipital spine and dorsal-fin origin 13+1(24), 14+1(65), 15+1(26), or 16+1(26). Circumpeduncular scales 13(18), 14(115), or 15(8).

Dorsal-fin rays i+10(99) or ii+10(42). Dorsal-fin origin situated posterior to vertical through pelvic-fin insertion, near middle of body. First dorsal-fin pterygiophore main body located of 8th and 9th vertebrae. Adipose-fin present. Anal-fin i+14(20), iii+15(18), ii+16(61), iii+16(24), ii+17(10), iii+17(5), ii+18(3). Antermost anal-fin pterygiophore inserting at 14th and 15th vertebrae. Anterior anal-fin margin slightly convex, with antermost rays more elongate and slightly more thickened than remaining rays, forming a distinct lobe. Remaining rays smaller with straight distal margin. Pectoral-fin rays i+9(8), i+10(113), or i+11(20). Tip of pectoral-fin not reaching pelvic-fin origin, when adpressed. Pelvic-fin rays i+7(120) or ii+7(21). Tip of pelvic-fin not reaching anal-fin origin, when

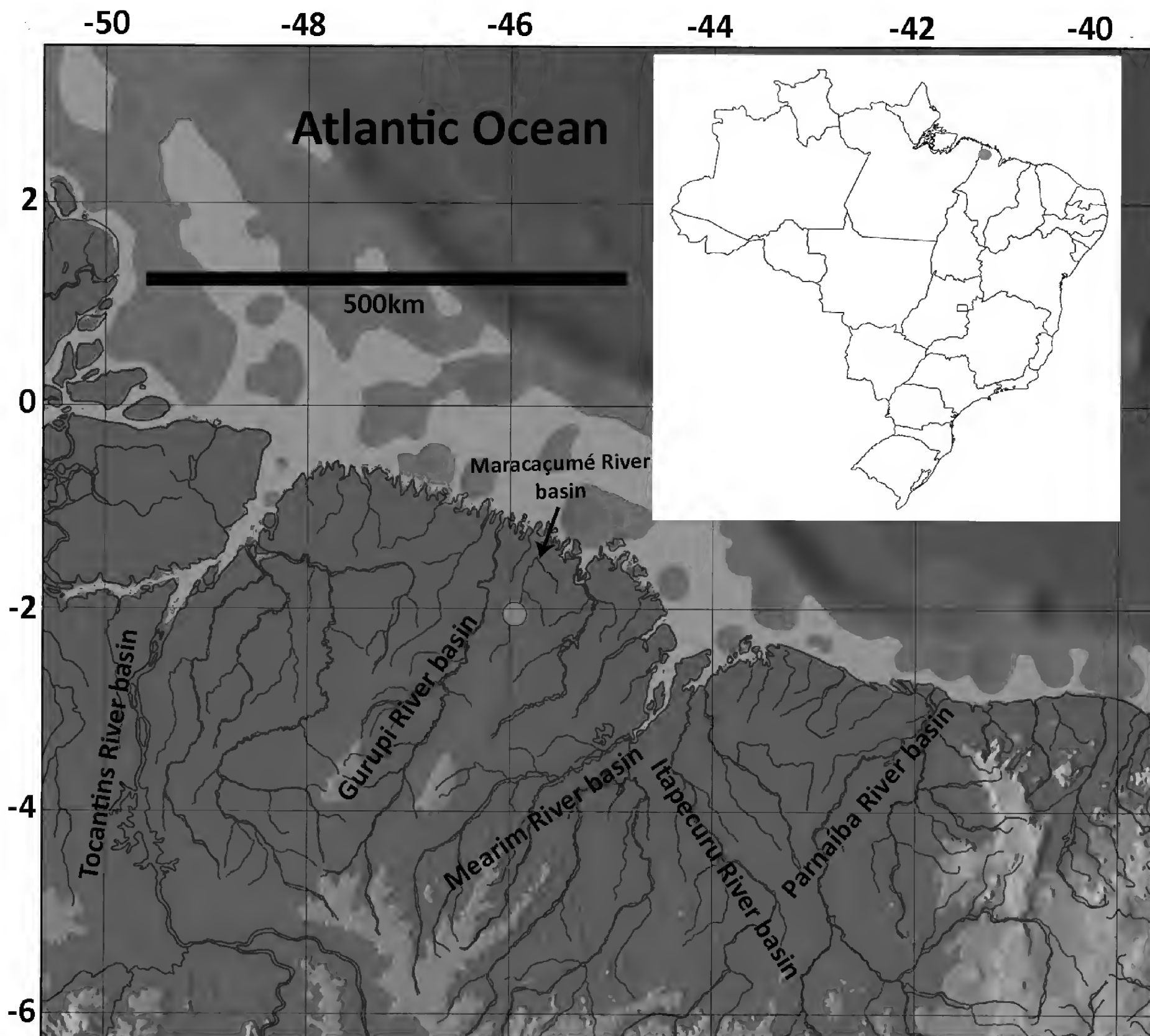


Figure 3. Type locality of *Aphyocharax brevicaudatus* sp. nov.

addressed. Caudal-fin with a sexually dimorphic pattern, described below (Fig. 1). Principal caudal-fin rays 10+9(130) or 10+10(11); dorsal procurrent rays 8(2), 9(3) or 10(27) and ventral procurrent rays 7(2), 8(3) or 9(27).

Branchiostegal rays 4(32). Supraneurals 6(4) 7(27) or 8(1). Total vertebrae 31 (1), 32(30) or 33(1).

Colour in alcohol. Ground colouration light brown to yellowish brown. Inconspicuous light brown to light gray stripe from humeral spot to caudal-fin base, more conspicuous on posterior half. Humeral region with one conspicuous dark brown to black humeral spot. Smaller dark brown or black chromatophores homogeneously scattered. Smaller dark brown or black chromatophores homogeneously scattered along body, except on chest. Head ground colouration similar to trunk, with dark brown chromatophores present on jaws, tip of snout, opercle, and dorsal portion of head. Dorsal, adipose, anal, caudal, pectoral, and pelvic fins hyaline to light brown.

Sexual dimorphism. Caudal-fin of mature males with upper lobe longer (about 2/3 longer) than lower one, while both caudal-fin lobes have similar length in females (Fig. 1). Gill glands were found in all analyzed mature males of *Aphyocharax brevicaudatus* sp. nov. and were always absent in females. They were always located on anteriormost portion of lower branch of first gill arch, extending posteriorly through variable number of gill filaments.

Etymology. The name *brevicaudatus* is a contraction of the Latin words *brevis* meaning “short” and *cauda* meaning “tail”, an allusion to the shorter caudal-fin lower lobe in the mature males of the new species.

Geographic distribution. *Aphyocharax brevicaudatus* sp. nov. is currently known only from a single locality, the Maracaçumé river basin, a small and isolated coastal river basin of the eastern Amazon region (Fig. 3).

Discussion

Several authors supported *Aphyocharax* as a monophyletic genus within Aphyocharacinae (Mirande 2010; Oliveira et al. 2011, Tagliacollo et al. 2012, Betancur-R. et al. 2018, Mirande 2018) and also the sister-group relationship between *Aphyocharax* and *Prionobrama* (e.g. Oliveira et al. 2011; Tagliacollo et al. 2012; Betancur-R. et al. 2018).

On the other hand, few studies focused on the intrageneric phylogenetic relationships within *Aphyocharax* (e.g. Tagliacollo et al. 2012), and its diversity is probably underestimated, with at least four undescribed species (Souza-Lima 2007) and several populations or species waiting for a taxonomic revision (Lima et al. 2013; Ohara et al. 2017; Brito et al. 2018).

Aphyocharax brevicaudatus sp. nov. is described here based on two distinct criteria and assumptions (PAA and WP). As mentioned in the Diagnosis (PAA), *Aphyocharax brevicaudatus* sp. nov. is unique among its valid congeners possessing the upper lobe of the caudal fin longer than the lower lobe in mature males (Souza-Lima 2003b; this study). This feature is generally rare among species of Characidae (Mirande 2010).

In our Bayesian inference phylogenetic analysis (Fig. 4), haplotypes of *A. brevicaudatus* sp. nov. clustered as an exclusive lineage with high node support (maximum posterior probability value) (WP). The hypothesis of this new species is strengthened from an integrative taxono-

my perspective, since it was based on evidence obtained from two independent criteria of species delimitation (see Dayrat 2005; de Queiroz 2007; Goldstein and Desalle 2010; Padial et al. 2010).

The closer relationship between *A. brevicaudatus* sp. nov. and *A. avary* is recovered with maximum posterior probability value. However the relationship between this clade (*A. brevicaudatus* sp. nov. and *A. avary*) and other congeners have low phylogenetic resolution, and discussions related to the phylogenetic positioning of this clade would be speculative with the data at hand.

Comparative material

***Aphyocharax avary*:** ANSP 39217, 1 (Holotype), Madeira River, about 200 miles east, Brazil. UFRO 018489, 3, Guajará municipality, Rondônia state, Brazil. UFRO016159, 62, Porto Velho municipality, Rondônia state, Brazil. UFRO 014317, 7, Novo Aripuanã municipality, Amazonas state, Brazil. MNRJ 10968, 11, Borba municipality, Iago de Borba (Madeira River Basin), Amazonas state, Brazil. CICCAA 02394, 38, Sororó River, Marabá municipality, Pará state, Brazil. ***Aphyocharax anisitsi*:** CICCAA 00867, 14, Pontes Lacerda municipality, Mato Grosso state, Brazil. CICCAA 01267, 6 C&S, Pontes Lacerda municipality, Mato Grosso state, Brazil. CAS 59697, 1, Asuncion municipality (radiograph and photograph of holotype), Par-

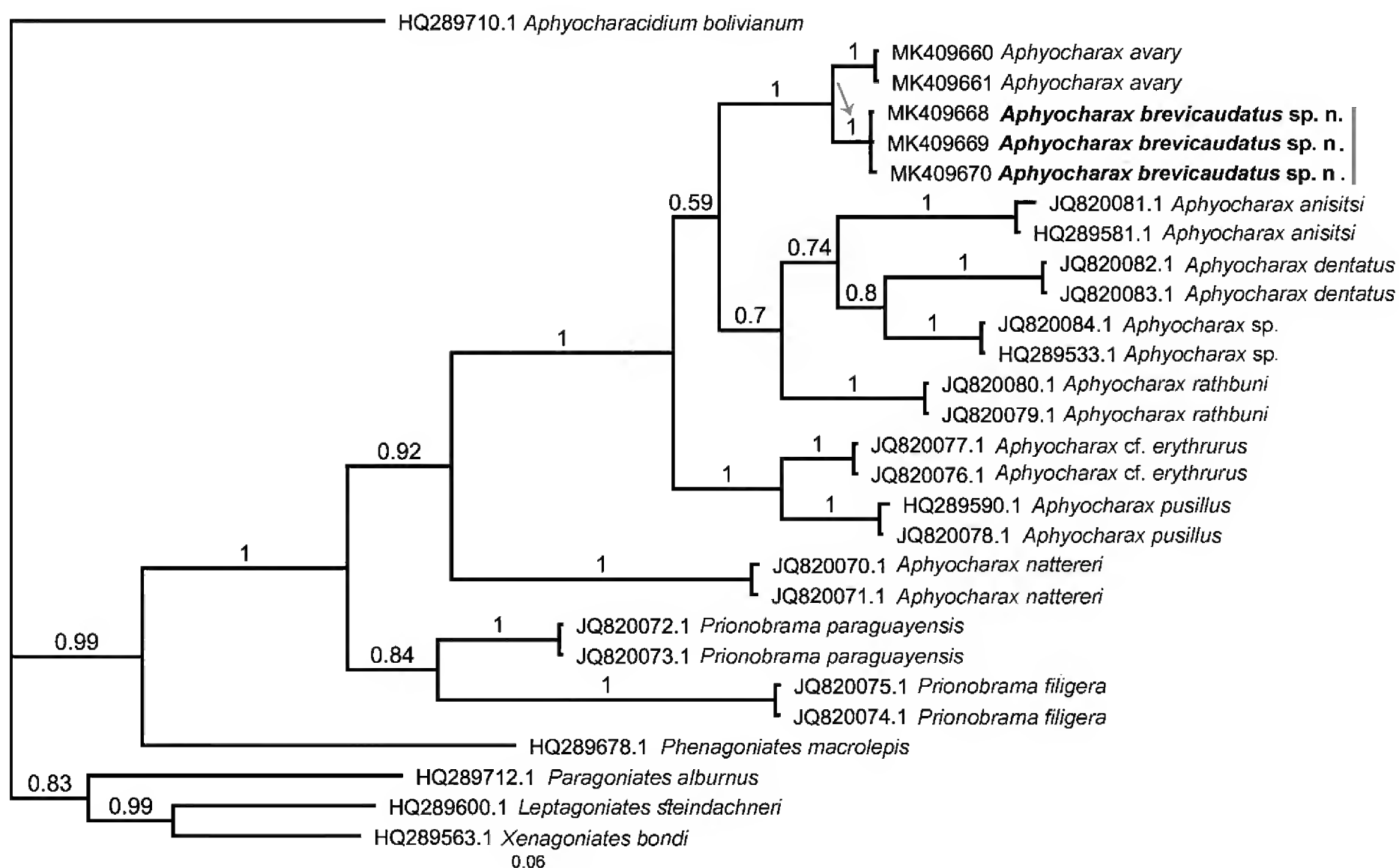


Figure 4. Bayesian inference tree including *Aphyocharax brevicaudatus* sp. nov. (red bar) and other congeners. Red arrow indicates the posterior probability of *A. brevicaudatus* node. Number above branches are posterior probability values.

aguay. *Aphyocharax dentatus*: ANSP 128718, 21, Lake Mozambique, Colombia. UFRJ 5571, 2, Rio Verde municipality, Mato Grosso do Sul state, Brazil. CAS 59722, 1, Laguna del Río Paraguay (radiograph and photograph of holotype), Asuncion municipality, Paraguay. *Aphyocharax erythrurus*: FMNH 53406, 1, Rockstone sandbank (photograph of paratype), Guyana. *Aphyocharax nattereri*: UFRJ 5783, 2, Poconé municipality, Mato Grosso state, Brazil. *Aphyocharax pusillus*: ANSP 178013, 4 (photographs of recently preserved specimens), Rio Napo (Amazon river basin), right bank just upstream from mouth of Mazan River, near town of Mazan, Loreto, Peru. BMNH 1867.6.13.46, 1 (syntype), Amazon river basin, Huallaga and Xeberos, Peru. BMNH 1867.6.13.58-59, 2 (syntypes), Amazon river basin, Huallaga and Xeberos, Peru. BMNH 1869.5.21.10, 1 (lectotype of *Chirodon alburnus*), Amazon River, Peru. BMNH 1869.5.21.11-13, 3 (paralectotypes of *Chirodon alburnus*), Amazon River, Peru. *Aphyocharax rathbuni*: CAS 76467, 1 (Radiograph and photograph of a Holotype), Paraguay basin, Arroyo Chagalalina, Paraguay. *Aphyocharax yekwanae*: FMNH 109278, 1 (radiograph of paratype), Bolivarian Republic, Venezuela. *Aphyocharax sp.*: CICCAA 00865, 11, Pontes e Lacerda municipality, Mato Grosso state, Brazil. CICCAA 00865, 4 C&S, Pontes e Lacerda municipality, Mato Grosso state, Brazil.

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Anatomical redescription of *Cyrenoida floridana* (Bivalvia, Cyrenoididae) from the Western Atlantic and its position in the Cyrenoidea

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Abstract

Members of the small bivalve family Cyrenoididae inhabit brackish waters of the eastern and western Atlantic Ocean. *Cyrenoida floridana* (Dall, 1896) from the western Atlantic is poorly known aside from shell descriptions. A detailed shell and anatomical study of *C. floridana* is here presented and compared with available data for Cyrenidae and Glauconomidae, two families of closest relationship according to recent phylogenetic studies. The species is characterized by valves externally covered by thin light brown periostracum; muscle scars and pallial line (without sinus) weakly impressed on the internal shell surface; a unique hinge pattern composed of cardinal and lateral teeth joining each other, right hinge with two laterals and two cardinals forming two inverted-V-shaped teeth and left hinge with two cardinals and one lateral forming a horizontal reversed F-shaped tooth; and microtubules inside the shell walls. Anatomically, the species presents unequal adductor muscles; demibranchs fused to each other along their posterior ends; a pair of totally fused, pigmented siphons; two pairs of siphonal retractor muscles; and a stomach with conjoined style sac and intestine, a single typhlosole, and three sorting areas. Evidence of shell parasitism is described.

Key Words

Anatomy, biodiversity, brackish water, Cyrenidae, freshwater, Glauconomidae, Heterodonta, Mollusca, taxonomy

Introduction

Cyrenoida Joannis, 1835, is the single genus of the small bivalve family Cyrenoididae and currently includes only six recognized extant species. Although previously assumed to extend into the Austral-Asian region (Pilsbry and Bequaert 1927), its known distribution includes temperate to tropical estuaries, marshes, and mangrove swamps of western Africa, both sides of the North American continent, and the western coast of Panama and adjacent islands (Joannis 1835; Morelet 1851; Dall 1896; Pilsbry and Zetek 1931; Morrison 1947; Huber 2010; MolluscaBase 2019). Because of its ecological position in the fringe area between freshwater and saltwater environments, the group has been left out from larger-scale

treatments of marine (e.g. Mikkelsen and Bieler 2007) and freshwater mollusks (e.g. Lydeard and Cummings 2019). *Cyrenoida* is poorly represented in museum collections, which, together with the fact that many of the original localities are difficult to access, has hindered detailed study of this taxon.

Several nominal species were introduced for West African members of this genus. These have been interpreted, based on shell morphology, as belonging to two fairly wide-ranging species (Huber 2010), the type species *Cyrenoida dupontia* Joannis, 1835, described from Senegal and extending to the Congo River (with synonyms *Cyrenella senegalensis* Deshayes, 1855, and *Cyrenoida rhodopyga*

Martens, 1891), and *C. rosea* (d'Ailly, 1896), described from Cameroon (including nominal subspecies *C. rosea brevidentata* Pilsbry & Bequaert, 1927 from Senegal). The fossil record of the group is poorly known, with a Pliocene species from southern Florida, *Cyrenoida caloosaensis* (Dall, 1896), recognized by Campbell (1993), and the modern species *Cyrenoida floridana* (Dall, 1896) interpreted as extending to the middle Pleistocene of Florida (Portell and Kittle 2010) and the Holocene of southern Texas (Neck and Herber 1981).

For the American Pacific coast (Coan and Valentich-Scott 2012), *Cyrenoida panamensis* Pilsbry & Zetek, 1931 was described from the western coast of mainland Panama (and is known from Costa Rica; Vargas-Zamora and Sibaja-Cordero 2011), and *C. insula* Morrison, 1946 from the Pearl Islands in the Gulf of Panama.

Another two species occur in the western Atlantic region, *Cyrenoida americana* Morelet, 1851, described from Cuba (and with published records from Puerto Rico and the Bahamas; Dall 1905), and *C. floridana* (Dall, 1896), the focus of the current treatment. Although rarely studied, the latter is a wide-ranging species along the western Atlantic and Gulf of Mexico coasts and has been cited as a prey item for both fish and bird species (Heard 1975, 1982; Kat 1978). It can be found living infaunally in muddy and sandy sediment colonized by halophytic plants, in estuaries and waters surrounding river mouths (Dall 1896, 1901; Kat 1982), the outer fringes of very low saline to freshwater marshes (Tunnell et al. 2010), as well as around freshwater ponds (this study).

The position of the family Cyrenoididae within the Heterodonta remained unresolved for a long time, with most authors including it in a broad concept of Lucinoidea (e.g. Prime 1860; Dall 1901; Lamy 1920; Chavan 1969; Vokes 1980; Boss 1982; Vaught 1989). Others placed it tentatively near the Corbiculidae (= Cyrenidae) (Thiele 1934) or as its own superfamily Cyrenoidoidea near groups such as Chamoidea and Galeommatoidea (Olsson 1961). A close relationship of Cyrenoididae with Lucinidae was questioned by Taylor and Glover (2006) and Williams et al. (2004) on anatomical grounds. The latter opinion was confirmed by Taylor et al. (2009) in the first molecular study that included a member of the family (*C. floridana*), which indicated a close relationship of Cyrenoididae with Cyrenidae (the latter as Corbiculidae) and Glauconomidae. They again elevated the rank to superfamily Cyrenoidoidea, which was adopted in some subsequent classifications (e.g. Bieler et al. 2010). Subsequent studies with additional molecular markers (Sharma et al. 2012; Combosch et al. 2017, Lemer et al. 2019) and combined morphological and molecular datasets (Bieler et al. 2014) confirmed the close relationship of Cyrenoididae, Cyrenidae, and Glauconomidae. The latter work combined them in the superfamily Cyrenoidea within the Neoheterodonte (the crown group of Imparidentia), its current position. The recent transcriptomic study by Lemer et al. (2019) included members of Cyrenidae [*Corbicula fluminea* (O. F. Müller, 1774) and *Polymesoda*

caroliniana (Bosc, 1801)], Glauconomidae (*Glauconome rugosa* Hanley, 1843), and Cyrenoididae (*C. floridana*). Interestingly, *Polymesoda* grouped with *Glauconome*, not *Corbicula* (which appeared as the basal taxon in this clade), indicating that Cyrenidae as currently understood (Bieler and Mikkelsen 2019) might not be monophyletic.

Whereas morpho-anatomical studies on this group have been limited, molecular data of *C. floridana* have been involved in several analyses, including recent transcriptomic studies exploring questions ranging from synonymous codon usage bias (Gerdol et al. 2015) to Imparidentia phylogeny (Lemer et al. 2019). To improve the morphological knowledge of Cyrenoididae and to contribute to the resolution in the Cyrenoidea clade, a detailed anatomical study of *C. floridana* is here presented. Its features are then compared to available data for members of Glauconomidae and several genera of Cyrenidae sensu lato.

Material and methods

A detailed list of examined material is presented following the anatomical description. The anatomical study is divided in two parts: shell analysis and soft part analysis. The shell analysis consisted of measurements and scanning electronic microscopy of the shell. The shell measurements were taken using a caliper or, in case of photos, using ImageJ software. The measurements used were shell length, height, and width; umbo length and height; dental shelf length and height; hinge teeth length and height; dorsal shell margin length; adductor muscle length, height, and area; and pallial line spacing from the ventral shell margin. The soft part analysis collected details of topology and morphology of systems and organs using photography and drawings under camera lucida. The soft part data were obtained from specimens preserved in ethanol. Dissection occurred with the specimens immersed in 70% ethanol. Final drawings were initially made in graphite and later remade on translucent paper with China ink, scanned, and edited using Photoshop CS3 software. The final drawings are average anatomical schemes based on information collected from several specimens. The number of specimens dissected varied according to the availability in collections and was expected to be sufficient to cover any feature affected by preservation methods, such muscular contractions, distensions limits, and presence or absence of delicate structures, or sexual stages of the specimens, and to detect maturation stages and gonadal filling. All soft parts here drawn are based on specimens in lot FMNH 328260.

The type materials of *C. floridana* and *C. guatemalensis* were examined from photographs, whereas additional samples were physically studied. Scanning electron microscopy (SEM) was provided by the Laboratório de Microscopia Eletrônica do Instituto de Biociências of the Universidade de São Paulo and by the Laboratório de Microscopia Eletrônica from Museu de Zoologia of the Universidade de São Paulo.

The following abbreviations are used in the anatomical descriptions and figures: **aa**: anterior adductor muscle; **an**: anus; **ar**: anterior pedal retractor muscle; **au**: auricle; **cc**: cerebral connective; **cg**: cerebral ganglia; **cn**: ctenidial nerve; **cp**: cerebropedal connective; **cv**: cerebrovisceral connective; **dd**: digestive diverticula; **dg**: digestive gland; **dh**: dorsal hood; **dm**: dorsal siphonal retractor muscles; **eo**: excurrent opening; **er**: esophageal rim; **es**: esophagus; **ex**: excurrent siphon; **fg**: food groove; **ft**: foot; **gf**: gill fusion; **gi**: gill; **go**: gonad; **gp**: genital pore; **gs**: gastric shield; **he**: heart; **id**: inner demibranch; **if**: mantle border inner fold; **in**: intestine; **io**: incurrent opening; **ip**: inner palp; **is**: incurrent siphon; **ki**: kidney; **lc**: left caecum; **lp**: left pouch; **lv**: large inverted-V-shaped tooth; **mf**: mantle border middle fold; **mo**: mouth; **mt**: major typhlosole; **na**: anterior adductor muscle nerve; **np**: nephropore; **nt**: minor typhlosole; **od**: outer demibranch; **of**: mantle border outer fold; **op**: outer palp; **pa**: posterior adductor muscle; **pg**: pedal ganglia; **pl**: pallial line; **pm**: pallial muscle; **pn**: pallial nerve; **pp**: papillae; **pr**: posterior pedal retractor muscle; **rc**: right caecum; **rn**: renal nerve; **sa1**: sorting area 1; **sa2**: sorting area 2; **sa3**: sorting area 3; **sm**: siphonal membrane; **sn**: dorsal siphonal muscle nerve; **sp**: siphons; **ss**: style sac; **st**: stomach; **sv**: small inverted-V-shaped tooth; **t1**: large lateral tooth of right valve; **t2**: large cardinal tooth of right valve; **t3**: small lateral tooth of right valve; **t4**: small cardinal tooth of right valve; **t5**: lateral tooth of right valve; **t6**: posterior cardinal tooth of left valve; **t7**: anterior cardinal tooth of left valve; **ve**: ventricle; **vg**: visceral ganglia; **vm**: ventral siphonal retractor muscles.

Institutional abbreviations: **ANSP**, Academy of Natural Sciences of Drexel University, Philadelphia, Pennsylvania, USA; **UF**, Florida Museum of Natural History, Gainesville, Florida, USA; **FMNH**, Field Museum of Natural History; **USNM**, National Museum of Natural History [United States National Museum], Smithsonian Institution, Washington, DC, USA.

Systematics

Family Cyrenoididae H. Adams & A. Adams, 1857 (1853). Synonym: Cyrenellidae J.E. Gray, 1853.

Genus *Cyrenoida* Joannis, 1835 (type species by monotypy: *Cyrenoida dupontia* Joannis, 1835). Synonyms include: *Cyrenella* Deshayes, 1836 (established in synonymy of *Cyrenoida*; available because it was used as valid before 1960, e.g. by Gray 1853); *Cyrenoidea* Dall, 1896 (unjustified emendation; the earlier use by Hanley (1846) is considered an incorrect subsequent spelling); *Cyrenodonta* has been credited by some authors to H. Adams & A. Adams, 1857, but it was introduced in synonymy of *Cyrenoida* and no pre-1960 use as a valid name has been located); *Cyrenoides* auct. is an incorrect subsequent spelling for *Cyrenoida* (G.B. Sowerby II, 1839).

Cyrenoida floridana (Dall, 1896)

Figs 1–41

Cyrenoidea floridana Dall 1896: 52; Simpson 1887–1889: 66 [nomen nudum]; Dall 1889: 50, 208 [nomen nudum]; Rhoads 1899: 48; Heard 1975: 22; 1982a: 23, fig. 24; 1982b: 131.

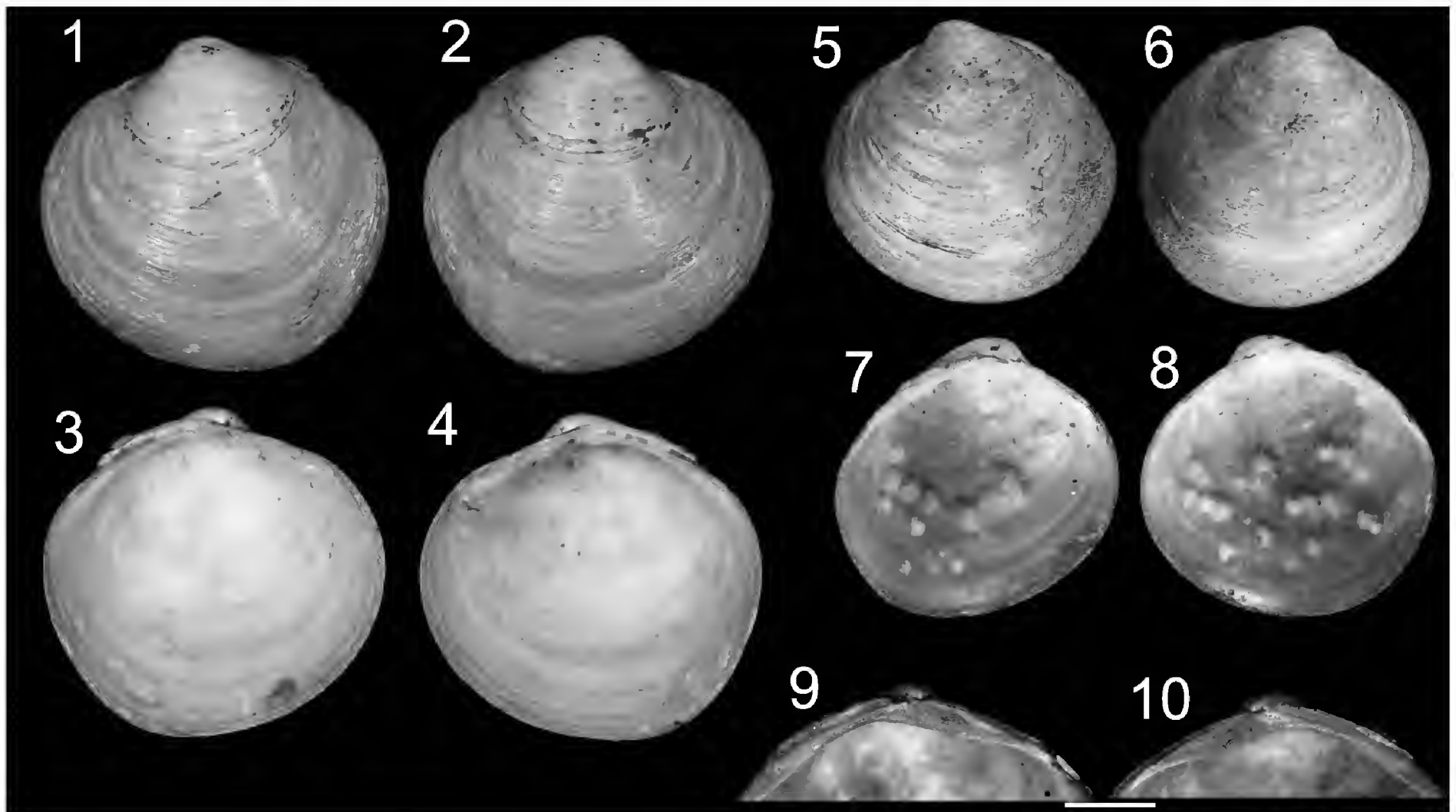
Cyrenoida floridana—Dall 1901: 817, pl. 42, fig. 7; Lamy 1920: 388; Pilsbry and Zetek 1931: 69; Smith 1951: 45 (pl. 16, fig. 11, pl. 18, fig. 8); Pulley 1952: 114–115, pl. 9, fig. 15; Morrison 1954: 9–10; Van Regteren Altena 1968: 157, 176; 1971: 5, 41, fig. 14; Waas 1972: 123; Abbott 1974: 466 (fig. 5383); Leathem et al. 1976: 93, figs 1–3; Kat 1978: 1–168, figs 1–91, tables 1–7; A1–A6; Neck and Herber 1981: 35–39; Kat 1982: 47, figs 1–3 (oocytes); Heard 1982a: 25, fig. 28j; Vokes and Vokes 1983: 39, 62, pl. 39, fig. 7; Neck 1985: 5; Bishop and Hackney 1987: 141, fig. 6; Turgeon et al. 1988: 36; 1998: 39; Camp et al. 1998: 11; Abbott and Morris 1995: 53, pl. 24, fig. 12; Redfern 2001: 219, pl. 92, fig. 898; Reece et al. 2004: 1116; Mikkelsen and Bieler 2000: 373; 2004a: 513; 2004b: 596; Lee 2009: 28, fig.; Turgeon et al. 2009: 728; Taylor et al. 2009: 10 (figs 4–8); Tunnell et al. 2010: 345; Redfern 2013: 400, fig. 1067; Bieler et al. 2014: 45 (fig. 3N); Arzul and Carnegie 2015: 33; González et al. 2015: 4, figs 1, 2; Combosch et al. 2017: table 1, figs 1, 2; Lemer et al. 2019: figs 1, 2.

Cyrenella floridana—Walker 1918: 88, fig. 232.

Cyrenoidea guatemalensis Pilsbry 1920: 221 (pl. 11, fig. 9); Clench and Turner 1962: 60.

Cyrenoida guatemalensis—Pilsbry and Zetek 1931: 69; Morrison 1946: 45.

Description. Shell (Figs 11–23): **External features:** Outline rounded, subcircular with ventral margin slightly posteriorly carinated (Figs 11, 12); equivalve, equilateral, ~6% longer than high, reaching maximum length of ~15 mm. Laterally inflated, width ~59% of total shell length (Figs 13–15). Externally white, adorned only with growth lines, showing ~3 thicker commarginal growth increments. Periostracum thin, slightly wrinkled, light brown. Walls thin, fragile. Umbones prosogyrous, low, ~5% of total shell height, large, length ~25% of total shell length, located at midpoint of shell length. Ligament parivincular, opisthodontic, long, ~39% of total shell length (Figs 15–17). Nymph long, ~20 times longer than wide, rectangular. Lunule and escutcheon absent. **Internal features:** Internal surface opaque white (Figs 16, 17). Adductor muscle scars and pallial line weak, very faintly impressed (outlined in Fig. 16). Anterior adductor muscle scar reniform, occupying ~1.5% of total internal surface; ventral portion ~2 times wider than dorsal portion; positioned at median third of valve height. Posterior adductor muscle scar oval, slightly pointed dorsally, occupying ~1.6% of total internal surface; located slightly more ventral than anterior muscle scar. Pallial line weak, formed by row of small pallial muscle scars, connected to middle portion of ventral surface of anterior adductor muscle to middle portion of ventral surface of posterior adductor muscle, inset from ventral shell margin by ~19.5% of total shell height, without pallial sinus. Microtubules of elongated conical shape, beginning with circular opening in interior shell wall, tapering toward but not reaching external surface (Figs 20–22). Internal surface of shell usually with aragonitic nodules of various sizes and quantities (Figs 16, 17, 23).

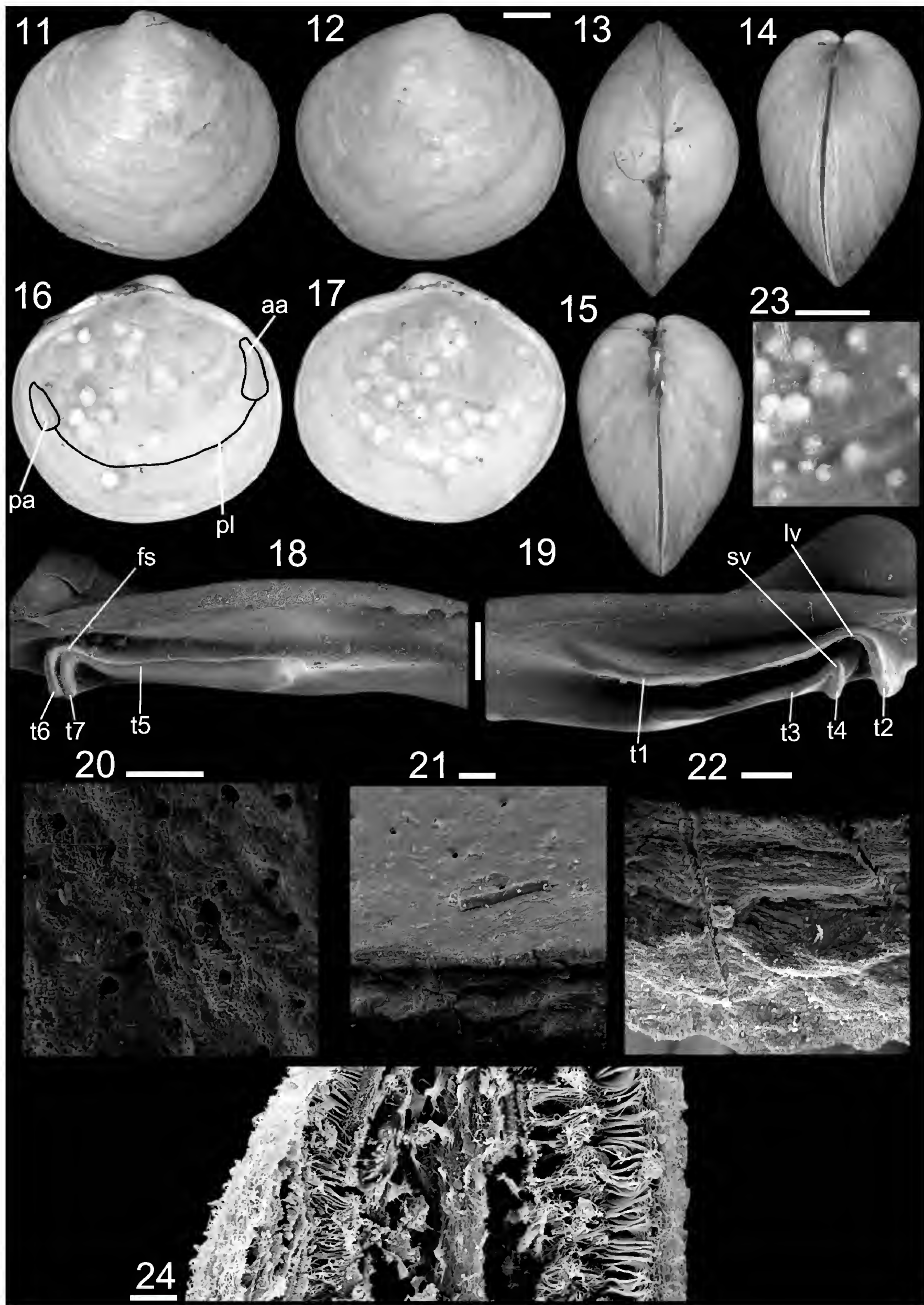


Figures 1–10. Syntypes of *Cyrenoida floridana* and lectotype of *C. guatemalensis*. **1–4.** *Cyrenoida floridana* (USNM 46846, length 12 mm, height 13 mm). **1.** Left valve, external view; **2.** Right valve, external view; **3.** Left valve, internal view; **4.** Right valve, internal view; **5–10.** *Cyrenoida guatemalensis* (ANSP 107532; length 8.6 mm, height 8.9 mm). **5.** Left valve, external view; **6.** Right valve, external view; **7.** Left valve, internal view; **8.** Right valve, internal view; **9.** Detail of left hinge; **10.** Detail of right hinge. Scale bar: 2 mm.

Hinge (Figs 16–19): Hinge restricted to central and anterior portion of dorsal margin, composed of lateral and cardinal teeth. **Right hinge** (Figs 17, 19): Dental shelf short and wide, triangular, running along entire length of anterior portion of dorsal margin, height equivalent to ~10 times dorsal margin width; composed of two laterals and two cardinals. Each cardinal tooth joining posteriorly with a lateral tooth, forming two inverted-V-shaped teeth, one large (Fig. 19: **lv**), one small (Fig. 19: **sv**). Large V-shaped tooth located near dorsal shell margin, formed by long and laminar lateral tooth (Fig. 19: **t1**) and short cardinal one (Fig. 19: **t2**). Lateral tooth length equivalent to ~56% of total dental shelf length, cardinal tooth length equivalent to ~22% of lateral tooth length; small V-shaped tooth located ventral to large V-shaped tooth (**lv**). Small lateral tooth (Fig. 19: **t3**) length ~30% shorter than large lateral tooth, whereas small cardinal tooth (Fig. 19: **t4**) ~40% shorter than dorsally located cardinal tooth (Fig. 19: **t2**). **Left hinge** (Figs 16, 18): Dental shelf narrow, fusiform, running along 30% of anterior portion of dorsal margin, height equivalent to ~3 times dorsal margin width; composed of three cardinal teeth, two cardinal and one lateral, forming horizontal reversed F-shaped tooth (Fig. 18: **fs**). Both cardinal teeth originating parallel and close to each other, (Fig. 18: **t6**, **t7**). Lateral tooth laminar (Fig. 18: **t5**), joining anterior cardinal tooth (Fig. 18: **t7**), length equivalent to 50% of total length of dorsal shelf. Both cardinal teeth equivalent to 20% of lateral tooth length. When articulated, left

valve tooth complex (**t5-t7**) fits within groove between right valve **t3-t4** and **t1-t2**.

Muscular system (Figs 25–27, 31, 34, 33): Anterior adductor muscle (**aa**) reniform in cross section, ~3 times taller than wide; ventral portion ~2 times wider than dorsal portion; occupying ~3% of total shell internal volume; located at middle third of shell height; clearly divided into quick and slow components (Figs 25, 26, 35), quick component occupying ~39% of anterior portion of muscle, dark grey in color, slow component occupying ~61% of posterior portion of muscle, light cream in color. Posterior adductor muscle (**pa**) elliptical in cross section, ~1.5 times wider than tall, ~20% shorter and ~2 times wider than anterior adductor muscle, occupying ~3% of total shell internal volume; located slightly ventral to anterior adductor muscle; clearly divided into quick and slow components (Figs 25–27, 34, 35), quick component occupying ~52% of posterior portion of muscle, dark grey in color, slow component occupying ~48% of anterior portion of muscle, light cream in color. Paired anterior pedal retractor muscles (**ar**) oval in section, thin, attached on shell at posterodorsal side of anterior adductor muscle insertion, area ~3% of that of adductor, length ~20% of shell length, left and right branches fused at mid-length. Paired posterior pedal retractor muscles (**pr**) oval in cross section, slightly laterally compressed, thin, ~40% longer than anterior pedal retractors; inserting on shell dorsally posterior adductor muscle, in area ~3% of that adductor, left and right branches fusing at dorsal ~20% of total muscle length. Pedal protractor



Figures 11–24. *Cyrenoida floridana*, shell and gills details. **11–22, 23.** UF 246126; **24.** FMNH 328260. **11.** Left valve, external view; **12.** Right valve, external view; **13.** Dorsal view of shell; **14.** Anterior view of shell; **15.** Posterior view of shell; **16.** Left valve, internal view, muscle scars and pallial line outlined; **17.** Right valve, internal view; **18.** Left hinge, SEM; **19.** Right hinge, SEM; **20.** Internal surface of shell, SEM, showing microtubule orifices; **21.** Detail of microtubule patch; **22.** Fractured shell showing microtubules partially through shell thickness; **23.** Detail of nodules at shell internal surface; **24.** Gill fragment, transverse section, SEM. Scale bars: 1 mm (**11–17, 23**); 200 μ m (**18, 19**); 20 μ m (**20–22**), 0.5 mm (**23**); 10 μ m (**24**).

muscles absent. Two pairs of siphonal retractor muscles (Figs 27, 31, 33); dorsal siphonal retractors (**dm**) ~3 times longer than wide; insertion at mantle bifid for half of total muscle length, 2 times as long as excurrent opening, originating laterally at half of siphonal base height; ventral siphonal retractors (**vm**) thin and translucent, ~3 times longer than wide, length ~50% of total length of dorsal siphonal muscle, originating at ventral end of incurrent siphon base.

Foot (Figs 25, 26, 33): Foot short, wedged-shaped, length equivalent to ~35% of total shell length, contracted height equivalent to ~27% of total shell height, laterally compressed, with small heel of length equivalent to ~23% of total foot length. Distal end acuminate. Byssal groove and byssus absent in adults.

Mantle (Figs 25–29): Mantle lobes symmetrical, thin, translucent white. Pallial muscles long, triangular, inserting from inner mantle fold region to ~16% of total mantle lobe height, arranged sparsely at ventral margin of mantle lobe; separated from each other by ~4 times pallial muscle basal width (Fig. 25: **pm**). Mantle border with three folds (Fig. 29); outer fold (**of**) thin, width ~5% of shell thickness, 5 times higher than wide; middle fold (**mf**) similar to outer fold, ~30% shorter; inner fold (**if**) short, ~3 times taller than wide. Middle fold with 30 small and short papillae, bordering entire pedal gape portion (Fig. 26: **pp**); each papilla taller than wide, with rounded tip, separated from adjacent papillae by width equivalent to 4 times papillar width. Periostracum between outer and middle folds. Mantle lobes totally free except for siphonal area. Anterior mantle fusion occurring at ~42% of anterior adductor muscle height; posterior mantle fusion occurring at ~70% of posterior adductor muscle height (Fig. 26). Siphonal area corresponding to ~30% of total mantle lobe length (Fig. 26). Incurrent and excurrent siphons originating from inner mantle fold; siphonal area equivalent to ~35% of total animal height and ~7% of length (Figs 26, 27); siphons externally fused, covered by small brown spots, internally separated by thick, smooth muscular wall (Figs 27, 28, 31); siphonal internal openings free, opening directly into pallial cavity; incurrent and excurrent siphons similar in size; ~5 times longer than wide; incurrent siphonal external tip bordered by one row of short papillae, papillae length equivalent to ~10% of total siphon length (Fig. 28: **pp**); excurrent siphonal tip with siphonal membrane (Fig. 28: **sm**).

Pallial cavity (Figs 25, 26, 30, 32, 33): Occupying ~50% of total internal shell volume (Fig. 25). Labial palps small, ~2% of total internal shell volume, triangular (Figs 26, 32), external surface smooth; outer (**op**) and inner hemipalps (**ip**) of similar size, ~60% narrower and 55% shorter than anterior adductor muscle insertion; outer hemipalp connected to mantle lobe by dorsal edge, at ~30% of palp length; inner hemipalp connected to visceral mass by dorsal edge, at ~20% of palp length; internal surface of each palp with ~10 tall, rounded transverse folds covering ~90% of inner palp surface, leaving thin smooth area at palp edges, corresponding to ~10% of total inner palp area. Folds decreasing in length toward

mouth, forming shallow channels directed to anterior and posterior portions of mouth (Fig. 32). Gill wide, ~60% times wider than outer hemipalp, equivalent to ~30% of total valve area (Fig. 25). Ctenidia eulamellibranch with two demibranchs (Fig. 30). Outer demibranch, fusiform, twice as long as wide; folded upon ~30% of its own area; covering pericardial and renal areas; connected to mantle lobe by tissue for ~15% of posterodorsal border length (Fig. 25); inner demibranch triangular, ~1.5 times longer than wide; folded upon 50% of its own area; covered by outer demibranch in area equivalent to ~20% of its own area; food groove along ventral surface of inner demibranch (Figs 30, 33: **fg**); demibranchs connected to each other at posterior end by tissue (**gf**), fusion length equivalent to 25% of total gill length (Figs 25, 33); each demibranch thin, fragile, without signs of chemosymbiotic bacteria (Figs 24, 30). Suprabranchial chamber ~1/3 of infrabranchial chamber volume (Fig. 26).

Visceral mass (Fig. 26): Triangular, occupying half of total internal shell volume, laterally flattened, 2 times as wide as muscular base; ~40% of anterodorsal portion filled by brown digestive gland (**dg**); remaining area filled by cream-colored gonad (**go**). Stomach and style sac located vertically in central portion of visceral sac.

Circulatory and excretory systems (Figs 26, 34): Pericardium located in posterodorsal region of visceral sac, between posterior region of umbonal cavity and dorsal surface of kidney (Fig. 34), ~2 times as long as wide; occupying ~25% of total visceral mass volume. Paired auricles (**au**) anteroposteriorly elongated, connecting to main axis of gills along ~1/3 of gill length; walls thin, translucent. Ventricle (**ve**) elongated, thick, located at central pericardial region, surrounding ~45% of intestine crossing pericardial area, connected to auricles at median portion of lateral walls. Kidney light brown, triangular, located posteroventral to visceral mass, between ventral wall of pericardium and dorsal surface of posterior pedal retractor muscles, occupying ~25% of total visceral mass volume. Nephropores (Fig. 26: **np**) small, located at anterior third of kidney length, near genital pore (Fig. 26: **gp**).

Digestive system (Figs 35–37): Palps and digestive gland as described above. Mouth small, located centrally between pairs of inner and outer labial palps. Esophagus (**es**) long, narrow, length ~30% and height ~10% of visceral sac length and height (Fig. 35), cylindrical, running separate from anterior adductor muscle between and parallel to anterior portion of paired anterior pedal retractor muscles; internal surface covered by longitudinal folds, forming esophageal rim at stomach entrance (Fig. 37, **er**) in anteroventral region. Stomach (**st**) wide, occupying ~30% of visceral sac volume, conical, funnel-like, located anterior to umbo (Fig. 35); length ~60% of total visceral sac length, ~30% of its height; posterior portion ~60% taller than anterior portion. Paired apertures to digestive caeca located ventrolaterally, turned toward ventral portion of visceral sac, located side by side at anterior portion of stomach. Dorsal hood (**dh**) long, thin, length ~40% of total stomach length, anteriorly bluntly pointed.

Left pouch (**lp**) located below anterior portion of dorsal hood, shallow, wide, occupying ~20% of external area of left stomach wall, with ducts to digestive gland connecting at its central region (Fig. 36: **dd**). Stomach internal surface mostly smooth, with three well-developed sorting areas (Fig. 37); first sorting area starting at left side of esophageal rim, running along dorsal wall of anterior stomach chamber, penetrating dorsal hood, narrow, comprised of small transverse folds (**sa 1**). Second sorting area originating ventral to first sorting area, at left side of esophageal rim, running along left wall of anterior stomach chamber, entering left pouch and dorsal hood, both on their ventral surfaces, broad, formed by thickening of stomach wall (**sa 2**). Third sorting area starting inside dorsal wall of dorsal hood, running along dorsal and right walls of posterior stomach chamber, until diffusing on ventral portion of right wall (**sa 3**). Gastric shield (**gs**) located at central dorsal wall, occupying ~40% of total gastric area, with two anterior projections, one dorsal at left border, penetrating dorsal hood, and one left ventral, penetrating left pouch. Two narrow, tall gastric ridges running along ventral stomach chamber, forming major and minor typhlosoles at style sac entrance (Fig. 37). Longer ridge originating posterior to left caecum, penetrating caecum and exiting its anterior end, running toward anterior portion of stomach, performing curve, penetrating anterior end of right caecum, exiting that caecum at its posterior end, penetrating style sac at its right side, forming major typhlosole (**mt**). Shorter fold originating at style sac entrance, at region of major typhlosole penetration into style sac, forming rim bordering style sac entrance and ultimately minor typhlosole (**nt**). Style sac (**ss**) connecting stomach ventrally (Fig. 35), tapering ventrally, ~3.3 times longer than wide, occupying ~12% of visceral sac total volume; style sac height equivalent to 50% of visceral sac length, and ~10% of its width. Intestine (**in**) thin, long, originating between typhlosoles, merging with style sac initially, narrowing after ventral end of style sac, passing ventrally below central stomach, penetrating pedal musculature at ~5% of foot height, contacting dorsal surface of posterior pedal retractor muscles, curving toward right, following posterodorsal portion of visceral sac, parallel to style sac; intestine total length ~7 times longer than style sac. Anus simple, sessile, on ventral surface of posterior adductor muscle (Fig. 31, 35: **an**).

Reproductive system (Fig. 26): Gonads with branched aspect, opaque, cream-colored. Paired gonoducts connected to gonadal acini branches along posterodorsal portion of visceral sac. Genital pores simple (**gp**), located at posterior portion of visceral mass, at ~20% of visceral mass height, near nephropore (**np**).

Central nervous system (Figs 38–41): Paired cerebral ganglia (Figs 38, 41: **cg**) surrounding dorsal surface of anterior esophagus, dorsal to external surface of outer labial palp, triangular, longer than wide (Fig. 38), length 50% of esophageal length. Each cerebral ganglion ~50% width of transverse section of esophagus. Cerebral commissure ~50% longer than ganglia length; anterior ad-

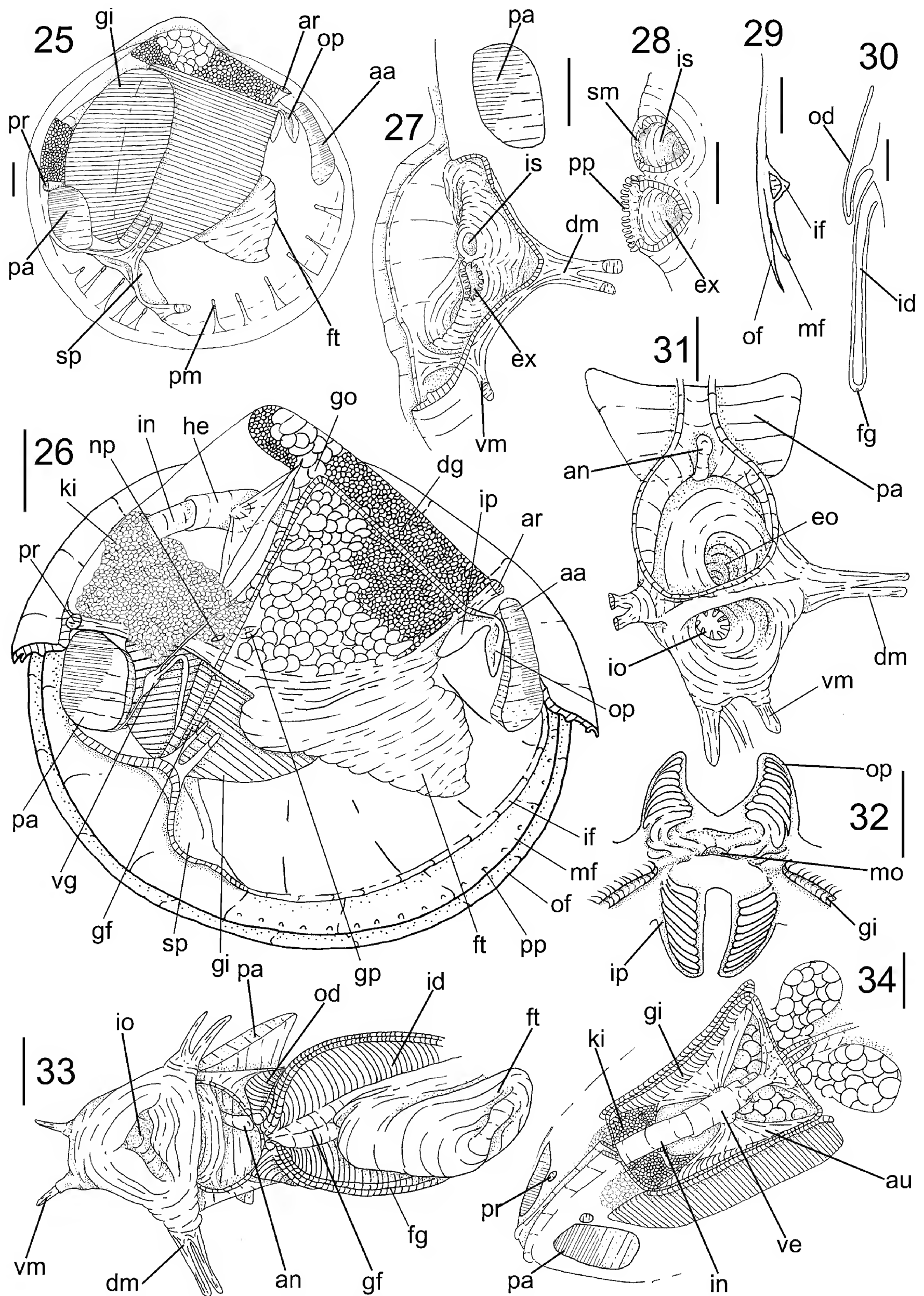
ductor muscle nerve (**na**) originating at anterior end of cerebral ganglion, contacting posterior surface of anterior adductor muscle, bifurcating into two main branches; internal branch penetrating posterodorsal third of muscle, diffusing into muscle; outer branch bordering posterior surface of anterior muscle until contacting pallial region and diffusing into muscle. Two additional pairs of nerves originating dorsally on cerebral ganglia, anterior to cerebrovisceral connective (**cv**) crossing visceral mass, contacting gonopore dorsally, bordering anterior portion of kidney and connecting dorsally with visceral ganglia, connecting cerebropedal connective (**cp**) running immersed in pedal muscles, connecting to anterior region of paired pedal ganglia (Figs 40, 41: **pg**). Paired visceral ganglia (Figs 39, 41: **vg**) fusiform, of similar length and height, length ~60% of cerebral ganglia length, partially fused medially, with subcentral groove; located ventral to paired posterior pedal retractor muscle, parallel with posterior adductor muscle, at dorsal tip connecting to cerebrovisceral connective (**cv**, as described above) and renal nerve (**rn**), penetrating kidney area; laterally originating ctenidial nerves (**cn**) running through central axis of posterior portion of gills; dorsally originating posterior adductor muscle nerve, penetrating mid-region of anterior surface of posterior adductor muscle; at ventral tip originating pallial nerve (**pn**), contacting anterior surface of ventral portion of posterior adductor muscle, running toward incurrent and excurrent siphonal muscles, reaching excurrent opening, originating single, short nerve (**sn**) that runs parallel to ~25% of dorsal siphonal muscle length, continuing parallel to mantle border, diffusing into mantle lobe edge. Paired pedal ganglia totally fused (Figs 40, 41: **pg**), oval, longer than wide, ~20% wider than visceral ganglia; located internal to posterior pedal retractor muscles, dorsal to foot insertion, at anterior tip connecting with cerebropedal connectives from cerebral ganglia; at posterior tip connecting two pairs of nerves, with dorsal pair running toward posterior region, inside posterior pedal retractor muscles; posteroventral pair curving ventrally, running into foot.

Habitat. Infaunal, in muddy sand; usually positioned vertically in about 2 cm depth (Kat 1978), in mangrove areas and brackish waters.

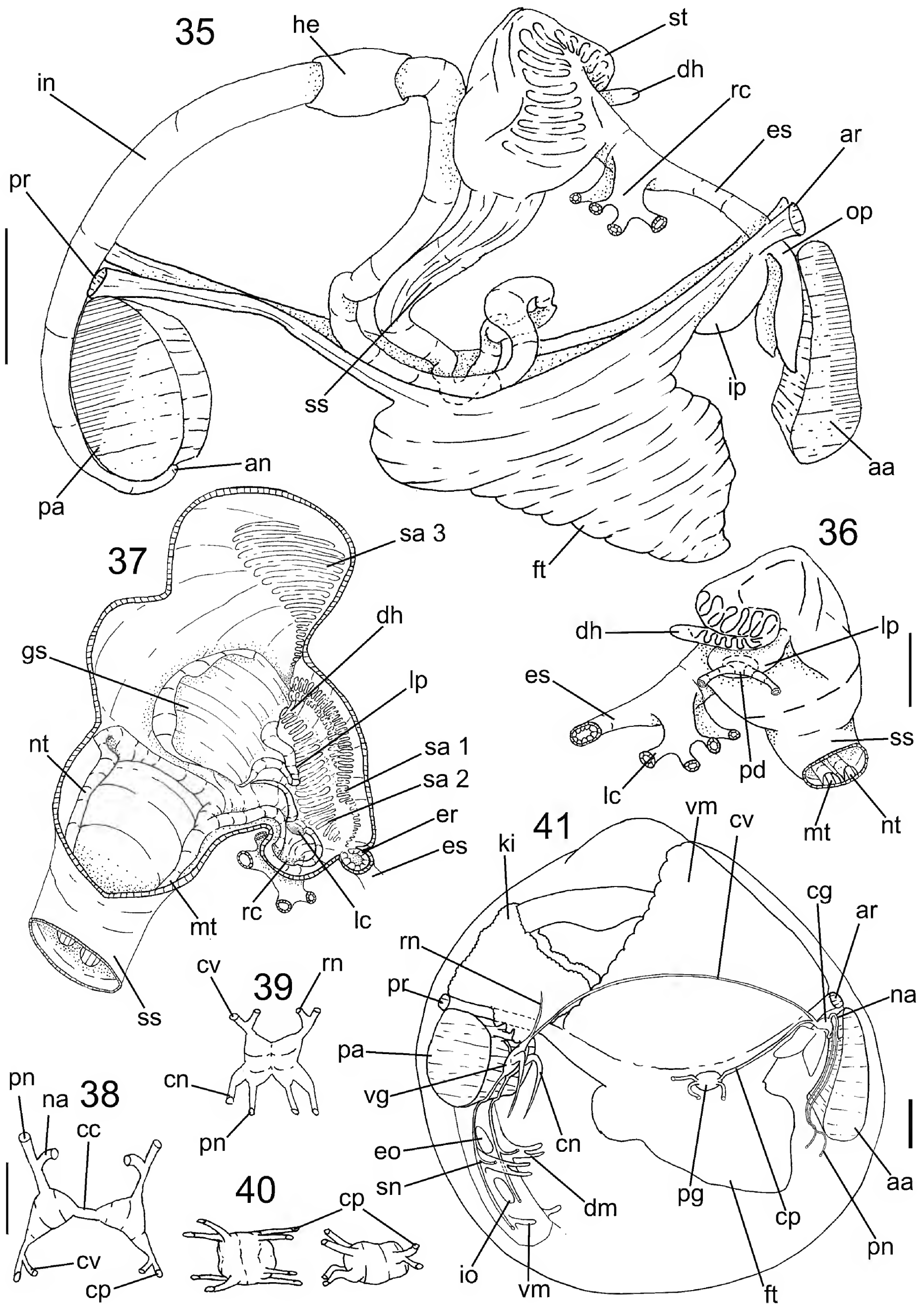
Measurements. (length by height by width, in mm): FMNH 328260 (specimen #1 of 4): 14.2 × 13.4 by 8.5; UF 122840 #1: 12.5 × 11.4 × 8; UF 264025 #1: 10.8 × 10.3 × 5.6; #2: 14.18 × 13.55 × 8.55.

Distribution. **USA:** eastern coast from Delaware to the Florida Keys, and Gulf of Mexico coast from western Florida to Texas; **Bahamas;** **Mexico:** Yucatan, Quintana Roo; **Guatemala;** **Bonaire** (Lee 2009); **Suriname.**

Type material. Syntypes: *Cyrenoidea floridana*: UNITED STATES OF AMERICA • **Florida**, Fort Myers, Everglades; 2 specimens; USNM 87735. Marco Island; 3 specimens;



Figures 25–34. Anatomy of *Cyrenoida floridana* (FMNH 328260). **25.** Right view valve removed, some structures seen by transparency of mantle lobe; **26.** Same, with mantle and gill removed; **27.** Incurrent and excurrent siphons, posterolateral view, right mantle lobe partially removed, some adjacent structures shown; **28.** Siphonal tips; right view, both partially sectioned longitudinally; **29.** Mantle border, section in its ventromedial portion; **30.** Gill, transverse section in its central portion; **31.** Incurrent and excurrent siphons, interior view, with details of their base and siphonal muscles; **32.** Labial palps, ventral view, outer hemipalps deflected dorsally; **33.** Posteroventral visceral region, ventral view, showing fusion of inner demibranchs in siphonal base; **34.** Pericardial region, posterodorsal view, dorsal mantle wall partially removed. Scale bars: 2 mm (25–28, 31, 33–34); 1 mm (29, 30, 32).



Figures 35–41. Anatomy of *Cyrenoida floridana* (FMNH 328260). **35.** Digestive tubes as *in situ*, right lateral view; **36.** Stomach, left lateral view; **37.** Stomach, right lateral view, right wall opened and deflected to show inner gastric surface; **38.** Cerebral ganglia, ventral view; **39.** Visceral ganglia, ventral view; **40.** Pedal ganglia; right figure in lateral right view, left figure in dorsal view; **41.** Nervous system topology, right lateral view. Scale bars: 2 mm (35–41, 40); 0.5 mm (38–40).

USNM 60974. 3 specimens, USNM 60975; Boca Ciega Bay; 3 specimens; USNM 60973. St Johns River mouth; 10 specimens; USNM 46846 (Figs 1–4). **Georgia**, Brunswick Island; 30 specimens; USNM 129197. *Cyrenoida guatemalensis*: **Lectotype**: GUATEMALA • Livingstone; ANSP 107532 (Figs 5–10). Note: Pilsbry's (1920) description of *C. guatemalensis* can be read as having been based on a single specimen and Van Regteren Altena (1971: 41) interpreted the specimen of ANSP 107532 as a holotype. However, Pilsbry is known for imprecisely indicating the type material at hand (P. Callomon, G. Rosenberg pers. comm.) and the existence of more than one original type specimen cannot be excluded. We accept Van Regteren Altena's (1971) action as a fixation of lectotype by inference of holotype under ICZN (1999) Article 74.6.

Examined material. UNITED STATES OF AMERICA • 10 valves; **Delaware**, Kent County, Bombay Hook; 01 Aug. 1954; Morrison and Rosso leg.; USNM 777892. • 10 valves; **New Jersey**, Delaware Bay, Cumberland County, Fortescue; 15 Jul. 1957; J.P.E. Morrison leg.; USNM 777894. • 6 valves; Delaware Bay, Cumberland County, Dividing Creek; J.P.E. Morrison leg.; 15 Jul. 1957; USNM 777895. • 20 valves; **Maryland**, Dorchester County; J.P.E. Morrison leg.; 11 Jul. 1954; USNM 777893. • 10 valves; Dorchester County, near Elliot, gullet of black duck; F.M. Uhler leg.; USNM 592260. • 8 valves; Queen Anne's County; 11 Jul. 1954; J.P.E. Morrison leg.; USNM 777890. • 12 valves; Arundel County, Deale, marshy, head of small inlet; 11 Jul. 1953; J.P.E. Morrison leg.; USNM 777887. • 6 valves; Arundel County; 15 Jul. 1953; J.P.E. Morrison leg.; USNM 777889. • 4 valves; Arundel County, Deale; 13 Jun. 1954; J.P.E. Morrison leg.; USNM 777888. • 6 valves; **North Carolina**, Beaufort, under algal mats; R.W. Heard leg.; USNM 678947. • 1 specimen; **South Carolina**, Horry/Georgetown counties, Murrell's Inlet, in black muddy sand under log near high tide line, S. edge of inlet along road; 03 Dec. 1955; J.P.E. Morrison leg.; USNM 1437782. • 6 valves; **Georgia**, McIntosh County, Fort King George Historic Site, Darien, exposed under drift logs and boards; 15 Dec. 1954; Cmdr. Miller leg.; USNM 707264. • 4 valves; Glynn County, Saint Simons Island; Oct. 1938; H.A. Rehder leg.; USNM 535386. • 1 valve; **Mississippi**, Jackson County, Halstead Bayou; Gulf Coastal Marine Laboratory leg.; UF 246126. • 15 valves; **Florida**, Wakulla County, St. Marks; 17 Jun. 1958; United States Fish and Wildlife Service leg.; USNM 612256. • 5 valves; Saint Johns County, Saint Augustine; F.E. Spinner leg.; ANSP 54330. • 6 valves; Saint Johns County, Halifax River; USNM 253659. • 12 valves; Volusia County, Daytona [Beach]; C.W. Johnson leg.; USNM 336943. • 2 valves; Marion County, creek SE of Ocala; 15 May. 1928; T. Van Hyning leg.; ANSP 152656. • 8 valves; Citrus County, Homosassa; E. Roper leg.; USNM 131462. • 4 specimens; Hernando County; G. Prime leg.; ANSP 68457. • 25 specimens; Hernando County, Aripeka; G. Prime leg.; ANSP 73905. • 20 valves; Pasco/Hernando counties,

Aripeka; L. Pine leg.; USNM 149932. • 10 valves; Hernando County, Little Blind Creek; 04 Dec. 1927; T. Van Hyning leg.; ANSP 149568. • 1 valve; Pasco/Hillsborough counties, Hillsborough River; E.J. Post leg.; USNM 591792. • 6 valves; Charlotte County, Punta Gorda; 1928; J.L. Madden leg.; USNM 592290. • 1 specimen; Glades County, Caloosahatchee River; C.W. Johnson leg.; ANSP 62888. • 5 valves; W Florida; C.W. Johnson leg.; ANSP 59610. • 30 valves; Collier County, Carnestown; 12 Apr. 1928; T. Van Hyning leg.; ANSP 152655. • 4 valves; Dade County, Miami; Olsen leg.; USNM 153404. • 10 valves; Dade County, Miami; 07 Apr. 01; Benedict leg.; USNM 330959. • 10 specimens; Dade County, Miami; S. N. Rhoads leg.; ANSP 77046. • 8 valves; Dade County, Miami; S. N. Rhoads leg.; ANSP 189416. • 16 valves; Lee County, Fort Myers; Hend. leg.; USNM 455820. • 16 valves; Lee County, Fort Myers; Henderson leg.; UNSM 425820. • 2 valves; Lee County, Fort Myers, Everglades; 1896; C.W. Johnson leg.; USNM 87735; syntype. • 20 valves; Monroe County, Big Pine Key; C. Margaret leg.; UF 122840. • 14 valves; Florida Keys, Monroe County, Big Pine Key; 27–28 Dec. 1956; C. Phillips, F. Philips leg.; FMNH 63059. • 31 valves; Florida Keys, Monroe County, pond on Big Pine Key; 1968; M. Teskey leg.; FMNH 293174. • 4 specimens + 15 valves; Florida Keys, Monroe County, Blue Hole quarry on Big Pine Key, Florida Keys; 024°42'21"N, 081°22'49"W; shoreline sediment at base of vegetation, salinity measured at 3 ppt; sta. FK-727; 03 May. 2004; R. Bieler, P.M. Mikkelsen leg.; FMNH 328260. • 67 valves; Florida Keys, Monroe County, Blue Hole quarry on Big Pine Key; 024°42'24"N, 081°22'48"W; sta. FK-794; 18 Nov. 2007; R. Bieler, P. Sierwald, E.A. Glover, J.D. Taylor leg.; same locality as in study by Taylor *et al.*, 2009; FMNH 333534. • 5 valves; Florida Keys, Monroe County, off mangrove island SE of Cudjoe Key; 024°38'12"N, 081°18'12"W; 1 m; sta. FK-745; 15 May. 2005; R. Bieler, P. Mikkelsen leg.; FMNH 333533. • 11 valves; Florida Keys, Monroe County, quarry on Big Pine Key, in sediment on shoreline rock; 024°41'56"N, 081°23'03"W; sta. FK-728; 03 May. 2005; R. Bieler, P. Mikkelsen leg.; FMNH 333535. • 3 valves; Florida Keys, Monroe County, mosquito ditch on Big Pine Key; 024°42'30"N, 081°23'02"W; sta. FK-939; 25 Apr. 2010; R. Bieler, P. Mikkelsen leg.; FMNH 333532. • 3 valves; Florida Keys, Monroe County, Spanish Harbor Key; sta. JG-708-0; 08 Jun. 2000; J. Gerber leg.; FMNH 308431. • 1 valve; Florida Keys, Monroe County, Ohio Key, land-locked pond adjacent to Ohio–Missouri Key bridge; 024°40'20"N, 081°14'36"W; sta. FK-723; 29 Apr. 2004; R. Bieler, P. Mikkelsen leg.; FMNH 314324. • 4 valves; Monroe County, Boca Chica Key; H. Hemphill leg.; ANSP 7983. **BAHAMAS** • 14 valves; **Grand Bahama Island**; 26°31'00"N, 78°46'30"W; J.N. Worsfold leg.; ANSP 374956. • 1 valve; Dover Sound, 26°35'05"N, 78°13'20"W, May. 1983; J. N. Worsfold leg.; ANSP 374350. • 2 valves; 26°31'00"N, 78°46'30"W; J.N. Worsfold leg.; ANSP 374957. • 6 valves; **Abaco**; C.W. Johnson leg.; USNM 425821. • 2 valves; S side of Abaco;

O. Bryant leg.; USNM 180503. MEXICO • 10 valves (1 figured specimen); **Quintana Roo**, Boca de Paila; Tulane University leg.; UF 264025. • 20 valves; Tulane University; Emily & Harold Vokes leg.; UF 264026. GUATEMALA • 2 valves; **Livingstone**; 1913; A. A. Hinkley leg.; syntype; ANSP 107532.

Discussion

Cyrenoida floridana and other *Cyrenoidea* anatomy

Recently, the family Cyrenoididae was classified together with Cyrenidae and Glauconomidae based on analyses of nuclear 18S and 28S rRNA genes (Taylor et al. 2009). This statement was corroborated using an integrative approach, with anatomical, molecular, and ontogenetic views (Bieler et al. 2014). In both cases, only one species each from Cyrenidae and Glauconomidae was used, and a robust discussion comparing morphological characters among the families was still lacking. Here a detailed discussion is provided, including morphological traits of the three families using available data from general traits of the family to details of species anatomy.

Very little information regarding *Cyrenoida floridana* has been available. What morphological data have been published are fragmented and lack details (e.g. Taylor et al. 2009; Bieler et al. 2014). Kat (1978) provided a histological and ecological study on the species, but only part of those results were formally published (Kat 1982).

Habitat: All three families that comprise Cyrenoidea are infaunal in soft sediments, inhabiting fresh to brackish waters worldwide. Most species present geographic distributions in Asia (e.g., Glauconomidae), but Cyrenidae includes species naturally distributed worldwide, except for Arctic and Antarctic regions, as well as introduced invasive species (Bieler and Mikkelsen 2019). Cyrenoididae is known only from African and American continents in brackish waters. Kat (1978) commented that *C. floridana* presents hermaphroditism, brooding behavior, juvenile dispersion by buoyance, thermal resistance, and site selection as adaptations to survive in intertidal areas of severe conditions subject to rapid environmental change.

Additional details about *C. floridana* habitat in Canary Creek, Delaware were provided by Kat (1978). There, the species lives buried horizontally in the first two centimeters of sediment. High sulfide concentration in the sediment appears to inhibit colonization, although the species can tolerate a wide range of salinity, suspended particles, temperature, pH, and moisture content. Highest population densities were found in moist sediment protected by a primary layer of halophytic vegetation and a secondary cover of filamentous algae.

Shell: As is common in fresh and brackish water bivalves (Cummings and Graf 2015), *C. floridana* presents a persistent periostracum covering the entire shell surface. In contrast to African *Cyrenoida* species, Cyrenidae,

and Glauconomidae that are covered in thick, brown to greenish periostracum (Huber 2015), *C. floridana* bears a thin periostracum. Periostracum in fresh and brackish water bivalves is a common feature, because such environments present much more corrosive properties (Cummings and Graf 2015) and this organic layer protects against shell corrosion. Kat (1978) noted that *C. floridana* periostracum is thicker near the shell border and almost invisible and iridescent near the umbo. Kat (1978) also described parallel folds in the thicker portions of periostracum in adult specimens of *C. floridana*. In living specimens, these folds create ridges that act to channel water when the bivalve is partially exposed, helping the animal to stay hydrated and thermally stable.

Shape among Cyrenoidea varies from rounded (Cyrenoididae), trigonal (Cyrenidae), to anteroposteriorly elongated with a straightening of the posterior shell margin (Glauconomidae) (Joannis 1835; Owen 1959; Boss 1982; Huber 2015). Some representatives present a gap between the valves at the posterior end of the shell, as in *Polymesoda* (Morton 1976) and *Glauconome* (Owen 1959).

Shell size among *Cyrenoida* species can be variable. The African *Cyrenoida* can reach 30 mm (e.g. *C. dupon-tia*) whereas the American *C. floridana* reaches only 14 mm. Despite the size difference, ecological and morphological characteristics allow African and American species assignment to the same genus, i.e., the habitat in brackish waters and the unique hinge pattern. Compared with other Cyrenoidea, *C. floridana* can be considered the smallest representative of the superfamily; Cyrenidae attain lengths of 39 to more than 150 mm and Glauconomidae between 20 and 79.5 mm (Huber 2015). Cyrenidae is the only family within this group that presents concentric ribs; the remaining species are adorned only with growth lines (Boss 1982; Huber 2015). Commarginal growth increments are here described for *C. floridana*. These thickened lines could be associated with seasonal growth anomalies or seasonal metabolic changes (Lewis and Cerrato 1997).

Hinge: Hinge pattern in Cyrenoidea is somewhat variable. Glauconomidae and Cyrenidae share the presence of at least three cardinal teeth positioned perpendicular to the shell umbo, and one of these teeth can be bifid (Boss 1982; Huber 2015). Members of Cyrenidae share with *C. floridana* the presence of lateral teeth, but those in Cyrenidae can be either smooth or serrate. Cyrenoididae, including African *Cyrenoida* and *C. floridana*, presents a combination of lateral and cardinal teeth forming a unique pattern.

Microtubules: The *C. floridana* shell presents microtubules that partially penetrate the shell. This feature is shared with some Cyrenidae, e.g., *Corbicula* species (Araújo et al. 1994), but is absent in others, e.g., *Polymesoda* (see Tan Tiu and Prezant 1989). According to Waller (1980), microtubules are more common in epifaunal than in infaunal bivalves and, based on studies in Arcidae, could be associated with photoreception, anchorage sites for the mantle, improvement of the surface for res-

piratory change, protection against boring organisms, or sites of ionic regulation. Rosso (1954) commented that microtubules could be involved in embryonic nourishment. Robertson and Coney (1979) stated that they could be used for monitoring water conditions, although this is unlikely given that they do not fully penetrate the shell. Tiu Tan and Prezant (1989) hypothesized that microtubules could act to lighten juvenile shells, aiding in planktonic dispersal, and to assist in anchoring the mantle to shell during locomotion or biomineralization. At any rate, microtubules occur in several bivalve families as a post-larval feature (Malchus 2010) and resemble the aesthetes found in some gastropods and polyplacophorans (Simone 2011), which mostly have receptor functions. Kat (1978) observed that the vast majority of tubules in *C. floridana* do not fully penetrate the shell and are filled with non-secretory, finger-like projections from the external layer of the mantle. The mantle includes blood sinuses that, when filled, could extend the projections inside the tubules, improving tissue attachment to the shell. Therefore Kat (1978) discarded any notion of secretory or sensory function and believed that the microtubules serve to anchor the mantle to the inner shell surface.

Pallial line: Another feature variable among Cyrenoidea is the pallial line. In *Cyrenoida floridana* it is weak, discontinuous, and without a sinus, whereas Glauconomidae presents a narrow, deep sinus, and in Cyrenidae, it varies between entire to including a shallow or deep sinus (Huber 2015). The difference between the presence of a sinus and pallial line intensity is due to size and form of the siphonal muscles, and the quantity of pallial muscles, respectively. Siphonal muscles in *C. floridana* are paired, short, and thin and insert on the pallial muscle insertion line; Glauconomidae and Cyrenidae have strong, long muscular bands that dislocate the pallial muscle insertion toward the interior of the valve (Owen 1959; Kurniushin and Glaubrecht 2002). Pallial muscles in *C. floridana* are spaced along the mantle border, creating a discontinuous pallial line, whereas Glauconomidae and Cyrenidae present powerful pallial muscles strongly marked on the internal surface of the shell (Owen 1959; Glaubrecht et al. 2003).

Main muscular system: All known species of Cyrenoidea present anterior and posterior adductor muscles, a pair of anterior pedal retractor muscles, and a pair of posterior retractor muscles (Owen 1859; Huber 2015); a pair of pedal protractor muscles are present in some Cyrenidae (Simone et al. 2015). The overall symmetry of the adductor muscles in Cyrenoidea and Glauconomidae is slightly anisomyarian, with the anterior adductor muscle reniform and the posterior adductor muscle oval, but some Cyrenidae are isomyarian (Morton 1976; Simone et al. 2015; Huber 2015).

Foot: Foot shape among Cyrenoidea varies between Cyrenidae, which bear a well-developed, strong, wide, axe-shaped foot, whereas Cyrenoididae and Glauconomidae have a wedged-shaped foot (Owen 1959; Mansur and Meier-Brook 2000; Huber 2015). Dall (1898) de-

scribed the *Cyrenoida floridana* foot as filiform, and this condition was used to classify the species in Lucinidae. The image of a living specimen included by Bieler et al. (2014, fig. 3 N) can be referenced to verify shape and color of foot in living condition. Kat (1978) commented that the foot of *C. floridana* can be extended by more than one shell length in the sediment, lacks a byssal gland, and in large individuals required up to 10 minutes to complete a burrowing cycle.

Mantle: The number of mantle folds and presence of papillae are very diverse among Cyrenoidea. In Cyrenidae, mantle papillae are relatively common (Boss 1982; Huber 2015), although they are not shared among all genera and species (Simone et al. 2015). Although three mantle folds are found in Cyrenidae (Morton 1976), the genera *Corbicula* and *Cyanocyclus* present four mantle folds, with the middle one doubled and forming papillae at the anteroventral portion of mantle border (Mansur and Meier-Brook 2000). *Cyrenoida floridana* and Glauconomidae present a three mantle folds arrangement, but in *C. floridana* the middle fold bears papillae, whereas this does not occur in Glauconomidae (Owen 1959). The degree of mantle fusion of both mantle lobes varies greatly. In Cyrenidae (Huber 2015; Simone et al. 2015) and *C. floridana*, fusion occurs only at the siphonal area, whereas Glauconomidae presents a wider fusion along the inner fold and internal surface of middle fold (Owen 1959), forming an anterior pedal gape.

Siphon: In Cyrenidae, the siphons can originate from the inner fold, as in *Polymesoda* (see Morton 1976) and *Cyanocyclus* (see Mansur and Meier-Brook 2000; as *Neocorbicula*) or from fusion of the inner fold and the internal surface of middle fold, as in *Corbicula* (see Mansur and Meier-Brook 2000). This second pattern is also found in Glauconomidae (Owen 1959), classified as type B by Yonge (1957). In *C. floridana*, the siphon originates as in *Polymesoda*, classified as a type A (Yonge 1957), but it presents a row of papillae described as type B by Yonge (1982).

Siphon length is variable in Cyrenoidea from long or short, fused or separated (Huber 2015). Glauconomidae presents long siphons totally fused, whereas Cyrenidae can show separated short to long siphons (Owen 1959; Morton 1976; Mansur and Meier-Brook 2000; Huber 2015). The siphons of *C. floridana* were shown in living condition by Bieler et al. (2014, fig. 3N); showing siphons with different lengths, with the excurrent siphon two times longer than incurrent, although the incurrent one has a wider opening than the excurrent; this can be explained by the different degree of contraction of the two siphons. Kat (1978) illustrated *C. floridana* siphons with the excurrent one being longer, but half of its length is due to the extroverted siphonal membrane. At any rate, the cyrenoidid siphons are not as long as those of the Glauconomidae, which reach ~50% of the animal length, but they are not as short as those of the cyrenid *Polymesoda erosa* (Solander, 1786) (Morton 1976). All three families share the pattern of the incurrent opening wider than the excurrent (Owen 1959; Morton 1976; Boss 1982;

Mansur and Meier-Brook 2000; Simone et al. 2015). The different sizes of incurrent and excurrent siphons in *C. floridana* is a reversed pattern from that of the Glauconomidae, in which the excurrent siphon is slightly shorter than the incurrent (Owen 1959); Cyrenidae presents siphons of similar lengths (Morton 1976; Mansur and Meier-Brook 2000; Simone et al. 2015).

The presence of papillar rows at the siphonal apertures is a common feature in all three families. They have, at least, one row of papillae at the external rim of the incurrent siphon (Morton 1956; Owen 1959; Glaubrecht et al. 2003). Glauconomidae, *C. floridana*, and some Cyrenidae present a siphonal membrane in the external excurrent siphonal opening, but some Cyrenidae genera, e.g. *Corbicula*, also can present papillar rows at this opening (Araújo et al. 1993; Glaubrecht et al. 2003). Glauconomidae and some Cyrenidae, such as *Corbicula* and *Polymesoda erosa* present papillae beyond the siphonal tip. In Glauconomidae, the external surfaces of both siphons present small papillae, especially on the ventral and dorsal surfaces (Owen 1959). In *Corbicula* and *P. erosa*, the papillae occur at the siphonal base in parallel rows, which can surround the siphonal base, as in *P. erosa* (see Morton 1976), or can be distributed along the entire mantle border up to the siphonal tip, as in *Corbicula* (Glaubrecht et al. 2003). According to Kat (1978), the siphonal papillae in *C. floridana* serve a regulatory function for the incurrent siphon. When incurrent water presents a high concentration of suspended material or the siphon tips are below the sediment surface, the papillae are positioned over the siphonal entrance, whereas in conditions of low suspended material, the siphons are held at maximum dilatation with the papillae away from the entrance.

The siphonal base or tips in all three families show pigment as rings or spots in pale to dark brown, orange, or black (Owen 1959; Morton 1976; Araújo et al. 1993; Glaubrecht et al. 2003).

Siphonal musculature is composed of siphonal retractor muscles that can be present as only one muscle band or divided into two bands, one dorsal and one ventral. In Glauconomidae and most Cyrenidae, the siphonal retractor muscle appears as one wide muscular band; it is fan-shaped in Glauconomidae (Owen 1959; Korniusshin and Glaubrecht 2002), but in *C. floridana* and *Polymesoda floridana* (Conrad, 1846) each present two muscular bands (Simone et al. 2015) with the dorsal band bifid in *C. floridana*.

Gills: Gills in Cyrenoidea are eulamellibranch and both demibranchs are present (Huber 2015). Both demibranchs are wide in *C. floridana*, and the anterior portion of the inner demibranch inserts between the labial palps. In Cyrenoidea, gill size is usually small, without insertion of the inner demibranch between the palps (Owen 1959; Morton 1976; Simone et al. 2015).

Stomach: The stomach of *C. floridana* presents the style sac and the midgut conjoined, the major typhlosoles penetrating both left and right caeca, presence of a normal gastric shield that penetrates at dorsal hood and left pouch, ducts from digestive diverticula opening into

the stomach via left pouch and both caeca, presence of sorting area at roof of anterior side of the dorsal hood and sometimes extending over the right wall of stomach, sorting area in the left pouch, and a sorting area at anterior roof of stomach from esophagus to dorsal hood. Gastric shield teeth and a cuticular lining of the stomach, coded in the morphological/molecular analysis by Bieler et al. (2014) and reaffirmed as having been observed by I. Temkin who conducted that part of the study (2019 pers. comm.), were not detected in the histological study by Kat (1978) nor in the present study. Kat (1978) also described two short caeca, one adjacent to the gastric shield and another near the intestinal groove, but those structures were not observed during this study. The main differences between *C. floridana* and other Cyrenoidea is that in Corbiculidae and Glauconomidae, digestive ducts open independently on the lateral wall of the stomach and Cyrenidae presents a sorting area on the anterior roof and posterior wall of the stomach.

Intestinal coiling among Cyrenoidea shows a simple, loose pattern, with few loops. Midgut course can be summarized as starting as style sac, running ventrally in the visceral sac, followed by a portion running anteriorly, forming a dorsal loop directing the intestine posteriorly, then following parallel to the style sac until leaving visceral sac, passing through the pericardium, crossing the dorsal surface of the kidney, and ending on the surface of posterior adductor muscle (Owen 1959; Morton 1976; Simone et al. 2015). This pattern is a little more complex in *Corbicula*, which presents several spiral coils at the anterior portion of the midgut (Araújo et al. 1993).

The anus of *C. floridana* is located on the ventral surface of the posterior adductor muscle (Fig. 35: **an**). This is a unique position. The anus in the Cyrenidae can be found at different points on the posterior surface of the posterior adductor muscle (Owen 1959; Morton 1976; Araújo et al. 1993; Simone et al. 2015).

In living specimens of *C. floridana*, Kat (1978) observed that the portion of the intestine posterodorsal to the anterior adductor muscle is folded when the intestine was empty, but straightened when the intestine was filled.

Excretory system: The kidney did not present any unusual gross features during this study. In histological sections, Kat (1978) described U-shaped tubules differentiated into anterior and posterior portions based on cell type. Also Kat (1978) described soft, rounded concretions of unknown composition in the kidney lumen and, because some were too large to be expelled, hypothesized that the kidney acts as a storage area for such concretions as a strategy to survive in intertidal environments.

Reproductive cycle: Little is known about the reproductive cycle of *C. floridana*. Kat (1978, 1982) described the reproductive physiology of *C. floridana*, identifying the species as a simultaneous hermaphrodite, describing four gonadal stages and observing developing juveniles in the demibranchs, indicative of brooding behavior, as in many Cyrenidae (Huber 2015). Kat (1978) also noticed that a few specimens in the studied population were purely males.

Based on the reproductive cycle of *C. floridana*, Kat (1978) discussed differing fertilization strategies, based on the number of embryos developing inside the gonad. Kat (1978) noticed that southern populations of *C. floridana* present a characteristic gonadal development and spawn twice a year, whereas northern populations present discreet alterations on gonadal development and successfully spawn only once. Due these differences Kat hypothesized that both populations are in process of differentiation.

Nervous system: Kat (1978) performed a histological study on *C. floridana* specimens and provided additional details about the nervous system, especially regarding microscopic nerve branching and the presence of statocysts on the pedal ganglia.

Parasitism: Calcareous nodules on the inside of *C. floridana* shells are sometimes visible in published photographs of this species, e.g. those by Abbott (1974) and Abbott and Morris (1995). They have been variously reported, e.g. by Van Regteren Altena (1971: 41) who referred to their presence on the type material of *Cyrenoida guatemalensis* (see Figs 7, 8) and stated that “the present Suriname specimens also possess blisters interiorly and I think that their presence is caused by some outward influence in all.” Nodules were noted frequently during this study, although the small numbers of specimens examined do not present a reliable percent occurrence in the species or any living population. They were neither mentioned nor figured in the morphological study by Kat (1978), which involved an unquantified “large number” of shells collected over nine months from the coast of Delaware. Each nodule seen during the present study presents as a small orifice on an igloo-shaped structure that could indicate parasitism by Trematoda (Huntley and De Baets 2015). Kat (1978) detected trematodes in sporocyst stages throughout the bivalve’s soft tissues in a small percentage of histological sections and notice that the infection negatively affected gonadal development and excretion. Also, histozoic and coelozoic parasitism by the haplosporidian protist *Minchinia* sp. has been reported in samples of *C. floridana* (Reece et al. 2004; Arzul and Carnegie 2015).

Conclusions

1. *Cyrenoida floridana* is morphologically characterized by valves externally covered by thin light brown periostracum; muscle scars and pallial line only faintly visible on the internal shell surface, and a unique hinge pattern.
2. The species presents microtubules on the interior shell wall.
3. Anatomically the species presents slightly unequal adductor muscles; few pallial muscles that are well separated from each other; an inner demibranch inserted between the labial palps; demibranchs fused to each other along their posterior ends; totally fused and pigmented siphons that originate from the inner mantle fold; two pairs of siphonal retractor muscles;

loose intestinal coiling; and the anus located on the ventral surface of the posterior adductor muscle.

4. *Cyrenoida floridana* shares a similar habitat, its gill morphology, most of the stomach complexity, and siphonal pigmentation with members of Cyrenidae and Glauconomidae. It differs from the latter two families in its hinge composition, small size, weak and discontinuous pallial line, few and separated pallial muscles at the mantle border, the presence of papillae along the entire ventral border of the mantle except the siphonal area, an excurrent siphon longer than the incurrent one, a bifid dorsal siphonal retractor muscle tip, demibranchs inserting between the labial palps, the absence of independently digestive ducts opening into the lateral side of stomach, and the anus located at the ventral surface of the posterior adductor muscle.
5. Calcareous nodules presenting single circular openings are common on the internal shell surface and could be associated with trematode parasitism.

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A new species in the genus *Heteromysoides* (Crustacea, Mysida, Mysidae) from Songkhla Lagoon, southern Thailand

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Abstract

A new mysid, *Heteromysoides songkhlaensis*, is reported from shallow water in the Songkhla Lagoon, southern Thailand. The new species is closely similar to *H. nana* in having a triangular rostrum and the eyestalk without a process at the anteromesial corner. However, the new species can be readily distinguished from *H. nana* by three setae on the inner margin and five setae on distal margin of the second segment of the mandibular palp; the carpopropodus of the fifth and sixth thoracic endopod of the new species is composed of four articles, and the telson of the new species is distally rounded, shorter than the sixth abdominal somite, and 1.3 times longer than its basal width; the spines on the telson form elongated spines from the distal to posterior margin. The new species also resembles *H. dennisi*, *H. simplex*, and *H. stenoura*; however, it differs by (1) the presence of a rounded distal margin of telson, and (2) absence of a sharp process on the distolateral corner of the eyestalk.

Key Words

Brackish water, *Heteromysoides songkhlaensis*, Thale Sap, Thale Sap Songkhla

Introduction

In Southeast Asia, about 210 species in the order Mysida (Crustacea) have been reported (Sawamoto 2014), and 48 of these species have been documented in Thailand (Tattersall 1921; Murano 1988, 1995; Fukuoka and Murano 2002; Hanamura et al. 2008, 2011; Moriya et al. 2015). Information about the mysid fauna in the Songkhla Lagoon system of southern Thailand has not been updated since Tattersall (1921), who reported *Rhopalophthalmus egregius* Hansen, 1910 and *Nanomysis siamensis* W. Tattersall, 1921.

During a study of variability of the recruitment abundance of *Metapenaeus* spp. in the hyperbenthos of Thale Sap and Thale Sap Songkhla in the Songkhla Lagoon system in 2018, several mysid specimens were collected. Among them, an undescribed species was discovered. The species showed morphological characteristics of the

genus *Heteromysoides* Băcescu, 1968: (1) the cornea of the eye, which is restricted to the anterolateral part of the eyestalk, is reduced in size, and (2) the pleopods are not sexually dimorphic. The known species of the genus primarily occupy shallow marine waters, including marine caves, in the tropical and subtropical regions of the world.

To date, 10 species have been reported in the genus *Heteromysoides*: *H. berberae* Băcescu & Müller, 1985 from Somalia, east Africa; *H. cotti* Calman, 1932 from the Canary Islands; *H. dennisi* Bowman, 1985 from the Caribbean Sea; *H. longiseta* Băcescu, 1983 from Heron Island, eastern Australia; *H. macrops* Murano, 1988 from northern Australia; *H. nana* Murano, 1998 from Channel Island, Northern Territory, Australia; *H. sahulensis* Murano, 1998 from the Sahul Shelf, Australia; *H. simplex* Han-

amura & Kase, 2001 from Okinawa, Japan; *H. spongicola* Băcescu, 1968 from Cuba and Grand Cayman; and *H. stenoura* Hanamura & Kase, 2004 from the Caribbean Sea.

In this paper, *Heteromysoides songkhlaensis* is newly described based on specimens collected in the Songkhla Lagoon system. This, the fourth mysid species known to occur in the Songkhla Lagoon and also the 49th in Thailand, is newly added to the Southeast Asian mysid fauna.

Material and methods

The Songkhla Lagoon system, also known as Songkhla Lake, is a large, shallow body of water located on the east coast of the Thai Peninsula in southern Thailand situated between 7°08'N and 7°48'N and between 100°07'E and 100°35'E. The lagoon system covers approximately 1,082 km² and comprises four distinct bodies of water: Thale Noi, Thale Luang, Thale Sap, and Thale Sap Songkhla (Fig. 1). The lagoon exhibits three water regimes, fresh, brackish, and salt water, which are arranged from north to south, respectively. The salty, southern end of the lagoon is connected to the Gulf of Thailand. Within the lagoon system, salinity ranges from 0 to 34 psu in Thale Sap Songkhla to almost zero in Thale Noi. In both Thale Sap and Thale Sap Songkhla, the substratum is primarily mud.

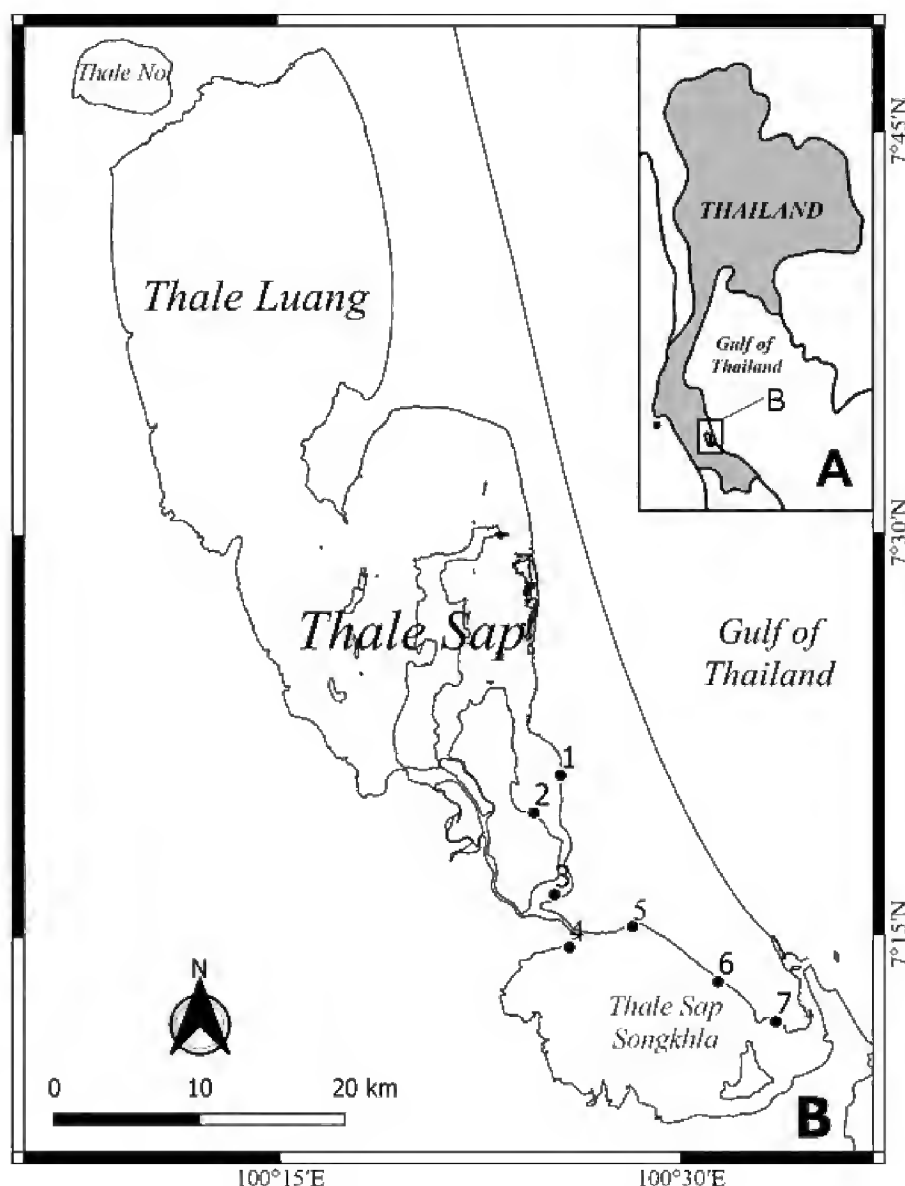


Figure 1. The map of the Songkhla Lagoon system, southern Thailand, shows seven sampling stations (black dot) where *Heteromysoides songkhlaensis* sp. nov. was collected. **St. 1.** Ban Bang Khiat; **St. 2.** Ban Koh Nang Kum; **St. 3.** Ban Laem Chak; **St. 4.** Ban Tai; **St. 5.** Ban Pa Khad; **St. 6.** Ban Bo Pab; **St. 7.** Ban Hua Khao.

Specimens were collected by using a modified Riley's hand-pushed net. Its mouth frame was 30 × 50 cm (height × width), the mesh sizes were 2 mm and 0.5 mm, and its side length 2.5 m. The net was pushed forward for 30 m along the shallow zone of Songkhla Lagoon at seven stations (Fig. 1). The specimens collected were fixed in 4% formalin in the field and brought back to the laboratory. In the laboratory, mysid specimens were sorted and then transferred to 70% ethanol for further study.

Using a micrometer installed in the eyepiece of the microscope, body length (BL) was measured from the tip of the rostrum to the distal end of the telson, excluding apical denticles. Illustrations were made with the aid of a camera lucida. The marginal setae of some appendages, especially the antennal scale, thoracopodal exopods, and uropod, were omitted from the illustrations. Terminology was based mainly on Tattersall and Tattersall (1951) and Wittmann et al. (2014). Specimens examined in this study are deposited in the collection of Prince of Songkla University Zoological Collection (**PSUZYC**), at the Princess Maha Chakri Sirindhorn Natural History Museum, Prince of Songkla University in Hat Yai, Songkhla, Thailand; Phuket Marine Biological Centre (**PMBC**) in Phuket, Thailand; Zoological Reference Collection (**ZRC**) of the Lee Kong Chian Natural History Museum, National University of Singapore and National Museum of Nature and Science, Tokyo (**NSMT**), Japan.

Systematic account

Heteromysoides songkhlaensis sp. nov.

<http://zoobank.org/DE6E674F-CEB3-4CAD-829C-8221F21E1F77>

Figs 2–4

Type material. *Holotype.* Adult male (BL 3.2 mm) (NMST-Cr 26744), Thale Sap, 7°20'58.68"N, 100°25'31.56"E, Ban Bang Khiat, Tambon Bang Khiat, Singha-Nakhon District, Songkhla Province, Thailand, 19 January 2019, at 1.3 m of depth with salinity of 0.39 psu, over a muddy substrate, coll. V. Lheknim, N. Tubtintong and R. Yolanda.

Allotype. Adult female with empty marsupium (BL 3.7 mm) (PSUZYC 20190119-02.01), Thale Sap Songkhla, 7°15'18.77"N, 100°28'11.86"E, Ban Pa Khad, Singha-Nakhon District, Songkhla Province, Thailand, 19 January 2019, at 1.3 m of depth with salinity of 0.47 psu, over a muddy substrate, coll. V. Lheknim, N. Tubtintong and R. Yolanda.

Paratypes. 1 adult male (BL 3.6 mm, dissected) (NSMT-Cr 26745), Thale Sap, 7°19'34.50"N, 100°24'31.45"E, Ban Koh Nang Kum, Koh Nang Kum, Pak Payoon District, Phattalung Province, Thailand, 18 May 2018, at 1.3 m of depth with salinity of 3.68 psu, over muddy substrate, coll. V. Lheknim, N. Tubtintong and R. Yolanda; 1 adult male (BL 3.4 mm, dissected) (PSUZYC 20180618-01.01) Thale Sap Songkhla, 7°13'14.67"N, 100°31'24.12"E, Ban Bo Pab, Sathing Mor, Singha-Nakhon District, Songkhla Province, Thailand, 18 June 2018, at 1 m of depth with salinity of 1.67 psu, over muddy substrate, coll. V. Lhek-

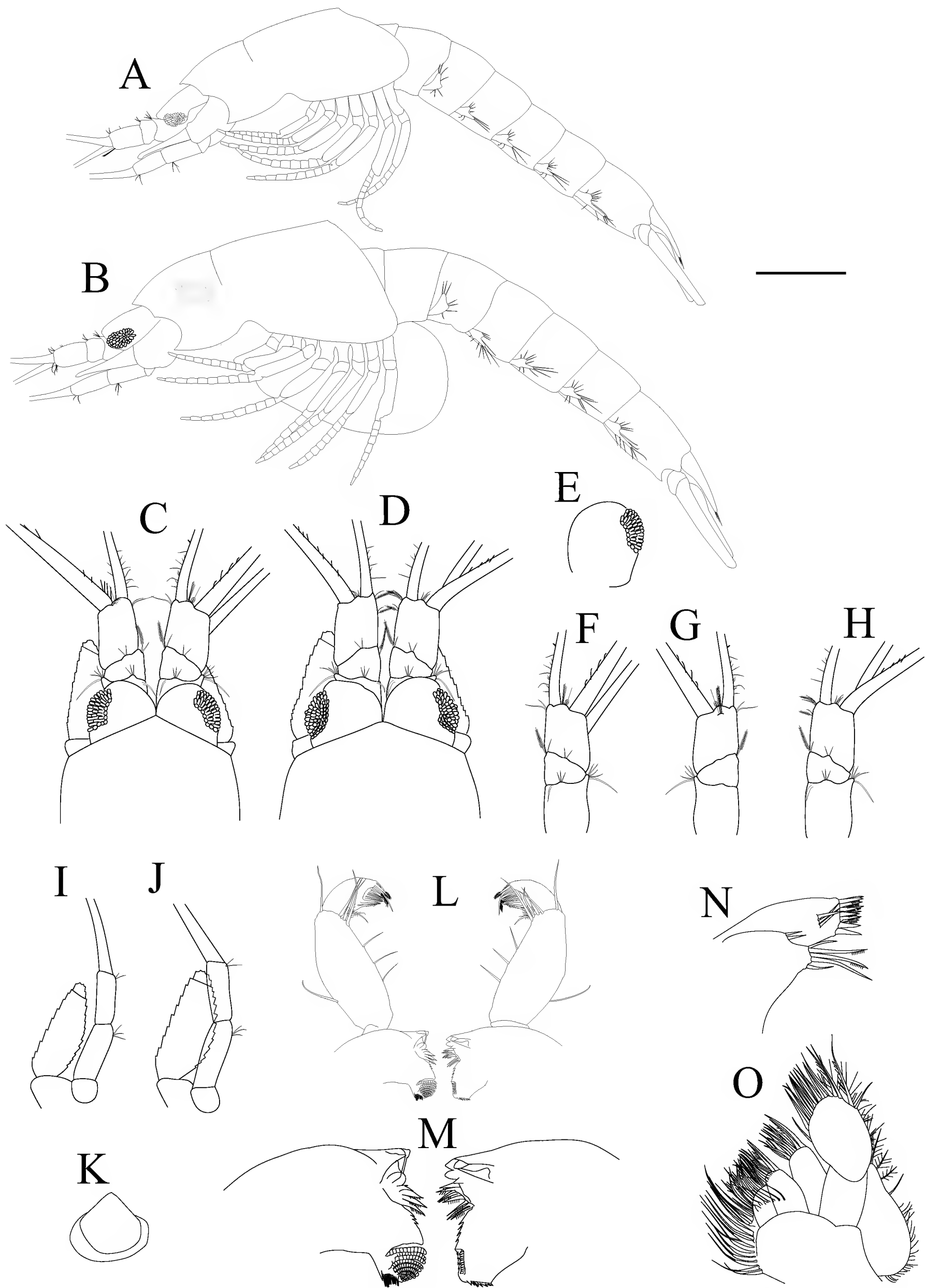


Figure 2. *Heteromysoides songkhaensis* sp. nov. Holotype, male (BL 3.2 mm, **A, C, E, F, G, I**) (NSMT-Cr 26744), allotype, female (BL 3.7 mm, **B, D, H, J**) (PSUZC 20190119-02.01), paratype, male (BL 3.6 mm, **L–O**) and female (BL 3.6 mm, **K**) (ZRC 2019.1095). **A, B.** Lateral view of whole body; **C, D.** Dorsal view of anterior body; **E.** Dorsal view of right eye; **F, H.** Dorsal view of right antennule; **G.** Ventral view of right antennule; **I, J.** Ventral view of antenna; **K.** Ventral view of labrum; **L.** Ventral view of mandibles with palps; **M.** External view of mandibles enlarged; **N.** Right maxillule; **O.** Right maxilla. Scale bars: 0.5 mm (**A, B**); 0.3 mm (**C, D, F–J**); 0.2 mm (**L**); 0.1 mm (**E, K, M–O**).

nim, N. Tubtintong and R. Yolanda; 1 adult male (BL 3.5 mm, dissected) (PMBC 11806), Thale Sap, 7°20'58.68"N, 100°25'31.56"E, Ban Bang Khiat, Tambon Bang Khiat, Singha-Nakhon District, Songkhla Province, Thailand, 18 July 2018, at 0.6 m of depth with salinity of 2.72 psu, over a muddy substrate, coll. V. Lheknim, N. Tubtintong and R. Yolanda; 1 adult female (BL 3.7 mm, dissected) (PMBC 11807), Thale Sap, 7°16'30.89"N, 100°25'17.21"E, Ban Laem Chak, Pak Ror, Singha-Nakhon District, Songkhla Province, Thailand, 18 April 2018, at 1.5 m of depth with salinity of 15.1 psu, over muddy substrate, coll. V. Lheknim, N. Tubtintong and R. Yolanda; 1 adult female (BL 3.1 mm, dissected) (NSMT-Cr 26746), Thale Sap Songkhla, 7°11'45.16"N, 100°33'33.76"E, Ban Hua Khao, Hua Khao, Singha-Nakhon District, Songkhla Province, Thailand, 18 April 2018, at 1.4 m of depth with salinity of 24.8 psu, over a muddy substrate, coll. V. Lheknim, N. Tubtintong and R. Yolanda; 2 adult females (BL 3.2 mm [dissected], 3.6 mm [not dissected]) (NSMT-Cr 26747), Thale Sap, 7°20'58.68"N, 100°25'31.56"E, Ban Bang Khiat, Tambon Bang Khiat, Singha-Nakhon District, Songkhla Province, Thailand, 18 May 2018, at 1.1 m of depth with salinity of 7.43 psu, over muddy substrate, coll. V. Lheknim, N. Tubtintong and R. Yolanda; 2 adult males (BL 3.6 mm, [dissected], 4.0 mm [not dissected]); 1 adult female (BL 3.6 mm, dissected) (ZRC 2019.1095), Thale Sap Songkhla, 7°14'32.41"N, 100°25'50.57"E, Ban Tai, Pak Ror, Singha-Nakhon District, Songkhla Province, Thailand, 18 November 2018, at 1.2 m of depth with salinity of 5.25 psu, over muddy substrate, coll. V. Lheknim, N. Tubtintong and R. Yolanda.

Description. Head and cephalic appendages. Carapace with anterior margin obtusely produced into wide, triangular rostrum (Fig. 2C, D); cervical groove distinct at anterior two-fifths, posterior margin excavated, leaving last thoracic somite uncovered in dorsal view, but sufficiently covered laterally (Fig. 2A, B): antero-ventral corner rounded (Fig. 2A, B). Eye slightly depressed, subglobular in dorsal aspect; cornea comprise of small tube-like ommatidia situated in antero-lateral part without ocular process (Fig. 2C–E). Antennule with first segment of peduncle longer than wide, with dorsal projection bearing 3 setae (Fig. 2F, H); distolateral corner of first segment greatly produced anteriorly, distal part with 5 setae; second segment shortest, with dorsal projection bearing 2 setae and distal part with 2 setae; third segment subequal to first segment, with dorsal projection bearing 4 setae dorsally, middle part with 2 setae at the mesial margin for female while no seta on male, respectively and 2 setae at distomesial corner for male while 3 setae for female; the lobe completed with several long setae on male (Fig. 2G) while no long setae on female. Antennal peduncle more robust in male than female and reaching 0.8 length of antennular peduncle and the sympod rounded (Fig. 2I, J); antennal scale elongated, elliptical with apical suture, setose all round, reaching middle part of third segment of antennular peduncle, nearly 3 times as long as wide, not reaching distal end of antennal peduncle (Fig. 2I, J). La-

brum triangular, without process or spine in anterior part but with expanded disto-lateral parts (Fig. 2K). Mandibular palp 3-segmented, second segment longest and widened at mid-length, with barbed setae on both margins, 3 on middle part of inner margin, 1 seta on proximal part of outer margin and 5 setae on the distal margin of the second segment (Fig. 2L); incisor process well developed and comprised of a series of teeth forming serrated sharp ridge; lacinia mobilis showing different shape in right and left mandibles, and spine row and molar process clearly visible (Fig. 2M). Maxillule well developed, basal lobe with spines densely, wider than precoxal lobe (Fig. 2N). Maxilla with 4 distal setae and smooth setae on exopod (Fig. 2O); distal segment of endopod longer than proximal one; basal and coxal endites well developed, with dense setae.

Thoracopods. Flagelliform part of first and eighth thoracopodal exopods composed of 8 segments (Figs 3A, 4C), while second to seventh thoracopodal exopods with 9 segments (Figs 3C, E, G, I, 4A, B). First thoracopodal endopod short and basis well developed, larger than endite; medial margins of carpus, propodus and dactylus heavily setose (Fig. 3A, B). Second thoracopodal endopod stout (Fig. 3C); basis with 2 setae; preischium with 1 seta, shorter than basis; ischium longer than preischium with 6 setae; merus longest, with 2 setae; carpopropodus 0.75 times as long as merus, with several barbed setae (Fig. 3D); dactylus 0.5 times as long as carpopropodus, 1.6 times as long as width, with several barbed setae (Fig. 3D). Third and fourth thoracopodal endopods similar in form (Fig. 3E, G) and more slender than second (Fig. 3C); basis with 2 setae; ischium slightly longer than merus, with 4–6 setae on inner margin; merus slightly shorter than carpopropodus; carpopropodus constituting 3 sub-segments with barbed setae, basal segment longest and second shortest; dactylus short, apex with long barbed seta and several setae (Fig. 3E–H). Fifth thoracopodal endopod longest (Fig. 3I), with similar morphological characters to sixth, seventh, and eighth (Fig. 4A–C). Sixth thoracopodal endopod (Fig. 4A) subequal in length to seventh and eighth (Fig. 4B, C); basis with 1 seta, ischium longer than merus, with several setae; merus with 6 setae; carpopropodus constituting 4 sub-segments, with several setae, basal segment longest, third segment shortest; dactylus short, with several setae. Penis (Fig. 4C) long, 0.8 times as long as ischium of eighth thoracopodal endopod, apex rounded, with several smooth setae.

Pleon and pleopods. Abdominal somites smooth, without hairs, spines or folds, ventral sternites without process, anterior 5 somites subequal in length, sixth somite 1.3 times as long as preceding somite (Fig. 2A, B). Five pleopods reduced to unsegmented lobes, not modified; first pleopod shortest, second to fourth ones subequal in length and fifth pleopod longest, 1.6 times as long as fourth (Fig. 4D–H).

Uropod and telson. Uropodal endopod slightly shorter than exopod, without spine on ventral side of statocyst region (Fig. 4I). Telson (Fig. 4K–N) subtriangular, 0.8 times as long as sixth abdominal somite, 1.3 times as long as basal width, excluding apical denticles, with 11–18 ar-

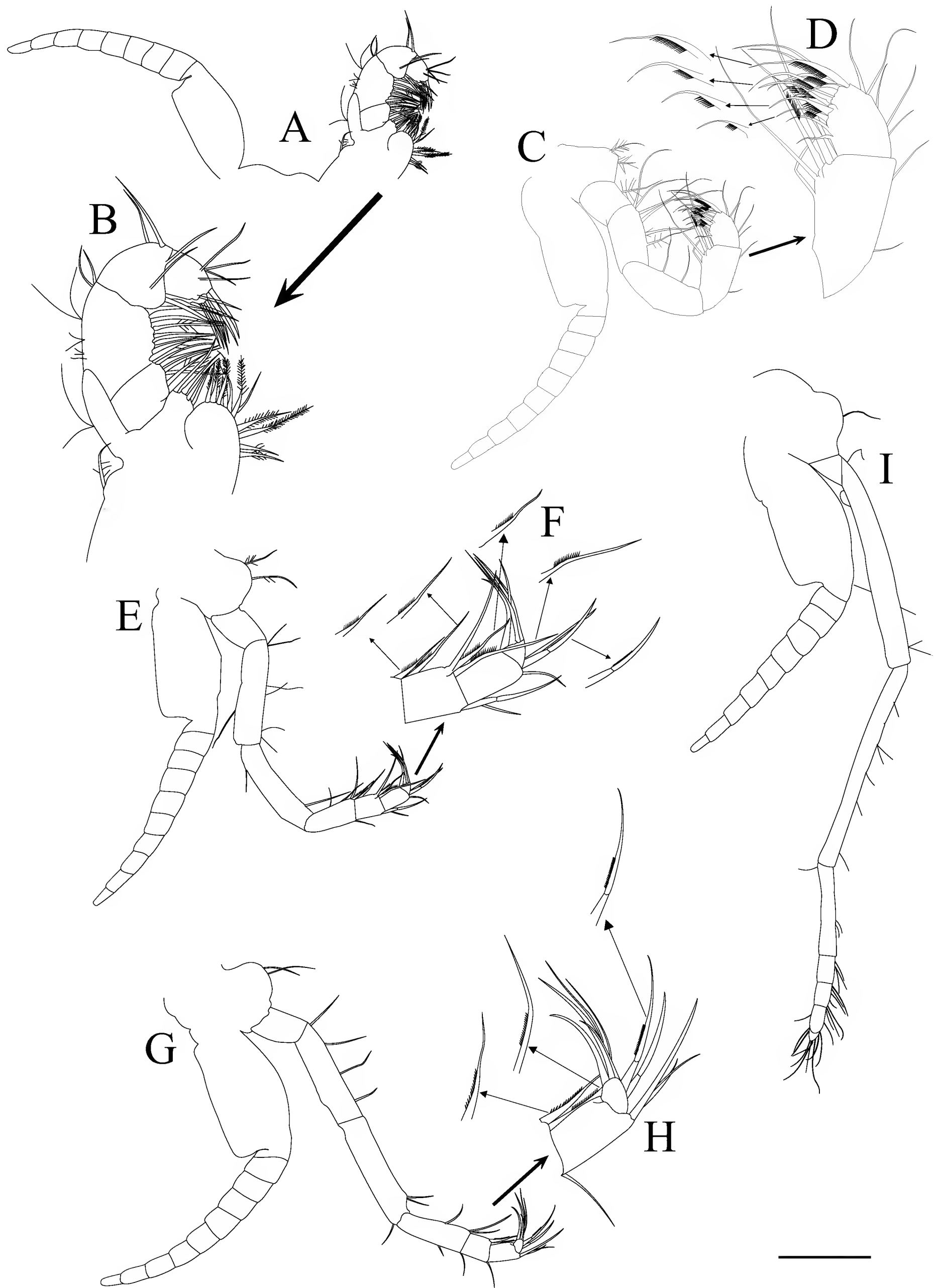


Figure 3. *Heteromysoides songkhlaensis* sp. nov. Paratype, male (BL 3.6 mm, A–I) (ZRC 2019.1095). **A.** Right first thoracopod; **B.** Right first thoracopodal endopod enlarged; **C.** Right second thoracopod; **D.** Carpopropodus, dactylus and setae enlarged; **E.** Right third thoracopod; **F.** Distal part of carpopropodus, dactylus and setae enlarged; **G.** Right fourth thoracopod; **H.** Distal part of carpopropodus, dactylus and setae enlarged; **I.** Left fifth thoracopod. Scale bar: 0.2 mm (A, C, E, G, I); 0.1 mm (B, D, F, H).

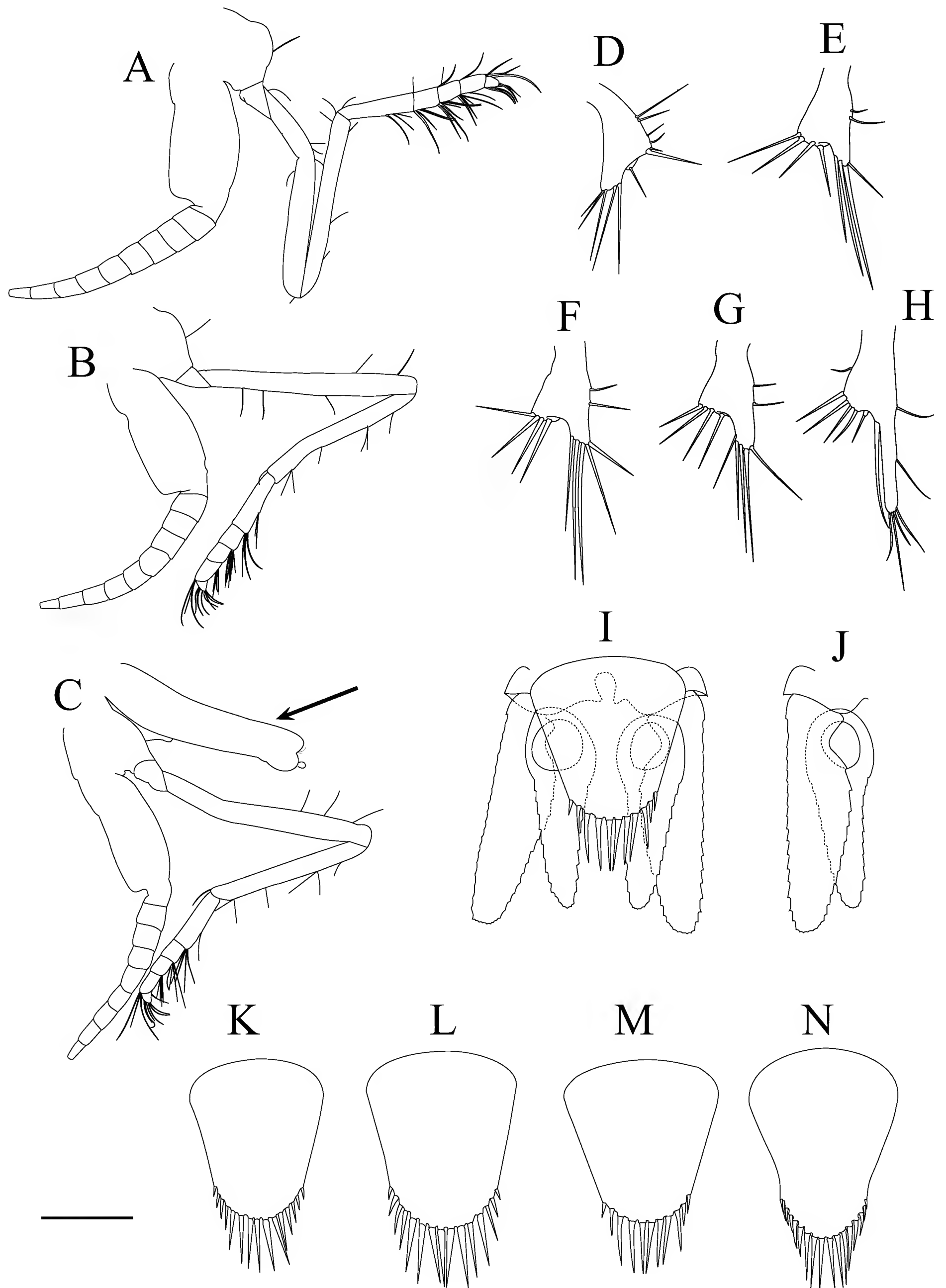


Figure 4. *Heteromysoides songkhlaensis* sp. nov. Holotype, male (BL 3.2 mm, **D–H, K**), (NSMT-Cr 26744), allotype, female (BL 3.7 mm, **L**) (PSUZC 20190119-02.01), paratype, male (BL 3.6 mm, **A–C, I, J, M**) and female (BL 3.6 mm, **N**) (ZRC 2019.1095). **A.** Right sixth thoracopod; **B.** Right seventh thoracopod; **C.** Right eighth thoracopod; **D–H.** Right first to fifth pleiopods; **I.** Dorsal view of telson and uropods; **J.** Ventral view of right uropod; **K–N.** Dorsal view of telson. Scale bars: 0.2 (**A–C, I–N**); 0.1 mm (**D–H**).

Table 1. Body length and the number of spines on the telson of *Heteromysoides songkhlaensis* sp. nov. from Songkhla lagoon, southern Thailand.

No.	Type of specimen	Sex	Body length (mm)	Number of spines
1	Holotype	Male	3.2	15
2	Paratype	Male	3.4	12
3	Paratype	Male	3.5	13
4	Paratype	Male	3.6	14
5	Paratype	Male	3.6	11
6	Paratype	Male	4.0	18
Range			3.2–4.0	11–18
7	Allotype	Female	3.7	15
8	Paratype	Female	3.1	12
9	Paratype	Female	3.2	17
10	Paratype	Female	3.6	19
11	Paratype	Female	3.6	17
12	Paratype	Female	3.7	16
Range			3.1–3.7	12–19

ticulated denticles in males and 12–19 in females on distal quarter margin (Table 1), increasing in length distally.

Etymology. This species is named after the locality, Songkhla Lagoon, where of the specimens were found.

Distribution. This species was captured in brackish waters above a muddy substratum at Thale Sap and Thale Sap Songkhla, Songkhla Lagoon, southern Thailand.

Discussion

Heteromysoides songkhlaensis is closely similar to *H. nana* in (1) having a triangular rostrum of the carapace, and (2) lacking a process at the anteromesial of the eyestalk. However, the new species can be distinguished from *H. nana* by several features: (1) the mandibular palp displays three setae on the inner margin and five setae at the distal margin of the second segment as opposed to two setae on the inner margin and three setae at the distal margin of the second segment in *H. nana*; (2) the carpopropodi of the fifth and sixth thoracic endopods of the new species is composed of four articles compared to five articles in *H. nana*; (3) the telson of the new species is distally rounded, shorter than the sixth abdominal somite, and 1.3 times longer than its basal width, while in *H. nana* the telson is slightly concave, longer than the sixth abdominal somite, and 1.6 times longer than its basal width; and (4) the spines on the telson are noticeably different in their arrangement from those of *H. nana*.

The new species also exhibits similarities to several other *Heteromysoides* species, e.g. *H. dennisi*, *H. simplex*, and *H. stenoura*, in having (1) the telson without a cleft or sinus at its distal end, and (2) the uropodal endopod without a spine on the inner mesial margin. However, the new species differs from them in having (1) the eyestalk without a sharp process at the disto-lateral part, and (2) the telson rounded, not truncated, at the distal margin.

Several species from the family Mysidae in South-east Asia have been found from brackish to full-strength seawater, e.g. *Mesopodopsis orientalis* (e.g., Hanamura et al. 2008), *Acanthomysis thailandica* (e.g., Ramarn et al. 2012), and *Rhopalophthalmus* spp. (e.g., Hanamura et al. 2011). So far, all described species of *Heteromysoides* have been found in seawater, whereas the new species was found in brackish waters. Further study would be needed to elucidate the exact relationship of the current geographical pattern and the origin of *Heteromysoides* species.

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The evolutionary terrestrialization of planarian flatworms (Platyhelminthes, Tricladida, Geoplanidae): a review and research programme

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Abstract

The terrestrialization of animal life from aquatic ancestors is a key transition during the history of life. Planarian flatworms form an ideal group of model organisms to study this colonization of the land because they have freshwater, marine, and terrestrial representatives. The widespread occurrence of terrestrial flatworms is a testament to their remarkable success occupying a new niche on land. This lineage of terrestrial worms provides a unique glimpse of an evolutionary pathway by which a group of early divergent aquatic, invertebrate metazoans has moved onto land. Land flatworms are among the first groups of animals to have evolved terrestrial adaptations and to have extensively radiated. Study of this terrestrialization process and the anatomical key innovations facilitating their colonization of the land will contribute greatly to our understanding of this important step in Metazoan history. The context and scientific background are reviewed regarding the evolutionary terrestrialization of land flatworms. Furthermore, a framework of a research programme is sketched, which has as its main objective to test hypotheses on the evolution of land planarians, specifically whether particular anatomical and physiological key innovations have contributed to their evolutionary successful terrestrial colonization and radiation. In this context special attention is paid to the respiration in aquatic and terrestrial planarians. The research programme depends on a comprehensive phylogenetic analysis of all major taxa of the land flatworms on the basis of both molecular and anatomical data. The data sets should be analyzed phylogenetically with a suite of phylogenetic inference methods. Building on such robust reconstructions, it will be possible to study associations between key innovations and the evolutionary terrestrialization process.

Key Words

adaptations, evolution, key innovations, land flatworms, model organisms, respiration, terrestrialization

Introduction

Charles Darwin was fascinated by planarian flatworms, and he was particularly struck by the fact that there is a group of planarians that actually live on land. As he wrote in a letter from 23 July 1832 to his mentor Henslow: “Amongst the lower animals, nothing has so much interested me as finding 2 species of elegantly coloured true Planariae inhabiting the dry forest.” And in a letter from 15 August 1832: “I have today to my astonishment found 2 Planariae living under dry stones....”. Darwin thought for a long time that he was the first person to

have discovered terrestrial flatworms. It was only in 1846 that it came to his attention that already in 1774 the Danish naturalist O. F. Müller had described the land flatworm *Microplana terrestris* (Müller, 1774) (Porter and Graham 2016).

Darwin (1983: 25) appropriately and succinctly described land flatworms as follows: “In general form they resemble little slugs, but are very much narrower in proportion, and several of the species are beautifully coloured with longitudinal stripes.” He took some of

the land flatworms that he had collected in Tasmania on board of the *Beagle* and managed to keep them alive for two months. He experimented on the animals by cutting some animals into half, and he discovered that after 25 days each piece had regenerated to an almost complete animal (Darwin 1983; Sluys 2016). Darwin was so much intrigued by his flatworm findings that in a letter of 22 May 1833, written when he was in Tierra del Fuego, he asked his sister Catherine to send him Dalyell's (1814) paper on several species of British freshwater planarians (Thomson 2009). In this paper Dalyell (1814) reported many observations on the biology of these worms, including a detailed study of their fission and regeneration (Ball and Reyoldson 1981). Since the days of Darwin and Dalyell our knowledge on the regenerative capacity of land planarians, and that of triclad flatworms in general, has greatly increased (cf. Reddien 2018; Rink 2018), as well as our knowledge on the morphology, taxonomy, phylogeny, and distribution of land flatworms (cf. Sluys and Riutort 2018 and references therein). The fact that delicate organisms such as free-living flatworms, most of which occur in freshwater or marine environments, are able to survive on land has received little attention. Thus far, no detailed studies have been undertaken that attempted to analyze how and when during their evolutionary history planarians conquered the terrestrial environment, which of their anatomical and physiological features enabled their colonization of the land, and which adaptations currently facilitate their occupation of the terrestrial niche.

Therefore, in the following I do not so much present the results of such studies, but provide a review of this subject and sketch the context, scientific background, and framework of a research programme in which land flatworms form the model group through which we may not only learn about their own terrestrialization but may be enlightened also on the early evolutionary terrestrialization of animal life in general. In this context, special attention is paid to the respiration in aquatic and terrestrial planarians. In addition, the results obtained during this putative research programme will also provide data for some collateral topics, such as biodiversity assessment and historical biogeography.

Early evolutionary terrestrialization of animal life, as exemplified by land flatworms

The terrestrialization of animal life from marine or freshwater ancestors is a key event in the history of life on earth, particularly because in the course of evolution "... transitions among physically different habitats... are rare" (Vermeij and Dudley 2000: 546; see also Vermeij 2010). Moving from an aquatic to a terrestrial niche is challenging due to the dramatically different demands each environment places on the physiology and structure of an organism, thus requiring numerous innovations.

Key innovations afford enhanced performance, promoting ecological opportunity. These innovations enable subsequent species diversification and radiation. For example, marine gastropod snails in several cases evolved terrestriality independently from amphibious ancestors by side-stepping a major constraint on land snail evolution, viz., the need to produce mucus for locomotion (Rosenberg 1996). Interestingly, mucus plays an important role in land flatworms: forming a slime trail for locomotion, slime threads by which they can cross spaces or lower themselves from heights, and a protective coat against drying. Apparently, the worms have followed a different adaptive pathway than the molluscs and were able to colonize the land without conserving mucus.

The land flatworms or planarians (Fig. 1) likely represent one of the first groups of animals that during evolution have colonized the land and have extensively radiated (see below: Impact and innovative aspects). Study of the evolutionary terrestrialization of the land flatworms and the key anatomical innovations facilitating this process will contribute greatly to our understanding of the early steps onto land of the Metazoa. Planarian flatworms (Platyhelminthes Claus, 1887, Tricladida Lang, 1884) form an ideal group of model organisms to study this process because they have freshwater, marine, and terrestrial representatives. Preadaptations for life on land are the conditions that (1) flatworms have internal fertilization, (2) the cocoons enveloping the eggs have a relatively hard shell, (3) the young hatch directly as young worms and not as larvae (Little 1983), and that (4) the worms produce mucus. Traditionally, three major groups of triclads were recognized: Paludicola Hallez, 1892 (freshwater planarians), Maricola Hallez, 1892 (marine triclads), Terricola Hallez, 1892 (land planarians). A fourth clade, the Cavernicola Sluys, 1990, was proposed by Sluys (1990). More recently, molecular phylogenetic studies have shown that one of the three paludicolan families is more closely related to the land planarians than to the other freshwater planarians (Baguña and Riutort 2004; Álvarez-Presas et al. 2008; see also Sluys and Riutort 2018).



Figure 1. Photograph of the South American land planarian *Polycladus gayi* (from Grau and Carbayo 2010).

Model organism: land planarians

Terrestrial planarians (Platyhelminthes, Tricladida, Geoplanidae Stimpson, 1857) are a relatively species-rich group (approx. 910 nominal species) with a worldwide, mainly pan-tropical, distribution (Fig. 2). The animals live typically in tropical jungles and wooded areas. Terrestrial planarians colonized the land hundreds of millions of years ago, but they still lack any special mechanism for water conservation (Kawaguti 1932). Although they require a humid environment, they cannot endure long submersion in water, in contrast to their marine and freshwater relatives (Froehlich 1955). The animals cannot endure heat and direct sunlight, otherwise they desiccate quickly (Kawaguti 1932). Because of these limitations they tend to remain hidden during the day in humid, but not wet, refuges, only emerging at night when the relative humidity of the air is high. Land planarians are fully terrestrial cryptozoic organisms because they are not tied to aquatic systems for reproduction. The worms are part of the soil ecosystem, living within the habitat of their prey (Ogren 1955; Ball and Sluys 1990; Ogren and Sheldon 1991). Terrestrial planarians are successful top-predators of other invertebrates such as snails, slugs, earthworms, isopods, insect larvae, and springtails; they themselves are rarely predated upon by other organisms, although some of their predators may be beetles, snails, and other land planarians (Boll and Leal-Zanchet 2018 and references therein). Land planarians search for, attack, and capture prey much larger than themselves, employing various techniques such as physical force, adhesive mucus, pharyngeal action, and pouring very effective digestive secretion over the surface of the live prey, or into it, by the protrusible pharynx.

The widespread occurrence of these terrestrial flatworms (Fig. 2) is a testament to their remarkable success occupying a new niche on land for hundreds of millions of years. This lineage of flatworms thus provides a unique glimpse of an evolutionary pathway by which a group of early divergent aquatic, invertebrate metazoans has moved onto land.

Objectives

The main objective of the research programme described here is to test hypotheses on the evolution of land flatworms, specifically whether particular anatomical and physiological key innovations have contributed to their successful terrestrial colonization and subsequent radiation (see below: Hypotheses testing). This first requires a comprehensive phylogenetic analysis of all major taxa of the land flatworms (e.g., for the current 55 genera; cf. Sluys et al. 2009). The project needs to construct this phylogeny on the basis of both molecular and anatomical data. This reconstruction forms the necessary basis and framework for subsequent comparative studies of key innovations, adaptive radiation, and historical biogeography of land flatworms, and on the early terrestrialization of animal life.

Key innovations, adaptive radiation, and terrestrialization

Understanding of the evolutionary dynamics of the following presumed key innovations, for example, may contribute to our insight in the evolution of land flatworms: (1) colonization of the land (on which occasions did the transition from water to land occur and were there reversals?); (2) contribution of the various kinds of anatomically complex creeping soles and (3) of mesenchymal body musculature (absent in freshwater and marine forms) to the effective terrestrialization; (4) contribution of cephalic specializations for the capture of prey to the adaptive radiation process; (5) the relation between the ecology and anatomy of the various taxa and their various types of pharynges (frequently totally different from freshwater and marine forms) for capturing and digesting prey; (6) the extent to which the various kinds of multi-cellular eyes of land flatworms (completely different from marine and freshwater forms) facilitated terrestrialization and adaptive radiation; (7) adaptation of particular sense organs, such as olfactory chemoreceptors, to the humid air of the terrestrial environment, in contrast to taste chemoreceptors that evolved in aquatic habitats; (8) the way in which the worms are able to cope with a major evolutionary constraint: the need to produce mucus for their locomotion, mucus for the most part being water; (9) the correlation between various body shapes (cylindrical, flat, etc.) on the one hand and water conservation and various terrestrial habitats (ranging from humid to rather dry) on the other hand, a cylindrical body considered to be more economical in terms of water conservation (Clark and Cowey 1958); (10) the manner in which the protonephridia adapted from an osmoregulatory system in aquatic ancestors to a resorptive system (saving water and/or eliminating metabolic wastes) in land flatworms; (11) the change from aquatic to terrestrial respiration.

Impact and innovative aspects

Phylogenetic studies, including those on flatworms in general and land flatworms in particular, are generally based on one-sided approaches, incorporating either morphological/anatomical data, or molecular data. Molecular studies might plot some morphological data on the resulting phylogenies to legitimize the molecular trees ('pseudo-morphology'; cf. Mooi and Gill 2010; Assis and Rieppel 2011; see also Williams and Ebach 2010). But for the land flatworms there are no studies that take an integrative approach with both kinds of data. This contrasts with the fact that many interesting scientific questions in this group of animals concern the evolution of their structures, key innovations, and adaptations (see above: Key innovations, adaptive radiation, and terrestrialization).

Land flatworms likely are among the first groups of animals that during evolution have colonized the land

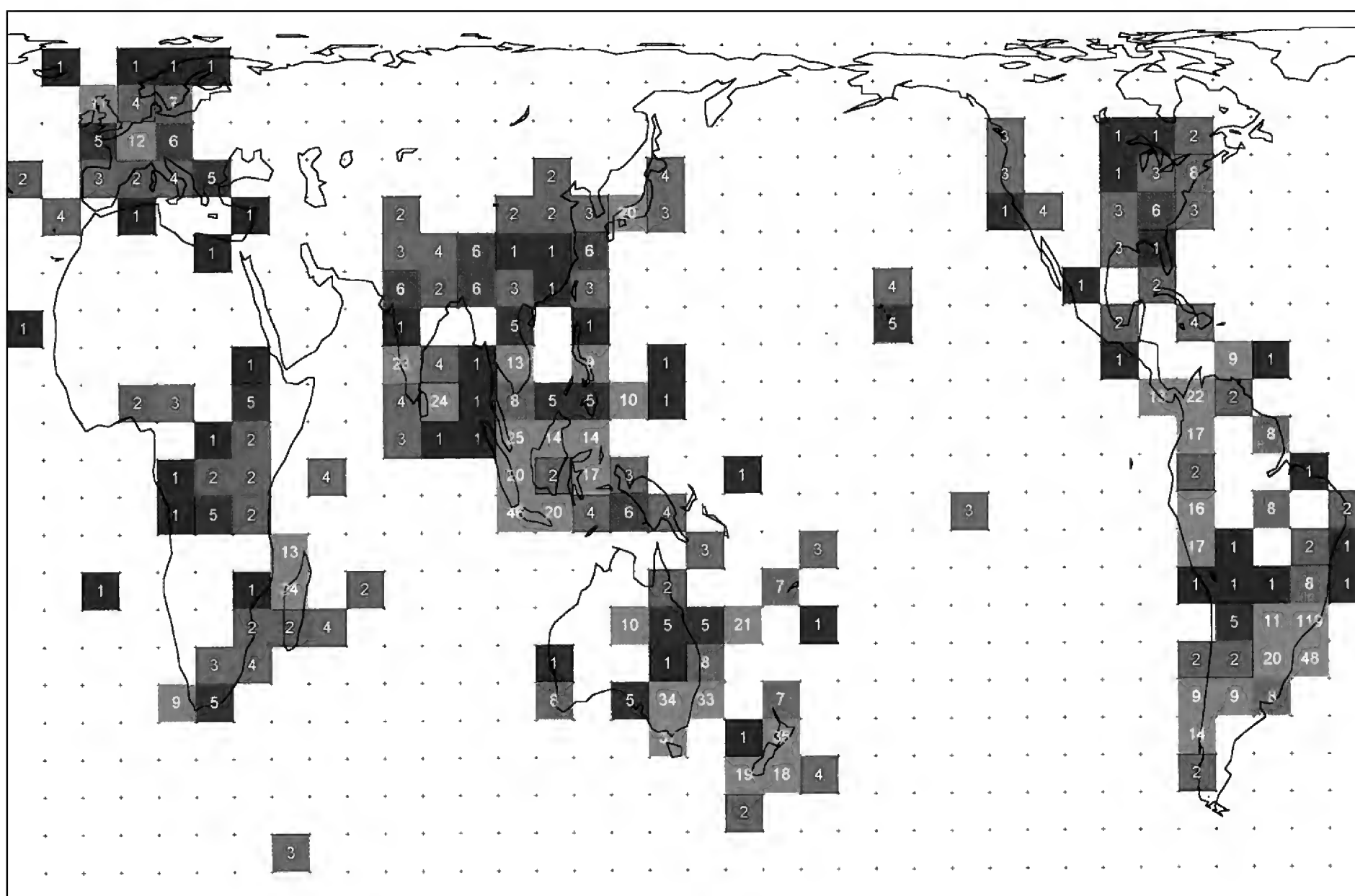


Figure 2. Map of species richness in land planarians on an equal area grid map; maximum in red, minimum in dark blue (from Sluys 1998). Over the past 20 years new discoveries have added to the number of native and introduced species. Nevertheless, the current pattern of biodiversity remains very similar to the one shown in this map, although now, for example, about 20 new species are recognized in Europe, 40 in southeastern and southern Brazil and northeastern Argentina, nine in the Australian territories, and six in New Zealand (Sluys 2016).

and have subsequently radiated extensively. According to fossil information arthropods would be the first animals to have colonized the land, with atmospheric oxygen levels as the major driver of successful colonization (Ward et al. 2006). However, phylogenetic trees suggest flatworms as one of the early colonizers (cf. Hedges and Kumar 2009). This is generally neglected and, therefore, the study proposed here will contribute to a more balanced representation of the evolutionary history of terrestrial animal life.

The fossil record of flatworms is sparse and hardly provides adequate calibration points for a molecular clock (cf. Pierce 1960; Alessandrello et al. 1988; Ruiz and Lindberg 1989; Poinar 2003); calibration points may have to be based on paleogeographical information, amber fossils, coprolites, or estimates of mutation rates (cf. Blaxter 2009 and references therein). Thus, the proposed project will also form a first step towards our understanding of the absolute timing of the early terrestrialization of animal life. It will facilitate the test of the hypothesis that terrestrialization is linked to atmospheric oxygen levels, as was proposed for arthropods (Ward et al. 2006). The project may thus contribute to the first few insights into the terrestrialization of the Lophotrochozoa Halanych et al., 1995 because our current understanding is mainly re-

stricted to the Ecdysozoa Aguinaldo et al., 1997 and the Deuterostomia Grobden, 1908 (cf. Labandeira 2005). Such issues may only be adequately addressed with the help of the phylogenetic trees generated during the research programme outlined here. These phylogenetic reconstructions will also form the long-awaited robust backbone for conservation biology studies in which land planarians function as indicator taxa (see Sluys 1999). Furthermore, triclad flatworms are a key group in historical biogeography because they do not possess larval dispersive stages. Therefore, they are excellent models for vicariance scenarios as explanations for current biogeographic patterns. Thus, the research programme will facilitate tests of the hypothesis that plate tectonics has been a major factor in their historical biogeography (cf. Sluys 1994, 1995).

For the morphological data I envision this programme to develop a formal knowledge representation (ontology) of planarian phenotypes and character states that leverages progress in this field (for a review, see Mabee et al. 2007) such that one of the outcomes will be a ‘Rosetta stone’ of concepts in planarian morphology that can be used not just to disambiguate characters and their states in the putative study but also to inform subsequent research questions in connecting genomic data and planarian phenotypes.

Phylogeny

Knowledge on the phylogenetic relationships within the Tricladida is based on phylogenetic analyses of molecular and morphological datasets (for a review, see Sluys and Riutort 2018). Attention has been paid mostly to: (1) the relationships between the higher taxa within the Tricladida (cf. Sluys 1989a; Carranza et al. 1998; Álvarez-Presas et al. 2008); (2) the affinities within the suborder of the Maricola (Sluys 1989b); (3) the higher taxon relationships within the freshwater planarians in general and within the family DugesIIDae Ball, 1974 in particular (Ball 1974; De Vries and Sluys 1991; Sluys 2001; Lázaro et al. 2009). Sluys and Kawakatsu (2006) explored the phylogenetic relationships within the freshwater families Dendrocoelidae Hallez, 1892 and Kenkiidae Hyman, 1937. More recent studies have resulted in an expanded character state matrix, including several new species and gene sequences, and in a robust phylogenetic tree for the higher taxa (Álvarez-Presas et al. 2008).

For decades the evolutionary relationships within the group of land flatworms have been neglected. Partial taxonomic revisions of the group have been published but these were rarely based on a phylogenetic analysis (cf. Ogren and Sluys 1998; Kawakatsu et al. 2005). It was only with the advent of molecular techniques that studies started to address the phylogenetic structure within the group (cf. Álvarez-Presas et al. 2008; Carbayo et al. 2013). On the basis of the results of these molecular studies, and in combination with anatomical data, a revised higher classification of planarian flatworms was proposed (Sluys et al. 2009), in which the subordinal taxonomic rank of the terrestrial planarians was downscaled to the level of family, viz., the Geoplanidae. However, these molecular studies suffer from the fact that they only incorporate relatively few exemplar species and then only for a small selection of land planarian taxa.

Methodology

Separate and combined analyses

It is proposed here to use both molecular and morphological data sets. To characterize their phylogenetic signal the character state matrices should be analyzed separately, using parsimony (morphology) and Bayesian methods (morphological as well as molecular). In addition, molecular and morphological data sets should be combined into one joint analysis. With respect to morphological and molecular characters two approaches may be followed: (1) morphology is merely optimized in post-tree analysis of the molecular results, or (2) morphological and molecular characters are combined into one data matrix. The first approach is favoured in many recent studies and considered to be the only contribution of morphology to phylogenetic analysis by Scotland et al. (2003); but see Jenner (2004) for a rebuttal. It is here

suggested that the second approach, i.e., combined analysis, is applied.

From an empirical perspective, it has been shown that morphology can have a profound effect on the combined analysis, irrespective of the fact that the number of molecular characters generally exceeds the number of morphological features (Jenner 2004; Assis 2009). Combined analyses may be different from the analyses of the separate data matrices and consensus trees may hide a phylogenetic signal that is generated by a total evidence analysis. Positive contributions of morphology to quantitative clade support measures in combined analyses have been observed for a large number of taxa (Jenner 2004).

Timetree calibration

As the fossil record of flatworms is sparse and does not provide adequate calibration points for a molecular clock, calibration of the phylogenetic timetrees has to be based on other kinds of data, such as, for example, paleogeographical information (see above: Impact and innovative aspects). This means, for example, that we will be looking for closely related taxa **a** and **b** that are endemic to the areas **A** and **B**, respectively. In addition, we will be looking for those areas **A** and **B** inhabited by endemic taxa for which paleogeographic data indicate the time since the two areas have fragmented from a single ancestral area. These two pieces of information, together with the molecular clock hypothesis, will enable one to date all cladogenetic and biogeographic events in the entire lineage of which **a** and **b** only form a part.

Within the triclad flatworms there is a good number of such disjunctions, due to vicariance events, within species or between closely related species, that may be tested as possible calibration points. For example, land planarians of the genus *Othelosoma* Gray, 1869 are restricted to Africa and India and have attained their current distribution when India and Africa started to separate at about 150 Mya. Table 1 specifies the taxa, and their presumed vicariance events and divergence times that may profitably be used for calibration.

One may perhaps be inclined to consider paleogeographical calibrations to be less ideal than fossil calibrations. In point of fact, the opposite may be the case. Fossil-calibrated molecular clocks at best provide minimum dates (Wilke et al. 2009). Therefore, it has been argued that clocks are best calibrated with reference to the distribution of molecular clades and associated tectonics (e.g., Azuma et al. 2008; Heads 2014).

Molecular dating is a rapidly developing field and therefore there is currently no single best method; each approach has its advantages and disadvantages. It is also important to note that in the phylogenetic tree of the Platyhelminthes, the triclads constitute one of the crown groups (cf. Baguña and Riutort 2004). This implies that the nodes below the Tricladida represent older taxa that therefore might be used as potential outgroups in the phylogenetic analysis.

Datasets and phylogenetic analysis

The molecular data matrix for this project may be derived from published data from GenBank, and new molecular sequences generated from fresh material of new taxa examined during the project. Previous studies have shown that the following genes provide the best resolution at the hierarchical levels of the phylogenetic tree of the triclads that form the focus of the putative research programme: nuclear 18S rDNA and 28S rDNA for resolving the deeper, more ancient branches in the tree, and mitochondrial COI to contribute signal on more recent splits (e.g. between and within genera) (Álvarez-Presas et al. 2008). Subsequently, another nuclear marker, the elongation factor 1-alpha (EF), was added to the list of informative markers for an intermediate level between family and species, contributing to resolution of the relationships between members of the Geoplaninae subfamily (Carbayo et al. 2013).

It has been suggested that many of the problems associated with the amplification and sequencing of planarian molecular markers may be solved by applying next generation sequencing (NGS) methodologies (Sluys and Riutort 2018). This new era has started already, and in recent years genomes and transcriptomes of freshwater planarians have already been sequenced (Egger et al. 2015; An et al. 2018; Grohme et al. 2018; Rozanski et al. 2018), contributing new anonymous nuclear markers that can be used as phylogenetic tools. There are even bioinformatic pipelines that can help in the discovery of these markers using NGS data as input (Frías-López et al. 2016). This has already been applied in freshwater planarians, and will soon be used also for terrestrial flatworms. Moreover, there is now available also information on other mitochondrial markers, in addition to COI, as whole mitogenomes were sequenced and annotated (Sakai and Sakaizumi 2012; Solà et al. 2015; Gastineau et al. 2019; Yang et al. 2019), contributing to the combination of nuclear and mitochondrial markers, thus obtaining better resolved phylogenies.

The project requires a large morphological data matrix of all major taxa of land planarians (e.g., for the current 55 genera; cf. Sluys et al. 2009). For this, the programme may be taking as leads the doctoral dissertations of both Dr L. Winsor (2003, James Cook University, Townsville)

and Dr F. Carbayo (2003, University of Sao Paulo). Both researchers made detailed character codings and scorings for taxa of land planarians. Dr Winsor mostly focussed on Australian taxa, while Dr Carbayo concentrated on South American species, although neither used these scorings for a subsequent phylogenetic analysis. During the project character codings and scorings may be extracted from these two doctoral theses and, subsequently, be combined, refined and also supplemented by scorings for taxa not examined by Winsor or Carbayo. Definition and scoring of morphological character states should comply with the most recent insights (cf. Sereno 2007).

The morphological, molecular, and combined data matrix may be analyzed using maximum parsimony (e.g., TNT; Goloboff et al. 2003), maximum likelihood (e.g., RaxML; Stamatakis 2014; IQtree; Nguyen et al. 2015), and Bayesian Inference (MrBAYES, Ronquist et al. 2012, and BEAST, Drummond et al. 2012). Informative genes should first be analyzed separately, but also combined in the form of concatenated datasets. Substitution model parameters may either be selected using nested likelihood ratio tests or explored using reversible jump Markov chain Monte Carlo methods (jModeltest, Darriba et al. 2012; Partitionfinder, Lanfear et al. 2017). Saturation tests should be performed using DAMBE (Xia 2017).

Molecular data may be analyzed also under a dynamic approach to homology. In the dynamic approach delineations are dependent upon the topology of the phylogenetic trees on which they are optimized. In this context hypotheses of homology are part of phylogenetic hypotheses and are subject to the same optimality criteria as the trees, viz., minimisation of evolutionary transformation events. The computer program POY (ver. 4.0 beta 2635; Wheeler et al. 2006, Varón et al. 2010) allows for phylogenetic tree searches under this dynamic homology or direct optimization approach.

Aquatic planarians should form one of the outgroups for the phylogenetic analysis. Particularly the freshwater family Dugesidae has been shown to share a close relationship with the land flatworms (see Sluys et al. 2009). But other freshwater groups, as well as marine triclads, should be included also as outgroups. Comparison with these freshwater and marine forms will reveal the adaptations that made possible the transition to land.

Table 1. Taxa, and their presumed vicariance events and divergence times that may be used for calibration of the timetrees.

Taxon	Vicariant distribution	Divergence time (Mya)
<i>Othelosoma</i> species	Africa (31 sp.)/India (7 sp.)	≤150
<i>Bipalium</i> species	Madagascar (23 sp.)/India & SE Asia (160 sp.)	90-50
<i>Girardia</i> species	N. America (4 sp.)/ S. America (39 sp.)	3,5
genus <i>Girardia</i> /genus <i>Dugesia</i>	N. & S. America (42 sp.)/Africa (21 sp.)	130-100
<i>Dugesia</i> species	E. Med. (12 sp.)/W. Mediterranean (10 sp.)	38-3
<i>Procerodes littoralis</i>	E. Atlantic/W. Atlantic	150
<i>Foviella affinis</i>	E. Atlantic/W. Atlantic	150
<i>Uteriporus vulgaris</i>	E. Atlantic/W. Atlantic	150
genus <i>Amblyplana</i> /genus <i>Geoplana</i>	Africa (9 sp.)/S. America (64 sp.)	100
<i>Romankenkius</i> species	S. South America (1 sp.)/Australia (12 sp.)	120

Hypotheses testing

Creeping sole

The research proposed here seeks to explore the evolution of terrestrialization of land flatworms in time and in correlation with presumed key morphological adaptations. As regards the time axis, this will be important both for direct reconstructions of when terrestrialization happened, as well as in the subsequent analysis of whether hypothesized key innovations co-vary in their location on the phylogeny with elevated diversification rates under a model of adaptive radiation (e.g., using the method of Ree 2005). It is here proposed that divergence dates estimates may be reconstructed from molecular data calibrated using previously published node ages (Hedges and Kumar 2009) in a relaxed molecular clock approach as implemented in BEAST (Drummond et al. 2012). As for covariance between traits (see above: Key innovations, adaptive radiation and terrestrialization), the general model will be that the radiation of flatworms, with presumably repeated terrestrializations, constitutes a natural experiment such that morphological changes hypothesized to be associated with terrestrialization co-vary with and co-occur in ancestral state reconstructions on a phylogenetic tree. Sophisticated comparative methods to correct for autocorrelation (because the different lineages are related to each other) have been developed, including Bayesian statistical methods that allow for phylogenetic uncertainty (e.g., Pagel and Meade 2006). Understanding of the evolutionary dynamics and consequences of such innovations will contribute to the unraveling of their genetic basis and their role in speciation events and, consequently, the adaptive radiation of this group of animals.

To give an example, the study will provide insight into the evolution of creeping soles, the latter defined as: “A flat or ridged modified strip of epithelium on the ventral surface of geoplanid triclad flatworms characterized by the presence of cilia . . . which provides propulsive forces by ciliary or muscular action, or by a combination of both” (Sluys et al. 2009: 1773). Traditionally, a narrow creeping sole is considered as the primitive character state, while medium to broad soles and loss of a creeping sole are seen as derived states. However, narrow soles may also secondarily result from partial reduction, while absence of a creeping sole altogether may be the ancestral state, as aquatic forms lack one. However, the evolution of creeping soles has never been analyzed within a phylogenetic context; the research programme developed here will be the first to do so. If the traditional view holds true, one would expect to infer the narrow creeping sole as the character state at the root of the tree, with transitions to medium or broad soles, or loss of a creeping sole, nearer the tips. Under the opposite scenario, the absence of a creeping sole being the ancestral state, one would consequently expect this state to be reconstructed

for the root of the phylogeny with alternately polarized state changes reconstructed nearer the tips. Likewise, expectations can also be formulated for body shape: if cylindrical body shapes indeed conserve water one would expect transitions to this morphology to coincide with, or follow terrestrialization when reconstructed on the phylogeny. In a similar way, all of the hypotheses mentioned above (see above: Key innovations, adaptive radiation and terrestrialization), as well as others that may arise during the study, can be tested.

Respiration in planarians

Introduction

A particular crucial feature that may be among the most difficult to examine and to plot its character states on the phylogenetic trees concerns the adaptation to terrestrial respiration. Planarian flatworms possess neither circulatory nor respiratory systems for transporting oxygen or digested food substances to the internal tissues. In these animals, oxygen is absorbed across the entire body wall and for this diffusion process water is required to dissolve oxygen and carbon dioxide in order to cross cell membranes. Clearly, this poses no problem for freshwater and marine planarians as they live in an aquatic habitat, but when ancestral planarians colonized the land, leaving this aquatic milieu must have formed a major hurdle, as the physical properties of water and air are so different. It is true that many land planarians live in habitats with a high humidity, but still these conditions greatly differ from a fully aquatic environment, while there are also terrestrial planarians that occur in mesophile and xerophile habitats (Froehlich 1955; Winsor et al. 1998).

Thickness of flatworms

The analysis of this subject is complicated by the fact that not much is known about the respiratory physiology of free-living flatworms in general and planarians in particular. Furthermore, most of these studies concern aquatic species. A striking example is McNeill Alexander’s (1979) conclusion that the maximum possible thickness of a free-living flatworm is 1.0 mm or at most 1.5 mm. His conclusion is based on an argument that involves the calculation of the diffusion rate of oxygen. In philosophical context McNeill Alexander’s type of functional explanation has been presented as an example of viability explanations, which are distinct from causal or historical explanations (Wouters 1995).

McNeill Alexander’s (1979) calculation is based on a number of factors, viz., (a) partial pressure of oxygen in water, (b) rate of gas diffusion, (c) the fact that oxygen mostly will diffuse through the dorsal body surface, as the ventral surface is in contact with the substrate, (d) the diffusion constant for oxygen diffusing through connective tissue, (e) density of flatworm tissue. When the known or estimated values for these variables are used

in a derivation using Fick's law of diffusion, "This calculation indicates that the maximum possible thickness for a flatworm ... is about 0.5 mm if oxygen diffuses in only from the dorsal surface, or 1.0 mm if it diffuses equally from the ventral surface.... A similar calculation for a cylindrical turbellarian indicates that the maximum possible diameter would be 1.5 mm This is probably why large flatworms are flat." (McNeill Alexander 1979: 185).

As flatworms rely entirely on oxygen diffusion through the surface, it is indeed advantageous to have a large surface area:volume ratio, i.e., to be flat and not cylindrical. In general, this holds true for aquatic species, while within species their thickness hardly or not at all increases with an increase in plan area of the body (Calow 1987). Another interpretation of the broad bodies of large land flatworms is that this facilitates capture and subdual of prey (cf. Cseh et al. 2017), i.e., forms an evolutionary adaptation to new kinds of terrestrial prey not encountered by their aquatic ancestors.

For an organism that relies on direct diffusion of oxygen Prosser (1973) provided a formula for the calculation of the thickness of the animal, based on the oxygen concentration of the medium, a diffusion coefficient K , and the rate of oxygen consumption. When the calculation is done for both water and air (Table 2) it reveals that air-breathers can be six times thicker because there is more oxygen in air than in water (it should be noted that there is uncertainty about the units in which thickness is expressed).

Nevertheless, the conclusion of McNeill Alexander (1979), as well as the calculation on which it is based, is open to a number of criticisms. First of all, it is certainly not the case that large flatworms are always very flat or thin. For example, "giant" freshwater species from Lake Baikal, such as *Bdellocephala bathyalis* Timoshkin & Porfirjeva, 1989, are certainly thicker than 0.5–1.0 mm (*B. bathyalis* measuring 3.3 mm in thickness in preserved condition; Sluys et al. 1998). And also the large land planarians are usually thicker, such as *Polycladus gayi* Blanchard, 1845 (4 mm thick), *Pseudogeoplana lumbricoides* (Schirch, 1929) (3.5 mm), *P. nigrofusca* (Darwin, 1844) (3 mm), *Geoplana rufiventris* Schultze & Müller, 1857 (2.3 mm) (Von Graff 1899). Although such measurements on the thickness are usually made on preserved specimens, and that thus fully stretched live specimens will be thinner, this does not necessarily compromise the picture. It should be realized that most of

the time the flatworms hide under stones or fallen logs, etc. and that during this resting period they are highly contracted, thus presumably approaching the condition of preserved specimens.

Another example of a thick flatworm-like animal is the basal bilaterian *Xenoturbella bocki* Westblad, 1950, which may reach a length of 2–3 cm and a thickness of 5 mm (Franzén and Afzelius 1987).

Another objection that may be raised against McNeill Alexander's (1979) calculation concerns his assumption that diffusion in flatworms is more or less equal to that in frog muscle and connective tissue, i.e., $2 \times 10^{-5} \text{mm}^2 \text{atm}^{-1} \text{s}^{-1}$. However, it is doubtful that the mesenchyme and gut tissue—forming the major component of the planarian body—have the same diffusion constant as frog muscles and connective tissue. Evidently, the diffusion constant of planarian tissue will not be equal to that in water ($6 \times 10^{-5} \text{mm}^2 \text{atm}^{-1} \text{s}^{-1}$) but perhaps $4 \times 10^{-5} \text{mm}^2 \text{atm}^{-1} \text{s}^{-1}$ would be a value that is more realistic for flatworms. This would then imply a higher rate of diffusion and, consequently, would allow the worms to be thicker.

For the rate (m) of oxygen consumption per unit volume of tissue, McNeill Alexander (1979: 185) used $0.1 \text{cm}^3 \text{oxygen g}^{-1} \text{h}^{-1}$, "or a little more". However, according to Hyman (1951: 207 and references therein) this may be higher, viz., $0.2\text{--}0.31 \text{cm}^3 \text{oxygen g}^{-1} \text{h}^{-1}$, that is "0.2–0.3 cc per gram per hour in adult worms." According to Moore (2006) it would be about $0.1\text{--}0.2 \text{ml oxygen g}^{-1} \text{h}^{-1}$ at 15°C .

A variable that is not taken into account by McNeill Alexander (1979) is the relationship between size and metabolic rate in flatworms. Although data are scant, generally respiratory rate decreases as size increases (Vernberg 1968).

Although McNeill Alexander's view on the maximum thickness of flatworm-like animals has been explicitly or implicitly endorsed (e.g., Ruppert et al. 2004; Moore 2006), he considered it merely "a very rough calculation in a textbook" and he conceded that "There are many doubtful assumptions in the calculation" (McNeill Alexander in litt., 22 August 1996).

Respiratory pigments

Apart from the doubtful assumptions in McNeill Alexander's calculation, another explanation for the empirical fact that flatworms frequently are thicker than 0.5–1.0 mm may lie in the presence of

Table 2. Data and results of thickness calculation according to Prosser's (1973) formula: $\text{thickness} = \sqrt{(8C_o(K/V_{o_2}))}$; oxygen concentration in medium (C_o) and K value (for muscle) from Prosser (1973); oxygen consumption (V_{o_2}) converted from value of 0.2ml/g/hr ($= 0.0033 \text{ml/g/min}$; see this paper).

Medium	Oxygen medium (ml/ml)	K (muscle; cm ² /min/atm)	Oxygen consumption (ml/g/min)	Thickness (units ?)
Water	0.00651	0.000014	0.0033	0.014864234
Air	0.2095	0.000014	0.0033	0.084322613

respiratory pigments, transporting oxygen across tissues. Hemoglobin is the most common respiratory pigment among invertebrates in general (Brusca and Brusca 2003). With respect to flatworms it has been reported mostly from parasitic helminths (Weber and Vinogradov 2001) as well as for a number of ecto- and endosymbiotic turbellarians, such as *Paravortex* Wahl, 1906, *Triloborhynchus* Bashiruddin & Karling, 1970, *Cleistogamia* Faust, 1924, *Serita* Cannon, 1982, *Paranotothrix* Cannon, 1982 (Jennings and Cannon 1987; Jennings 1988, 1997). Hemoglobin is known also from the free-living flatworms, viz., a species of *Phaenocora* Ehrenberg, 1835 (Vernberg 1968; Weber and Vinogradov 2001). It has been hypothesized that presence of hemoglobin in the entosymbiotic graffiid rhabdocoel *Paravortex scrobiculariae* (Graff, 1882) represents an adaptation to the oxygen-poor conditions to which this species is subjected, in contrast to the well-aerated habitats of other species, such as *P. cardii* (Hallez, 1908) and *Graffilla buccinicola* Jameson, 1897, which lack hemoglobin (Jennings 1981). Unfortunately, oxygen carrying components such as hemoglobin have not been studied in planarians. Winsor (1998) mentioned the possible respiratory role of uroporphyrins (other than hemoglobin) present in the rhabdoids of *Platydemus manokwari* de Beauchamp, 1962. Potential presence of hemoglobin may be deduced from the presence of non-epidermal pigments, often situated in or around specific organs, such as the brain and the pharynx (Jennings 1981, 1988; Jennings and Cannon 1987). In planarians, body colouration generally is due to the presence of granular pigments located in the mesenchyme directly below the dorsal epidermis (Sluys and Riutort 2018), while in most species of the freshwater genus *Girardia* Ball, 1974 the pharynx is also pigmented. Therefore, red pigment at other locations in the planarian body may point to the presence of hemoglobin. However, I have rarely observed pigment to be present at such other locations, at least in histological preparations, suggesting that hemoglobin is absent in triclad flatworms.

Respiration in triclads and other free-living turbellarians

Oxygen consumption in planarians and other free-living turbellarians has been studied chiefly in freshwater species (cf. Vernberg 1968; Heitkamp 1979) and only once in a terrestrial species (Daly and Matthews 1982). An important result that emerged from these studies is the relationship between body size and respiration, in that generally smaller animals have a higher rate of oxygen consumption than larger specimens, when determined on a weight-specific basis; however, some species showed the reverse correlation, while for others no relationship could be established between body size and oxygen uptake (Vernberg 1968 and references therein; Heitkamp 1979).

Rates of oxygen consumption may be determined and expressed in different ways and are generally influenced by the temperature of the habitat. The type of response to changes in temperature varies per species, as some species are eurythermal and others much more stenothermal in their ecological requirements (Vernberg 1968 and references therein). Therefore, respiration rate frequently is expressed as microliters-O₂-per-(milli-)gram-wet weight-per hour ($\mu\text{LO}_2/(\text{m})\text{g}/\text{WW}/\text{h}$) at a particular temperature. Another way to express oxygen consumption is by calculating the coefficient *b*, or the regression slope of a particular power function for the relation between body size and respiration. Unfortunately, the value of *b* varies much as it greatly depends on the size of the animals, their physiological condition, and many external factors (Heitkamp 1979).

For five species of freshwater planarians (*Dugesia gonocephala* (Dugès, 1830), *Crenobia alpina* (Dana, 1766), *Polycelis nigra* (Müller, 1774), *P. felina* (Dalyell, 1814), *Schmidtea polychroa* (Schmidt, 1861)) the following values were found for oxygen consumption ($\mu\text{LO}_2/\text{g}/\text{WW}/\text{h}$), measured at a temperature of about 15 °C: 170, 240, 135, 199, 116, respectively (Vernberg 1968). Unfortunately, these values for triclad flatworms cannot be compared directly with those determined for various microturbellarians as these were calculated per milligram wet weight ($\mu\text{LO}_2/\text{mg}/\text{WW}/\text{h}$), resulting in the following values, measured at a temperature of 15 °C: 1.242 (*Dalyellia viridis* (Shaw, 1791)), 0.688 (*Opisthomum pallidum* Schmidt, 1848), 0.168 (*Mesostoma ehrenbergi* (Focke, 1836)), ranging between 0.298 and 0.700 (eight different populations of *Mesostoma lingua* (Abildgaard, 1789)) (Heitkamp 1979).

The habitat temperature of the tropical terrestrial land planarian *Bipalium kewense* Moseley, 1878 is usually much higher than that of the aquatic triclads mentioned above, albeit that this invasive species has established itself outdoors in, for example, several North American states, the West Indies, Portugal, French Guiana, and France (Sluys 2016; Justine et al. 2018). The oxygen consumption of *B. kewense* specimens from outdoor localities in Arkansas, USA was determined at temperatures varying between 27–33 °C, which yielded respiration rates ($\mu\text{LO}_2/\text{g}/\text{WW}/\text{h}$) ranging between 113–290 (Daly and Matthews 1982). It is noteworthy that these values are in the same order of magnitude as those determined for freshwater planarians.

The coefficient *b* based on oxygen consumption of entire specimens of *B. kewense* ranged between 0.686–0.753, as measured at temperatures ranging between 27–33 °C (Daly and Matthews 1982). These values are in the same order of magnitude as those determined for the freshwater triclads *Crenobia alpina* (0.66), *Dugesia gonocephala* (0.82), and *Polycelis felina* (0.82) and the microturbellarians *Mesostoma ehrenbergi* (0.625), *M. lingua* (0.850), and *Opisthomum pallidum* (0.880) (Heitkamp 1979 and references therein).

Terrestrial respiration

Terrestrial flatworms face two problems that involve mutually conflicting adaptations, viz., desiccation and respiration. A cylindrical body, with less surface area:volume ratio, will minimize water loss but restricts diffusion of oxygen to the internal tissues. Probably this is the reason why smaller terrestrial species tend to be round or oval in cross-section, e.g., species of the land planarian genus *Microplana* Vejdovsky, 1890. Therefore, large species tend to be flattened to create a large surface area:volume ratio in order to facilitate diffusion of oxygen to the deep tissues. Nevertheless, the generally large and particularly long species of the land planarian subfamily Bipaliinae Von Graff, 1896 also have a more or less cylindroid body in cross-section.

The partial pressure of oxygen in well-aerated water in equilibrium with air is 0.21 atm (McNeill Alexander 1979) and results in about 9 mgO₂/l at 20 °C. Evidently, the actual amount of dissolved oxygen available at a particular aquatic habitat depends on the temperature, depth, altitude, and the mixing properties of the water (e.g., running water in shallow streams mixing better with air). The amount of oxygen in air is about 30 times that of water (Little 1990; Moore 2006), amounting to about 210 ml O₂, weighing 280 mg, in 1 L of air (Schmidt-Nielsen 1975), while the diffusion rate of oxygen through air is much faster than through water (3 million times faster through air; Prosser 1973).

In the present context it suffices to realize that, thus, availability of sufficient oxygen would not have formed a stumbling-block during an evolutionary transition from water to a terrestrial environment. But, clearly, the organisms needed to evolve respiratory adaptations enabling them to extract oxygen from the air, as opposed to their ancestors, which had evolved in an aquatic habitat.

One such adaptation may be the production of mucus, which is secreted by both aquatic and terrestrial planarians. Mucus plays several important roles in the life of a planarian flatworm and is produced by various kinds of gland. Secretions from glands at the body margin produce a slime trail that facilitates the gliding movement of both aquatic and terrestrial triclads, effectuated by the propulsive force of cilia on the ventral body surface (Jones 1978). Many species of land planarians do not have such dedicated marginal glands, and various types of mucus are secreted from their creeping sole and/or ventral surface. Sticky mucus discharged by cephalic glands partakes in the capture of prey and has neurotoxic properties (cf. Thielicke and Sluys 2019 and references therein). The mucus of triclad flatworms also has repellent properties as the worms are only rarely eaten by other animals since their surface secretions appear to have repugnatorial function (Hyman 1951; Winsor 1998).

As mucus is produced also in aquatic triclads it could well be that these various functions already formed evolutionary preadaptations of similar functions in land planarians. Perhaps the secretion produced by the marginal adhesive zone is an exception as it has been suggested

that it may not provide a lubricant for locomotion in the land planarians but form a moisture-retaining sealant in a resting animal (Winsor 1998). However, one function does not exclude the other.

Production of surface secretions may also have formed a preadaptation for respiration in the terrestrial environment as it covers the body with a “watery” layer that presumably improves the uptake of oxygen. This may be related to the possible role, including respiration, of substances (porphyrins) in rhabdoids that are conspicuous in the dorsal/dorso-lateral epithelium (and microrhabdites over the ventral surface) of land planarians (see above). To the best of my knowledge, this aspect of mucus secretion and respiration in land flatworms has never received any attention.

Evidently, uptake of oxygen through the body wall is only the first step in the respiration process. Hereafter, the oxygen needs to be transported to tissues deeper inside the planarian body. In the absence of respiratory pigments (see above: Respiratory pigments) this can be achieved only by means of diffusion. This implies that also the internal tissues must have a sufficient amount of water in order to be able to dissolve oxygen and carbon dioxide. Maintaining a sufficient level of hydration may be unproblematic for freshwater planarians but may require certain adaptations in marine and terrestrial forms. In particular, land planarians have no physiological or anatomical adaptations for water retention (Kawaguti 1932). On the one hand land planarians have practically no water-saving adaptations, while on the other hand they avoid wet environments and thus are considered to be stenohygic hygrococles (Froehlich 1955). It should here be noted that the situation may not be as absolute as suggested by Kawaguti’s (1932) findings, in that land flatworms may prevent desiccation by encasing themselves in mucus. Further, there may be also biochemical adaptations (secondary metabolism; see Campbell 1965) in land planarians for the elimination of carbon dioxide and nitrogenous waste that appear to facilitate water retention, such as the secretion of calcium salts (Percival 1925), which is consistent with being a stenohygic hygrococle. In contrast to land planarians, freshwater species are subjected to osmotic influx of water and therefore must continuously regulate its volume with the help of their protonephridial system.

One way to assess the hydration of the planarian body is to determine the osmolarity of the tissues, which is expected to vary inversely with the degree of hydration (Jones et al. 2004). The osmolarity of the freshwater planarians *Schmidtea polychroa* and *Girardia dorocephala* (Woodworth, 1897) was 125–128 mOsm kg⁻¹ and 126 mOsm kg⁻¹, respectively, while that of the marine triclad *Procerodes littoralis* (Ström, 1768) ranged between 217–272 mOsm kg⁻¹ (Jones et al. 2004 and references therein). Tissue osmolarity for the terrestrial planarian *Arthurdendyus triangulatus* (Dendy, 1896) ranged between 187.8–257.5 mOsm kg⁻¹, depending upon the laboratory conditions (relatively dry or fully hydrated)

under which the specimens were kept (Jones et al. 2004). These data show that tissue osmolarity in land flatworms is higher than that of freshwater planarians. This means that terrestrial flatworms are less hydrated than freshwater species and that the former are able to maintain a higher osmolarity because they are less prone to influx of water. Evidently, the necessary amount of water that land triclads require for upholding their respiratory physiology is extracted from their frequently, but not always, humid environments. It is a matter of fact that for already millions of years land planarians have successfully evolved the necessary adaptations for exploiting the terrestrial environment but that our understanding of these solutions is still in its infancy.

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An illustrated catalogue of Rudolf Sturany's type specimens in the Naturhistorisches Museum Wien, Austria (NHMW): Red Sea bivalves

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Abstract

Rudolf Sturany, the curator of molluscs of the Natural History Museum of Vienna between the late 19th and early 20th century described 21 species of bivalves from the Red Sea collected by the pioneering expeditions of the vessel “Pola” which took place between 1895 and 1898. We here list and illustrate the type material of these species, provide the original descriptions, a translation into English, and curatorial and taxonomic comments. All species are illustrated in colour and with SEM imaging. To stabilize the nomenclature, we designate lectotypes for *Gastrochaena weinkauffi*, *Cuspidaria brachyrhynchus*, and *C. dissociata*, whose type series contained specimens belonging to other species. This paper concludes the series on the type specimens of marine molluscs described by Sturany from the “Pola” expeditions.

Key Words

Bivalvia, deep-sea, Indo-Pacific province, Pola expeditions

Introduction

The Red Sea lies in a key biogeographic position and shows a high level of endemism (Edwards and Head 1987; Janssen and Taviani 2015; DiBattista et al. 2016; Bogorodsky and Randall 2019). Separated by the Indian Ocean by a shallow sill, its biodiversity is hypothesized to be the result of recolonization from the Gulf of Aden after the Last Glacial Maximum (Taviani 1998). At the other end, the Suez Canal connects it to the Mediterranean Sea, which has been invaded by hundreds of tropical species triggering the so-called Lessepsian invasion, one of the largest marine bioinvasions in the marine realm (Por 1978; Galil et al. 2015). Both aspects are of major biogeographic interest because they offer insights into the processes of dispersal, build up, and merging of faunas. Such processes cannot be properly studied without a thorough knowledge of the taxonomy of Red Sea species and the relations with those of nearby areas.

It is not uncommon, for example, to encounter clearly non-native organisms in the Mediterranean Sea and not being able to assign them unambiguously to a species (e.g. Steger et al. 2018).

Knowledge on type specimens is a fundamental first step for sound taxonomic work and the publication of type catalogues is recommended also by the International Commission on Zoological Nomenclature (ICZN 1999, 72F.4).

Rudolf Sturany, curator of the molluscan collection at the Natural History Museum in Vienna (NHMW) between the late 19th and early 20th century, described 56 species of Red Sea molluscs based on the pioneering expeditions of the vessel “Pola” between 1895 and 1898, the first to explore the deep-sea regions of the basin (Scheffbeck 1996; Stagl 2012; Janssen and Taviani 2015). However, his work went unnoticed for long, possibly also due to the use of the German language (Huber and Eschner 2011).

The “Pola” samples are also an irreplaceable source of baseline data in this era of global change. Climate warming, eutrophication, and coastal development are serious pressures on the Red Sea ecosystem (e.g. Raitsos et al. 2011; Naumann et al. 2015; Hall et al. 2018). Although not always recognized as such, the NHMW and the other institutions that preserve similar historical samples are a strategic asset in global change research (Johnson et al. 2011; Lister 2011; Albano et al. 2014; Dayan and Galil 2017).

We here conclude our work to document the type specimens of Sturany's marine taxa, started with the Red Sea gastropods (Albano et al. 2017) and continued with the deep-sea Mediterranean species (Albano et al. 2018), by treating the bivalves described from the Red Sea. We provide high-quality optical and SEM images and, to help overcome the language barrier, we translate all original German descriptions into English.

The year of publication of the Red Sea bivalves

This paper focuses on the 21 bivalve taxa described by Sturany in 1899 (Table 1). This work was published in the volume 69 of the journal *Denkschriften der kaiserlichen Akademie der Wissenschaften/Mathematisch-Naturwissenschaftliche* as part of a separate series on reports of the “Commission für oceanographische Forschungen” dated 1901. However, preprints (“Besonders abgedruckt”) with double pagination were published in 1899 (date on their frontispiece) and are present in the library of the Natural History Museum of Vienna; therefore, this should be considered the correct year of publication for all new names. A similar situation occurred for some Red Sea gastropods (Albano et al. 2017).

Materials and methods

The “Pola” material is entirely stored in the NHMW (Stagl et al. 1996). Type series of Sturany's species were segregated. Most species were represented by holotypes or very small series. In the latter case, we identified the syntypes best matching the original description and selected lectotypes when appropriate to stabilize the nomenclature (ICZN 1999). A taxon list in alphabetical order with page and figure numbers in this paper is provided in Table 1.

For each species, we provide references to the original description and figure, indicate the original localities, list the type material, reproduce the original description, and translate it into English. All the mentioned inventory numbers refer to the Mollusca collection of NHMW. The systematic arrangement follows Bouchet et al. (2010). The reassessment of the current taxonomic status of Sturany's names is beyond the scope of this paper, and we relied on the published literature to add some comments in this regard. The material studied by Sturany comes from off-shore “stations” (Table 1) and coastal “localities” (Tables 2, 3); we maintained this terminology. In the two tables, we report the collecting sites with their original orthography in German and a modern name between square brackets. The coordinates are those provided by Sturany. Any citation to the International Code of Zoological Nomenclature (ICZN 1999) should be considered to its online version, which includes all recent amendments.

Most photographs were shot with a Nikon SMZ25 microscope; large shells were photographed with a Canon 350D camera, a 50 mm lens, and extension tubes. SEM images were taken with a JEOL JSM-6610LV using low vacuum without any coating. Specimen measurements have been added for holotypes.

Table 1. List of treated taxa in alphabetic order, with original and current name, current family placement, and figure in this paper.

Taxon	Current name	Family	Page	Figure
<i>akabana</i> , <i>Cardita</i>	<i>Centrocardita akabana</i> (Sturany, 1899)	Carditidae	564	4
<i>bracheon</i> , <i>Raeta</i>	<i>Raeta bracheon</i> Sturany, 1899	Anatinellidae	571	8
<i>brachyrhynchus</i> , <i>Cuspidaria</i>	<i>Cuspidaria brachyrhynchus</i> Sturany, 1899	Cuspidariidae	585	16
<i>deshayesi</i> , <i>Gastrochaena</i>	<i>Gastrochaena deshayesi</i> Sturany, 1899	Gastrochaenidae	579	13
<i>dissociata</i> , <i>Cuspidaria</i>	<i>Cuspidaria dissociata</i> Sturany, 1899	Cuspidariidae	587	17
<i>elachista</i> , <i>Limopsis</i>	<i>Limopsis elachista</i> Sturany, 1899	Limopsidae	559	4
<i>hypopta</i> , <i>Chione</i>	<i>Timoclea hypopta</i> (Sturany, 1899)	Veneridae	578	12
<i>intracta</i> , <i>Lyonsia</i>	<i>Poromya intracta</i> (Sturany, 1899)	Poromyidae	595	21
<i>pexiphora</i> , <i>Gastrochaena</i>	<i>Dufoichaena pexiphora</i> (Sturany, 1899)	Gastrochaenidae	582	14
<i>potti</i> , <i>Cuspidaria</i>	<i>Cuspidaria potti</i> Sturany, 1899	Cuspidariidae	589	18
<i>raveyensis</i> , <i>Diplodonta</i>	<i>Transkeia raveyensis</i> (Sturany, 1899)	Ungulinidae	575	11
<i>siebenrocki</i> , <i>Amussium</i>	<i>Parvamussium siebenrocki</i> (Sturany, 1899)	Pectinidae	561	2
<i>siebenrocki</i> , <i>Tellina</i>	<i>Jitlada bertini</i> (Jousseume, 1895)	Tellinidae	573	9
<i>squamosina</i> , <i>Tridacna</i>	<i>Tridacna squamosina</i> Sturany, 1899	Cardiidae	566	5
<i>steindachneri</i> , <i>Amussium</i>	<i>Propeamussium steindachneri</i> (Sturany, 1899)	Pectinidae	563	3
<i>steindachneri</i> , <i>Cuspidaria</i>	<i>Cuspidaria steindachneri</i> Sturany, 1899	Cuspidariidae	591	19
<i>subcandidus</i> , <i>Solecurtus</i>	<i>Solecurtus subcandidus</i> Sturany, 1899	Solecurtidae	573	10
<i>sulphurea</i> , <i>Scintilla</i>	<i>Scintillula lutea</i> (Lamarck, 1818)	Galeommatidae	566	6
<i>thauomasia</i> , <i>Pseudoneaera</i>	<i>Pseudoneaera thauomasia</i> Sturany, 1899	Cuspidariidae	593	20
<i>variabilis</i> , <i>Scintilla</i>	<i>Scintillula variabilis</i> (Sturany, 1899)	Galeommatidae	569	7
<i>weinkauffi</i> , <i>Gastrochaena</i>	<i>Lamychaena weinkauffi</i> (Sturany, 1899)	Gastrochaenidae	583	15

Table 2. Off-shore stations of the “Pola” expedition with bivalves (from Sturany 1899).

Station number	Locality	Coordinates	Depth [m]
9	“südlich von Yenbo” [south of Yanbu’ al Bahr, Saudi Arabia]	23°21'N, 37°37'E	-791
27	–	23°41'N, 37°23'E	-747
41	“zwischen Mersa Halaib und Jidda” [between Halayeb, Egypt, and Jeddah, Saudi Arabia]	22°4'N, 38°E	-2160
44	“vor Jidda” [off Jeddah, Saudi Arabia]	21°36'N, 38°33'E	-902
47	“bei Yenbo” [Yanbu’ al Bahr, Saudi Arabia]	23°41'N, 38°9'E	-610
48	“vor Yenbo” [off Yanbu’ al Bahr, Saudi Arabia]	24°5'N, 37°45'E	-700
51	“bei Sherm Sheikh” [near Abu Ghusun, Egypt]	24°15'N, 35°37'E	-562
56	“bei Mersa Dhiba” [Mersa Dhiba, Egypt]	25°23'N, 34°55'E	-582
61	“nächst den Hassani-Inseln” [near Al Hasani, Saudi Arabia]	24°35'N, 36°51'E	-828
72	“bei der Insel Shadwan” [Shadwan Island, Egypt]	27°25'N, 34°30'E	-1082
76	“südlich der Insel Sanafir” [south of Sanafir Island]	27°43'N, 34°47'E	-900
81	“unweit von Ras Abu Massahrib, Noman Insel” [close to Ras Abu Massahrib, Noman Island, Saudi Arabia]	26°34'N, 35°33'E	-825
87	“bei Ras Mallap im Golfe von Suez” [Ra’s Mal’ab in the Gulf of Suez, Egypt]	29°7.6'N, 32°56'E	-50
94	“bei Nawibi im Golfe von Akabah” [Nuweiba, Gulf of Aqaba, Egypt]	28°58.6'N, 34°43.7'E	-314
96	“nördlicher Theil des Golfes von Akabah” [northern part of the Gulf of Aqaba]	29°13.5'N, 34°47.8'E	-350
106	“südlich von Jidda” [south of Jeddah, Saudi Arabia]	21°2'N, 38°41.4'E	-805
109	“westlich von Jidda” [Jeddah, Saudi Arabia]	21°19'N, 37°39'E	-890
114	“zwischen Suakim und Lith” [between Suakin, Sudan, and Al Lith, Saudi Arabia]	19°38'N, 37°55'E	-535
117	“südlich von Raveya” [south of Raveya, Sudan]	20°16.9'N, 37°33.5'E	-638
121	“westlich von Kunfidah” [west of Al Qunfudhah, Saudi Arabia]	18°51.9'N, 39°5.4'E	-690
128	“bei Akik Seghir” [Akik Seghir, Eritrea]	18°7.7'N, 39°11.2'E	-457
130	“westlich von Kunfidah” [west of Al Qunfudhah, Saudi Arabia]	19°17'N, 39°37'E	-439
138	“östlich von Akik Seghir” [east of Akik Seghir, Eritrea]	18°3'N, 40°14.7'E	-1308
145	“östlich von J. Dahalak” [east of Dahlak Island, Eritrea]	16°2.6'N, 41°13.5'E	-800
156	“nördlich von Jidda” [north of Jeddah, Saudi Arabia]	22°51'N, 38°2'E	-712
170	“bei der Insel Noman” [Noman Island, Saudi Arabia]	27°0.2'N, 35°17.6'E	-690
176	“bei Koseir” [El Quseir, Egypt]	25°57'N, 34°36.1'E	-612

Table 3. Coastal localities of the “Pola” expedition with bivalves (from Sturany 1899).

Locality number	Locality	Coordinates/region
10	“Nawibi” [Nuweiba, Egypt]	Gulf of Aqaba
12	“Dahab (Mersa Dahab)” [Dahab, Egypt]	Gulf of Aqaba
16	“Shadwan-Insel” [Jazirat Shakir, Egypt]	Northern Red Sea, 28–26°N
25	“Sherm Sheikh (Mersa Sheikh)” [near Abu Ghusun, Egypt]	26–24°N
27	“Port Berenice” [Berenice Troglodytica, Egypt]	24–22°N
30	“Mersa Halaib” [Halayeb, Egypt]	24–22°N
31	“Jidda (Djeddah)” [Jeddah, Saudi Arabia]	22–20°N
32	“Raveiya (Mahammed Ghul)” [Gul Mohammad, Saudi Arabia]	22–20°N
37	“Ras Turfa” [near Jazan, Saudi Arabia]	18–16°N
41	“Massawa (Massaua)” [Massawa, Eritrea]	16–11°N
43	“Kamaran-Insel” [Kamaran Island, Yemen]	16–11°N

Systematic list of taxa

Family Limopsidae Dall, 1895

Limopsis elachista Sturany, 1899

Figure 1

Sturany 1899: 268, plate IV, figures 1–4.

Original localities. Station 48, off Yanbu’ al Bahr, Saudi Arabia, 24°5'N, 37°45'E, -700 m. Station 106, south of Jeddah, Saudi Arabia, 21°2'N, 38°41.4'E, -805 m. Station 117, south of Raveya, Sudan, 20°16.9'N, 37°33.5'E, -638 m.

Type material. Syntypes: NHMW 84346: 2 valves, station 48; NHMW 84347: 3 valves, station 106; NHMW 84348: 2 specimens, station 117 (one specimen in original figure).

Original description. *Von den Stationen 48, 106, 117 (638–805 m); einige wenige Schalen.*

Die Schale ist winzig klein, schwach gewölbt, ein wenig schief gewachsen, doch nahezu kreisförmig, so hoch wie breit.

Der Oberrand ist gerade und wird von den ein wenig aus der Mitte nach vorne gerückten Wirbeln überragt; Vorder-, Unter- und Hinterrand sind gerundet. Die äussere Sculptur besteht aus einer zarten, aber deutlichen Streifung im Sinne des Wachstums, sowie aus Radialstreifen, die entweder nur die vordere und mittlere Partie der Schale auszeichnen, oder, was die Regel ist, bis rückwärts reichen; die davon betroffenen Stellen zeigen also ein feines Gitterwerk.

Die Grundfarbe der Muschel ist schmutzigweiss bis gelblich; darüber ziehen in der Regel drei radial gestellte, gelbbraune Bänder, die jedoch von wechselnder Breite sind und in verschiedener Combination fehlen können.

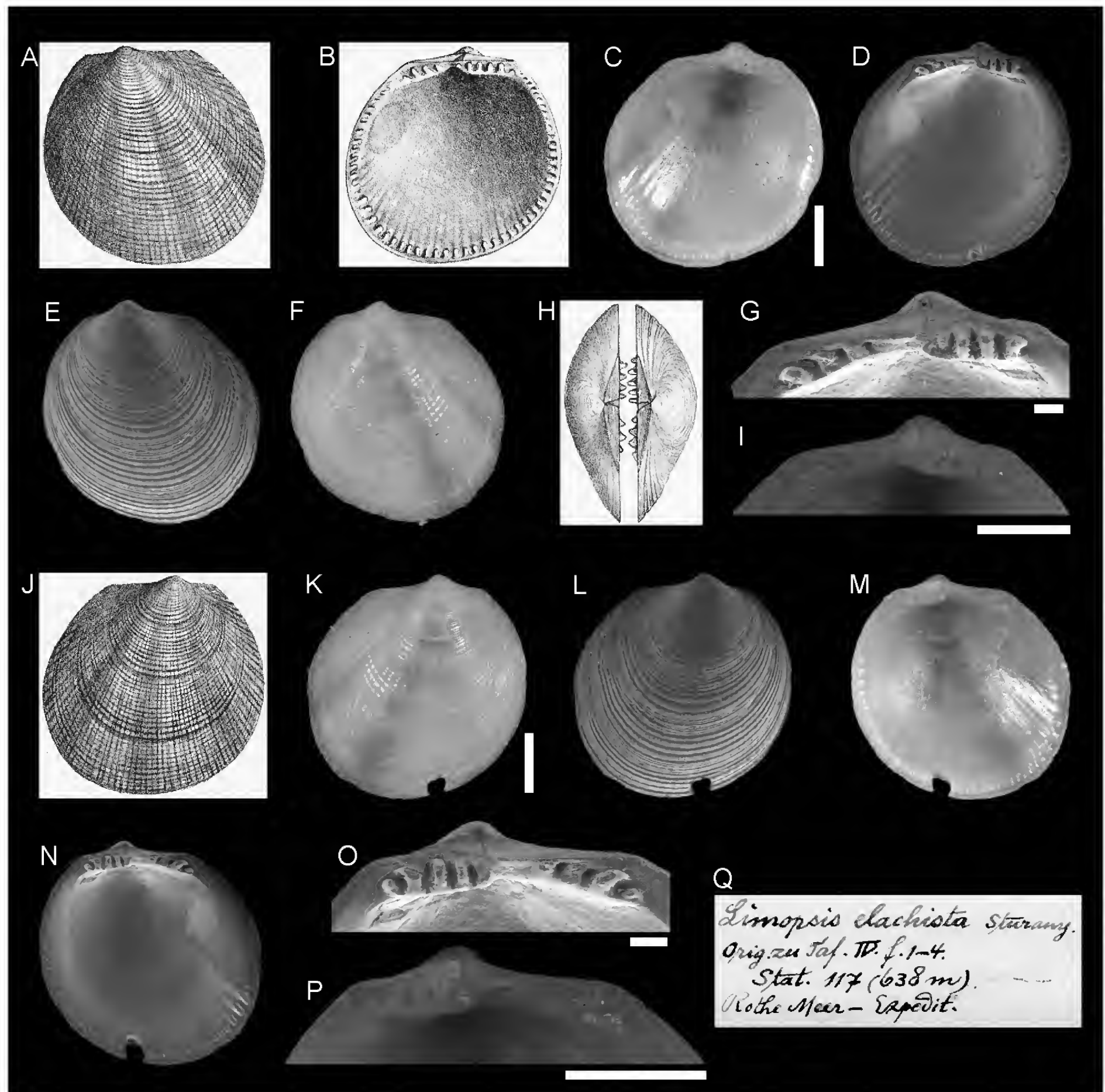


Figure 1. *Limopsis elachista* Sturany, 1899, Station 48, south of Raveya, Sudan, -638 m. A, B, H, J Original figures. C–F, G, I, K–P Figured syntype NHMW 84348: right valve interior (C, D), exterior (E, F), and hinge detail (G, I); left valve exterior (K, L), interior (M, N), and hinge detail (O, P). Q Original label. Scale bars: 1 mm (C, I, K, P); 0.2 mm (G, O).

Das Innere der Schale ist vor Allem mit einem relativ kräftigen Schloss ausgestattet. Dieses besteht in jeder Schale aus 7 Zähnen, und ist diese Zahnreihe in der Wirbelgegend unterbrochen, so dass die Formel 3:4, respective 4:3 zu verzeichnen ist; mitunter gesellt sich zu den 7 normalen Zähnen in der rechten Schale noch je ein ganz kleiner Zahn an den beiden äussersten Enden der Reihe. Das Innere der Schale ist ferner noch durch eine stark gekerbte Peripherie und durch eine verwischte Radialstreifung ausgezeichnet.

Die Länge und Höhe der Muschel misst 3,5–3,7 mm, die Dicke beträgt circa 2.2 mm.

Es sind nur wenig Exemplare, die bei der Abfassung der Diagnose in Betracht kommen konnten. Wie sehr trotzdem

die oben angedeuteten wechselnden Charaktere der neuen Art bei den verschiedenen vorliegenden Schalen sich combinieren, mögen die folgenden Beispiele zeigen.

Eine linke Schale von Station 48 ist bänderlos und zeigt hauptsächlich in ihrer hinteren Partie die Gittersculptur; eine zweite (rechte) Schale von derselben Station ist allenthalben gegittert und hat ein breites Mittelband, während die seitlichen Radialbänder nur schwach ausgebildet sind. Von der Station 106 liegen zwei rechte, allenthalben gegitterte Schalen vor; bei der einen ist nur das hintere Radialband ausgebildet, die andere ist wieder bänderlos. Von Station 117 habe ich das hier abgebildete, mit drei Bändern ausgezeichnete Exemplare vor mir (deren Bezahnung sich ausdrücken lässt mit der Formel;

rechts 5 + 4, links 4 + 3), sowie ein solches, bei dem das vordere Band fehlt.

Die neue Art ist verwandt mit L. torresi Smith aus der Torresstrasse.

Translation. From stations 48, 106, 117 (638–805 m); a few valves.

The shell is tiny, slightly arched, a little oblique, but almost circular, as high as long.

The dorsal margin is straight and overlapped by the umbo, which is slightly tilted forward; the anterior, ventral and posterior margins are rounded. The outer sculpture consists of a delicate but distinct striation consisting of both growth [concentric ridges], as well as of radial costae, which are expressed only over the anterior and central parts of the shell, or, as is the rule, reach posteriorly; the affected areas show a fine reticulate structure.

The basic colour of the shell is dirty white to yellowish; usually there are three radial yellow-brown rays of varying expression across the median area which, however, can be missing in different combinations.

The interior of the valve is equipped with a relatively strong hinge. This consists in each valve of 7 teeth, and this row of teeth is interrupted in the umbo region, so that the formula 3:4, respectively 4:3 is recorded; sometimes a very small tooth joins the 7 normal teeth in the right shell at the two extreme ends of the row. The interior of the shell is also characterized by a strongly notched periphery and blurred radial incisions.

The length and height of the shell measure 3.5–3.7 mm, the thickness is about 2.2 mm.

There are only a few specimens that could be considered when writing the diagnosis.

Nevertheless, the above indicated variable characters of the new species may be combined in the various valves present, as the following examples may show.

A left valve of Station 48 lacks colour bands and shows the reticulate sculpture mainly over the posterior area; a second (right) valve from the same station is reticulate on all sides and has a wide central band, while the lateral radial bands are weak. From station 106 there are two right valves, entirely reticulate sculptured; in one, only the rear radial band is formed, the other is again without bands. From station 117, I have the three-banded specimens pictured here (dentition can be expressed by the formula: right 5 + 4, left 4 + 3), as well as one in which the front band is missing.

The new species is related to *L. torresi* Smith from the Torres Strait.

Family Pectinidae Rafinesque, 1815

Amussium siebenrocki Sturany, 1899

Figure 2

Sturany 1899: 269–270, plate IV, figures 5–8.

Type locality. Station 72, Shadwan Island, Egypt, 27°25'N, 34°30'E, –1082 m.

Type material. Lectotype: NHMW 84355: 1 valve, station 72, designated by Dijkstra and Janssen (2013). Paralectotypes: NHMW 84177: 1 valve, station 72; NHMW 84353: 1 valve, station 44; NHMW 84354: 1 valve, station 48; NHMW 84356: 5 valves; NHMW 84357: 5 valves; NHMW 84358: 10 valves.

Original description. *Von den Stationen 44, 48, 72, 91, 106, 109 (700–1082 m); einige wenige Schalen.*

Die Muschel ist klein, ungleichseitig, sehr wenig gewölbt, von fast kreisförmiger Gestalt, schmutzig weiss-er oder gelber Farbe aussen und milchweisser Farbe innen. Der fein zugespitzte Wirbel ist mittelständig; unter ihm liegt an der Schlossleiste die kleine Ligamentgrube.

Die rechte Schale ist kleiner und flacher als die linke, ist aussen gleichförmig concentrisch gestreift in ihrer Hauptpartie und mit Radialsculptur versehen auf dem vorderen Öhrchen, indem nämlich hier dicht aneinander gereiht 6–8 beschuppte Rippchen vom inneren Winkel nach dem convexen vorderen Ende des Öhrchens ziehen. Das hintere Öhrchen besitzt gleichsam als Fortsetzung der allgemeinen concentrischen Streifung feine, hier fast senkrecht gestellte Linien. Die Innenseite der rechten Schale besitzt 10 weisse Radialrippchen, die knapp vor dem Rande knotig verdickt endigen, und ausser ihnen lassen sich meist noch die Andeutungen von je einer Rippe an der inneren Basis der Öhrchen constatiren. Die 10 Hauptrippen scheinen nach aussen als weisse Radiallinien schwach durch. Der Oberrand ist äusserst schwach gekerbt.

Die linke Schale ist grösser und aussen ganz anders sculptirt. Es findet sich hier ausser der concentrischen Streifung noch eine sehr wechselnde, nichts weniger als constante Anzahl von Radialrippen vor. Einige davon beginnen in kurzer Entfernung vom Wirbel, andere etwa erst in der Mitte der Schalenhöhe; bei allen ist aber an ihren Kreuzungspunkten mit der concentrischen Streifung eine schwache Schuppenbildung zu constatiren. An den Öhrchen sind wieder die Querstreifen der Hauptpartie in senkrechter Richtung fortgesetzt, am vorderen Öhrchen sogar ein paar Radialrippen vorhanden. Das Innere der linken Schale ist glänzend; hier tritt die Berippung in gleicher Anzahl auf wie in der rechten Schale; aber die weissen Rippen reichen hier nicht bis hart an den Rand, sondern endigen mit ihren Verdickungen schon etwas entfernter davon.

[Tabelle mit Maßangaben!]

Abweichend von dem in der Diagnose erwähnten regelrechten Verhalten erscheint eine rechte Schale von der Station 44 (6,9 : 7,0 mm); hier schieben sich zwischen die vorderen Radialrippen der Innenseite noch 3 ganz kurze Rippchen, welche, da sie unten am Rande stehen, die relativ weiten Abstände von je 2 Rippenendigungen gleichsam ausfüllen.

Die neue Art ist verwandt mit der Tiefsee-Form des Mittelmeeres, A. hoskynsi Forbes.

Translation. From stations 44, 48, 72, 91, 106, 109 (700–1082 m); a few valves.

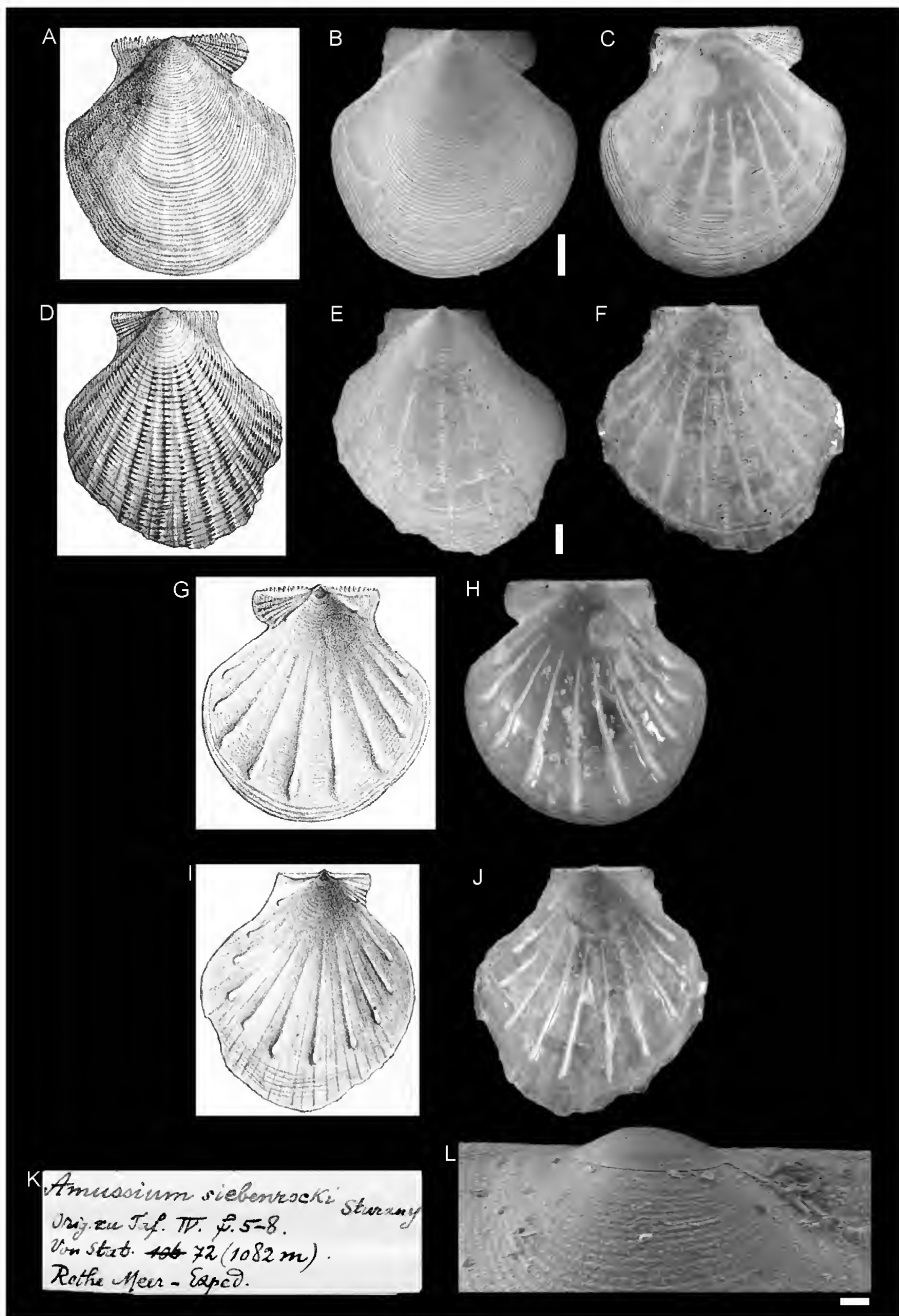


Figure 2. *Amussium siebenrocki* Sturany, 1899, Station 72, Shadwan Island, Egypt, -1082 m. **A, D, G, I** Original figures (rotated by 180°). **B, C, E, F, H, J, L** Lectotype NHMW 84355: right valve exterior (**B, C**), interior (**H**), and hinge detail (**L**). Left valve exterior (**E, F**) and interior (**J**). **K** Original label. Scale bars: 1 mm (**B, E**), 0.1 mm (**L**).

The clam is small, inequilateral, slightly curved, of almost circular shape, dirty white or yellow outside and milky white inside. The finely pointed beak [umbo] is central; below there is the small ligament pit at the hinge margin.

The right valve is smaller and flatter than the left, externally the main part (disc) is uniformly concentrically ridged but with radial sculpture on the anterior auricle, of 6–8 scaly ribs radiating from the inner angle to the convex anterior end of the auricle. The posterior auricle, as a continuation of the general concentric striation, possesses fine lines, here almost vertical. The inside of the right shell has 10 white radial ribs, which terminate with a thick nodule just before the margin, and besides these, the traces of one rib on the inner base of the auricles can usually be ascertained. The 10 main ribs appear on the outside as weak white radial lines. The upper margin is very slightly notched.

The left valve is larger and externally sculptured very differently. In addition to the concentric striation, there is also a very variable, nothing less than constant number of radial ribs. Some of them begin at a short distance from the umbo, others only in the middle of the valve; in all, however, faint scales can be observed at their points of intersection with the concentric ridges. At the auricles, the horizontal ridges of the main part are continued in the vertical direction, on the anterior auricle even a few radial ribs are present. The inside of the left shell is shiny; here the ribs occur in the same numbers as in the right valve; but the white ribs do not closely reach the edge, but end with their thickenings a little before.

[Table with dimensions]

Deviating from the normal behaviour mentioned in the diagnosis, a right shell appears from the station 44 (6.9: 7.0 mm); here 3 very short ribs raise in between the anterior radial ribs of the internal side, which, since they are at the edge, they almost fill the relatively wide distances of two ridge ends.

The new species is related to the deep-sea form of the Mediterranean *A. hoskynsi* Forbes.

Amussium steindachneri Sturany, 1899

Figure 3

Sturany 1899: 269, plate IV, figures 9–12.

Type locality. Akik Seghir, Eritrea, 18°7.7'N, 39°11.2'E, –457 m.

Type material. Lectotype: NHMW 84350: 1 valve, station 128, designated by Dijkstra and Janssen (2013). Paralectotypes: NHMW 84351: 5 valves, station 128; NHMW 84352: 2 valves, station 130; NHMW 92602: 3 valves, station 128.

Original description. *Von den Stationen 128 und 130 (439–457 m); einzelne Schalen.*

Die Muschel ist klein, ungleichschalig, fast kreisförmig, schwach gewölbt und glänzend, besitzt zarte, fein

zugespitzte Wirbel und darunter in der Schlossleiste eine dreieckige Ligamentgrube.

Die rechte Schale ist kleiner, aber dicker als die linke, ist milchweiss und durchscheinend. An ihrer ziemlich glatten, nur von ein paar stärkeren, aber unregelmässig auftretenden Anwachslineien durchzogenen, sehr stark glänzenden Aussenseite scheinen 6 weisse Rippen durch, die an der Innenseite radial angeordnet sind und bis an den Rand reichen, wo sie mit schwachen, knopfförmigen Verdickungen endigen. Überdies verläuft über die innere Basis eines jeden Öhrchens noch eine Rippe, die allerdings nur schwach entwickelt ist und nach aussen kaum durchzuscheinen vermag.

Das vordere Öhrchen ist vorne abgerundet (convex) und schwach quergestreift, d. i. concentrisch mit dem Vorderrande; das hintere ist fast rechtwinkelig abgestutzt. Der Oberrand der rechten Schale ist zart gekerbt.

Die linke Schale ist grösser, aber dünner als die rechte, ist glatt bis auf mikroskopisch feine Spuren von Quer- und Radialstreifen und stark durchscheinend. Durch zahlreiche über die ganze Aussenseite verbreitete Flecken von weisser Farbe und hauptsächlich gegen den Rand zu auftretende Flecken oder Streifchen von gelber oder orangerother Farbe gewinnt die etwas mehr gewölbte Schale ein charakteristisches Aussehen, das noch erhöht wird durch die kräftig Orangeroth oder gelb durchblickenden Radialrippen der Innenseite. So wie in der rechten Schale sitzen auch in der linken Schale 6 knotig verdickte Hauptrippen, welche in der Wirbelgegend, nicht weit vom Schlossrande entfernt, ihren Ursprung nehmen und, radial verlaufend, in einiger Entfernung vom convexen Rande endigen: ferner kommen auch hier noch zwei kleinere Rippchen an der inneren Basis der Öhrchen hinzu.

Das vordere Öhrchen ist hier ein wenig concav, das hintere rechtwinkelig abgestutzt. Beide sind zum Unterschiede vom Haupttheile der Schale etwas deutlicher senkrecht gestreift.

[Tabelle mit Maßangaben!]

*Angesichts der bunten linken Schale dieser neuen Art wird man an die gefleckte Form erinnert, die Dall von seinem *A. pourtalesianum* erwähnt.*

*Dass im Gegensatze zu den Verhältnissen der rechten Schale die inneren Radialrippen der linken Schale weit entfernt vom Unterrande endigen, steht im Zusammenhange mit der grösseren Ausdehnung, dem grösseren Umfange der linken Schale. Sind nämlich die Schalen zusammengeklappt, so decken sich gewissermassen Anordnung und Länge der beiderseitigen Radialrippen vollständig und ragt der glatte, radienlose Unterrand der linken Schale um so viel hervor, als diese Schale eben grösser ist. Diese Thatsache ist sowohl bei *A. steindachneri* m. wie bei der folgenden Art zu constatiren.*

Translation. From stations 128 and 130 (439–457 m); single valves.

The clam is small, inequilateral, almost circular, slightly arched and shiny, and has delicate, finely pointed beaks and a triangular ligament pit beneath in the hinge margin.

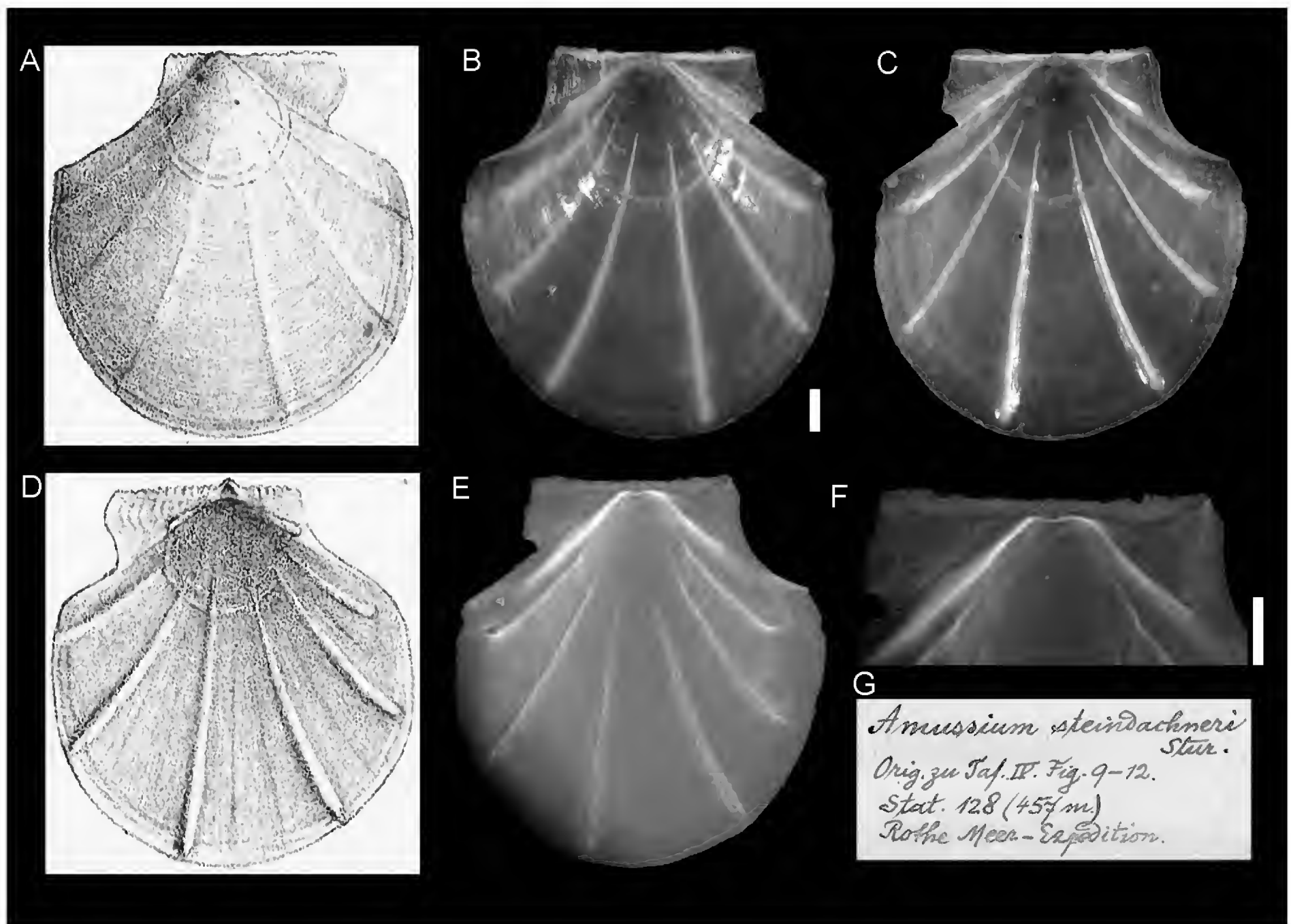


Figure 3. *Amussium steindachneri* Sturany, 1899, Station 128, Akik Seghir, Eritrea, -457 m. **A, D** Original figures (rotated by 180°). **B, C, E, F** Lectotype NHMW 84350: right valve exterior (**B**), interior (**C, E**), and hinge detail (**F**). **G** Original label. Scale bars: 1 mm.

The right valve is smaller, but thicker than the left, and is milky white and translucent. Its fairly smooth, very strongly glossy exterior, is crossed only by a few thicker but irregular growth lines. Six white ribs are arranged radially on the inside and reach the edge where they end with weak, button-shaped thickenings. Moreover, above the inner base of each auricle there is a rib which is only weakly developed and is hardly visible on the outside.

The anterior ear is anteriorly rounded (convex) and slightly striated, i.e. concentric with the margin; the rear is truncated almost at right angles. The upper margin of the right shell is delicately incised.

The left shell is larger, but thinner than the right, and is smooth, except for microscopic traces of transverse and radial ridges, and highly translucent. Through numerous white patches spread all over the outside and marks or lines of yellow or orange-red colour appearing towards the edge, the slightly more rounded shell acquires a characteristic appearance, which is enhanced by the strong orange-red or yellow-looking radial ribs on the inside. There are six nodular thickened main ribs in the right and the left valve, which originate in the umbo region, not far from the edge of the hinge, and terminate radially, in some distance from the convex margin; additionally, there are two smaller ribs to the inner base of the auricles.

The anterior auricle is a little concave, the posterior rectangular. In contrast to the main part of the valve both are slightly more vertically striped.

[Table with dimensions]

Considering the colourful left valve of this new species, one is reminded of the spotted shape which Dall mentioned in *A. pourtalesianum*.

In contrast to the proportions of the right shell, the inner radial ribs of the left valve are ending far away from the ventral margin, which is related to the greater elongation and size of the left valve. If the valves are paired, the arrangement and length of the radial ribs on both sides completely coincide, and the smooth, lower edge of the left shell, without radial sculpture, protrudes as much as this valve size. This fact can be stated for both *A. steindachneri* m. and the following species [*A. siebenrocki*].

Family Carditidae Férussac, 1822

Cardita akabana Sturany, 1899

Figure 4

Sturany 1899: 267–268, plate III, figures 10–12.

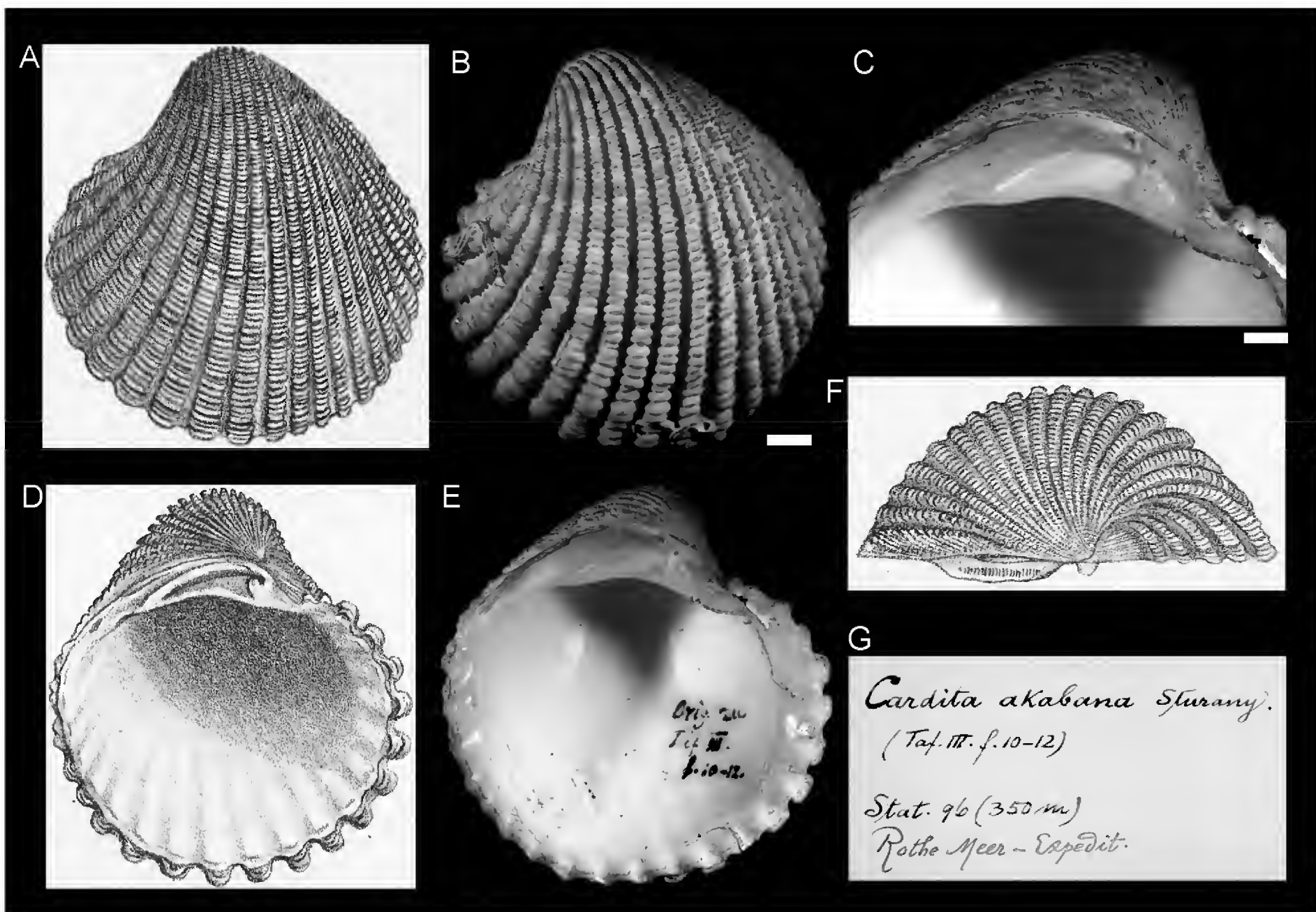


Figure 4. *Cardita akabana* Sturany, 1899, northern part of the Gulf of Aqaba, –350 m. **A, D, F** Original figures. **B, E, C** Figured syn-type NHMW 84343: right valve exterior (**B**), interior (**E**), and hinge detail (**C**). **G** Original label. Scale bars: 3 mm (**B**); 2 mm (**C**).

Type locality. Station 96, northern part of the Gulf of Aqaba, 29°13.5'N, 34°47.8'E, –350 m.

Type material. Syntypes: NHMW 84343: 2 valves, station 96 (one specimen in original figure).

Original description. Von Station 96 (350 m); zwei einzelne linke Schalen.

Die Schale ist gross, abgerundet, aufgeblasen und ungleichseitig, aussen ockergelb mit hellen, unregelmässig vertheilten Flecken, innen rein weiss.

Der Wirbel ist nach innen und vorne gedreht und überragt den Schlossrand um ein Bedeutendes; vor ihm liegt vertieft eine herzförmige, gestreifte Lunula. Vom Wirbel ziehen radial angeordnet 23 Rippen zum Rande. Sie sind meist gleich breit und breiter als ihre vertieft liegenden und undeutlich oder schwach quergestreiften Zwischenräume; in der hinteren Partie der Schale allerdings können mitunter die Rippen (etwa 5–6 an Zahl) weniger breit sein und dafür die Zwischenräume relativ weiter von einander abstehen. Die Rippen sind dicht mit geldrollenartig angeordneten Querwülsten oder Scheiben besetzt, die umso grösser sind, je weiter sie vom Wirbel entfernt liegen.

Der Rand der geöffneten Muschel ist kreisförmig, und nur am Übergange des Hinterrandes in den Unterrand ist eine schwache Winkelung zu verzeichnen. Entsprech-

end den Endigungen der Radialrippen sind die Ränder stark crenelirt.

Das Schloss der linken Schale besteht aus einem stumpfen Zahn, der direct unter dem Wirbel aus einer Schlossleiste hervortritt, und aus einer kleinen zahnartigen Erhebung vor demselben am Oberrande dort, wo die erste kurze Radialrippe endigt. Hinter dem Mittelzahn liegt eine lange und tiefe, dreieckige Grube, und auf diese folgt ein langer, dicker, bogiger und lamellenartiger Hinterzahn, der von dem das äussere Ligament tragenden hinteren Oberrande noch durch eine Vertiefung getrennt und oben wie unten fein quergestreift ist. Unter der Schlossleiste liegt die tiefe Aushöhlung der Wirbelgegend.

Die eine linke Schale ist 26,2 mm lang, 21,1 mm hoch und 12,2 mm dick; die andere (ebenfalls linke) misst 28,7, respective 30,2 und 14,1 mm.

Die neue Art, von der mangels rechter Schalen das Schloss leider nur unvollständig beschrieben werden konnte, erinnert einigermassen an *Cardita cardioides* Rve.

Translation. From Station 96 (350 m); two single left valves.

The shell is large, rounded, inflated and inequilateral, ochre coloured outside with bright, irregularly distributed spots, inside pure white.

The umbo turns inward and forward and clearly protrudes the edge of the hinge, it is reclined with a heart-

shaped, striated lunula. Twenty-three radial ribs run from the beak to the margins. They are usually the same width or wider than the interspaces which are indistinctly or weakly radially striate; over the posterior part of the shell, however, sometimes the ribs (about 5–6 in number) may be less wide and the interspaces stand farther apart. The ribs are densely covered by many bar-shaped varices or discs, which get larger the farther they are away from the beak.

The margin of the open bivalve is circular, and only at the transition from the posterior to the ventral edge is a weak angulation recorded. Coinciding with the ends of the radial ribs the edges are strongly crenulate.

The hinge of the left valve consists of an obtuse tooth, which emerges directly underneath the beak from the hinge margin, and of a small tooth-like bump at the dorsal margin where the first short radial rib ends. Behind the middle tooth lies a long and deep triangular pit, followed by a long, thick, curved and lamellar posterior tooth, which is separated from the posterior upper margin, supporting the outer ligament by a depression, and is finely striated above and below. Below the hinge margin, the deep cavity of the umbo area lies.

The first left valve is 26.2 mm long, 21.1 mm high and 12.2 mm thick; the other (also left) measures 28.7, respectively 30.2 and 14.1 mm.

The new species, which unfortunately could not be described completely due to the lack of right valves, is reminiscent of *Cardita cardioides* Reeve.

Family Cardiidae Lamarck, 1809

Tridacna elongata var. *squamosina* Sturany, 1899

Figure 5

Sturany 1899: 283–284, not figured.

Type locality. Yemen, Red Sea, Kamaran Isl., ca 15°17'N; 42°37'E, shallow water.

Type material. Lectotype: NHMW 107075: 2 valves (1 specimen), station 43 designated by Huber and Eschner (2011). Paralectotypes: NHMW 107076: 8 valves (4 specimens), station 12; NHMW 107077: 4 valves (2 specimens), station 10.

Original description. *Die stattliche Reihe der vorliegenden Schalen veranlasst mich, die in der Reeve'schen Monographie abgebildete Tr. compressa als Jugendform der elongata Lm. aufzufassen und ihren Namen einzuziehen, hingegen eine Varietät besonders hervorzuheben, die systematisch zur Tr. squamosa Lm. hinüberführt. Diese mit squamosina nov. var. zu bezeichnende Form liegt von den Localitäten 12, 14 und 43 in mehreren Exemplaren vor und ist durch die hauptsächlich gegen den Unterrand blättrig aufgestellten Querschuppen der Rippen ausgezeichnet.*

Translation. The impressive series of shells induces me to consider the *Tridacna compressa* depicted in Reeve's monograph as a young form of *T. elongata* Lamarck, and to cancel this name, and to highlight a variety that is systematically close to *Tr. squamosa* Lamarck. This form should be designated as *squamosina* nov. var. and several specimens are present from the localities 12, 14 and 43 and it is distinguished by the foliated transverse scales of the ribs mainly towards the lower margin.

Comments. Sturany introduced the name *squamosina* for a variety of *Tridacna elongata* Lamarck, 1819; it has a subspecific rank according to the Art. 45.6.4 of the ICZN. This species had been poorly known for a long time but was recognised as a distinct entity on the basis of a molecular phylogeny with the mitochondrial gene 16s rRNA (Richter et al. 2008). However, Richter et al. (2008) described this entity with the new name *Tridacna costata* which was recognised as a junior synonym of *T. squamosina* by Huber and Eschner (2011).

Family Galeommatidae Gray, 1840

Scintilla sulphurea Sturany, 1899

Figure 6

Sturany 1899: 286, plate VII, figures 6–9.

Type locality. Locality 25, near Abu Ghusun, Egypt, 26–24°N.

Type material. Holotype: NHMW 38098, fixed by monotypy.

Original description. *Von der Localität 25; ein einziges Exemplar.*

Die Muschel ist elliptisch gestaltet, massig gewölbt, an den Rändern ganz schliessend, ziemlich dickschalig, durchscheinend, dicht und ziemlich stark concentrisch gestreift, aussen und innen schwefelgelb gefärbt und glänzend.

Der Wirbel überragt den Schlossrand nur wenig und endet mit einem winzigen, glashell glitzernden Bläschen vor der Mitte der Schale am Schlossrande. Die Schlossleiste trägt, entsprechend dem Gattungscharakter, ausser einem nahe herangerückten Nebenzahn noch einen kräftigen Hauptzahn in der rechten Schale und 2 Hauptzähne in der linken Schale, von denen der vordere stärker als der hintere ist. Das braungefärbte Ligament liegt in dem grubenförmigen Zwischenraume zwischen Haupt- und Nebenzahn (fig. 7), welchen es jedoch nicht ganz ausfüllt, und ist bei der geschlossenen Muschel von aussen nur wenig sichtbar.

Der vordere Oberrand fällt sanft nach vorne und bildet mit dem nahezu senkrecht gestellten, also ziemlich gerade (sogar wenig nach rückwärts) abgestutzten Vorderrand fast einen Winkel (eine sogenannte »runde Ecke«). Ebenso gestaltet ist der Übergang von Vorder- in Unterrand; der letztere verläuft nicht ganz gerade, sondern zeigt eine

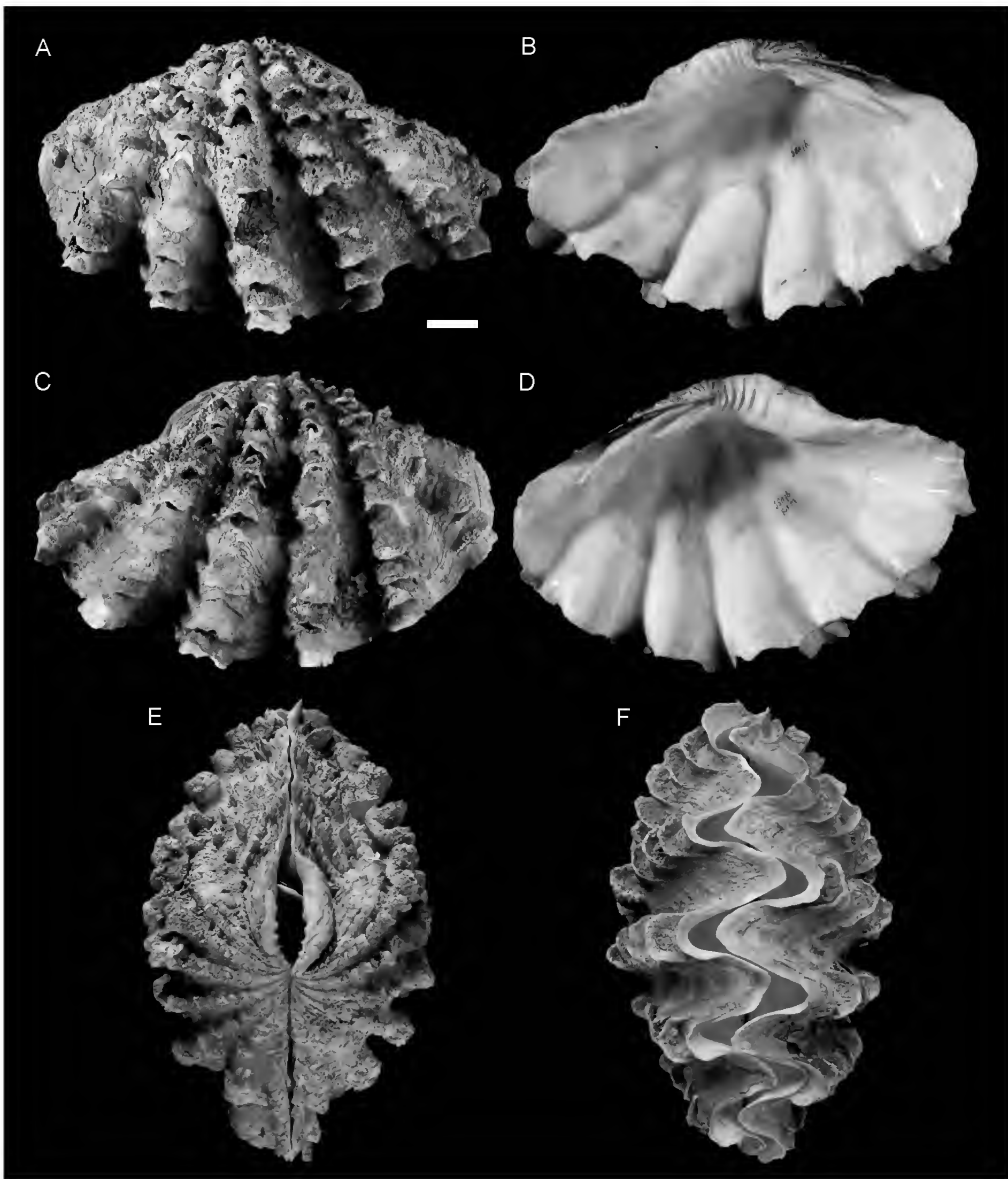


Figure 5. *Tridacna elongata* var. *squamosina* Sturany, 1899. A–F. Lectotype NHMW 107075: right valve exterior (A) and interior (B), left valve exterior (C) and interior (D), back view (E), front view (F). Scale bar: 2 cm.

geringe Concavität und verbindet sich in rundem Bogen mit dem convexen Hinterrande, der andererseits auch mit dem etwas aufwärts ziehenden hinteren Oberrande im Bogen verbunden ist.

Länge der Muschel 9,0, Höhe 6,3, Dicke 4,7 mm.

Es wollte mir nicht gelingen, die hier beschriebene Form mit einer der zahlreichen bestehenden Arten zu identificiren, von denen als die nächst verwandten

genannt seien: *Sc. tenuis* Desh., *semiclausula* Sow., *oblonga* Sow., *pisum* Sow. und *hydrophana* Desh.

Translation. From locality 25; one single specimen.

The clam is elliptical in shape, massively arched, completely closing at the edges, rather thick, translucent, densely and rather strongly concentrically lirated, outside and inside sulphurous in colour and shiny.

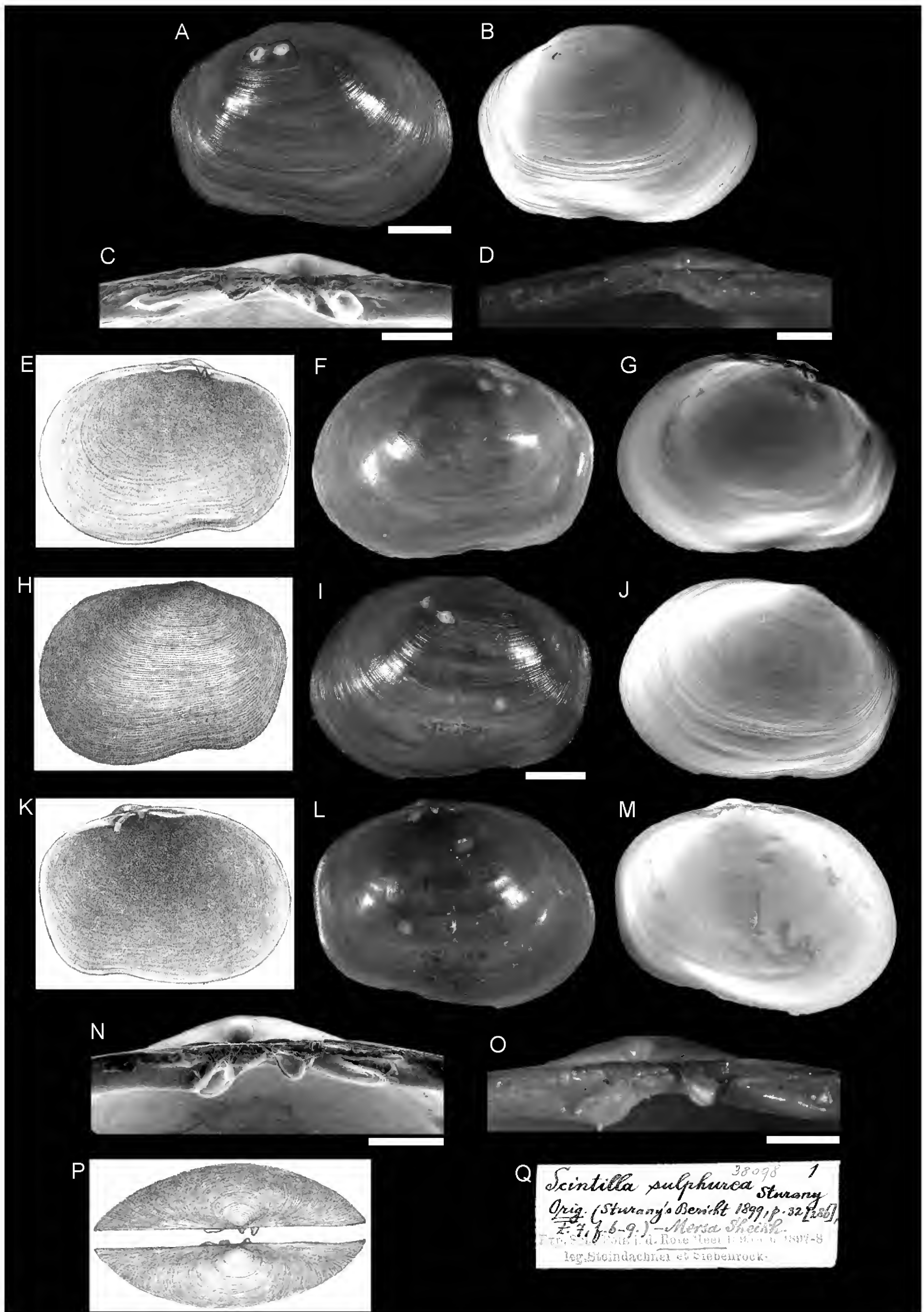


Figure 6. *Scintilla sulphurea* Sturany, 1899, near Abu Ghusun, Egypt. A–D, F, G, I, J, L–O Holotype NHMW 38098: left valve exterior (A, B) interior (F, G), and hinge detail (C, D); right valve exterior (I, J), interior (L, M), and hinge detail (N, O). E, H, K, P Original figures. Q Original label. Scale bars: 0.5 mm (C, D, N, O); 2 mm (A, I).

The umbo slightly protrudes over the hinge edge and ends with a tiny glassy glittering blister just before the centre of the shell at the hinge edge. The hinge margin, according to its generic character, has, in addition to a closely adjacent lateral tooth, a strong cardinal tooth in the right valve and two cardinal teeth in the left valve, of which the anterior is stronger than the posterior. The brown-coloured ligament lies in the pit-like spaces between the cardinal and lateral tooth (Fig. 7), which it does not completely fill, and is only slightly visible from the outside in the closed shell.

The anterior upper margin gently declines and almost forms an angle (a so-called “round corner”) with the almost vertical (even slightly backwards facing) truncated front edge. Equally designed is the transition from anterior to lower margin; the latter does not run quite straight but is slightly concave and connects in a circular arc with the convex posterior margin, which on the other hand is also connected with the slightly ascending posterior margin.

Length of the shell 9.0, height 6.3, thickness 4.7 mm.

I did not succeed in identifying the form described here with one of the numerous existing species, of which the most related are: *Sc. tenuis* Deshayes, *semiclausula* Sowerby, *oblonga* Sowerby, *pisum* Sowerby and *hydrophana* Deshayes.

Comments. This taxon is currently considered a junior synonym of *Scintillula lutea* (Lamarck, 1818) (Huber 2015).

Scintilla variabilis Sturany, 1899

Figure 7

Sturany 1899: 287, plate VII, figures 1–5.

Original localities. Locality 27, Berenice Troglodytica, Egypt, 24–22°N; locality 30, Halayeb, Egypt, 24–22°N; locality 41, Massawa, Eritrea, 16–11°N.

Type material. Syntypes: NHMW 38099: 1 specimen, locality 27; NHMW 37416: 1 specimen (in alcohol), locality 41; NHMW 37417: 2 specimens (in alcohol), locality 30.

Original description. *Von den Localitäten 27, 30 und 41.*

Die Muschel ist von elliptischer Gestalt, massig gewölbt, dickschalig, an den Rändern sich vollständig schliessend, dicht und ziemlich stark concentrisch gestreift, schwach durchscheinend, innen und aussen milchweiss und glänzend. Der Wirbel überragt den Schlossrand nur mit seinem bläschenförmigen Ende und steht in der vorderen Hälfte der Schale.

Das Schloss besteht in der rechten Schale aus einem kräftigen Hauptzahn 1 und einem nahe herangerückten Seitenzahn; in der linken Schale aus 2 schwächeren, ungleich starken Hauptzähnen und einem Nebenzahne. Das

dunkelgefärbte Ligament ist von aussen schwach zu sehen, ist auch hauptsächlich erst unter dem Schlossrande, wo für seine Aufnahme ein Ausschnitt der Schlossleiste zwischen Haupt- und Seitenzahn besteht, stärker, und zwar etwa kugelig entwickelt (figs 2 und 4).

Bei älteren Exemplaren ist der Umriss der Muschel fast der einer Ellipse; nirgend sind sogenannte »Ecken« gebildet, sondern alle Übergänge (von Ober- und Unter- in Vorder- und Hinterrand) sind abgerundet. Bei jüngeren Schalen jedoch grenzen sich die verschiedenen Ränder etwas schärfer von einander ab und ist hier und dort eine »stumpfe Ecke« oder ein Winkel gebildet. Auch ist hier zu bemerken, dass Ober- und Unterrand nicht streng parallel zu einander verlaufen müssen, sondern dass sich die höchste Stelle der Muschel in der Regel rückwärts befindet, indem die Muschel vorne etwas niedriger gebaut ist.

[Tabelle mit Maßangaben!]

Leider habe ich mich veranlasst gesehen, der stattlichen Artenreihe der Gattung Scintilla einen neuen Namen hinzuzufügen, da sich die vorliegende, in verschiedenen Altersstufen verschieden aussehende Form mit keiner der zahlreichen bisher bekannt gewordenen Scintillen mit Sicherheit identificiren lässt. Als die nächsten Verwandten möchte ich u. A. Sc. cumingii Desh. von Panama und Sc. candida Desh. von den Philippinen bezeichnen.

Translation. From localities 27, 30 and 41.

The clam is elliptical in outline, massively arched, thick, completely closing at the edges, dense and with rather strong concentric ridges, slightly translucent, milk-white and shiny inside and outside. The umbo protrudes the hinge edge only with its vesicular end and stands in the anterior half of the shell.

In the right valve, the hinge consists of a strong central tooth and a close lateral tooth; in the left valve, of two weaker, unequally strong main teeth and one lateral tooth. The dark-coloured ligament is hard to see from outside, it is mainly under the hinge margin, where there is a nearly spherical area between the central and posterior teeth for its inclusion (figs 2 and 4).

In older specimens, the outline of the shell is almost elliptical; the so-called “corners” are not formed, but all margins (from dorsal and ventral to anterior and posterior) are rounded. In younger shells, the different margin edges are a little sharper, and here and there an “obtuse corner” or an angle is formed. It should also be noted that the dorsal and ventral margin do not have to be strictly parallel, so that the highest point of the shell is usually posterior and positioned slightly lower in the front.

[Table with dimensions]

Unfortunately, it seemed necessary to add a new name to the impressive series of species in the genus *Scintilla*, since the present form, which looks different at different ages, cannot be identified with any of the numerous established *Scintilla*. As closest relatives, I would like to name *S. cumingii* Deshayes from Panama and *S. candida* Deshayes of the Philippines.

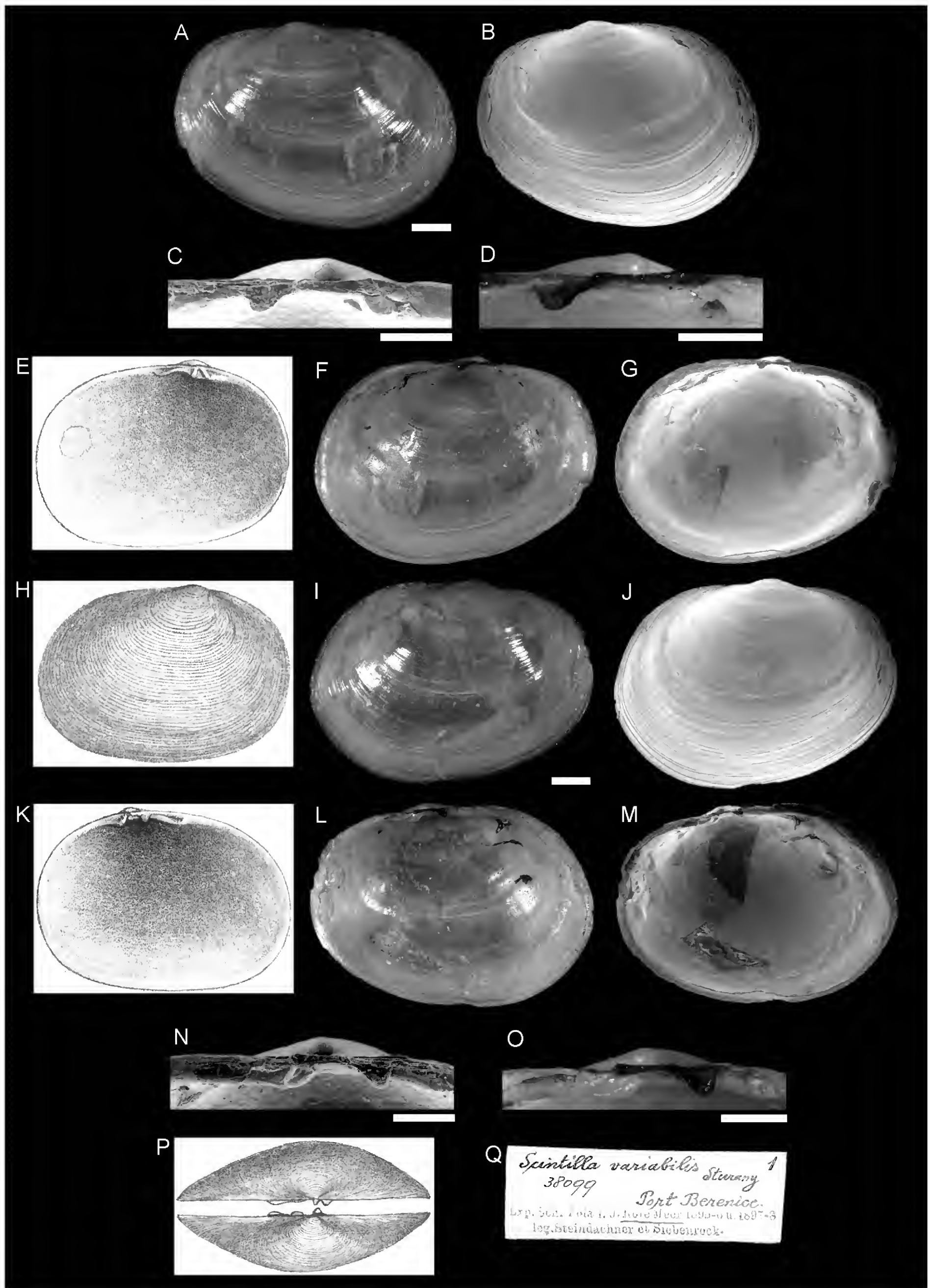


Figure 7. *Scintilla variabilis* Sturany, 1899. A–D, F, G, I, J, L–O Syntype NHMW 38099: left valve exterior (A, B), interior (F–G) and hinge detail (C, D). Right valve exterior (I, J), interior (L, M) and hinge detail (N, O). E, H, K, P Original figures. Q Original label. Scale bars: 0.5 mm (C, D, N, O); 2 mm (A, I).

Family Anatinellidae Deshayes, 1853

Raeta bracheon Sturany, 1899

Figure 8

Sturany 1899: 266, plate III, figures 1–6.

Type locality. Station 87, Ra's Mal'ab in the Gulf of Suez, Egypt, 29°7.6'N, 32°56'E, –50 m.

Type material. Syntypes: NHMW 84335: 2 valves, station 87 (in original figure).

Original description. *Von Station 87 (50 m), eine rechte und eine linke Schale, die jedoch nicht zueinander gehören.*

Die Muschel ist gross, Cuspidaria-förmig, mässig gewölbt, dünn, durchscheinend, aussen milchweiss, matt, concentrisch gefaltet, innen glänzend.

Der Wirbel liegt ein wenig vor der Mitte der Schale und überragt den Schlossrand nicht besonders stark. Die vordere Hälfte der Schale ist gewölbt, die hintere abgeflacht und schnabelförmig ausgezogen.

Der vordere Oberrand geht im Bogen in den gewölbten Vorderrand und dieser ebenso in den convexen Unterrand über. Der hintere Oberrand fällt schief ab zum abgerundeten Hinterende des Schnabels, die untere Begrenzung des Schnabels ist ebenfalls von einer schiefen Linie gebildet; der Winkel des Rostrums ist circa 60°.

Zwischen den concentrisch angeordneten Falten der Oberfläche, welche nach innen vollständig durchgeprägt sind, liegen noch mikroskopisch feine concentrische Streifen (in der Regel 5–6 Streifen zwischen 2 Falten). Gegen den Unterrand zu werden die Zwischenräume der Faltung enger; die Falten selbst sind, entsprechend der Form der Schale, in ihrem Verlaufe mehrfach geknickt, besonders am Oberrande.

Von Muskeleindrücken sind im Inneren der Schale zu sehen: ein langgestreckter, fast senkrecht stehender, nur wenig gekrümmter vorne nächst dem Vorderrande und ein etwa kreisförmiger rückwärts am hinteren Oberrande, wo das Rostrum entspringt.

Von oben betrachtet, lässt die Muschel ein undeutlich begrenztes, schmales und längliches Feld vor dem Wirbel erkennen (lunula).

Das Schloss besitzt ein inneres Ligament, welches in einer länglichen, etwa dreieckigen Grube liegt; unmittelbar davor stehen in der rechten Schale zwei senkrecht gestellte Mittelzähne parallel zu einander; über demselben, also am Schlossrande und gewissermassen als obere Begrenzung der Ligamentgrube, liegt ein ziemlich starker Zahn von gleicher Länge wie die Ligamentgrube; ferner sind leistenförmige Seitenzähne, vorne und rückwärts je einer, zu constatiren; dieselben sind vom Oberrande durch Vertiefungen getrennt. In der linken Schale ist nur ein senkrechter Mittelzahn wahrnehmbar, welcher vor der Ligamentgrube steht; im übrigen liegen hier die Schlossverhältnisse wie in der rechten Schale.

Die vorliegende rechte Schale ist 30,5 mm lang und 20 mm hoch, die linke Schale 29 mm lang und 19,5 mm hoch.

*Die neue, anscheinend nur geringe Tiefen des Roth-en Meeres bewohnende Raeta-Art ist nun die erste für das eigentliche erythräische Seebecken bisher bekannt gewordene aus dieser Gattung. In Aden kommt nach Shopland *R. abercrombiei* Melvill vor, deren Originalfundort Bombay ist, und mit der meine Art nicht zu verwechseln ist.*

Translation. From station 87 (50 m), one right and one left valve, which do not belong to the same individual.

The clam is large, *Cuspidaria*-shaped, moderately arched, thin, translucent, outside milky white, dull, concentrically folded, shiny inside.

The umbo is slightly anterior to the centre of the shell and does not much protrude the hinge edge. The anterior part of the valve is arched, the posterior on the same plane and subrostrate.

The anterior upper margin shades off in a curve to the arched anterior margin and continues into the convex lower margin. The posterior upper margin slopes off to the rounded rear end of the beak, while the lower marking of the beak is formed by an oblique line; the angle of the rostrum is about 60°.

Between the concentrically arranged folds, which are completely imprinted on the inside, microscopically fine concentric striae are present (usually 5–6 striae between two folds). Towards the lower margin, the spaces between the folds become narrower; the folds themselves, according to the shape of the shell, are repeatedly flexed, especially at the upper margin.

Muscle scars can be seen in the interior of the shell: one elongated, almost vertical, slightly curved near the anterior margin and another almost circular at the posterior margin, where the rostrum originates.

Viewed from above, the clam shows an indistinct, narrow and elongated area in front of the umbo (lunula).

The hinge has an inner ligament, which lies in an elongated, approximately triangular pit; directly in front of it, in the right shell, two perpendicular median teeth are parallel to each other. At the edge of the hinge, and as a kind of upper restriction of the ligament pit, a fairly strong tooth lies and is of the same length as the ligament pit; in addition, bar-like lateral teeth, one in front and one on the back are separated from the upper margin by depressions. In the left valve, only one vertical median tooth is perceptible, in front of the ligament pit; otherwise, hinge conditions are the same as in the right shell.

The present right valve is 30.5 mm long and 20 mm high, the left valve 29 mm long and 19.5 mm high.

This new species is the first for the Red Sea basin known from this genus inhabiting apparently only shallow waters. According to Shopland, *R. abercrombiei* Melvill occurs in Aden, its original location is Bombay and should not be confused with my species.

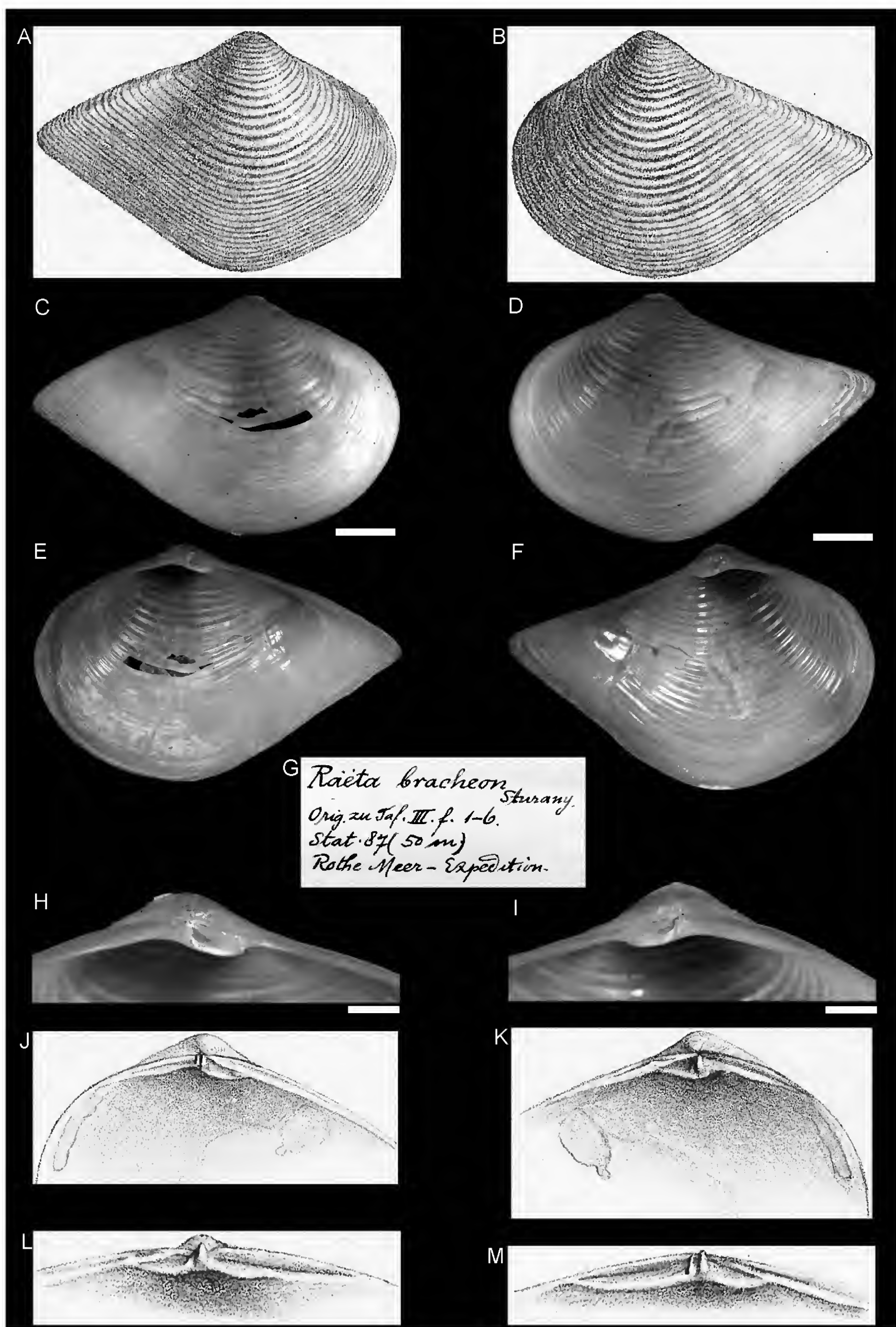


Figure 8. *Raeta bracheon* Sturany, 1899, Station 87, Ra's Mal'ab in the Gulf of Suez, Egypt, 50 m. **A, B, J–M** Original figures. **C–F, H, I** Figured syntypes NHMW 84335: right valve exterior (**C**) interior (**E**), and hinge detail (**H**); left valve exterior (**D**), interior (**F**), and hinge detail (**I**). **G** Original label. Scale bars: 5 mm (**C, D**); 2 mm (**H, I**).

Family Tellinidae Blainville, 1814

Tellina siebenrocki Sturany, 1899

Figure 9

Sturany 1899: 278, plate VI, figures 4–7.

Type locality. Locality 45, Ras Mujamila, Yemen, 16–11°N.**Type material.** Holotype: NHMW 38016, fixed by monotypy.**Original description.** *Von der Localität 45; ein einziges, aber schön erhaltenes Exemplar.*

Die Muschel ist dickschalig, ungleichseitig und fast gleichschalig, wenig gewölbt, eiförmig mit schnabelig vortretendem Hinterende; aussen stark glänzend und etwas opalisierend, rosafarbig im Grundtone und purpurroth gefärbt in der Wirbelgegend, innen glänzend und mehr minder orangegelb, in der Wirbelgegend schwach durchscheinend. Sie ist concentrisch gestreift, und zwar ziemlich dicht und unregelmässig (etwas gröber am Unterrande) und ist durch Spuren von radialer Streifung aussen sowohl wie innen ausgezeichnet.

Die Wirbel sind mittelständig und stehen einander am Schlossrande dicht gegenüber. Vor dem Wirbel fällt der Rand der Schale in schwachem, etwas herausgekrümmten Bogen schief herab; er verbindet sich bogig mit Vorder- und Unterrand; hinter dem Wirbel senkt sich der Rand schief und etwas convex herab zu dem kurzen, und abgeschlossenen Rostrum, das unten, am Übergange in den schwach convexen Unterrand, eine schwache Concavität aufweist.

Das Schloss der rechten Schale besitzt direct unter dem Wirbel zwei divergirende, freistehende Cardinalzähne, wovon der hintere gespalten ist, einen nahe herangerückten vorderen und einen längeren, ebenfalls nicht weit entfernt stehenden Lateralzahn; über diese Lateralzähne ist der Rand leistenförmig hervorgezogen. In der linken Schale ist ein kaum gespaltenen Cardinalzahn zu verzeichnen, eingefasst von Gruben für die gegenüberstehenden Zähne der rechten Schale. Die Seitenzähne werden hier vertreten durch zahnartig vorgezogene Ränder vorne und rückwärts, welche in die entsprechenden Vertiefungen zwischen den Lateralzähnen und Rändern der rechten Schale passen. Das braune Ligament der Muschel liegt aussen hinter dem Wirbel.

Vom Wirbel zieht in jeder Schale eine schwache kielartige Erhebung zum schnabelförmigen Ende der Schale, wodurch also rückwärts eine lanzettförmige Area entsteht.

Die Muskeleindrücke sind deutlich; der vordere ist aufrechtstehend oval, der hintere rund. Die Mantelbucht reicht bis zum vorderen Muskeleindruck, steigt unter dem Wirbel ziemlich hoch hinauf und endigt vorne ziemlich spitz.

Länge der Muschel 15,7, Höhe 11,3 und Dicke 6,2 mm.

Die neue Art hat die Gestalt einer T. producta Sow. einer T. culter Hanl. (d. i. eine Form von den Philippinen, die auch eine ähnliche Farbe besitzt), einer T. cuspis Hanl. einer T. brevicostata Sow. etc.; die beiden letzteren sind,

abgesehen von anderen viel wichtigeren Unterschieden, auch viel grösser in ihren Umrissen.

Translation. From locality 45; a single, but well-preserved specimen.

The clam is thick, inequilateral and is almost equivalve, little arched, egg-shaped with a protruding beaked posterior end; outside strongly glossy and somewhat opalescent, with a pinkish background and purple coloured in the umbonal region; on the inside, glossy and more or less orange-yellow, slightly translucent in the umbonal region. It has concentric striae, rather dense and irregular (somewhat coarser at the lower margin) and is marked by traces of radial striation both externally and internally.

The beaks are centred and stand close to each other at the hinge edge. In front of the beak, the valve margin is sloping down in a faint, slightly arched curve; and curved again when connecting the anterior and ventral margins; behind the beak, the edge slopes convexly down to the short and closed rostrum, which is weakly concave below and then merges into the weakly convex lower margin.

The hinge of the right valve has directly below the umbo, two diverging free-standing cardinal teeth, of which the posterior is split, closely adjacent is an anterior lateral tooth; over these lateral teeth the edge is extended and ridge-shaped. The left shell has a weakly split cardinal tooth, surrounded by pits for the opposing teeth of the right shell. The lateral teeth are represented by anterior and posterior tooth-like margins which fit into the corresponding pits between the lateral teeth and the edges of the right valve. The brown ligament of the clam lies externally behind the umbo.

From the umbo, a weak keel-like elevation in each valve runs to the beak-shaped end of the valve, thus creating a lancet-shaped area backwards.

The muscle scars are light; the anterior is upright oval, the posterior round. The pallial sinus extends to the anterior muscle scar, rises quite high under the umbo and ends quite pointedly.

Length of the shell 15.7, height 11.3 and thickness 6.2 mm.

The new species has the shape of *T. producta* Sowerby, *T. culter* Hanley (a form of the Philippines, which has a similar colour), *T. cuspis* Hanley, *T. brevicostata* Sowerby, etc.; the latter two, apart from other much more important differences, are also much broader in their outlines.

Comments. It is considered a junior synonym of *Tellina bertini* (Jousseume, 1895) (Oliver 1992).

Family Solecurtidae d'Orbigny, 1846

Solecurtus subcandidus Sturany, 1899

Figure 10

Sturany 1899: 260–261, plate I, figures 1–4.

Type locality. Station 94, Nuweiba, Gulf of Aqaba, Egypt, 28°58.6'N, 34°43.7'E, –314 m.

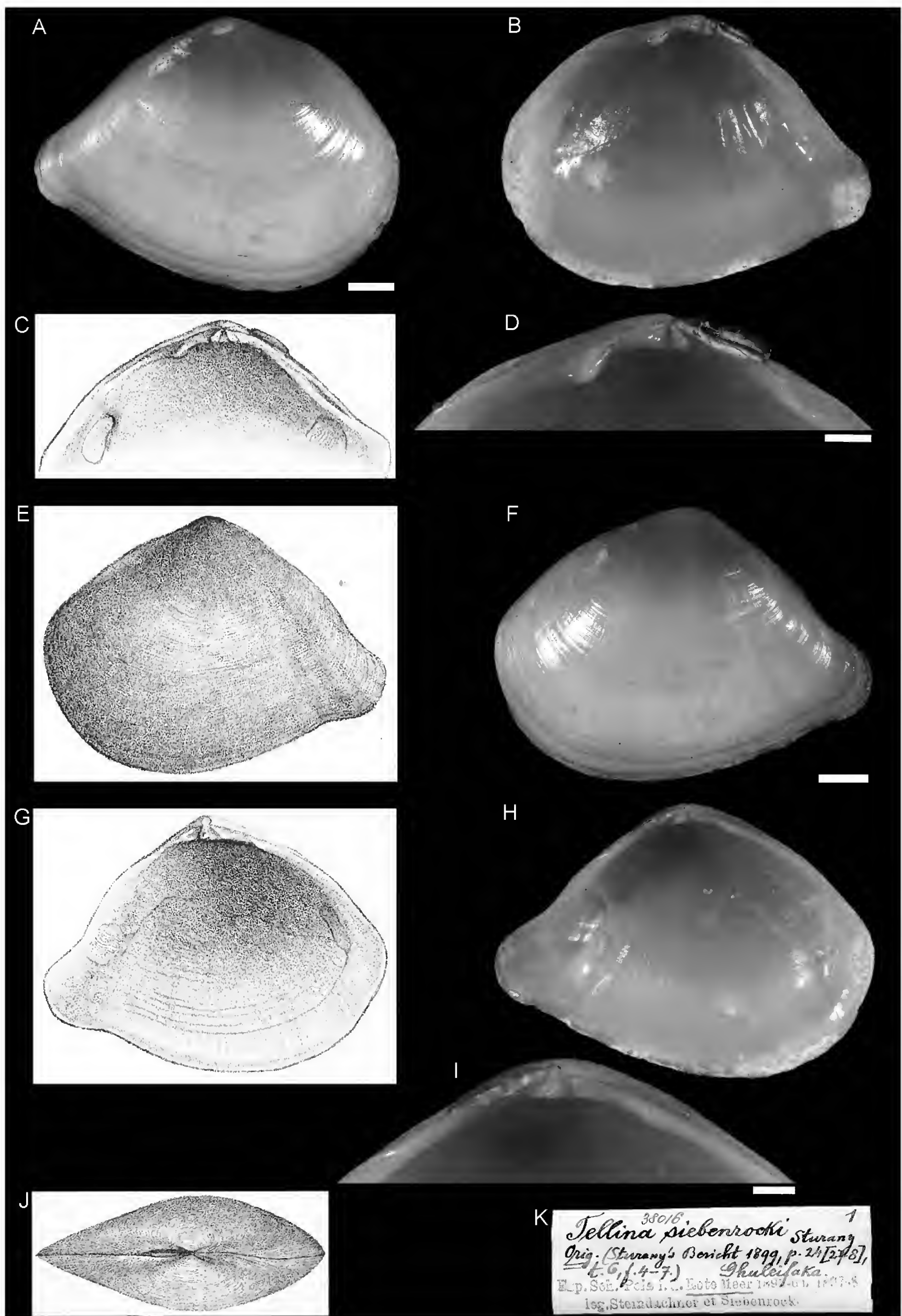


Figure 9. *Tellina siebenrocki* Sturany, 1899, locality 45, Ras Mujamila, Yemen. **A, B, D, F, H, I** Holotype NHMW 38016: right valve exterior (**A**), interior (**B**), and hinge detail (**D**); left valve exterior (**F**), interior (**H**), and hinge detail (**I**). **C, E, G, J** Original figures. **K** Original label. Scale bars: 1 mm (**D, I**); 2 mm (**A, F**).

Type material. Holotype: NHMW 84296, fixed by monotypy.

Original description. *Ein einziges Exemplar von Station 94 (314 m).*

Die Muschel klafft an beiden Enden, ist wenig gewölbt, langgestreckt oval, ziemlich festschalig, schwach durchscheinend und ein wenig glänzend, aussen weiss mit Spuren gelber Zeichnung, innen rein weiss.

Die Sculptur derselben ist im Allgemeinen fein und undeutlich. Aus der dichten concentrischen

Streifung treten gegen die Ränder der Schalen zu mehrere Anwachsstreifen kräftig hervor; eine Radiärstreifung fehlt nur in der vorderen Schalenpartie, in der Mitte treten sehr schief gestellte Streifen auf, in der hinteren Schalenpartie stehen aufrechte Streifen, die jedoch ein- bis zweimal gekrümmt sind, und zwar oben mit dem Bogen nach vorne, unten mit dem Bogen nach hinten (vide fig. 1).

Der Oberrand der Muschel weicht wenig von einer Geraden ab, vorne ist er schwach abfallend, hinter dem Wirbel minimal eingebogen; der Unterrand ist ganz gerade; Vorder- und Hinterrand gehen oben und unten mit »runden Ecken« in Ober- und Unterrand über.

Der Wirbel steht vor der Mitte, ist schwach zugespitzt und überragt den Schlossrand wenig.

Aus der Schlossleiste ragen in der rechten Schale 2 spatenförmige Zähne hervor, von denen der hintere bedeutend kräftiger entwickelt und länger ist; in der linken Schale befindet sich nur 1 schwächerer Hauptzahn, der vorne und rückwärts von einer Grube umstellt wird. Hinter den genannten Zähnen liegt auf vorgezogenem Rande das Ligament.

Die Mantelbucht ist zungenförmig und reicht bis über die Wirbelregion hinaus in die vordere Schalenpartie.

Die Länge der Muschel beträgt 30, die Breite 12,4, die Dicke circa 7 mm.

Die nächstverwandten Arten sind S. divaricatus Lischke aus Japan und S. candidus Renier aus dem Mittelmeer und dem Atlantischen Ocean. Die erstgenannte Art unterscheidet sich hauptsächlich dadurch, dass die Querlinien vorne nicht so schief gestellt sind wie bei der neu aufgestellten Form, und dass sie rückwärts, respective oben runzelig werden, auch anders geknickt erscheinen. Bei S. candidus Renier ist die Quer- (oder Radial-) streifung ähnlich ausgebildet wie bei S. subcandidus m., doch ist jene Muschel gewölbter und relativ höher. Beiden in Vergleich gezogenen Arten gegenüber ist die neue Art überdies durch die besonders stark entwickelte Bezahnung ausgezeichnet.

Translation. One single specimen from station 94 (314 m).

The clam gapes at both ends, is slightly arched, elongated oval, quite hard-shelled, weakly transparent and a little shiny, white with slight yellowish shading on the outside, pure white on the inside.

The sculpture is generally fine and indistinct. From the dense concentric striation, a number of growth lines emerge most prominently at the margins of the valves; a radial striation is missing only over the anterior part of the shell, in the middle part very oblique incisions are pres-

ent, over the posterior part there are upright ridges, which are once or twice sinuous, in fact they have the concavity to the front dorsally, and to the back ventrally (see fig. 1).

The upper margin of the clam deviates little from a straight line; it is slightly sloping, minimally sloping behind the umbo; the lower margin is very straight; above and below, the anterior and posterior margin change with “rounded corners” into the upper and lower margins.

The weakly pointed umbo is located anteriorly and protrudes little beyond the hinge edge. Two flat teeth protrude from the hinge edge in the right valve, the most posterior of which is much more prominent and long; in the left valve there is only one weaker central tooth, which is enclosed by a cavity in the front and back. The ligament lies behind the aforementioned teeth on an elongated edge.

The pallial sinus is tongue-shaped and reaches beyond the umbo region into the anterior part of the shell.

The length of the shell is 30 mm, height 12.4, thickness 7 mm.

The closest related species is *S. divaricatus* Lischke from Japan and *S. candidus* Renier from the Mediterranean Sea and the Atlantic Ocean. The first species is mainly distinguished by less tilted transverse lines compared to the newly described form, and by a rugose structure on the back, with a differently tilted appearance. In *S. candidus* Renier, the lateral (or radial) striation is developed in a similar way as in *S. subcandidus* m., however, the shell is more rounded and relatively higher. Furthermore, the new species is distinguished by the strongly developed dentition compared to both species.

Family Ungulinidae Gray, 1854

Diplodonta raveyensis Sturany, 1899

Figure 11

Sturany 1899: 285–286, plate VI, figures 8–11.

Type locality. Locality 32, Gul Mohammad, Saudi Arabia, 22–20°N.

Type material. Holotype: NHMW 38097 lost; see comments.

Original description. *Von der Localität 32; ein tadello-ses Exemplar.*

Die Muschel ist fast kreisförmig im Durchschnitte, ziemlich festschalig, stark gewölbt; aussen etwas glänzend, mit feiner, dicht stehender, concentrischer Punktstreifung ausgestattet, in der Farbe schmutzigweiss bis gelblich mit einigen hellgrauen, nach innen durchschimmernden Zonen; innen reinweiss, glatt und glänzend am Rande, rauh und matt in der Mitte.

Die Wirbel sind stark ausgehöhlt, stehen vor der Mitte, sind mit ihren stumpfen Spitzen nach innen und vorne gekehrt und stehen sich an dem Schlossrande gegenüber, den sie nicht viel überragen. Eine Lunula ist kaum ausgebildet.

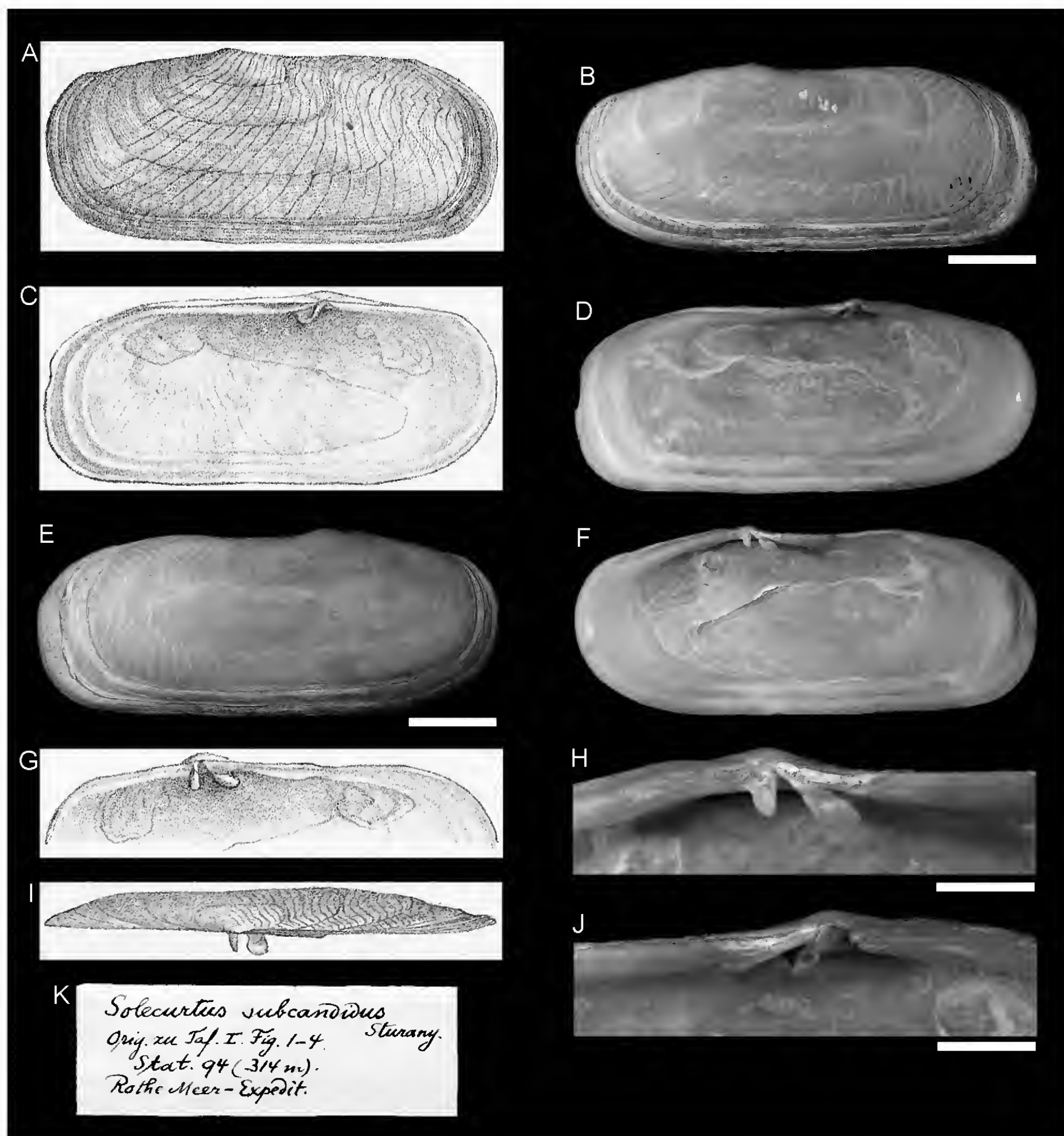


Figure 10. *Solecurtus subcandidus* Sturany, 1899, Station 94, Nuweiba, Gulf of Aqaba, Egypt, -314 m. **A, C, G, I** Original figures. **B, D–F, H, J** Holotype NHMW 84296: left valve exterior (**B**), interior (**D**), and hinge detail (**J**), right valve exterior (**E**), interior (**F**), and hinge detail (**H**). **K** Original label. Scale bars: 5 mm (**B, E**); 2 mm (**H, J**).

Der vordere Oberrand fällt schief ab und geht im Bogen in den Vorderrand über; ebenso ist der Übergang von Vorder- in Unterrand und von Unter- in Hinterrand schön gerundet, nur der vom Wirbel schief abfallende hintere Oberrand bildet an seinem Übergange in den Hinterrand einen schwach ausgeprägten Winkel, der nicht viel mehr als 100–110° beträgt.

Das Schloss besteht aus einem inneren Ligament direct unter dem Rande und aus einer auffallenden Bezeichnung. Die letztere besteht in der rechten Schale in 2 divergirenden Mittelzähnen unter dem Wirbel, von denen

der hintere gegabelt ist und die voneinander durch eine dreieckige Grube getrennt sind. In der linken Schale sind ebenfalls zwei Mittelzähne zu sehen, von denen aber der vordere gespalten ist und der hintere einfach bleibt. Auch hier sind dieselben voneinander durch eine dreieckige Grube in der breiten Schlossleiste getrennt, und hier wie dort liegt vor dem vorderen Mittelzähne eine schwache Vertiefung, die nach vorne rinnenförmig verläuft, und hier wie dort liegt das Ligament gleich hinter dem hinteren Mittelzahn, schief vom Wirbel herab nach hinten ziehend.

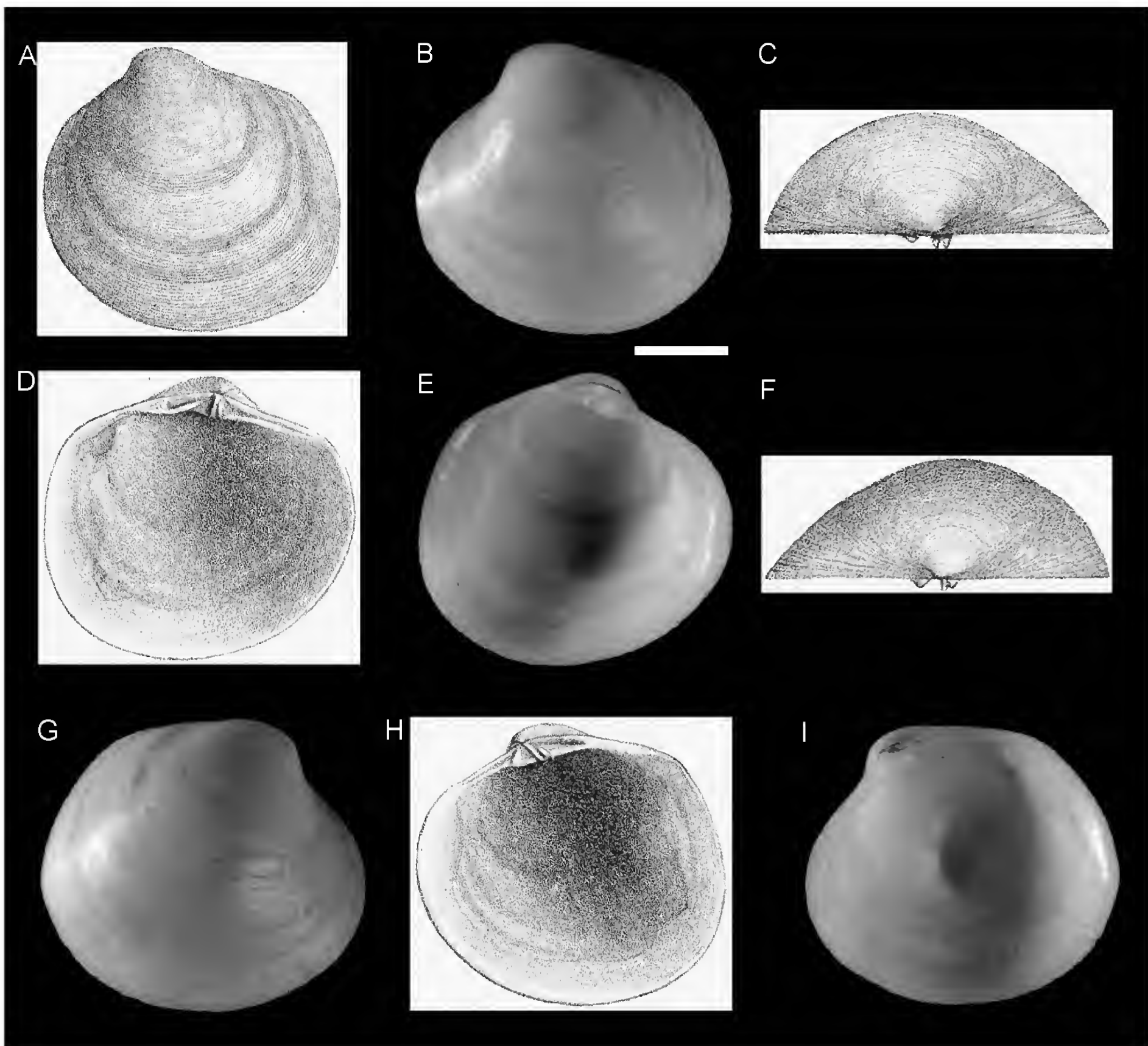


Figure 11. *Diplodonta raveyensis* Sturany, 1899, locality 32, Gul Mohammad, Saudi Arabia. **A, C, D, F, H** Original figures. **B, E, G, I** Holotype NHMW 38097 left valve exterior (**B**) and interior (**E**); right valve exterior (**G**) and interior (**I**). Photo courtesy Henk Dekker. Scale bar: 3 mm.

Der Mantelrand verläuft parallel dem unteren Rande der Schale und endigt vorne und rückwärts an den Muskeleindrücken.

Länge der Muschel 10,4, Höhe 9,8, Dicke 7,3 mm

*In der Gestalt ist diese neue Art wohl ähnlich der *Lucina globularis* Lam., welche nach Jousseume auch im Rothen Meere vorkommen soll; ferner der nunmehr in die Gattung *Diplodonta* verwiesenen *Lucina rotundata* Turton, für welche die Bezeichnung ganz so beschrieben wird, wie wir sie bei der neuen Art gesehen haben und die von Reeve für »Mediterranean and southern shores of Britain«, von Smith und Shopland für Aden, von Caramagna sogar für Assab im südlichsten Theile des Rothen Meeres angegeben wird. Von dieser *L. rotundata* Turton ist aber meine Art schon durch die geringe Grösse genügend verschieden.*

Mysis tumida A. Ad., in der Gestalt der neuen Art ebenfalls ähnlich, ist nur wenig grösser, jedoch durch das Merk-

mal »striolis confertis radiantibus et concentricis obsolete decussata« hinreichend als verschieden gekennzeichnet.

Translation. From locality 32, one perfect specimen.

The clam is nearly circular, quite hard-shelled, strongly arched; slightly shiny on the outside, with fine, compact, concentric dotted striation, of dirty white to yellow colour with some light grey, translucent to the inside zones; pure white on the inside, smooth and shiny on the edge, rough and matt in the middle.

The beaks are strongly extended, positioned anteriorly, tilted to the inside and to the front with obtuse tips and touch each other at the hinge edge, which they do not protrude by much. The lunula is hardly developed.

The anterior upper margin goes down and merges with the frontal margin in a curve; also, the transition from the anterior to the lower margin and from the lower to

the posterior margin is nicely rounded; only the unevenly sloping posterior upper margin forms at its junction a weakly developed angle of no more than 100–110°.

The hinge is formed by an inner ligament directly beneath the margin and by a prominent dentition.

The latter consists of two divergent middle teeth below the umbo, which are separated from each other by a triangular cavity and the posterior one is bifurcate. In the left shell, there are also two middle teeth; however, the anterior one is bifurcate and the posterior is ordinary. Also in this case, they are separated by a triangular cavity within the broad hinge margin and in both cases there is a shallow deepening in front of the central tooth, which proceeds towards the front in a groove, and in both cases the ligament lies right behind the posterior central tooth.

The pallial line proceeds parallel to the lower margin of the shell and ends in the front and posteriorly at the muscle scars.

Length of the shell 10.4, height 9.8, thickness 7.3 mm.

In its shape, this new species apparently resembles *Lucina globularis* Lamarck which according to Jousaume occurs also in the Red Sea. Furthermore, there is a similarity to *Lucina rotundata* Turton, now placed in the genus *Diplodonta*, for which the dentition is described just as we have seen it in the new species and which was named by Reeve for “Mediterranean and southern shores of Britain”, by Smith and Shopland for Aden, and by Caramagna even for Assab in the southernmost part of the Red Sea. My species, however, is different enough because of the small size from this *L. rotundata* Turton.

Mysis tumida A. Adams, also similar in shape to the new species, is only slightly smaller, but adequately differentiated by the characterization “*striolis confertis radiantibus et concentricis obsolete decussata*” [reticulate sculpture of compact radial and obsolete concentric striae].

Comments. The holotype was lost while on loan.

Family Veneridae Rafinesque, 1815

Chione hypopta Sturany, 1899

Figure 12

Sturany 1899: 281–282, plate VII, figures 10–14.

Original localities. Locality 10, Nuweiba, Egypt, Gulf of Aqaba; locality 16, Jazirat Shakir, Egypt, northern Red Sea, 28–26°N.

Type material. Syntypes: NHMW 38049: locality 16, 5 valves (one specimen in original figure).

Original description. *Von den Localitäten 10 und 16.*

Die Muschel ist oval bis dreieckig, dickschalig, wenig gewölbt, aussen weiss bis gelb mit unregelmässig in grösseren oder kleineren braunen Flecken vertheilter Zeichnung, innen violett oder weiss.

Die Schale ist an ihrer Oberfläche radial und der Länge nach von Furchen durchzogen, die tief einschneiden und eine bemerkenswerthe Felderung hervorrufen. So stehen mehr als dreissig derbe Radialrippen dicht aneinander, die am Wirbel schwach entspringen und gegen den Rand zu stark werden, und welche eben durch die Quersfurchen eine Gitterung erhalten. In der hinteren Schalenpartie sind die Felder schuppig oder dornig ausgebildet, doch ist dies nur bei jungen Exemplaren gut zu sehen.

Die an der Spitze violett oder roth gefärbten Wirbel stehen etwas vor der Mitte der Schale und überragen den Schlossrand nur wenig. Der vordere Oberrand fällt vom Wirbel schief und etwas bogig herab in den gerundeten Vorderrand, welcher auch mit dem Unterrand bogig verbunden ist.

Der hintere Oberrand verläuft etwas schief nach rückwärts und hinab zum Hinterrand, mit dem er unter einem kaum merklichen, stumpfen Winkel sich verbindet, während wieder Hinter- und Unterrand an dem im Alter etwas ausgezogenen Hinterende der Muschel bogig verbunden sind. Eine Kerbung der Ränder, entsprechend den äusseren Endigungen der Radialrippen, ist nur bei jungen Exemplaren auffallend entwickelt; bei diesen ist dann innerhalb der Kerbung auch jene allen Chionen zukommende Strichelung besonders gut zu sehen, die bereits an den Oberrändern beginnt und ringsum zieht.

Vor den Wirbeln liegt eine deutlich begrenzte, lanzettförmige Lunula, hinter derselben das äussere Ligament. Die Schlossleiste trägt im Allgemeinen 2 divergirende Zähne und 3 Gruben in der rechten Schale sowohl wie in der linken. Bei jungen Exemplaren ist des Näheren zu sehen, dass die Grube vor dem vorderen Zahn der rechten Schale noch von einem schwachen Zähnchen überstellt ist, ferner dass der hintere Hauptzahn der linken Schale vorne etwas gespalten ist und darauf noch ein schwacher, leistenförmiger Zahn folgt, der schief nach rückwärts läuft.

Der Mantelrand ist rückwärts kurz zungenförmig eingebuchtet.

[Tabelle mit Maßangaben!]

Translation. From locality 10 and 16.

The clam is oval to triangular, thick-shelled, poorly arched, white to yellow on the outside with a pattern of irregularly sized, brown spots, purple or white on the inside.

The shell is radially and longitudinally carved by deep grooves on its surface, causing a notable sculpture. Over thirty compact radial ribs are densely arranged, they are initially weak at the umbo and become stronger towards the margin and become cancellate when crossing the concentric grooves. In the posterior part of the shell, the sculpture is scaly or thorny; however, this is clearly visible only in young specimens.

The umbos are violet or red at their tips, they are positioned anteriorly and protrude the hinge margin only slightly. The anterior dorsal margin declines from the umbo with a slight curve into the rounded anterior margin, which is also connected to the ventral margin.

The posterior dorsal margin slopes slightly backwards and downwards to the posterior margin, with which it

connects in a hardly noticeable obtuse angle, while posterior and upper margins are connected again in a curve at the posterior end of the bivalve, which is slightly extended in older specimens. A crenulation of the margin, due to the endings of the radial ribs, is noticeably developed only in young specimens. Here, within the crenulations, the finer sculpture typical for all *Chione* is especially visible, it already starts at the upper margins and continues all around the shell.

A clearly confined, elongate lunula lies in front of the umbos, located behind them there is the external ligament. The hinge margin generally shows two diverging teeth and three pits in both the right and left valves. In young specimens, small teeth surround the pit in front of the central tooth of the right valve; furthermore, the posterior central tooth of the left valve is slightly split at the tip and is followed by a weak, elongated oblique tooth.

The pallial sinus is slightly indented posteriorly in a tongue-shape.

[Table with dimensions]

Family Gastrochaenidae Gray, 1840

Gastrochaena deshayesi Sturany, 1899

Figure 13

Sturany 1899: 273–274, plate V, figures 1–7.

Type locality. Locality 37, near Jazan, Saudi Arabia, 18–16°N.

Type material. Syntypes: NHMW 37982: locality 37, 4 specimens (one specimen in original figure).

Original description. *Von der Localität 37 (Ras Turfa); einige wenige abgestorbene Exemplare.*

Die Muschelliege eingeschlossen in einem Kalkgehäuse, das aus 6–7 aneinander gegliederten Ringen besteht. Der vorderste ist kopfförmig oder kugelig aufgeblasen und am grössten, nach hinten zu verschmälern sich die Ringe, und der letzte, kleinste besitzt die Öffnung für den Austritt der Siphonen. Das Kalkgehäuse sitzt meist einer fremden Molluskenschale auf oder ist mit dem Gehäuse eines zweiten Individuums verklebt.

Die Muschel ist länglich oder nahezu viereckig, stark gewölbt und gedreht, ziemlich dickschalig, ventral weit geöffnet, so dass ein lang herzförmiger Hiatus entsteht, und hat ihre wenig eingedrehten Wirbel fast am vordersten Rande stehen, wo die Muschel am höchsten ist. Ober- und Unterrand sind mitunter parallel; erstere verläuft vom Wirbel nach hinten zuerst aufwärts, dann ein wenig concav, letzterer ist stark nach aussen gebogen und verläuft überdies etwas concav. Der Vorderrand fällt nahezu senkrecht vom Wirbel herab, der Hinterrand ist ein convexer, aufrecht stehender Bogen.

Die Schalen sind schmutzigweiss bis gelb und werden diagonal, d. i. vom Wirbel zum Unterrande, von einer

Depression durchzogen, wodurch sie sich hier abflachen und einander nähern. In der vorderen, stark gewölbten Hälfte der Schale, also vor der Depression, ist eine grobe Längsstreifung bemerkbar, in der hinteren und oberen Partie (hinter der Depression) treten aus der hier aufrecht stehenden Streifung in der Regel 5 mit dem Hinterrande gewissermassen concentrisch gestellte Wachsthumslinien auf. Dieselben sind auch im Inneren der Schale markirt und dürften mit der Articulation der äusseren Kalkhülle mehr minder correspondiren, d. h. gleichzeitig mit der Anlage eines neuen Ringes aussen dürfte innen ein Wachsthum der Schale stattfinden.

Im Inneren der Schale liegt hinter der Mitte ein grosser, runder Muskeleindruck, vorne am Vorderrande liegen ein paar ganz kleine, undeutliche Eindrücke unter einander.

Die Bezeichnung des Schlossrandes ist in der Regel gleich Null; nur ausnahmsweise tritt rechts ein zahnförmiger Stumpf auf, dem dann links eine kleine Grube entspricht.

[Tabelle mit Maßangaben!]

Reeve bildet in seiner Monographie der Gattung Gastrochaena einige Formen ab, die mit der vorliegenden als neu beschriebenen Art zweifellos grosse Ähnlichkeit besitzen. Es ist dies vor Allen die Sowerby'sche G. ovata von Panama. Während die fig. 16a bei Reeve zwei mit einander verklebte Kalkgehäuse darstellt, ganz ähnlich einem mir vorliegenden Doppalexemplar von Ras Turfa, sind in fig. 16b die vom Kalkgehäuse eingeschlossenen Schalen zur Abbildung gebracht. Die letzteren zeigen wohl ebenfalls die Merkmale der stark hervortretenden Anwachsstreifen in der hinteren Schalenpartie, doch kann ich mich zu einer Identificirung der Exemplare aus dem Rothen Meere mit G. ovata Sow. schon mit Rücksicht auf das Vorkommen der letzteren in Panama nicht entschliessen.

Die zweite bei Reeve abgebildete Form, welche ein ähnliches Kalkgehäuse besitzt, ist G. pupina Desh. In der bisherigen Literatur über die Mollusken des Rothen Meeres stösst man auf eine Angabe Mc. Andrew's, wonach im Suez-Golfe Teredo (Uperotis) pupina Desh. vorkommen soll; diese Bestimmung wird später von Cooke in »Guetera lagenula Gould (= cymbium Spengl.)« richtig gestellt.

Wenn man bedenkt, dass diese beiden Bestimmungen sich auf das gleiche Material beziehen, so fällt es schwer, sich vorzustellen, was für eine Gastrochaena-Form den beiden Herren eigentlich vorgelegen war; denn G. pupina Desh. scheint etwas ganz Anderes zu sein als G. lagenula Gould. Ist Mc. Andrew der Sache näher gekommen, so kann es wohl sein, dass die Exemplare aus dem Golfe von Suez denen ganz gleichgestaltet waren, die hier beschrieben wurden, d. h. dass sie von einem gegliederten Kalkgehäuse, ähnlich dem von Reeve, fig. 17, abgebildeten, eingeschlossen sind. Es würden dann die Angaben Mc. Andrew's und Cooke's die Literatur-Vorläufer zu der hier neu begründeten Art vorstellen und möglicherweise auch die (citirte) Deshayes'sche Beschreibung hieher zu ziehen sein als die blosser Bekanntmachung der äusseren Kalkhülle. Gastrochaena ovata Sow. aber ist jedenfalls die nächstverwandte Form dazu.

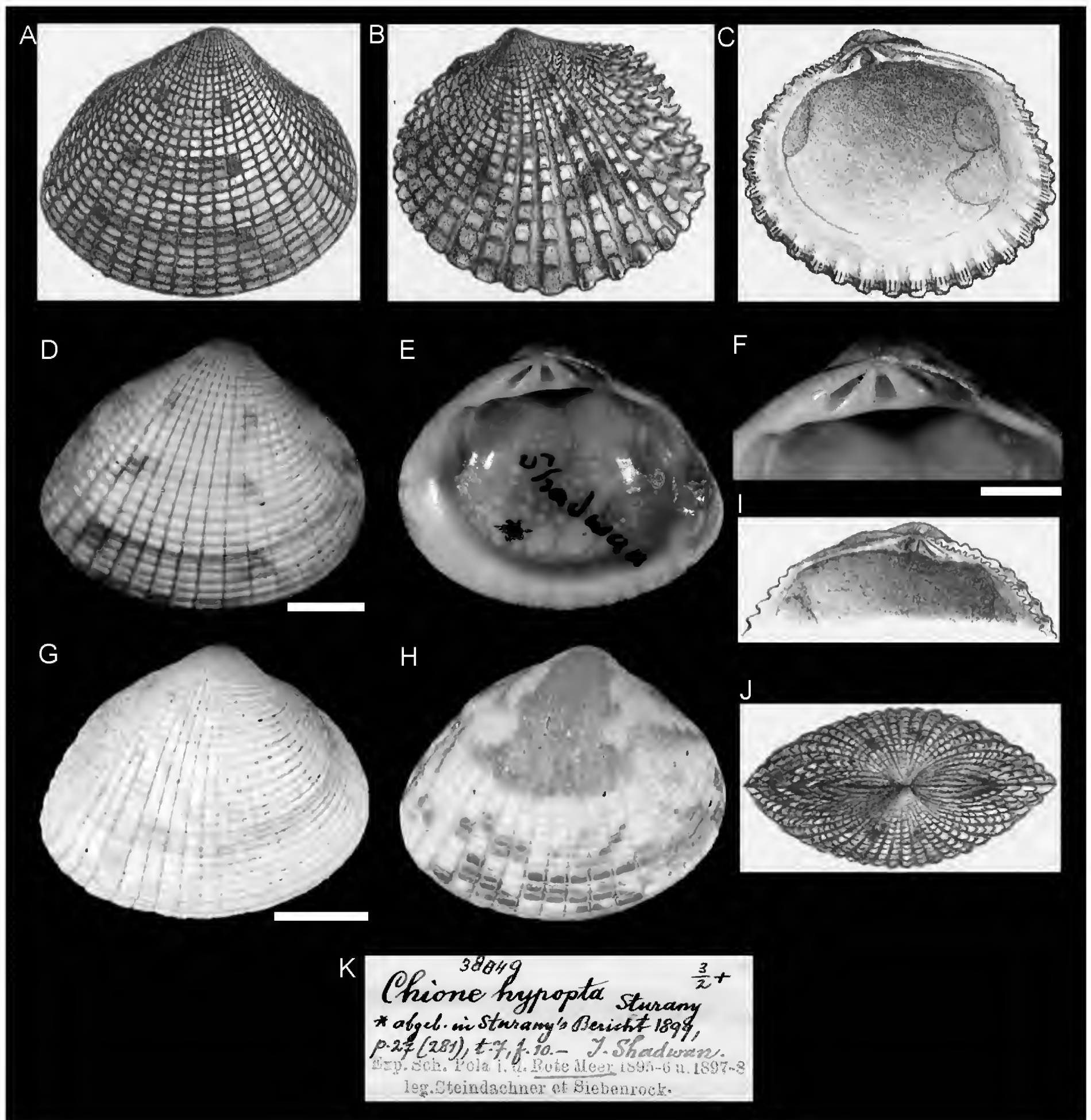


Figure 12. *Chione hypopta* Sturany, 1899, locality 16, Jazirat Shakir, Egypt, northern Red Sea. A–C, I, J Original figures. D–H Syntypes NHMW 38049: figured syntype right valve exterior (D), interior (E) and hinge detail (F); other syntypes, right valves exterior (G–H). K Original label. Scale bars: 6 mm (D); 5 mm (G); 3 mm (F).

Betreffs der Methode, nach der die Öffnung der festen Kalkhülle zu empfehlen ist, möchte ich mittheilen, dass es mit einer kräftigen Pinzette wohl möglich ist, vom untersten Ende, an der Siphon-Öffnung ansetzend, kleine Stücke soweit abzubröckeln, dass man die im Innern liegende Muschel (respective deren Schalen) erreichen kann. Verlässlicher ist es aber, über die Länge des ganzen Kalkgehäuses Salzsäure aufzustreichen und, diesen Vorgang mehrmals wiederholend, die Hülle endlich zu durchbrechen.

Translation. From locality 37 (Ras Turfa); a few dead specimens.

The bivalve lies enclosed in a calcified case, which consists of 6–7 connected segments. The foremost is the largest, head-shaped or globularly inflated, the rings become narrower towards the back, the last and smallest one has an aperture for the siphons.

The calcareous shell is most often attached to another mollusc shell or is agglutinated to the shell of another specimen. The bivalve is elongated or almost quadrangular, strongly curved and contorted, quite thick-shelled, gaping on the ventral side so that a long heart-shaped hiatus is formed, and has its little twisted umbos standing almost at the foremost edge, where the shell is thickest.

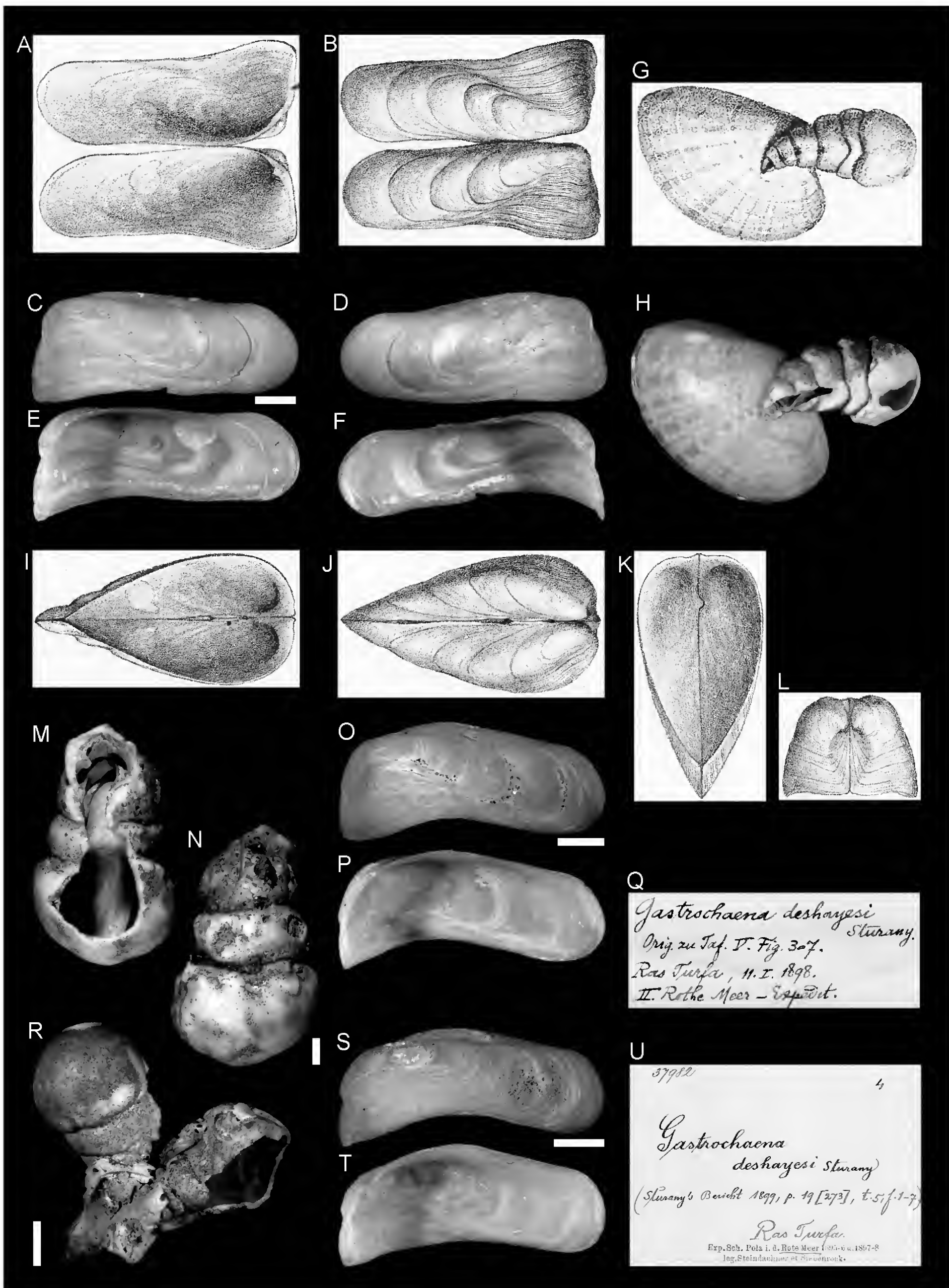


Figure 13. *Gastrochaena deshayesi* Sturany, 1899, locality 37, near Jazan, Saudi Arabia. **A, B, I–L** Original figures. **C–F, M, N** Figured syntype NHMW 37892/1: left valve exterior (**C**), interior (**F**); right valve exterior (**D**), interior (**E**); case (**M, N**). **H, O, P** Syntype NHMW 37892/2: left valve exterior (**O**), right valve interior (**P**) and case (**H**). **R–T** Syntype NHMW 37892/3: case (**R**), left valve exterior (**S**), right valve interior (**T**). **Q, U** Original labels. Scale bars: 2 mm (**C, N, O, S**), 4 mm (**R**).

The dorsal and ventral margins are occasionally parallel; the former runs from the umbo to the posterior end at first upwards, then with a little concavity, the latter is curved strongly outwards and then continues with a slight concavity. The anterior margin drops from the umbo almost vertically, the posterior margin has a convex curvature.

The valves are dirty-white to yellow and bear a depression diagonally, that is from the umbo to the ventral margin, where they are flattened and in contact. Anteriorly, in the strongly curved half of the shell, meaning in front of the depression, a rough longitudinal striation is noticeable; posteriorly on upper part (behind the depression), emerging from the striation there are usually five growth lines which are to some extent concentrically aligned with the posterior end.

Such growth lines are also visible in the inner part of the shell and correspond more or less to the segmentation of the calcified outer case, i.e. growth on the valves seems to take place simultaneously to the development of a new ring on the case.

On the inside of the shell located behind the mid-line there is a large, round muscle scar; at the anterior margin, there are a few very small, hardly noticeable scars one below one another.

The dentition at the hinge edge is usually non-existing; only as an exception there may be a tooth-shaped stub on the right side, and accordingly a small cavity on the left.

[Table with dimensions!]

Reeve displays some forms of the genus *Gastrochaena* in his monograph, which undoubtedly show great similarity to this newly described species and especially Sowerby's *G. ovata* from Panama.

While fig. 16a depicts two agglutinated calcified cases, similar to a double specimen available to me from Ras Turfa, fig. 16b presents the shells enclosed by the case. The latter also shows well the features of the strongly emerging growth lines in the posterior part of the shell; however, I cannot decide on the identification of the specimens from the Red Sea with *G. ovata*, considering the occurrence of the latest ones in Panama.

The second form depicted in Reeve, which has a similar calcified shell, is *G. pupina* Deshayes. Within the so far published literature on the molluscs of the Red Sea, one comes across a mentioning of Macandrew, according to which *Teredo (Uperotis) pupina* Deshayes occurs in the Gulf of Suez; this identification is later corrected by Cooke in "*Guetera lagenula*" Gould (= *cymbium* Spengler). Considering that these identifications refer to the same material, it is difficult to imagine which form of *Gastrochaena* was actually available to these two gentlemen, as *G. pupina* seems to be something completely different from *G. lagenula*. If Macandrew came closer to the truth, the specimens from the Gulf of Suez were possibly entirely similarly shaped to those described here, i.e. enclosed by a subdivided calcified case, similar to that depicted by Reeve, fig. 17. In that case, the descriptions by Macandrew and Cooke would present the precursors of the literature on the here newly established species

and possibly the (cited) Deshayes' description should be moved here instead of just the notification of the outer calcified case. *Gastrochaena ovata* Sowerby, however, is the nearest related form to it.

Concerning the method to open the strong calcified case, I would like to announce that, using strong forceps, it is well possible to break small pieces from the lower end, starting at the siphon aperture and reach the bivalve lying within. It is more reliable, however, to apply hydrochloric acid along the length of the entire shell and, repeating the procedure several times, finally breaking through.

Comments. This is a junior synonym of *Cucurbitula cymbium* (Spengler, 1783) (Oliver 1992).

Gastrochaena pexiphora Sturany, 1899

Figure 14

Sturany 1899: 274, plate VI, figures 1–3.

Type locality. Locality 31, Jeddah, Saudi Arabia, 22–20°N.

Type material. Lectotype: NHMW 37983: 1 specimen (right valve broken into two pieces and soft parts in alcohol), locality 31, designated by Nielsen (1986).

Additional material. NHMW 37374: 1 specimen, locality 27 or 31 (identified as *G. dentifera* Dufo, 1844 by C. Nielsen).

Original description. *Von den Localitäten 27 und 31; einige wenige Exemplare.*

Die Muschel ist langgestreckt, vorne am niedrigsten, in der Mitte oder rückwärts am höchsten, von schmutziggelber bis gelber Farbe, dickschalig, in ihrer ganzen Ausdehnung stark gewölbt, mit einer besonders auffallenden Verdickung am Hinterende, an der Bauchseite von vorne bis rückwärts offen, so dass ein eiförmiger Hiatus entsteht.

Die Anwachsstreifen sind in der vorderen Partie parallel dem Unterrande, in der hinteren Partie parallel dem Hinterrande angeordnet, erfahren also entsprechend der Diagonale der Schale eine Knickung; sie sind vorne stärker und dichter, rückwärts zarter und schwächer. Die Wirbelgegend ist frei von einer concentrischen Streifung, ebenso das verdickte Hinterende der Muschel.

Der Wirbel steht fast am vorderen Ende der Muschel; der niedrige, convexe Vorderrand ist über denselben nur ein wenig vorgezogen, der Oberrand verläuft nach oben und rückwärts in einem ziemlich starken Bogen, der Hinterrand fällt steil und schwach convex herab und bildet mit dem hinteren Oberrand sowohl wie mit dem Unterrande einen rechten Winkel. Der Unterrand ist stark nach aussen gewölbt, verläuft aber sonst ziemlich gerade.

Das äussere Ligament ist gelbbraun und reicht vom Wirbel bis kaum zur Hälfte der Muschel; die Schlossleiste ist mit einem deutlichen Zahne ausgestattet.

[Tabelle mit Maßangaben!]

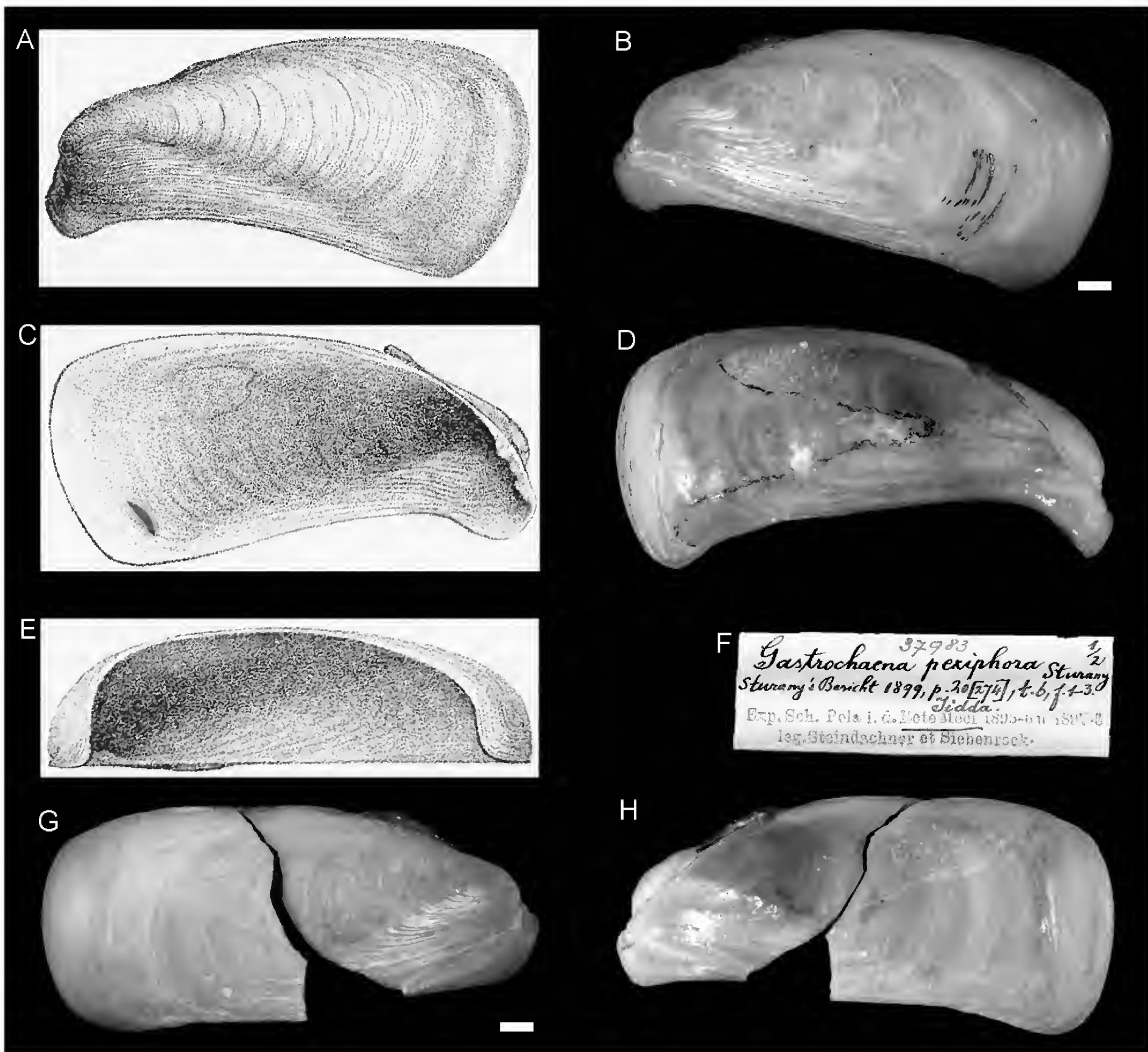


Figure 14. *Gastrochaena pexiphora* Sturany, 1899, locality 31, Jeddah, Saudi Arabia. **A, C, E** Original figures. **B, D, G, H** Lectotype NHMW 37983: left valve exterior (**B**), interior (**D**), right valve exterior (**G**), interior (**H**). **F** Original label. Scale bars: 1 mm.

Translation. From localities 27 and 31; a few specimens.

The shell is elongated, lowest at the front, highest in the centre and posteriorly, of dirty white to yellow colour, thick, strongly arched, with a particularly pronounced thickening at the posterior end, gaping on the ventral side from front to back so that an oval hiatus results.

The growth lines are parallel to the ventral margin in the front section, arranged parallel to the margin also posteriorly, thus appearing bent along the diagonal of the valve; they are stronger and denser at the front, finer and weaker at the back. The beak region is without concentric striation, as is the thickened posterior end.

The umbo is almost at the front end of the shell; the low, convex anterior margin is only slightly protruding, the dorsal margin runs upwards and backwards in a quite strong arc, the posterior margin falls steeply and is slightly convex, forming a right angle with the posterior dorsal and ventral margin. The ventral mar-

gin is strongly arched outwards, but otherwise runs quite straight.

The outer ligament is yellow-brown and extends from the umbo to barely half of the shell; the hinge margin has a distinct tooth.

***Gastrochaena weinkauffi* Sturany, 1899**

Figure 15

Sturany 1899: 275, plate V, figures 8–11.

Type locality. Locality 27, Berenice Troglodytica, Egypt, 24–22°N.

Type material. Lectotype: NHMW 37985, 1 specimen (in original figure, soft parts in alcohol), here designated. Paralectotypes: NHMW 37986: 2 specimens, locality 12.

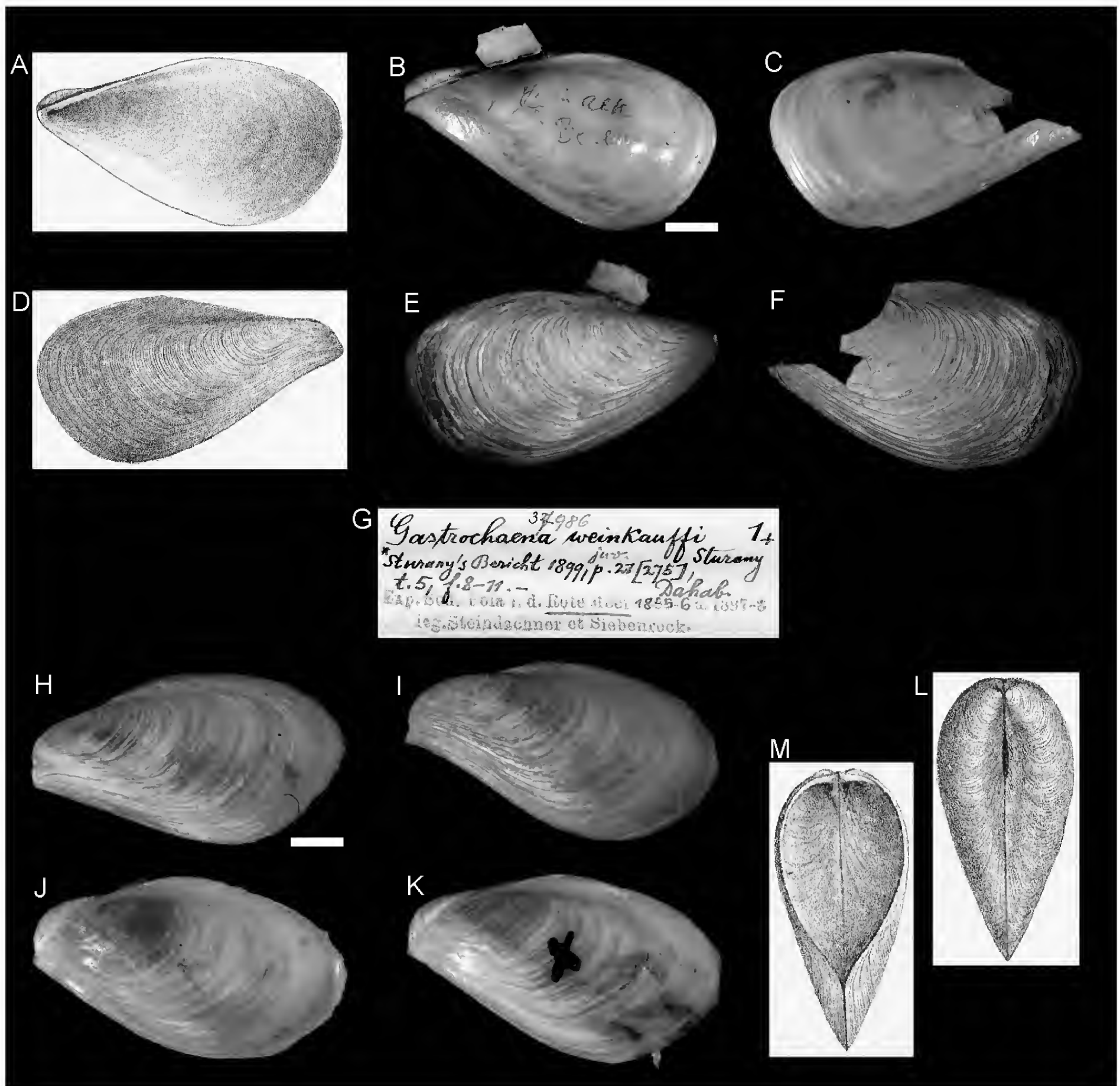


Figure 15. *Gastrochaena weinkauffi* Sturany, 1899, locality 27, Berenice Troglodytica, Egypt. **A, D, L, M** Original figures in Sturany, 1896. **B, C, E, F** Lectotype NHMW 37985: right valve interior (**B**), exterior (**E**), left valve interior (**C**), exterior (**F**). **H–K** Paralectotype NHMW 37986: left valve exterior (**H, I**), interior (**J, K**). **G** Original label. Scale bars: 5 mm (**B**), 1.5 mm (**H**).

Additional material. NHMW 37375, 7 specimens (in alcohol), mixture from localities 12, 25, 27, 32, 41 and 43 (identified as *G. gigantea* Deshayes, 1830 by K. Kleemann).

Original description. Von den Localitäten 12, 25, 27, 32, 41 und 43; ganz junge und erwachsene Exemplare in geringer Anzahl.

Die Muschel ist stark gewölbt, in der vorderen Partie ventral offen, vorne am niedrigsten, rückwärts am höchsten; sie ist im Allgemeinen von ovaler Gestalt und zeigt eine starke, dichtstehende Streifung im Sinne des Wachstums; die Streifen ziehen entlang dem Unterrande, dann im Bogen aufwärts, concentrisch mit dem runden Hinter-

rande, um schliesslich am Oberrande zu endigen. In der Jugend sind die Streifen zart und fein, im Alter kräftiger.

Die Wirbel sind ausgehöhlt und stehen nahezu an der vordersten Spitze der Schale; von einem ganz kurzen, niedrigen Vorderrand entspringt der schief nach unten und hinten gleitende, stark nach aussen gewölbte Unterrand, dem sich der halbkreisförmige Hinterrand als äussere Begrenzung der rückwärts mächtig entwickelten Schale anschliesst. Der hintere Oberrand verläuft gerade und geht ohne Winkelbildung in den Hinterrand über.

Das äussere Ligament ist hornbraun oder dunkel und reicht ungefähr bis zur Mitte der Schale. Von einer Bezähmung kann nicht die Rede sein, wohl aber von einer

Verdickung des Schlossrandes; nur bei jungen Exemplaren tritt der Rand etwas zahnartig hervor.

[Tabelle mit Maßangaben!]

Die hier beschriebene Art erinnert im Allgemeinen an *Gastr. dubia* Penn., ferner speziell das grosse Exemplar (von Berenice) an *G. grandis* Desh. Es ist möglich, dass wir es mit derselben Form zu thun haben, welche Weinkauff aus dem Rothen Meere vor sich gehabt hat, und die ihn veranlasste, die mediterrane *G. dubia* Penn, auch für dieses Gebiet anzugeben; ich habe aber von einer Identifizierung der mir vorliegenden Exemplare mit der Pennant'schen Art aus mehreren Gründen absehen müssen.

Vor Allem will ich die hier besprochene Art nicht mit *G. rüppellii* Desh. verwechselt wissen, die von den meisten späteren Autoren für ein Synonym der *G. dubia* Penn, angesehen wird, was mir im Hinblick auf die bisher publicirten Abbildungen derselben jedoch gewagt erscheint; ferner scheint mir die »neue« im Rothen Meer ziemlich weit verbreitete Art, respective Form, zu deren Beschreibung ich mich gewiss nicht leichten Herzens entschlossen habe, durch die Verleihung eines neuen Namens und durch eigene Abbildungen gebührend hervorgehoben zu sein und eine neuerliche Revision der Frage viel eher zu gestatten, als wenn sie blindlings mit *G. dubia* Penn, identificirt worden wäre.

Translation. From localities 12, 25, 27, 32, 41 and 43; very young and adult specimens in low numbers.

The species is strongly arched, gaping in the front ventral part, lowest in the front, highest in the back; overall it presents an oval shape and shows a strong and closely spaced striation according to shell growth; the striae proceed along the lower margin and further upwards, concentrically with the rounded posterior margin and finally ending at the upper margin. In juvenile specimens, the striae are delicate and subtle, growing more prominent with age.

The umbos are extended and positioned at the most anterior tip of the shell; arising from a very short and low anterior margin, the ventral margin is strongly arched outwards, with a semi-circular connection to the posterior margin of the posteriorly strong developed shell. The dorsal margin proceeds straight and passes into the posterior margin without angulation.

The outer hinge ligament is horn brown or dark and reaches approximately the middle of the shell. There is no dentition worth mentioning; however, there is an obvious thickening of the hinge margin; only in young specimens does the margin emerge in a slightly tooth-like manner.

[Table with dimensions]

The species described here mostly reminds of *Gastrochaena dubia* Pennant and also the large specimen (from Berenice) of *G. grandis* Deshayes. We might possibly be dealing with the same form, which Weinkauff had lying in front of him from the Red Sea and which made him report the Mediterranean *G. dubia* for this region. However, I had to refrain from identifying the specimen at hand with Pennant's species for a number of reasons. Most importantly, I

do not want the species described here to be confused with *G. rüppellii* Deshayes, which is viewed as a synonym of *G. dubia* Pennant by most later authors, which though seems risky to me, with regard to the publications to date. I certainly did not bring myself light-heartedly to the description of this "new" species, which is quite widespread in the Red Sea; however, a revision of this issue is much more likely if I granted a new name and separate illustrations than if it had been identified blindly with *G. dubia* Pennant.

Comments. This species has been placed in genus *Lamychaena* by Carter et al (2008). The original series contains two species: *G. weinkauffi* and seven specimens identified as *G. gigantea* (by K. Kleemann). Therefore, the specimen matching the original illustration and sizes is here designated as lectotype to stabilize the nomenclature.

Family Cuspidariidae Dall, 1886

Cuspidaria brachyrhynchus Sturany, 1899

Figure 16

Sturany 1899: 263–264, plate II, figures 1–6.

Original localities. Station 41, between Halayeb, Egypt, and Jeddah, Saudi Arabia, 22°4'N, 38°E, –2160 m. Station 48, off Yanbu' al Bahr, Saudi Arabia, 24°5'N, 37°45'E, –700 m. Station 106, south of Jeddah, Saudi Arabia, 21°2'N, 38°41.4'E, –805 m. Station 121, west of Al Qunfudhah, Saudi Arabia, 18°51.9'N, 39°5.4'E, –690 m. Station 128, Akik Seghir, Eritrea, 18°7.7'N, 39°11.2'E, –457 m. Station 130, west of Al Qunfudhah, Saudi Arabia, 19°17'N, 39°37'E, –439 m.

Type material. Lectotype: NHMW 84323: 1 specimen (in original figure), station 121, here designated. Paralecotypes: NHMW 84320: 1 specimen, station 41; NHMW 84321: 5 valves, station 48; NHMW 84322: 1 valve (fragment), station 106; NHMW 84325: 1 valve, station 130.

Original description. *Von den Stationen 41, 48, 106, 121, 128 und 130 (439–2160 m); einzelne Schalen oder Exemplare.*

Die Muschel ist mittelgross, schön gewölbt, dünnschalig, durchscheinend, kaum gestreift. Sie fällt vorne schief herab und endigt rückwärts unter starker Einschnürung der Schale mit einem kurzen schmalen Rostrum.

Der Wirbel liegt wenig vor der Mitte und überragt den Schlossrand. Der Übergang von Vorder- und Unterrand vollzieht sich nicht unter Winkelbildung, sondern im Bogen; rückwärts ist der Unterrand seicht eingebuchtet, da wo sich der schwach gestreifte Schnabel ansetzt und vom Wirbel herab mehr oder minder senkrecht die Depression zieht. Der hintere Oberrand ist ziemlich gerade (nicht concav) und bildet eine sanft herabgleitende obere Begrenzung des Rostrums.

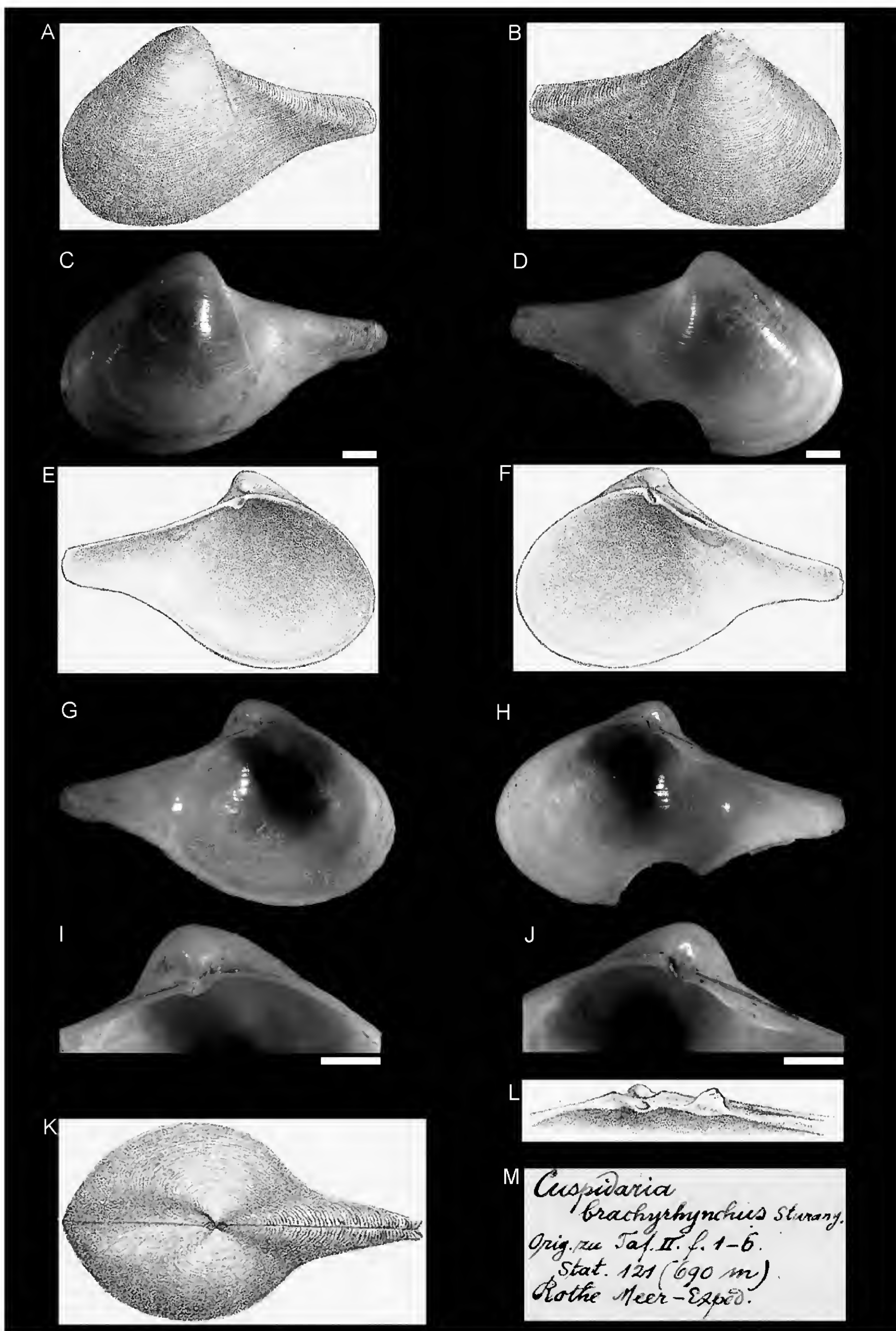


Figure 16. *Cuspidara brachyrhynchus* Sturany, 1899, Station 121, west of Al Qunfudhah, Saudi Arabia, 18°51.9'N, 39°5.4'E, -690 m. **A, B, E, F, K, L** Original figures. **C, D, G–J** Lectotype NHMW 84323: left valve exterior (**C**), interior (**G**), and hinge detail (**I**); right valve exterior (**D**), interior (**H**), and hinge detail (**J**). **M** Original label. Scale bars: 1 mm.

Im Schlosse der rechten Schale ist der hintere Zahn relativ gut entwickelt und vorstehend; die Ligamentgrube ist klein und schief nach hinten geneigt, eine Leistenbildung vor derselben kaum sichtbar. In der linken Schale sind bloss die Schlossränder beiderseits etwas vorgezogen und ist auch hier die Ligamentgrube klein und schief.

[Tabelle mit Maßangaben!]

Diese neue Art hat die Gestalt der vom »Investigator« an den »Andaman Islands« gedrehten Cuspidaria approximata E. A. Smith, mit der sie nahe verwandt zu sein scheint. Sie ist von ihr nur durch die geringere Grösse unterschieden (C. approximata misst 15:11:9½ mm) und durch den gänzlichen Mangel von Radialrippen.

Translation. From stations 41, 48, 106, 121, 128 and 130 (439–2160 m); single valves or specimens.

The bivalve is medium-sized, globose, thin, translucent, barely sculptured. It slopes obliquely anteriorly, and posteriorly it ends with a strong constriction into a short narrow rostrum.

The umbo is slightly in front of the mid-line and protrudes the hinge margin. The transition from the anterior to the ventral margin is not angulate, but curved; posteriorly, the ventral margin is shallowly indented; where the weakly striated rostrum is attached, there is a depression running almost vertically downwards from the umbo. The posterior dorsal margin is quite straight (not concave) and forms a gently descending upper line at the rostrum.

In the hinge of the right valve, the posterior tooth is relatively well developed and protruding; the ligament pit is small and tilted backwards, a ridge formation is barely visible in front of it. In the left valve, only the hinge margins are slightly protruding on both sides, the ligament pit is small and oblique.

[Table with dimensions]

This new species has the form of *Cuspidaria approximata* E.A. Smith from the “Investigator” cruise to the Andaman Islands, to which it seems closely related. It can be distinguished from it only by the smaller size (*C. approximata* measures 15: 11: 9½ mm) and by the complete lack of radial ribs.

Comments. The lot NHMW 84322 contained two fragments belonging to *C. steindachneri* which have been moved to lot NHMW 13016. We thus selected a lectotype, to unambiguously identify this species and stabilize the nomenclature. The lot NHMW 84324 (station 128) is missing at least since the time of cataloguing as reported in the collection inventory book written in 1987.

Cuspidaria dissociata Sturany, 1899

Figure 17

Sturany 1899: 262–263, plate II, figures 7–10.

Type locality. Station 106, south of Jeddah, Saudi Arabia, 21°2'N, 38°41.4'E, –805 m.

Type material. Lectotype: NHMW 84318: 1 right valve (in original figure), station 106, here designated. Paralectotypes: NHMW 84319: 2 valves, station 106.

Original description. *Einige wenige Schalen (halbe Exemplare) und Fragmente von Station 106 (805 m).*

Die Muschel ist mittelgross, mässig gewölbt, ziemlich festschalig, kurz und breit geschnabelt, aussen grob längsgestreift und schmutzig weiss, innen rein weiss, ziemlich glatt und glänzend.

Die Wirbel liegen in der vorderen Hälfte und überragen die Schlossleiste.

Indem die Muschel in einem ziemlich runden Bogen schief abfällt, geht der vordere Oberrand ohne Winkelbildung in den Vorderrand über, und dieser ist ebenso mit dem Unterrand verbunden, dessen hinterer Theil am Ursprunge des Schnabels, wo eine leichte Depression vom Wirbel herabläuft, schwach eingebuchtet ist. Der hintere Oberrand der Schale bildet die schief abfallende obere Begrenzung des kurzen und verhältnissmässig breiten Schnabels.

Das Schloss der rechten Schale ist durch einen relativ sehr mächtigen, horizontal gelegenen Zahn hinter dem Wirbel ausgezeichnet, während die linke Schale keine solche Differenzierung des Schlossrandes erkennen lässt; die Ligamentgruben sind in beiden Schalen gering entwickelt.

[Tabelle mit Maßangaben!]

Mit der vorhergehenden Art haben die eben betrachteten Exemplare die Streifung der Oberfläche, mit der folgenden die Grösse und die Gestalt gemeinsam. Mit C. brachyrhynchus m. war sie auf dem Grunde der Station 106 vergesellschaftet gefunden worden.

Translation. A few valves (single valves) and fragments from station 106 (805 m).

The bivalve is medium-sized, moderately globose, quite thick, short and broadly rostrate, roughly concentrically lirated and dirty white on the outside, pure white, rather smooth and shiny on the inside.

The beaks are located in the front half and protrude the hinge margin.

The valve profile slopes down in a round arc, the anterior dorsal margin merges with the anterior margin without any angle, and this is connected with the ventral margin, the posterior part of which is slightly indented at the origin of the beak, from where a slight depression runs down. The posterior dorsal valve margin forms an oblique slope at the short and relatively wide rostrum.

The hinge of the right valve is characterized by a relatively strong, horizontally located tooth behind the beak, while the left valve shows no such differentiation of the hinge edge; the ligament pits are poorly developed in both valves.

[Table with dimensions]

These specimens have in common with the previous species [*C. steindachneri*] the external sculpture, the size and shape. It has been found together with *C. brachyrhynchus* m. at the sea bottom of station 106.

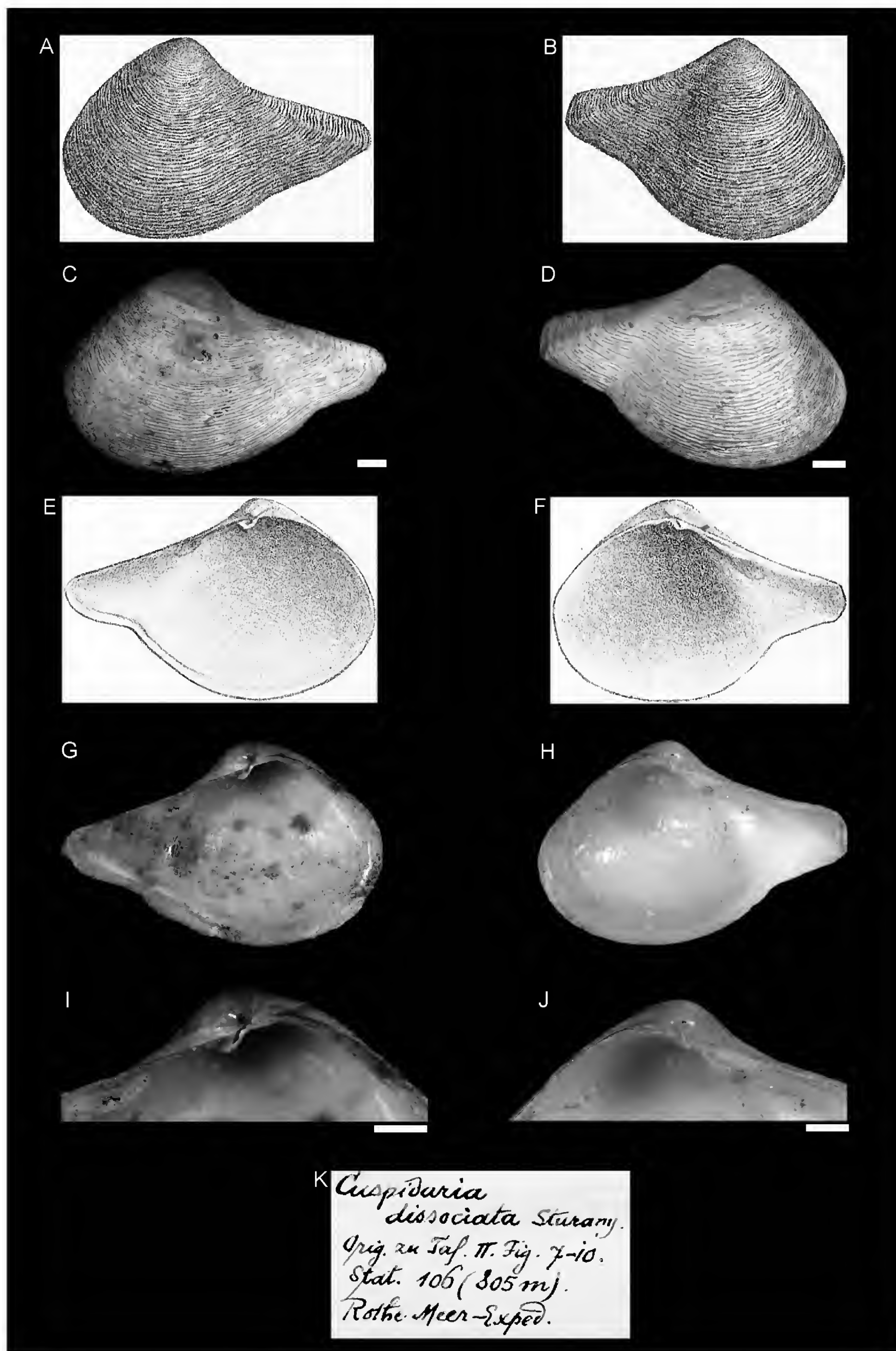


Figure 17. *Cuspidaria dissociata* Sturany, 1899, Station 106, south of Jeddah, Saudi Arabia, 21°2'N, 38°41.4'E, -805 m. **A, B, E–F** Original figures. **C, D, G–J** Lectotype NHMW 84318: left valve exterior (**C**), interior (**G**), and hinge detail (**I**); right valve exterior (**D**), interior (**H**), and hinge detail (**J**). **K** Original label. Scale bars: 1 mm.

Comments. The lot NHMW 84319 contained two fragments belonging to *C. steindachneri* which have been moved to lot NHMW 13017. We thus selected a lectotype to unambiguously identify this species and stabilize the nomenclature.

***Cuspidaria (Cardiomya) potti* Sturany, 1899**

Figure 18

Sturany 1899: 264–265, plate I, figures 10–16.

Original localities. Station 27, Red Sea, 23°41'N, 37°23'E, –747 m; Station 48, off Yanbu' al Bahr, Saudi Arabia, 24°5'N, 37°45'E, –700 m; Station 51, near Abu Ghusun, Egypt, 24°15'N, 35°37'E, –562 m; station 56, Mersa Dhiba, Egypt, 25°23'N, 34°55'E, –582 m.

Type material. Syntypes: NHMW 84326: 1 valve, station 27; NHMW 84327: 6 valves, station 48; NHMW 84328: 1 specimen (in original figure), station 51; NHMW 84329: 1 valve, station 56.

Original description. *Von den Stationen 27, 48, 51, 56 (562–747 m); einzelne ganze Exemplare oder Schalen.*

Die Muschel ist sehr klein, zart, milchweiss, durchscheinend, kurz geschnäbelt. Die Schalen sind mässig gewölbt, mit zarten, aber deutlichen Radialrippchen und dazwischen concentrischer Streifung ausgestattet. In der vorderen Schalenpartie stehen dicht aneinander Radialrippchen von verschiedener Stärke, nach hinten folgen auf sie in weiteren Abständen 3 kräftigere Rippen, zwischen denen allerdings mitunter noch einzelne schwächere eingeschlossen sind. Die concentrische Streifung ist vorne allenthalben deutlich ausgeprägt, wodurch sie zu einer schönen Gittersculptur führt, in der hinteren Partie ist sie hauptsächlich unten am Rande ausgebildet; frei davon bleibt meist die Partie zwischen Wirbel und Rostrum.

Der Oberrand ist gerade, horizontal und wird durch die ziemlich median gestellten Wirbel in 2 ungleiche Theile getrennt. Der kurze vordere Oberrand geht unter einem ziemlich weiten Winkel in den schief abfallenden Vorder- rand über, der hintere Oberrand bildet die obere Begrenzung des senkrecht abgestutzten Rostrums, das hier noch mit einigen schiefen (diagonalen) Rippchen geziert ist. Der Unterrand ist schön convex bis zum Grunde des Schnabels, wo dann der Rand concav wird. Hier, am Grunde des Schnabels und an den Endigungen der stärkeren Radialrippen ist entsprechend dem eingebuchteten Schalenrande auch die concentrische Streifung nach oben gewölbt. Im Inneren der Schale scheinen die Radialrippen der Aussen- seite durch und ist die Kerbung des Unterrandes (eine Folge der Radialsculptur!) besonders ins Auge fallend.

Bezüglich des Schlosses der rechten Schale ist zu sagen, dass unter dem Wirbel eine kleine Ligamentgrube liegt und darauf nach rückwärts ein kräftiger Zahn folgt, der, gerade hervorstehend, mit der Schale durch eine Stützlamelle verbunden ist. Der folgende hintere Ober-

rand ist verdickt und lamellenartig vorgezogen, unter demselben liegt eine schiefe, faltenartige Erhöhung oder Verdickung der Schalenwand als hintere Grenze zu dem scharfen und tiefen Muskeleindrucke. Der vordere Ober- rand ist gleichsam verdoppelt.

Das Schloss der linken Schale besitzt eine Ligament- grube, hinter welcher der Oberrand eine zahnartige Ver- dickung oder einen deutlich vorragenden Zahn trägt.

[Tabelle mit Maßangaben!]

Von verwandten Formen nenne ich die viel grössere und mit 4–5 Hauptradialen ausgezeichnete Cuspidaria (Cardiomya) alcocki Smith, welche der »Investigator« in der »Bay of Bengal« gedredet hat, ferner die erythräi- sche Art Neaera (Cardiomya) pulchella A. Ad., die aber ebenfalls grösser ist und einen convexen Oberrand besitzt.

Die neue Art habe ich zu Ehren des Commandanten der »Pola«, des Herrn Linienschiffs-Capitäns Paul Edlen von Pott, benannt.

Translation. From stations 27, 48, 51, 56 (562–747 m); some whole specimens or valves.

The bivalve is very small, fragile, milky white, transparent, with a short rostrum. The valves are slightly sculptured, with fine but distinct radial ribs and concentric striae in between.

On the anterior part of the shell, there are radial ribs of different strengths arranged close to each other. Three strong ribs are following with broader interspaces towards the posterior; between them, however, single more weakly developed ones may be noticed. The concentric sculpture is distinctly developed everywhere at the front and leads to a beautiful reticulate sculpture; in the posterior part it is mainly developed near the margin; the part between the umbo and the rostrum has none in most cases.

The dorsal margin is straight, horizontal and is divided into two uneven parts by the umbo, which is located rather medially. The short dorsal margin merges into the declining anterior margin within quite a wide angle; the posterior dorsal margin forms the upper boundary of the vertically truncated rostrum, which is decorated here with several uneven (diagonal) ribs. The ventral margin is beautifully convex until the base of the rostrum, where the margin turns concave. Here, at the base of the rostrum and at the endings of the stronger radial ribs, the sculpture is curved upwards, analogous to the indented shell edge. On the inside of the valve, the radial ribs of the outside are visible in transparency and the sculpture of the ventral margin (a consequence of the radial sculpture!) is especially remarkable.

Concerning the hinge on the right valve, it is worth mentioning that beneath the umbo there is a small ligament cavity and thereupon towards the back a strong tooth follows, which, sticking out vertically, is connected to the shell by a supporting lamella. The following posterior dorsal margin is thickened and the lamellar sculpture continues to the front; beneath it, an oblique wrinkle-like elevation or thickening of the shell wall lies as the posterior margin to the sharp and deep muscle scars. The anterior dorsal margin is thickened.

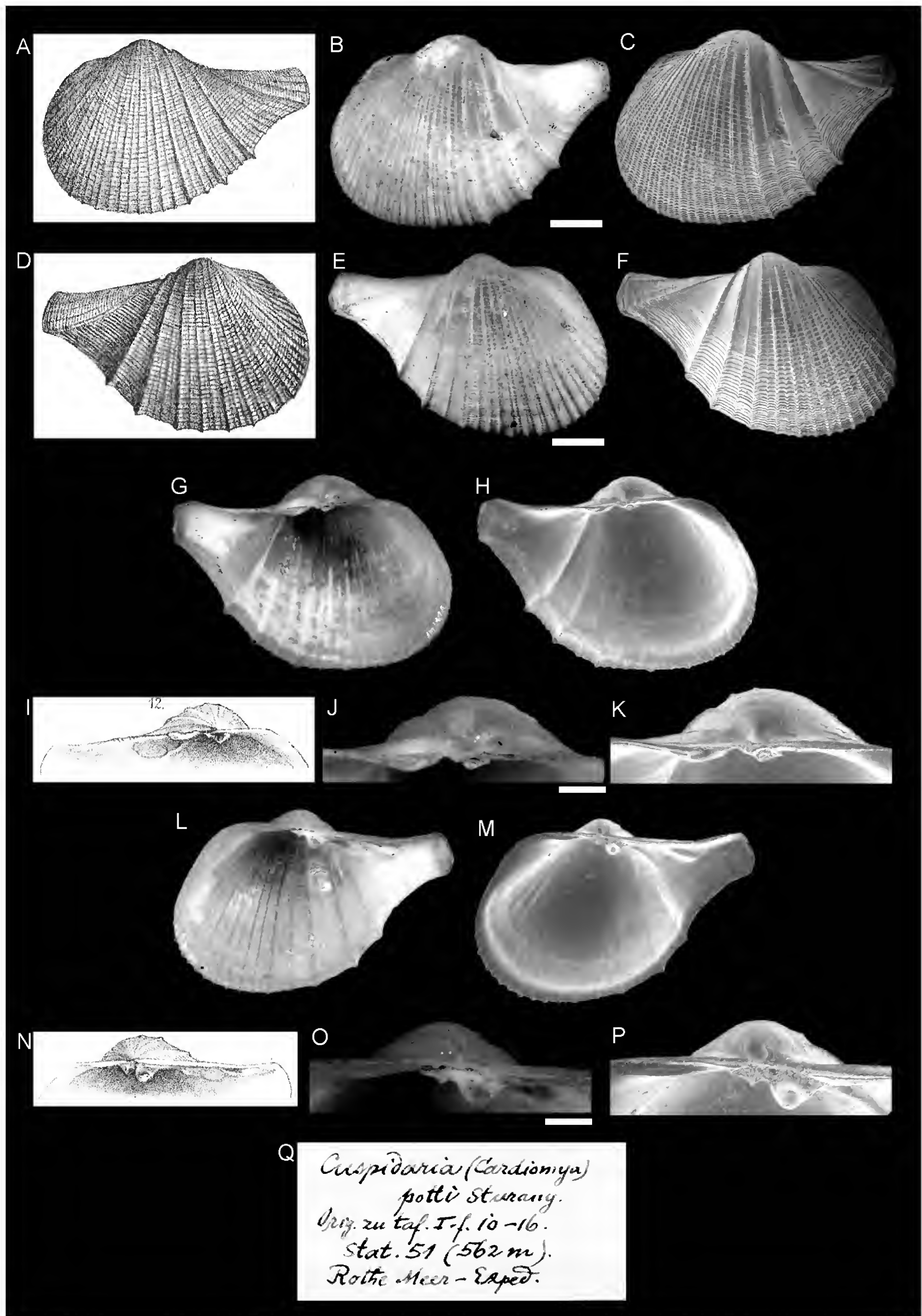


Figure 18. *Cuspidaria potti* Sturany, 1899, Station 51, near Abu Ghusun, Egypt, -562 m. A, D, I, N Original figures. B, C, E-H, J-M, O, P Figured syntype NHMW 84328: left valve exterior (B, C), interior (G, H) and hinge detail (J, K). Right valve exterior (E, F), interior (L, M), and hinge detail (O, P). Q Original label. Scale bars: 1 mm (B, E); 0.5 mm (J, O).

The hinge of the left valve features a ligament cavity, behind which the dorsal margin bears a tooth-like thickening without a clearly protruding tooth.

[Table with dimensions]

Of the related forms I mention the much larger and equipped with 4–5 main radials *Cuspidaria* (*Cardiomya*) *alcocki* Smith, which was dredged by the “Investigator” in the Bay of Bengal, moreover the Erythraean species *Neaera* (*Cardiomya*) *pulchella* A. Adams, which is also larger and has a convex upper edge.

I named the new species in honour of the commander of the “Pola”, captain Paul Edlen von Pott.

Comments. It is considered a junior synonym of *Cardiomya alcocki* (E.A. Smith, 1894) (Poutiers and Bernard 1995), which bears, however, a stronger sculpture and a less reticulated aspect.

Cuspidaria steindachneri Sturany, 1899

Figure 19

Sturany 1899: 261–262, plate I, figures 5–9.

Original localities. Station 9, south of Yanbu’ al Bahr, Saudi Arabia, 23°21'N, 37°37'E, –791 m; Station 47, Yanbu’ al Bahr, Saudi Arabia, 23°41'N, 38°9'E, –610 m; station 48, off Yanbu’ al Bahr, Saudi Arabia, 24°5'N, 37°45'E, –700 m; station 61, near Al Hasani, Saudi Arabia, 24°35'N, 36°51'E, –828 m; station 72, Shadwan Island, Egypt, 27°25'N, 34°30'E, –1082 m; station 76, south of Sanafir Island, 27°43'N, 34°47'E, –900 m; station 81, close to Ras Abu Massahrib, Noman Island, Saudi Arabia, 26°34'N, 35°33'E, –825 m; station 94, Nuweiba, Gulf of Aqaba, Egypt, 28°58.6'N, 34°43.7'E, –314 m; station 96, northern part of the Gulf of Aqaba, 29°13.5'N, 34°47.8'E, –350 m; station 109, Jeddah, Saudi Arabia, 21°19'N, 37°39'E, –890 m; station 121, west of Al Qunfudhah, Saudi Arabia, 18°51.9'N, 39°5.4'E, –690 m; station 138, east of Akik Seghir, Eritrea, 18°3'N, 40°14.7'E, –1308 m; station 145, east of Dahlak Island, Eritrea, 16°2.6'N, 41°13.5'E, –800 m; station 156, north of Jeddah, Saudi Arabia, 22°51'N, 38°2'E, –712 m; station 170, Noman Island, Saudi Arabia, 27°0.2'N, 35°17.6'E, –690 m; station 176, El Quseir, Egypt, 25°57'N, 34°36.1'E, –612 m.

Type material. Syntypes: NHMW 84311: 1 specimen (in original figure), station 121; NHMW 84301: 5 valves, station 9; NHMW 84302: 1 valve, station 47; NHMW 84303: 1 valve, station 48; NHMW 84304: 1 valve, station 61; NHMW 84305: 1 specimen, station 72; NHMW 84306: 3 valves, station 76; NHMW 84307: 2 valves, station 81; NHMW 84308: 1 valve, station 94; NHMW 84309: 2 valves (belonging to the same specimen?), station 96; NHMW 84310: 1 specimen, station 109; NHMW 84312: 3 valves, station 138; NHMW 84313: 4 valves, station 145; NHMW 84314: 2 valves, station 156; NHMW 84315: 1 valve, station 170; NHMW 84316: 2

valves (belonging to the same specimen?), station 176; NHMW 84317: 3 valves (2 fragments), station 91.

Additional material. NHMW 13016: 1 valve (fragment ex NHMW 84322, *C. brachyrhynchus*, separated by Janssen 1994), station 106; NHMW 13017: 2 valves (fragments ex NHMW 84319, *C. dissociata*, separated by Janssen 1994), station 106.

Original description. Von den Stationen 9, 47, 48, 31, 72, 76, 81, 94, 96, 109, 121, 138, 145, 156, 170, 176 (314–1308 m).

Die Muschel ist verhältnissmässig gross und dickschalig, aufgeblasen, aussen schmutzigweiss, dicht concentrisch gestreift, innen rein weiss, glatt und glänzend. Sie ist mit einem langen, relativ schmalen (bloss circa 2½ mm breiten) Rostrum ausgestattet, dessen Ränder parallel zu einander verlaufen und dessen Ende schwach gerundet abgestutzt ist.

Der Wirbel ist nach rückwärts und innen gebogen und liegt, da der Schnabel der Muschel so mächtig entwickelt ist, in der vorderen Hälfte der Schale. Vorne fällt die Muschel in gerundetem Bogen in den Vorderrand ab, der sich ebenso in den Unterrand fortsetzt, rückwärts tritt dieselbe zu dem ungefähr in der Mitte ihrer Gesammthöhe hervortretenden Schnabel in einem concaven Bogen. Auch der Unterrand buchtet sich rückwärts, am Ursprünge des Rostrums ein wenig ein. Vom Wirbel läuft schief herab zu dieser letzterwähnten Einbuchtung eine Depression, ferner in der Diagonale des Schnabels ein ebenfalls vom Wirbel herabziehender Wulst. Dieser trennt den noch concentrisch (längs-) gestreiften unteren Theil des Schnabels von seinem senk recht gestreiften oberen Theil. Der Schlossrand ist von dem Wirbel bedeutend überragt; ungefähr parallel zu seiner hinteren Partie verläuft eine am Wirbel entspringende Linie, wodurch ein langes, schmales Feld entsteht, das überdies etwas vertieft liegt (area). Die Bezeichnung der rechten Schale besteht aus 2 leistenförmigen Seitenzähnen, von denen aber nur der hintere gut entwickelt ist und deutlich hervorrägt, während der vordere sozusagen nur eine Verdoppelung des vorderen Oberrandes darstellt. Zwischen den beiden liegt schief nach hinten gekehrt die Ligamentgrube, und dem hinteren Zahne folgt ein starker Muskeleindruck. Die linke Schale besitzt ausser der Ligamentgrube keine eigentlichen Schlossbestandtheile; der hintere Oberrand ist nur zuweilen leistenförmig verlängert und verräth bloss durch eine undeutliche Vertiefung die Stelle, wo der Zahn der rechten Schale einlenkt.

Die Proportionen von Länge, Höhe und Dicke der Schalen wechseln wie folgt:

[Tabelle mit Maßangaben]

Die neue Art ist verwandt mit der vom »Investigator« an der Westküste von Indien erbeuteten Cusp. macrorhynchus E. Smith. Der Schnabel der letzteren entspringt aber in horizontaler Verlängerung des hinteren Oberrandes, also bedeutend höher als bei der eben besprochenen Art aus den Tiefen des Rothen Meeres, so dass auch der Sinus an der Basis des Schnabels grösser erscheint.

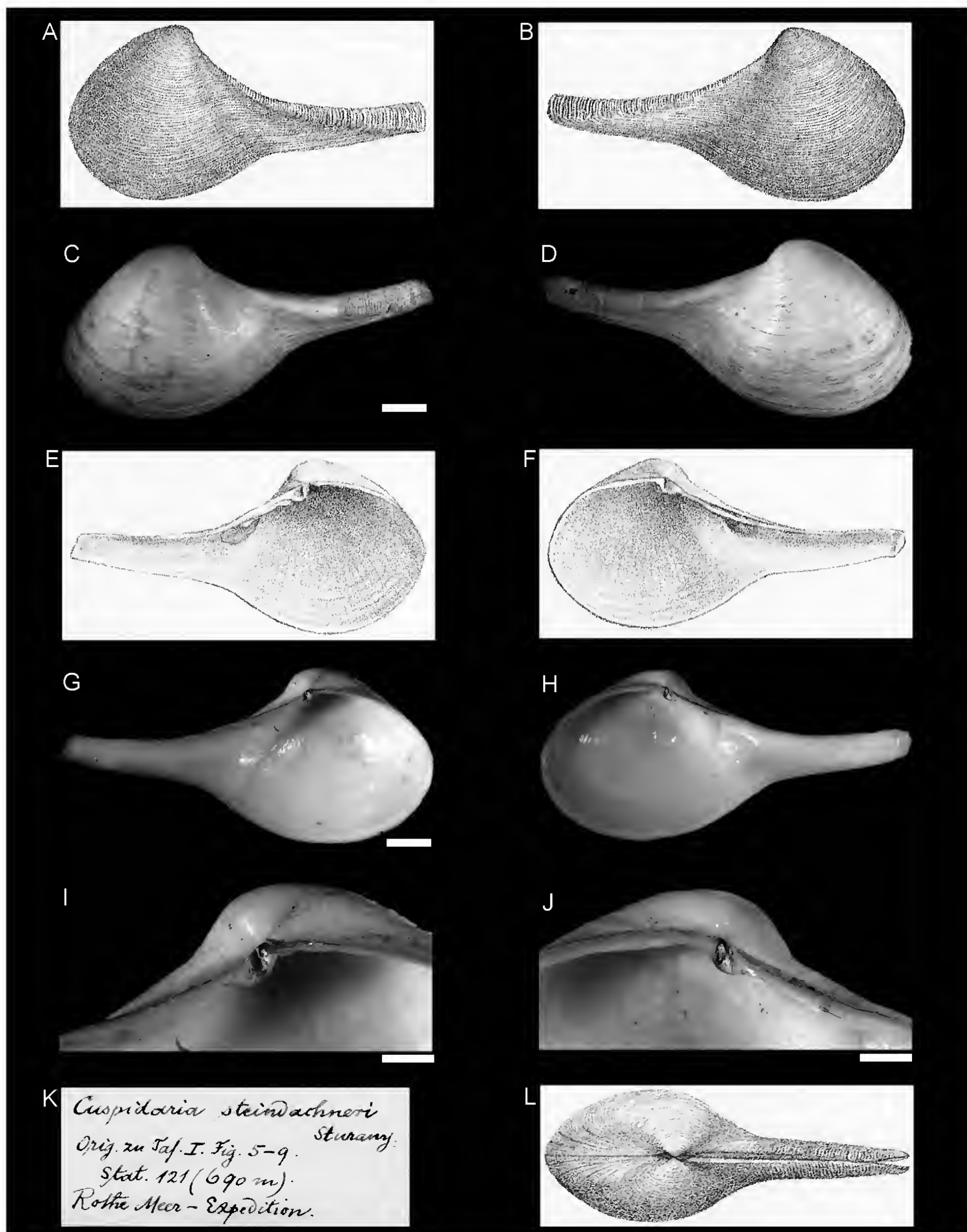


Figure 19. *Cuspidaria steindachneri* Sturany, 1899, station 121, west of Al Qunfudhah, Saudi Arabia, -690 m. **A, B, E, F, L** Original figures. **C, D, G–J** Figured syntype NHMW 84311: left valve exterior (**C**), interior (**G**) and hinge detail (**I**). Right valve exterior (**D**), interior (**H**) and hinge detail (**J**). **K** Original label. Scale bars: 3 mm (**C, G**); 1 mm (**I–J**).

Translation. From stations 9, 47, 48, 31, 72, 76, 81, 94, 96, 109, 121, 138, 145, 156, 170, 176 (314–1308 m).

The shell is proportionally large and thick-shelled, globose, dirty-white on the outside, densely concentrically

striate, pure white on the inside, smooth and shiny. The rostrum is long and relatively slender (only ca 2½ mm wide), its margins run parallel to each other and its end is truncated and slightly rounded.

The umbo is curved backwards and inwards and lies in the front half of the shell, as the rostrum is so strongly developed. Anteriorly, the valve margin drops down in a rounded curve towards the front margin, which continues into the ventral margin, the same proceeds backwards in a concave arc towards the rostrum, which starts approximately in the middle of the total height. The ventral margin is also indented a little in the back at the base of the rostrum. From the umbo, a depression runs obliquely towards this mentioned indentation; furthermore, on the diagonal of the rostrum there is an also downwards oriented keel, which separates the concentrically (longitudinally) sculptured lower part of the rostrum from its vertically sculptured upper part. The hinge margin is considerably protruded by the umbo; approximately parallel to its posterior part originating at the umbo there is a line, which creates a long, narrow deepened area. The dentition of the right valve consists of two ridge-like lateral teeth, only the posterior of which is well developed and clearly emerging, while the anterior represents almost a doubling of the anterior upper margin. Between the two, there is the ligament pit and after the posterior tooth there is a strong muscle scar. The left valve has no real hinge parts, with the exception of the ligament pit; the posterior upper margin is sometimes elongated and ridge-shaped and an indistinct deepening hints at the indentation of the tooth in the right valve.

The proportions of length, height, and thickness of the shell change as follows:

[Table with dimensions]

The new species is related to the *Cuspidaria macro-rhynchus* E.A. Smith captured by the “Investigator” on the west coast of India. However, the beak of the latter originates as a horizontal extension of the posterior dorsal rostrum, therefore remarkably higher than in the just described species from the depths of the Red Sea, so that also the sinus at the base appears larger.

***Pseudoneaera thaumasia* Sturany, 1899**

Figure 20

Sturany 1899: 265–266, plate II, figures 11–16.

Original localities. Station 48, off Yanbu’ al Bahr, Saudi Arabia, 24°5'N, 37°45'E, –700 m; station 72, Shadwan Island, Egypt, 27°25'N, 34°30'E, –1082 m; station 121, west of Al Qunfudhah, Saudi Arabia, 18°51.9'N, 39°5.4'E, –690 m; station 130, west of Al Qunfudhah, Saudi Arabia, 19°17'N, 39°37'E, –439 m.

Type material. Syntypes: NHMW 84330, 1 specimen (in original figure), station 48; NHMW 84331, 2 valves, station 48; NHMW 84332, 1 valve, station 72; NHMW 84333, 1 specimen, station 121; NHMW 84334, 1 valve, station 130.

Original description. *Von den Stationen 48, 72, 121 und 130 (439–1082 m); meist nur einzelne Schalen.*

Die Muschel ist milchweiss, durchscheinend, gewölbt und besitzt ein schwach schnabelförmig vorgezogenes Hinterende, an dem sie etwas klafft. Die Wirbel sind aufgeblasen, kehren sich mit ihren Spitzen zu einander nach innen und hinten und überragen den Schlossrand. Ihre Stellung ist ungefähr in die Mitte der Muschel verlegt. Ein eigentlicher Oberrand fehlt, indem die Muschel nach vorne sowohl wie rückwärts schief abfällt. Die vordere Begrenzung ist im Umriss ein schwach convexer, die rückwärtige ein ziemlich gerader, die untere ein stark convexer Rand; die ersteren bilden miteinander einen Winkel von mehr als 90°, der Unterrand buchtet sich rückwärts ähnlich wie bei den echten Cuspidarien seicht ein, wodurch unter gleichzeitiger Abflachung der hinteren Schalenpartie eine geringe Schnabelbildung entsteht. An der hinteren Abdachung der Muschel ist eine schmale, flach ausgebreitete, etwas längsgestreifte Partie durch einen beiderseits von der Wirbelgend zum Hinterende verlaufenden Kiel abgegrenzt (area). Von einer Längsstreifung der Oberfläche ist gewöhnlich nur rückwärts etwas wahrzunehmen; noch seltener, und zwar nur bei durchfallendem Lichte, gewahrt man eine äusserst zarte und unregelmässige Radialstreifung.

Das Schloss der rechten Schale besteht aus einer ganz seichten, undeutlichen Grube für das innere Ligament und zwei divergirenden Zähnen, die an ihren nach dem Inneren der Muschel gekehrten Enden frei stehen und ungleich lang sind. Sie entspringen von den Oberrändern und sind, scharf davon abstehend, durch eine kurze und zarte Brücke mit denselben verbunden. Betrachtet man die rechte Schale von oben, so sieht man vor dem vorgezogenen Wirbel einen kurzen Stumpf, hinter demselben einen längeren schief abstehen; es sind die beiden vorerwähnten Zähne.

In der linken Schale gewahrt man unter dem Wirbel eine schief nach unten und hinten gestellte Ligamentgrube und vor dieser ein schwaches, kaum hervortretendes Zähnchen.

Die Muskeleindrücke der Schale erinnern an die Verhältnisse bei den Cuspidarien.

[Tabelle mit Maßangaben!]

Als Commentar zu den eben angeführten Beispielen der Proportionen sei erwähnt, dass das Exemplar von Station 121 relativ schmal, also weniger aufgeblasen ist; dass bei dem grösseren Exemplare von Station 48 eine concentrische Streifung deutlicher ausgeprägt ist, als die Regel wäre, und auch die Schnabelbildung mehr ins Auge fällt; und dass dies endlich auch bei dem Exemplare von Station 130, dem grössten der vorliegenden, der Fall ist. Bei dem letzteren ist überdies die erwähnte Bildung einer hinteren, horizontalen Partie, die kantig begrenzt wird, besonders hervorzuheben, sowie die zarte und unregelmässige, nur bei durchfallendem Lichte wahrnehmbare Radialstreifung.

Die neue Art, welche hier als der Typus einer neuen Gattung aufgestellt wird, sieht von aussen der mediterranen Neaera abbreviata Forbes vollständig gleich, hat aber – wie zur Genüge hervorgehoben wurde – ein gut verschiedenes Schloss. Wenn ich schliesslich mit einigen Worten noch die Gattung Montacuta streife, so geschieht es nur, um die grosse Ähnlichkeit der M. acuminata Smith mit Pseudoneaera thaumasia m. in der äusseren Gestalt hervorzuheben.

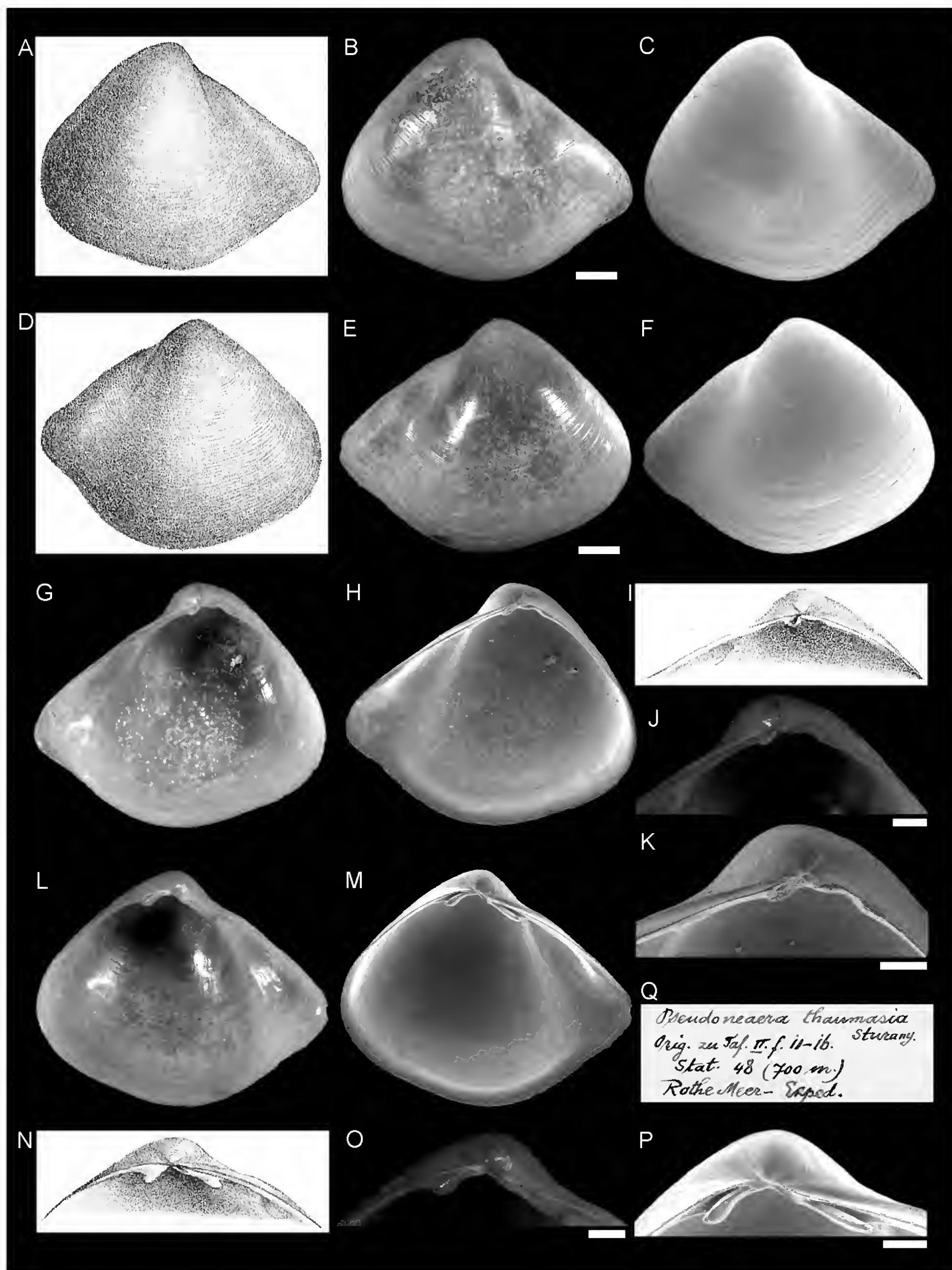


Figure 20. *Pseudoneaera thaumasia* Sturany, 1899, Station 48, off Yanbu' al Bahr, Saudi Arabia, -700 m. **A, D, I, N** Original figures. **B, C, E-H, J-M, O, P** Figured syntype NHMW 84330: left valve exterior (**B, C**), interior (**G, H**) and hinge detail (**J, K**); right valve exterior (**E, F**), interior (**L, M**) and hinge detail (**O, P**). **Q** Original label. Scale bars: 1 mm (**B, E**); 0.5 mm (**J, K, O-P**).

Translation. From stations 48, 72, 121 and 130 (439–1082 m); mostly only single valves.

This bivalve is milky-white, transparent, curved and possesses a poorly elongated posterior end, which it is slightly gaping. The umbos are inflated, turned towards each other and backwards at their tips, and protrude from the hinge margin. Their position is approximately in the middle of the shell. An actual dorsal margin is missing, as the valve drops down obliquely in the front and back. The anterior margin is weakly convex in its contour, the posterior has a rather straight margin, the ventral a strongly convex margin. The first two together form an angle of more than 90°, the lower margin shallowly indents backwards, as in true *Cuspidaria*, and forms a short rostrum under a flattening of the posterior shell part. Posteriorly, there is a narrow, flat, faintly longitudinally striated area confined by a keel running at both sides from the umbo region towards the back. The longitudinal striation at the surface is normally noticeable only posteriorly; even less frequently, and only in transparency, a very faint and uneven radial striation is visible. The hinge of the right valve consists of a very shallow, indistinct groove for the inner ligament and two diverging teeth which stand free at their inwards-turned endings and are of different length. They originate at the upper margin, stick out sharply, and are connected to it by a short fragile bridge. Observing the right valve from above, one can see a short stump in front of the elongated umbo, behind which a longer one stands out lopsided; those are the previously mentioned teeth. In the left valve beneath the umbo, there is a ligament pit tilted downwards and backwards and in front of it a weak, barely emerging tooth.

The muscle scars of the shell indicate a relationship with *Cuspidaria*.

[Table with dimensions]

It should be mentioned, as a comment on the proportions of the examples just mentioned, that the specimen from station 121 is rather slim, meaning less inflated; that a concentric striation in the specimen from station 48 is more prominent than normal, and also the rostrum is stronger; and that this is finally also the case in the specimen from station 130, the largest one. Concerning this last one, it should be especially underlined the mentioned formation of a posterior, horizontal rostrum, which is delimited by an angle, just like the slender and uneven radial striation, which is visible only in transparency.

The new species, which is described here as the type species of a new genus, externally resembles completely the Mediterranean *Neaera abbreviata* Forbes, however possesses—as emphasized enough—a well distinguished hinge. If I finally consider the genus *Montacuta* with a few words, this is only to emphasize the great external similarity of *M. acuminata* Smith with *Pseudoneaera thaumasia* m.

Comments. *Pseudoneaera* is a new genus introduced by Sturany (1899).

Family Poromyidae Dall, 1886

Lyonsia intracta Sturany, 1899

Figure 21

Sturany 1899: 261, plate III, figures 7–9.

Original localities. Station 72, Shadwan Island, Egypt, 27°25'N, 34°30'E, –1082 m; station 114, between Suakin, Sudan, and Al Lith, Saudi Arabia, 19°38'N, 37°55'E, –535 m; station 121, west of Al Qunfudhah, Saudi Arabia, 18°51.9'N, 39°5.4'E, –690 m; station 130, west of Al Qunfudhah, Saudi Arabia, 19°17'N, 39°37'E, –439 m.

Type material. Syntypes: NHMW 84297: 10 fragments of three valves (3 umbos can be recognized), station 72; NHMW 34298: 2 valves (belonging to the same specimen?, left valve fragmented into 5 pieces), station 114; NHMW 84299: 2 valves (belonging to the same specimen?, in original figure), station 121; NHMW 84300: 1 valve, station 130.

Original description. *Von den Stationen 72, 114, 121 und 130 (535–1082 m); meist nur einzelne Schalen oder Bruchstücke.*

Die Muschel ist mittelgross, mässig gewölbt, gerundet oval, am Hinterende ein wenig klaffend. Die zarten, ungleichseitigen Schalen sind durchscheinend, glasig und spröde, besitzen aussen und innen einen schönen Perlmutterglanz und sind aussen dicht mit Punkten besetzt, die in zahlreichen, dichtstehenden Radialreihen angeordnet sind und der ganzen Muschel eine rauhe Oberfläche verleihen. Von querstehenden Anwachsstreifen sind nur einige wenige, ganz zarte sichtbar.

Die Wirbel liegen in der vorderen Schalenpartie und kehren ihre Spitzen nach innen und vorne, überragen also den Schlossrand. Schief und im Bogen vom Wirbel nach vorne abfallend, zeigt die Muschel am Übergange in den schön convexen Unterrand keinen Winkel, während am Übergange des schief abfallenden hinteren Oberrandes in den abgestutzten Hinterrand ein stumpfer Winkel zu verzeichnen ist. An jener Stelle ist das Hinterende der Muschel schwach abgeflacht und vorgezogen, und über diese Partie zieht ein äusserst schwach ausgeprägter Radialstreifen vom Wirbel herab zum Übergange von Hinter- und Unterrand, indem gewissermassen eine Radialreihe von Punkten zu einer geschlossenen Linie vereinigt ist.

Das Schloss ist zahnlos, besitzt aber ein Ligament, das – im Gegensatz zu den Merkmalen der Gattung Lyonsia – nicht unter dem Rande, das heisst im Innern der Muschel gelegen ist, sondern noch am Rande selbst liegt, so dass es im zusammengeklappten Zustande der Muschel noch von aussen zu sehen ist. Für die Aufnahme oder Lagerung des Ligaments ist eine seichte Grube direct unter dem Wirbel jeder Schale bestimmt, aus der sich bei einiger Vorsicht jenes lichtgelb gefärbte Ligament herausheben lässt; sie liegt in dem Schalenrande, der an der betreffenden Stelle (direct unter

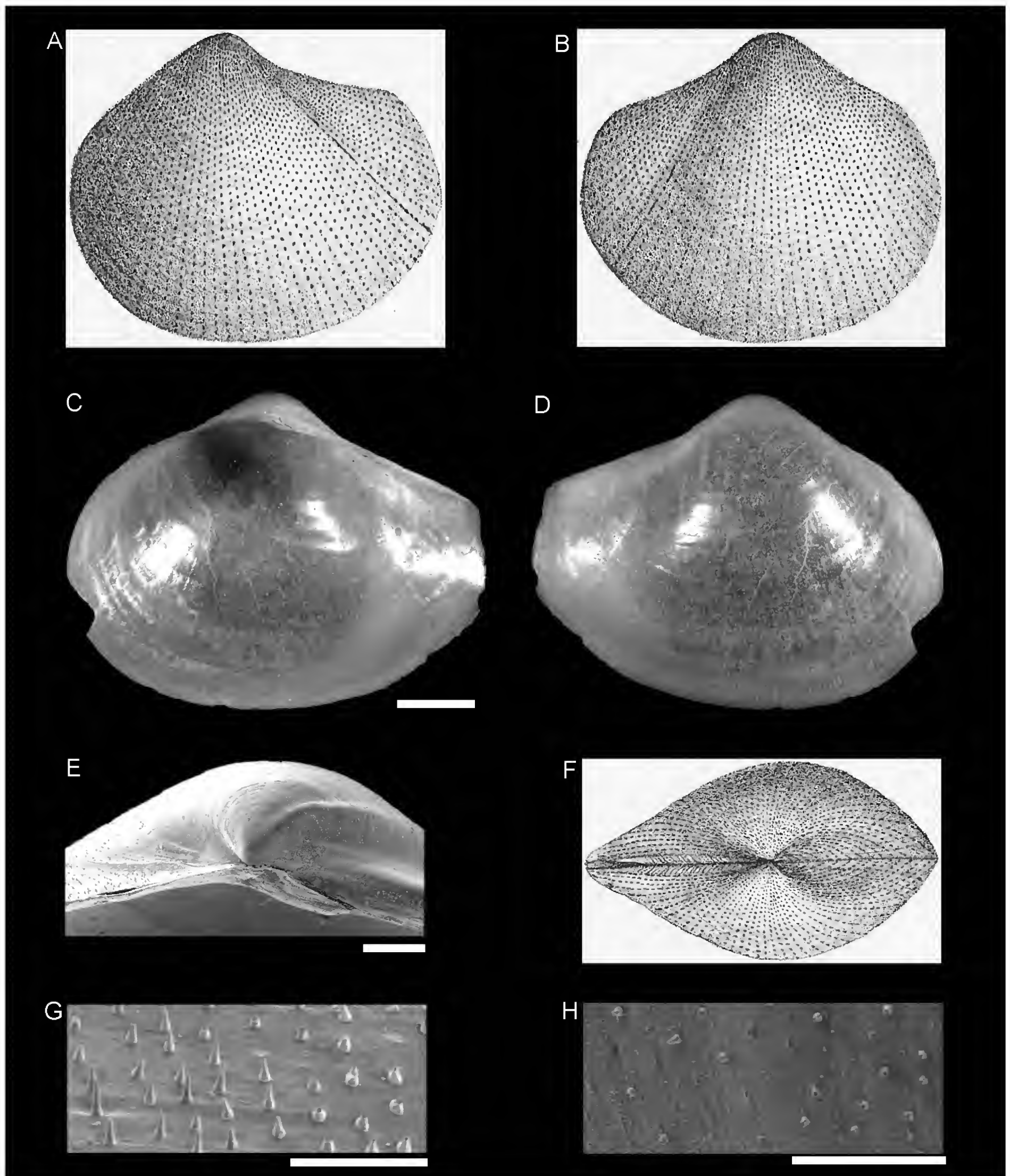


Figure 21. *Lyonsia intracta* Sturany, 1899, Station 130, west of Al Qunfudhah, Saudi Arabia, -439 m, **A, B, F** Original figures. **C–E, G, H** Syntype NHMW 84300: right valve interior (**C**), exterior (**D**), hinge detail (**E**) and sculpture details of the posterior (**G**) and anterior (**H**) valve parts. Scale bars: 1 mm (**C**); 0.5 mm (**E, G, H**)

dem Wirbel) sockelartig verdickt ist, und verläuft horizontal nach rückwärts. Noch wäre zu erwähnen, dass der Hinterrand einer jeden Schale – gleich hinter dem äusseren Ligamente – lamellenartig aus der Mittellinie hervortritt, und dass diese horizontal gestellten Lamellen beiderseits von einem Kielstreifen abgegrenzt werden, der am Wirbel entspringt und gegen das klaffende Hinterende der Muschel zieht (hinteres schmales Feld,

area). Vorne ist ein solches Feldchen (lunula) kaum wahrzunehmen.

[Tabelle mit Maßangaben!]

Der eigenthümliche Glanz der Schale, ferner die Andeutung von Radialrippchen am Hinterende (man beachte jenes eine erwähnte!) deuten auf die Gattung *Lyonsia*, zu deren Charakteren allerdings die Anlage des Ligaments oberhalb des Schlossrandes nicht recht passen will.

Translation. From stations 72, 114, 121, and 130 (535–1082 m); mostly only single valves or fragments.

This bivalve is medium sized, moderately inflated, oval rounded, slightly gaping posteriorly. The delicate, inequilateral shells are transparent, glassy and brittle, possess a beautiful mother-of-pearl shine and are closely beset with pustules on the outside, which are arranged in numerous tight radial rows and create a rough surface on the entire shell. Only very few delicate concentric growth lines are visible. The umbos are located at the anterior part of the shell and turn their beaks to the inside and the front, thus protrude the hinge margin. Dropping down in a curve and lopsided from the umbo towards the front, the bivalve does not show any angle at the transition to the nicely convex lower margin, while an obtuse angle is seen at the transition of the posterior dorsal margin to the truncated posterior margin. Here, the posterior end of the shell is weakly flattened and pulled forward, and a very weakly developed radial keel proceeds across this part down from the umbo towards the transition from the posterior to the ventral margin, as in a way a radial row of dots is united into a closed line.

The hinge is toothless, but possesses a ligament which – in contrast to the genus *Lyonsia* – is not located below the margin, meaning on the inside of the shell, but still at the margin itself, so that it is still visible from the outside when the shell is closed. To host the ligament there is a shallow indentation directly below the umbo of each shell, out of which the light yellow-coloured ligament can be extracted with some caution; it lies in the shell margin hidden at its place (directly below the umbo) and runs horizontally towards the back. It should also be mentioned that the posterior margin of each shell – directly behind the outer ligament – emerges as a lamella from the mid-line and that these horizontally positioned lamellae are confined on both sides by a keel, which originates at the umbo and tears towards the gaping posterior end of the bivalve (hind narrow field, area). In the front, such an area (lunula) is hardly recognizable.

[Table with dimensions!]

The peculiar shine of the shell, plus the trace of radial ribs at the posterior end (note the one mentioned!), suggests the genus *Lyonsia*, to whose characteristics the rudimentary ligament above the hinge margin does not quite fit.

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