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Photo de couverture: *Carassius praecipuus*, a new species of goldfish from Laos, see article of M. Kottelat in this issue.

REVUE SUISSE DE

# ZOOLOGIE

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## On *Starengovia* Snegovaya, a genus of Asian nemastomatines (Arachnida: Opiliones: Nemastomatidae)

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**Abstract:** Two species of the genus *Starengovia* Snegovaya, 2010 from Kyrgyzstan and Pakistan are characterized; *S. kirgizica* Snegovaya, 2010 is redescribed and *S. ivanloebli* proposed as a new species. They belong to the easternmost representatives of the subfamily Nemastomatinae. Both species are separated by some 650 km in north to south direction; the Pakistan record extends nemastomatine distribution to the northwest of the Himalayas. *Mediostoma pamiricum* Staręga, 1986 probably belongs to *Starengovia* as well. Within Nemastomatinae *Starengovia* displays plesiomorphic characters (extremely short glans of penis, armed with inconspicuous robust spicules) and apomorphic ones (long, distinctly inflated base of penis; large lateral foliate wing-like structures on truncus penis). The foliate-wing character is unique among Nemastomatidae. *Starengovia* may represent a relict line in the early evolution of nemastomatine harvestmen.

**Keywords:** Relicts - taxonomy - new species - Kyrgyzstan - Tadjikistan - Uzbekistan - Pakistan - Himalayas.

### INTRODUCTION

The subfamily Nemastomatinae of the family Nemastomatidae is an entirely Palaearctic group of small to minute, mainly soil-dwelling harvestmen. Their core distribution lies in western, central and southeastern Europe and extends to the Caucasus where a genera- and species-rich fauna occurs. At the eastern edge of the range, in Kyrgyzstan and the Tadjik Republic (Pamirs), currently only one species in each country is known. No nemastomatines from areas east of the Urals (Farzalieva & Esyunin, 1999) bordering western Siberia and eastern Kyrgyzstan (Snegovaya, 2010) and the Tadjik Pamirs (Staręga, 1986) were hitherto known. Surprisingly, the discovery of a single minute species in a genus of its own from the southwestern Chinese province of Yunnan extended nemastomatine distribution for some 3000 km to the southeast (Martens, 2016). The aim of this paper is to better characterize the genus *Starengovia* within the Nemastomatinae and to describe a new species from the Pakistani northwestern Himalayas.

### MATERIAL AND METHODS

Original line drawings were produced using a camera lucida attached to a Carl Zeiss research microscope. Measurements were taken by means of a micrometer disc attached to a Leitz stereomicroscope. Measurements

of the penis were taken from the original drawings. The automontage photographs were produced with a Leica Z6 APO A.

**Abbreviations for morphological terms:** Apo apophysis, Cx coxa, do dorsal, Fe femur, la lateral, Mt metatarsus, Op gen Operculum genitale, Pt patella, Ta tarsus, Ti tibia, Tu oc Tuber oculorum, ocularium, Tr trochanter, vc ventral. All measurements are given in mm.

#### Museum acronyms:

- CJM Working collection of J. Martens, Mainz, Germany
- MHNG Muséum d'histoire naturelle de Genève, Switzerland
- SMF Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt am Main, Germany
- ZMMU Zoological Museum of the Moscow State University, Moscow, Russia

### TAXONOMIC PART

#### Family Nemastomatidae Genus *Starengovia* Snegovaya, 2010

**Type species:** *Starengovia kirgizica* Snegovaya, 2010: 351 (by monotypy).

**Remarks:** A genus of Nemastomatidae in the subfamily Nemastomatinae, presently comprising two species. Gender of genus name is female.

**Emended diagnosis:** Small species (up to 1.7 mm body length, females being larger than males), dorsal scutum with lines of anvil-shaped tubercles along margins of all scutal areas. Pairs of marked para-median tubercles on opisthosomal areas of dorsal scutum. Apophysis on basal cheliceral article of male well-marked but low, with a distad-directed hook, discharge area for secretion in a bowl-like excavation on medial side of apophysis. Its inner wall perforated by numerous minute pores, apparently the extrusion area for cheliceral gland secretion.

Genital morphology of males: Characterized by rather unspecialized truncus penis, moderately slender, not markedly inflated; muscle-containing inflated base of penis large, rather compact, deeply incised medially, occupying about one fourth to one third of truncus length, truncus in straight continuation of inflated base. Glans inconspicuous, small, short, not well differentiated from truncus; armament of glans simple, with few stiff spicules in a dorsally and ventrally symmetrical arrangement, stylus short, straight to slightly curved.

**Distribution:** Hitherto only two males of one species were known from Kyrgyzstan, a second species is here described from Pakistan. Staręga (1986) provisionally named a single female from the Tadjik Republic as "*Mediostoma*" *pamiricum* Staręga, 1986. The locality of this specimen is about half way between and approximately 360 km from *Starengovia* records in Kyrgyzstan and in Pakistan and thus this female may also belong to *Starengovia*. This assumption is backed by characters of external morphology (Fig. 6B; see Discussion).

**Name:** It refers to Wojciech Krzysztof Staręga (1939-2015), a distinguished Polish arachnologist who worked on systematics and taxonomy of European, Asian and African harvestmen (Žabka, 2015).

**Relationships:** Rows of anvil-like tubercles forming lines and encircling the dorsal scutum magnum or parts of it and all or some of the dorsal scutal areas (probably equivalents to "somites") are present in seve-

ral nemastomatine genera and are documented for *Mitostoma* Roewer, 1951, *Carinostoma* Kratochvíl, 1958 (Martens, 1978a) and *Acromitostoma* Roewer, 1951 (Rambla, 1983). These structures are excessively developed in all New World ortholasmatines. According to the (still incomplete) molecular-based results of Schönhofer & Martens (2012), these dorsal ornaments developed independently in at least two different lineages. Two of the relevant genera analyzed, namely *Carinostoma* and *Mitostoma*, are placed on different branches of the molecular-based tree and are not closely related.

Alternatively, this dorsal armament may have been lost at various stages of nemastomatine evolution. This assumption is backed by the fact that nearly all ortholasmatine genera and species exhibit rich and elaborate scutal ornamentations. It is reduced in the few known Asian species (Shear & Gruber, 1983; Shear, 2010; Zhang & Zhang, 2013). Thus, lines of anvil-shaped tubercles may represent a plesiomorphic character within the Nemastomatidae, an element of the nemastomatid "Bauplan". In addition, equally shaped thorns turn up as coxal-rim denticles in most species of Nemastomatidae. If plesiomorphic, this character would not be useful to infer phylogenetic relationships.

### *Starengovia kirgizica* Snegovaya, 2010

Figs 1-5, 7-17, 20-26

*Starengovia kirgizica* Snegovaya, 2010: 352 (types not examined). – Schönhofer & Martens, 2012: 410 (discussion of phylogenetic placement, molecular-based phylogenetic tree). – Martens, 2016: 449 (discussion of phylogenetic placement). – Schönhofer, 2013: 47 (species mentioned).

**Material examined:** CJM 7649; 2 males; Kyrgyzstan, Fergansky Mountain Ridge, Babush Ata Mountains, above Arslanbob, at and near Yarodar Research Station, *Juglans regia* woodland, path to ravine, 41°19'N 72°58'E, 1400 m; H. Read leg. 17.5.1993. – CJM 6576; 4 males, 8 females; same locality, 1440-1500 m; S. Dashdamirov leg. 8.5.1990. – CJM 7650; 15 males, 14 females; same locality; W. Schawaller & J. Martens leg. 16.-18.5.1993. – CJM 7651; 6 males, 4 females; SMF; 2 males, 2 females; same locality; W. Schawaller & J. Martens leg. 15.5.1993. – ZMMU;

### Key to the currently known *Starengovia* species

- Distributed in Kyrgyzstan (one record also in Uzbekistan), larger species (male 1.5-1.75 mm, female 1.6-2.2 mm body length), para-median tubercles of dorsal scutum conical, relatively high (Figs 1, 3, 5), sometimes present on first free opisthosomal tergite (Fig. 5); penis with alae of wings, their tips bent to ventral side (Figs 20-24)..... *S. kirgizica*
- Distributed in northwestern Pakistan, smaller species (male 1.3-1.5 mm, female 1.3-1.65 mm body length), para-median tubercles of dorsal scutum peg-like, low, slender (Figs 6, 27, 29), not present on first free opisthosomal tergite; penis with alae of wings straight, not bent to ventral side (Figs 38-41)..... *S. ivanloebli* sp. n.





Figs 1-4. *Starengovia kirgizica*. (1) Body of male in dorsal view. (2) Same in ventral view. (3) Body of female in dorsal view. (4) Same in ventral view. Scale: 0.5 mm.

1 female; Kyrgyzstan, Chatkal Mt. Ridge, Sary Chelek Reserve, Suk-Bulak valley, litter, K. Mikhajlov leg. 7.7.1983. – CJM 7652; 1 male; Kyrgyzstan, Sary Chelek Nature Reserve, Tumanyak valley, open *Juglans regia* woodland, under stones and logs, 41°51'N 71°57'E, 1500 m; H. Read leg. 29.5.1993. – ZMMU; 2 females; same locality; K. Mikhajlov leg. 12.7.1983. – CJM 7653; 1 male, 1 female; same locality: Kodea Ata river valley, *Juglans*, *Malus*, *Picea*, under logs and stones, 71°57'E 41°51'N, 1500-1800 m; H. Read leg. 29.5.1993. – CJM 7654; 2 males, 5 females; MHNG; 5 males, 5 females; W. Schawaller & J. Martens leg. 29./30.5.1993. – ZMMU; 3 males, 3 females; same locality; W. Schawaller & J. Martens leg. 28.5.1993. – CJM 7655; 8 males, 3 females; same locality; W. Schawaller & J. Martens leg. 28.5.1993. – ZMMU; 1 male; same locality; D. Milko leg. 28.-31.5.1993. – ZMMU; 2 males, 8 females; same locality; S.I. Golovatch leg. 28.-31.5.1993. – ZMMU; 1 male, 1 female, same locality, Arkit, *Juglans regia* and *Acer turkestanica*, 1300 m; A.B. Ryvkin leg. 3.7.1983. – ZMMU; 1 male, 1 female, same locality, Kil'tesay stream, *Juglans regia*, 1300 m; A.B. Ryvkin leg. 4.7.1983. – ZMMU; 1 female, same locality, Karatungun canyon, *Picea schrenkiana* stands, 1400 m; A.B. Ryvkin leg. 10.7.1983. – CJM 7660; 2 males, 3 females, same locality, Kil'tesay canyon, *Juglans regia* with *Abies semenovi* forest, 1300 m; A.B.

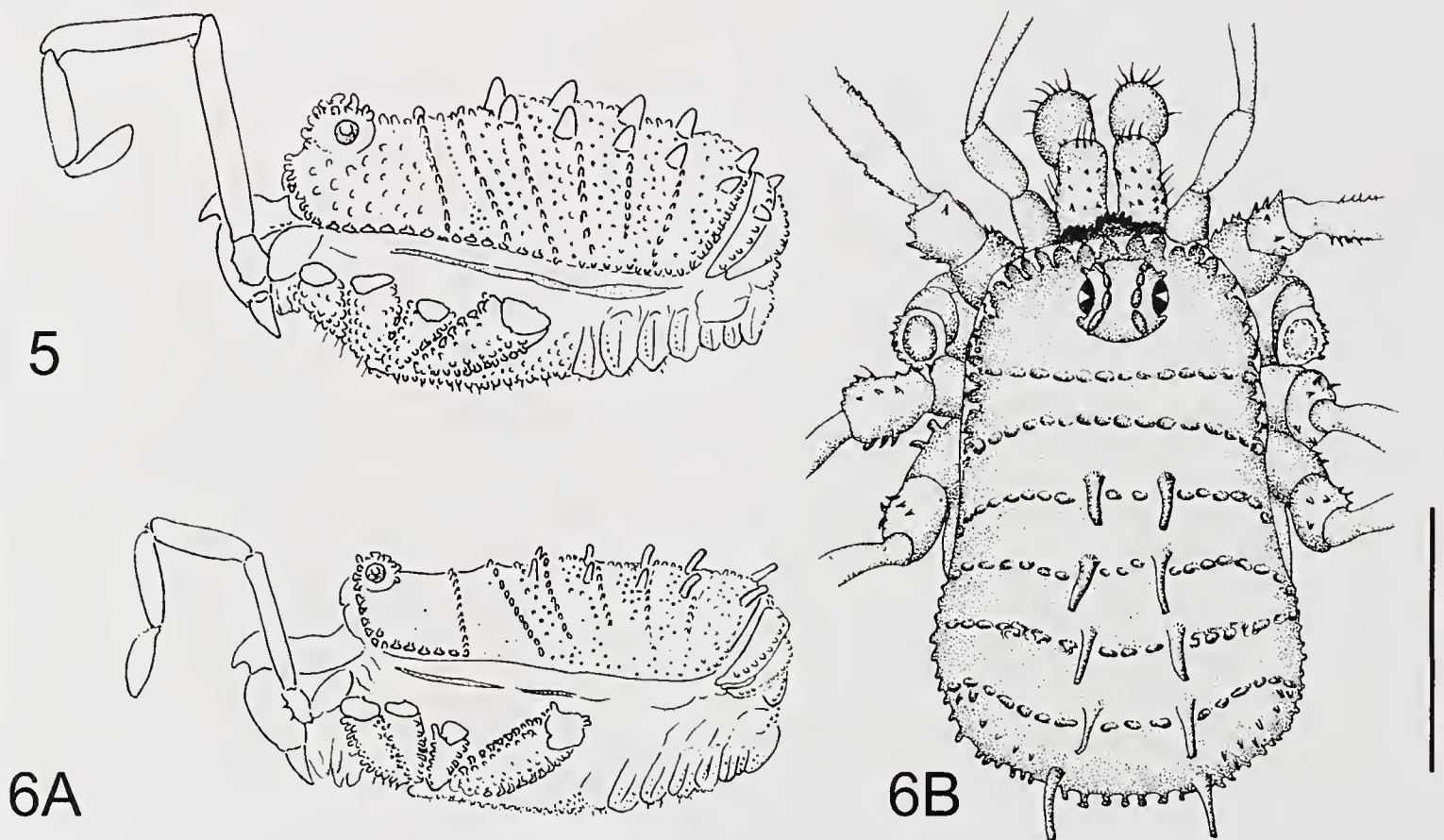
Ryvkin leg. 17.9.1983. – CJM 7656; 1 male, 1 female; Kyrgyzstan, N. Sovetskoye S. Alash Mt. Ridge, *Juglans regia* and *Crataegus* woodland with grassy glades, in litter, 41°11'N 72°39'E, 1200-1550 m; H. Read leg. 26.5.1993. – CJM 7657; 2 males; same locality; W. Schawaller & J. Martens leg. 25.5.1993. – ZMMU; 1 male; same locality; S.I. Golovatch leg. 26.5.1993. – CJM 7658; 1 male; Uzbekistan, Uckargan; J. Martens leg. 27.5.1993.

**Extended diagnosis:** Characterized by genital morphology (form of wings of truncus penis, by size of inflated basal region of truncus), size (larger body than in *S. ivanloebli* sp. n.) and by armament of dorsal scutum and free opisthosomal tergites (large, conical para-median tubercles on opisthosomal areas I-V and on first free opisthosomal tergite in few specimens only).

**Name:** Named after the country in which the type specimens were collected.

**Description (male)**

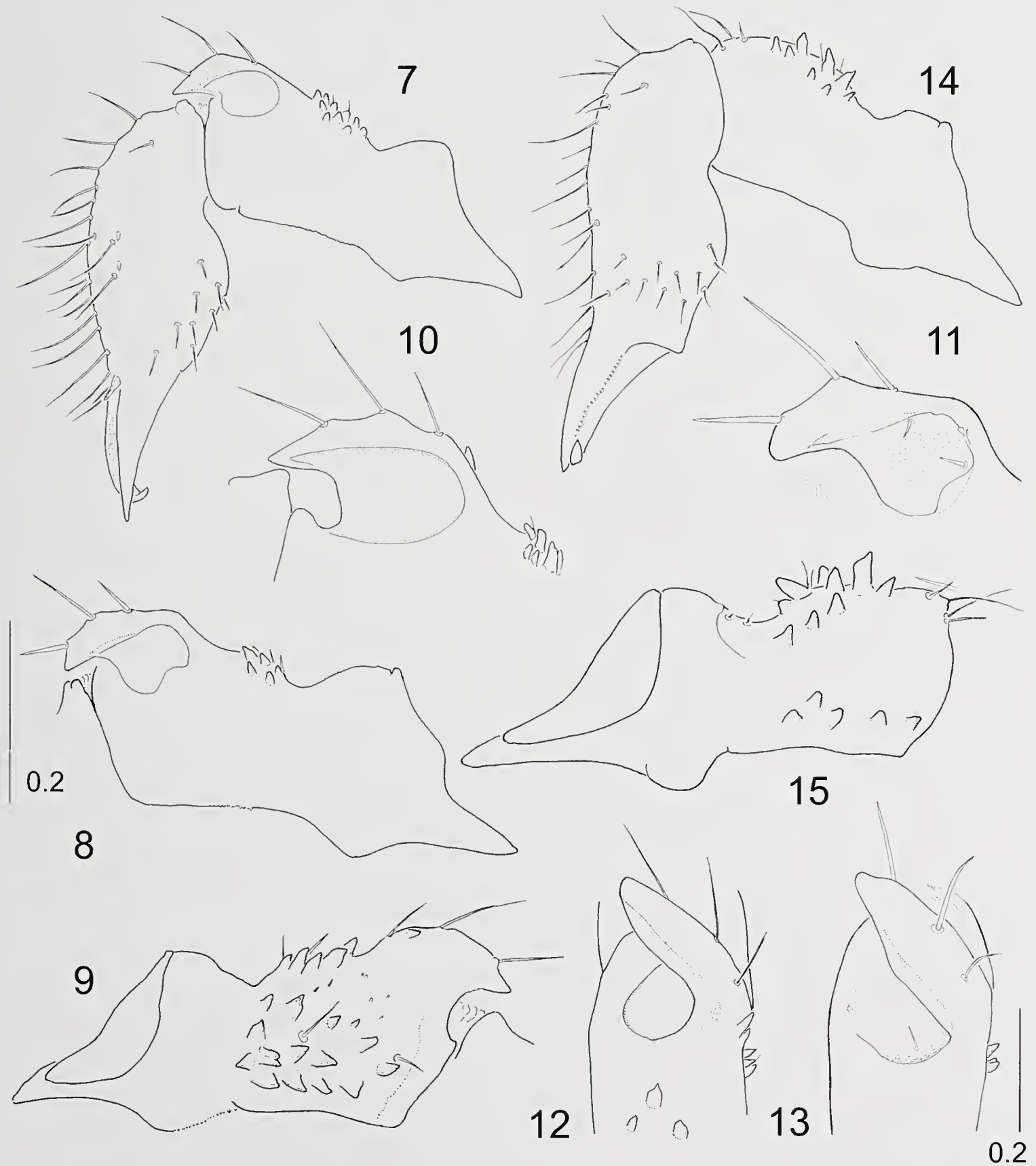
*Body, dorsal side* (Figs 1-5): Scutum uniformly light to dark brown (depending on time past final moult), without any golden or silver markings. Anterior and lateral margins of prosomal area I of dorsal scutum with a continuous line of closely spaced anvil-shaped tubercles of different sizes, largest on front of prosoma. Additional lines of anvil-shaped tubercles across the



Figs 5-6B. Body of male in lateral view (5-6A) and in dorsal view (6B). (5) *Starengovia kirgizica*. (6A) *S. ivanloebli* sp. n. (6B) *Mediosstoma pamiricum* Starega, 1986; reproduced from Starega (1986). Scale: 1 mm.

scutum: First (anteriormost) straight, second bent forwards, third and fourth straight, fifth and sixth line bent backwards. Tubercles of fourth, fifth and sixth line smaller and more or less interrupted (only few low tubercles present) in median part only, nearly lacking laterally. Opisthosomal areas I-V each with a

pair of quite large conical para-median tubercles; these tubercles posteriorly slightly further apart from each other than anteriorly. First free opisthosomal tergite in few specimens also carrying a pair of such tubercles. In addition, prosomal and opisthosomal areas with scattered low rounded tubercles.



Figs 7-15. *Starengovia kirgizica*. 7-13. Right chelicera of male. (7) Entire chelicera in prolateral view. (8) Basal article in prolateral view. (9) Same in retrolateral view. (10-11) Cheliceral apophysis in prolateral view. (12-13) Same in dorsal view. 14-15. Right chelicera of female. (14) Entire chelicera in prolateral view. (15) Basal article in retrolateral view. Scales: 0.2 mm (Figs 7-9, 14-15; Figs 10-13).

*Tu oc* relatively large, low, touching front margin of dorsal scutum, covered by few strong anvil-shaped tubercles.

*Body, ventral side* (Figs 2, 4-5): Cx I-IV pro- and retro-laterally with a line of strong anvil-shaped tubercles, rear and front line of consecutive Cx touching each other. Cx surface coarse, covered with relatively large and closely spaced tubercles. Op gen covered by much fewer, large, low, rounded tubercles; free sternites with few tubercles at rear margins; all light brown.

*Legs*: Quite different in some populations. Relatively short (but variation considerable; see below: Dimensions), male Fe I and III stout and markedly spindle-shaped, in females less pronounced (Sari Chelek, Alash), or Fe I and III slender, not spindle-shaped and whole leg considerably longer (Yarodar).

In all populations Tr with several large rounded tubercles; Fe, Pt and Ti of legs unarmed except for few minute light hairs on Mt, and Ta with few scattered long hairs. Coarse surface especially on Fe to Ti. No "comb-teeth" (Kammzähnen) as illustrated by Gruber (1976) for *Mediostoma*. Variable numbers of pseudo-articulations on Fe of legs II-IV.

*Pedipalp* (Figs 16-17): Slender and relatively long (in terms of *Starengovia* morphology), no article noticeably inflated; all articles except Tr bearing clavate setae, these most conspicuous on Pt, Ti and Ta; distal end of male Ti slightly curved downwards. No article with special armament in males and females.

*Chelicera of male* (Figs 7-15): Rather stout; basal article with strong pointed tubercles laterally and dorsally, a bulky frontad-directed Apo distinctly surpassing front margin of proximal article; Apo with a broad basis, approximately as long as high (in lateral view), upper side smoothly rounded and dorso-distally projecting into a pointed hook. In dorsal view Apo inclined anteriorly, towards longitudinal axis of article. Prolaterally Apo excavated nearly over its total length, forming a bowl-like excavation or hole. 2nd cheliceral article moderately inflated, with few long scattered bristles mostly on frontal surface.

*Male genital morphology* (Figs 20-26): Truncus penis (Figs 20-22) moderately slender; basis forming a large inflated part (occupying slightly less than one third of whole penis length) well differentiated from rest of truncus; inflated part compact and deeply split medially, completely filled by two penial muscles, their tendons spanning hole truncus length up to glans. Truncus parallel-sided (in do/ve view), slightly enlarged at level of wings, beyond wings narrowing toward glans; in lateral view narrowest above inflated basal part, from there slightly widening toward wings. One thin, fine hyaline and triangular wing on each lateral side in distal part of truncus, totally flattened, lateral corners slightly curved to ventral side (Figs 20-24).

Glans (Figs 25-26) only inconspicuously outlined, short, starting where two tendons are attached to inner truncus

wall; stylus short, a continuation of the glans, tapering to distal asymmetrical opening of seminal duct, slightly curved (in lateral view). Short, stiff and unspecialized spinules forming armament of glans, their arrangement symmetrical in ventral view.

**Female** (Figs 14-15): Characters largely as in male but lacking the dorso-distal cheliceral Apo.

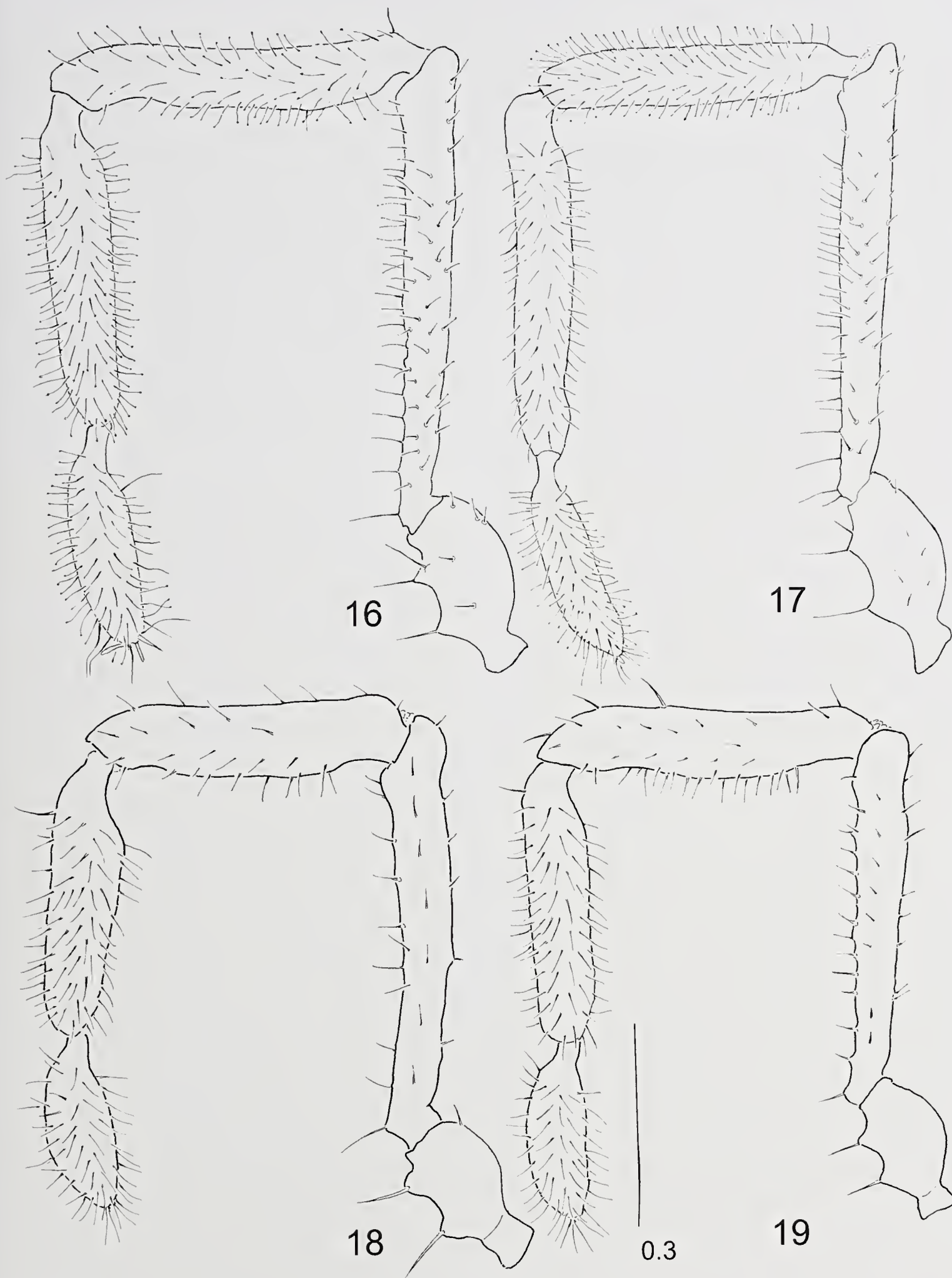
**Measurements**: Body length: Sary-Chelek and Alash: males: 1.5-1.75 (n=10), Uckargan male: 1.6. Females: 1.6- 2.2 (n=10). Leg II length, male, female in parentheses (two males from Yarodar and Uckargan, two females from Yarodar and Sari Chelek): Fe 1.1/1.5 (1.4/2.0) Pt 0.35/0.4 (0.5/0.5) Ti 0.75/1.2 (1.2/1.5) Mt 1.4/2.05 (1.75/2.4), Ta 1.1/1.6 (1.6/1.7). Pedipalp length (Sari Chelek): Fe 0.7 (0.9), Pt 0.6 (0.7), Ti 0.5 (0.6), Ta 0.3 (0.4). Penis length: 1.1.

**Variation**: The para-median tubercles of the dorsal scutum differ in size and shape in different populations. They are low and stout in individuals of short-legged populations (Sari Chelek, Alash), longer (up to twice as long) in long-legged populations (Yarodar). There is also variation within populations though to a generally much smaller extent. In addition, the dorsal scutum has either irregularly arranged anvil-shaped tubercles or these are partly arranged in transversal lines.

**Distribution**: The species is known from three localities in Kyrgyzstan and from one in Uzbekistan. The Kyrgyz specimens were collected at the Sary Chelek Biosphere Reservation about 60 km northwest of Tash-Kumyr, from the Fergansky Mountain Ridge in the Babush Ata Mountains above Arslanbob and from north of Sovetskoye in the Alash Mt. Ridge. The animals were collected in various habitats, mostly in open walnut (*Juglans regia*) forests, in riverine bushy stands, mostly under stones and old wood, and, mainly in the Sary Chelek area, also in various coniferous forest types. These opilionids were mostly sifted from soil litter and turned out to be quite common in all three areas. They were collected by different people independently from the same localities. Altitudinal records range from 1200 to 1800 m.

**Type locality**: Kyrgyzstan, Alash Mountain Ridge, Alash river valley, near Alash, 1550 m.

**Remarks**: *Starengovia kirgizica* was originally described on the basis of two males. A more detailed description is presented here. Judging from the rich material available, *S. kirgizica* has considerable variation in the shape of the dorsal scutal armament and in the length of legs, which is pronounced in leg II and IV. This leg variation is not correlated with body size, which is homogeneous throughout all populations. Also genital and cheliceral morphology of males does not vary noticeably. A detailed genetic investigation should check if more than one species is involved.



Figs 16-19. Pedipalps in prolateral view. (16-17) *Starengovia kirgizica*. (18-19) *S. ivanloebli* sp. n. (16, 18) Male. (17-19) Female. Scale: 0.3 mm.

***Starengovia ivanloebli* sp. n.**

Figs 6A, 18-19, 27-43

**Holotype:** MHNG; male; Pakistan, Swat District, above Utrot, 35°30'N 72°28'E, 2500 m; C. Besuchet and I. Löbl leg. 13.5.1983.

**Paratypes:** MHNG; 1 male, 2 females; same locality as for holotype. – MHNG; 4 males, 17 females; Swat, Malam Jabba, 34°48'N 72°35'E, 2300 m; 9.5.1983. – MHNG; 1 male, 1 female; Swat, above Miandam, 35°03'N 72°34'E, 2300 m; 10.5.1983. – MHNG; 1 male; Swat, above Utrot, 35°30'N 72°28'E, 2500-2600 m; 14.5.1983. – MHNG; 3 males, 11 females, 1 juvenile; Swat, valley of Ushu, ascent to Kalam, 35°27'N 72°34'E, 2300 m; 15.5.1983. – MHNG; 1 male, 5 females; SMF; 2 males, 2 females; Swat, above Miandam, 2400-2500 m; 17.5.1983. – MHNG; 1 male; Swat, Malam Jabba, 2500-2600 m; 18.5.1983. – MHNG; 1 male; Chitral, Lawarai Pass, 35°19'N 71°49'E, 2600 m; 23.5.1983. – MHNG; 3 males; CJM 7659; 3 males, 1 female; Hazara, above Naran, 34°54'N 73°39'E, 2600 m; 1.6.1983. All specimens leg C. Besuchet and I. Löbl.

**Diagnosis:** Characterized by genital morphology (form of alae and of inflated basal part of truncus), size (species smaller than *S. kirgizica*) and armament of dorsal scutum (para-median tubercles peg-like, low and slender, not present on first free opisthosomal tergite).

**Name:** The name is given in honour of Ivan Löbl who during numerous expeditions collected large numbers of soil arthropods, especially in the Himalayas and other parts of Asia. His contributions to entomology are striking.

**Description (male)**

**Body, dorsal side** (Figs 6A, 27-30): Scutum uniformly light brown to dark brown (depending on time since final moult), without any golden or silver markings. Anterior and lateral margins of prosomal area I of dorsal scutum with a continuous line of closely spaced anvil-shaped tubercles of different sizes, largest on front of prosoma. Additional lines of anvil-shaped tubercles across the scutum: First (anteriormost) in male more or less straight (in female straight), second line bent forwards, third line mostly straight but slightly bent backwards laterally, fourth straight, fifth and sixth line slightly bent backwards. Tubercles of fourth, fifth and sixth line smaller and more or less interrupted (only few low tubercles present) in median part only, nearly lacking laterally.

Median part of opisthosomal areas I-V with two slender and low, peg-like para-median tubercles slightly inflated distally and rounded at tip; distance between para-median tubercles slightly increasing posteriorly, all opisthosomal areas with several irregularly arranged low tubercles, very few on opisthosomal area I and on first free opisthosomal tergite, absent on prosomal scutal area

I around Tu oc. First free opisthosomal tergite without enlarged para-median tubercles.

**Tu oc** relatively small, low, touching front margin of scutum, densely covered with 10-12 anvil-shaped tubercles.

**Body, ventral side** (Figs 28, 30): Cx I-IV pro- and retro-laterally with a line of strong anvil-shaped tubercles, rear and front line of consecutive Cx touching each other. Op gen covered with rather large low, rounded, irregularly arranged tubercles; free sternites with few tubercles at margins; all light brown.

**Legs:** Rather short and slender (in terms of nemastomatid morphology); Cx with several large tubercles; Fe, Pt and Ti of legs I, III and IV slightly inflated (less so in female), Fe, Pt and Ti of leg I unarmed except for few minute light hairs, less so on Mt and Ta, there few scattered long hairs. Surface rough, no denticulation and no "comb-teeth" (Kammzähnen) as figured by Gruber (1976) for *Mediostoma*. Various numbers of pseudo-articulations on femora of legs II-IV.

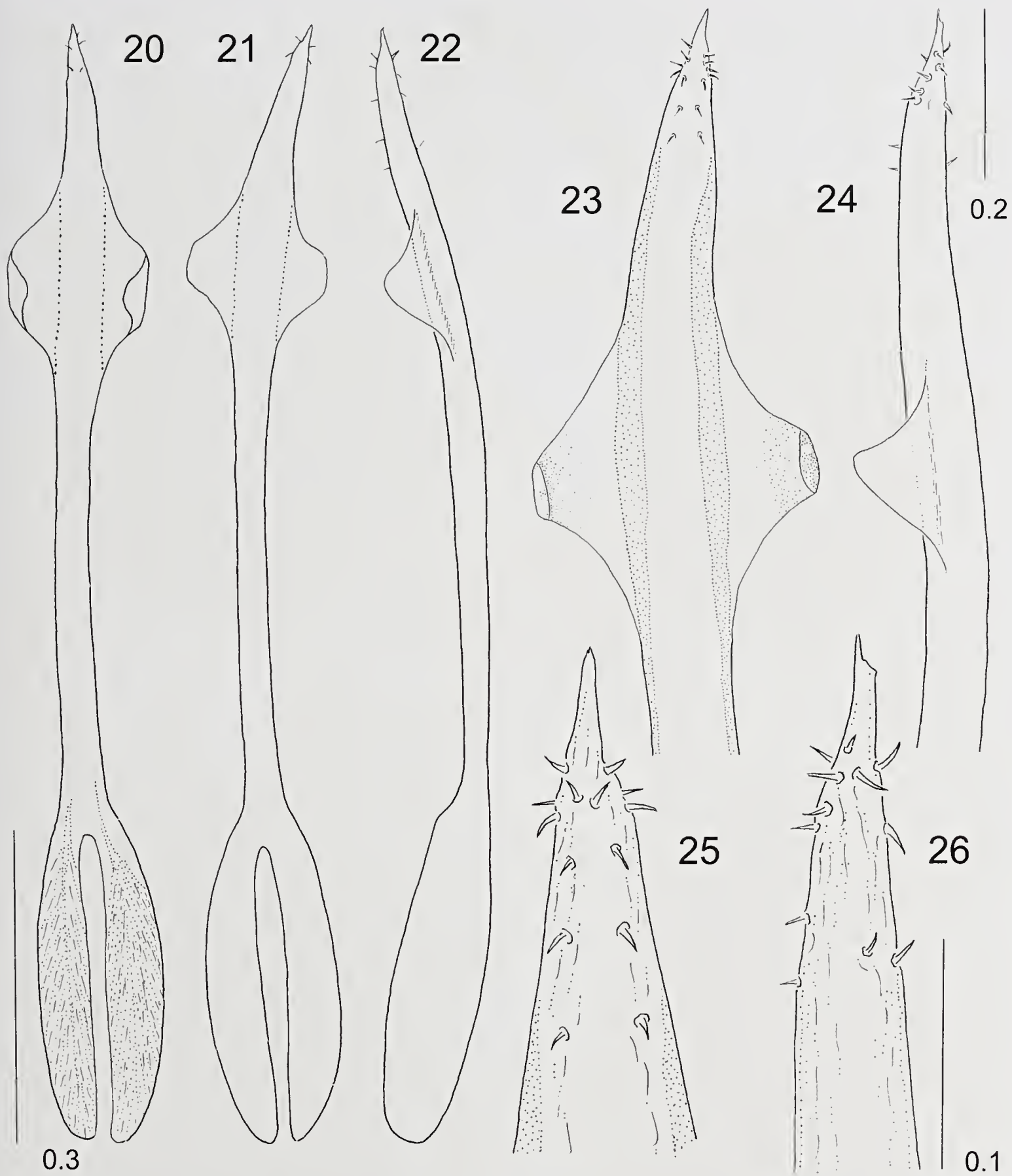
**Pedipalp** (Figs 18-19): Robust and short (in comparison with other nemastomatids), shorter than in *S. kirgizica*, male Ti slightly inflated proximally; all articles except Tr bearing clavate setae, most conspicuous on Pt, Ti and Ta (not indicated in Figs 18-19). In male and female no article with special armament.

**Chelicera** (Figs 31-37): Rather stout; basal article with a bulky frontad-directed Apo distinctly surpassing front margin of article; Apo with a broad basis, approximately as long as high (in lateral view), upper side smoothly rounded and dorso-distally projecting into pointed hook. In dorsal view Apo markedly inclined towards midline. Apo medially excavated for nearly its total length, forming a bowl-like excavation or hole. 2nd cheliceral article moderately inflated, with few long scattered bristles, situated mainly frontally.

**Male genital morphology** (Figs 38-43): Truncus penis (Figs 38-39) moderately slender; basis forming a large inflated part (occupying about one third of whole penis length) well differentiated from rest of truncus; inflated part compact, deeply incised in the middle and completely filled by penial muscles, their tendons spanning hole truncus length up to glans. Truncus narrowest above inflated part (in do/ve view), slightly widening toward lateral wings, beyond wings successively tapering to glans. One thin, fine and hyaline wing (Figs 38-41) on each lateral side of distal part of truncus, totally flattened, rectangular, abruptly and widely truncate, not pointed.

Glans (Figs 42-43) only inconspicuously outlined, short, starting where tendons are attached to inner truncus wall; stylus short, a continuation of glans, tapering to distal asymmetrical opening of seminal duct, slightly curved (in lateral view). Short, stiff and unspecialized spicules forming armament of glans; their arrangement symmetrical in ventral view (Fig. 42).

**Female** (Figs 29-30, 36-37): Largely as male but lacking dorso-distal Apo of first article of chelicera. This



Figs 20-26. *Starengovia kirgizica*, male genital morphology. (20) Truncus penis in ventral view. (21) Same in dorsal view. (22) Same in lateral view. (23) Distal part of truncus in ventral view. (24) Same in lateral view. (25) Glans penis in ventral view. (26) Same in lateral view. Scales: 0.3 mm (Figs 20-22); 0.2 mm (Figs 23-24); 0.1 mm (Figs 25-26).

article armed with pointed tubercles laterally. Form of anvil-shaped lines of tubercles of dorsal side slightly different (Fig. 29 cf. Fig. 27, see also “Body, dorsal side”).

**Measurements:** Body length, male 1.3-1.5 (n=10), female 1.3-1.65 (n=10). Leg II length: male, female in parentheses: Fe 1.25 (1.25), Pt 0.35 (0.4), Ti 0.9 (0.9), Mt 1.5 (1.45), Ta 1.25 (1.2). Pedipalp length: male, female in parentheses: Fe 0.5 (0.5), Pt 0.45 (0.4), Ti 0.4 (0.35), Ta 0.2 (0.2). Penis length: 1.0.

**Variation:** One of the peg-like para-median tubercles on opisthosomal area V of the dorsal scutum may lack (Fig. 27); on the first free opisthosomal tergite (corresponding to opisthosomal tergite VI) such tubercles are absent (Fig. 6).

**Distribution:** Known from eight localities in northwestern Pakistan, close to the northwestern fringes of the Himalayan chain. The species was found in three major administrative units of the country, Swat and Chitral Districts and Hazara Division, all mountainous areas in the northwest of the country, just west of the upper reaches of the Indus river.

Detailed habitat descriptions by the collectors refer to soil litter in open pine (*Pinus*), fir (*Abies*), spruce (*Picea*) and cedar (*Cedrus*) forests, in moist grassy glades, under stones and rotten wood and at moist riverine localities. Near Naran animals were found on June 1, under stones close to the actual snow line at 2600 m. Altitudinal records stretch from 2100 m (Murree) to 2600 m (Utrot, Malam Jabba, Naran, Lawarai Pass) and indicate occurrence of this species in a narrow altitudinal belt of just 500 m.

Most remarkably, *S. ivanloebli* sp. n. was collected together with two undescribed species of *Biantes* Simon, 1885 (Biantidae, a truly tropical family) at Malam Jabba, Naran to Kaghan, above Naran. One Kaghan series contained only five *Biantes* specimens, no *Starengovia*. The genus *Biantes* has undergone a tremendous radiation in the Himalayas; from Nepal alone 18 species were described (Martens, 1978b). Nearly all altitudinal zones there are inhabited by species in mostly narrow altitudinal belts stretching from the Terai lowlands to above 4000 m near the timberline. Many additional Biantidae species from Nepal and the Indian Himalayas await formal description. The Pakistani records of *Biantes* are the northwestern-most known within Asia. There they meet nemastomatines near their southeastern border.

## DISCUSSION

### Genus level systematics

Nemastomatidae are divided into two subfamilies, Nemastomatinae in the West Palaearctic, with hitherto only three outlying species in Central Asia and southwestern China, and Ortholasmatinae in North

and Central America, with few outlying species with a narrow geographical distribution in East Asia (Shear & Gruber, 1983; Shear, 2010; Schwendinger & Gruber, 1992). Nemastomatine generic division is mainly based on male genital and cheliceral morphology, and presently displays a relatively high degree of stability. Successively, papers of Kratochvíl (1958), Šilhavý (1966), Martens (1978a, 2006), Staręga (1976), Gruber & Martens (1968) and Gruber (1976, 1979, 2007) contributed much to our understanding of this subfamily. A first, still incomplete molecular-based analysis corroborated the present taxonomy and systematics and underlines that characters hitherto used are suitable for generic division and placement of species (Schönhofer & Martens, 2012). Presently, the subfamily comprises 17 genera (Schönhofer, 2013; Martens, 2016) with a strong presence in the western Palaearctic, especially in mountainous areas in southwestern, central and southeastern Europe. Most species there are known from the Iberian Peninsula with the Pyrenees (Prieto, 2008), from the Alps (Martens, 1978a) and from the Balkan Peninsula (Kratochvíl, 1958; Staręga, 1976). Also the Caucasus is a centre of nemastomatine diversity (Martens, 2006). It harbors endemic genera and, additionally, several of them display remarkable radiation into small-range species (Martens, 2006; Schönhofer, 2013).

### Taxonomic characters

The species of *Starengovia* presented here are typical representatives of Nemastomatinae, which lack the ortholasmatine hood projecting from the anterior margin of the dorsal scutum and which are characterized by a number of specific traits in their genital morphology. In *Starengovia* the large pair of membrane-like flaps of the distal part of the truncus penis is diagnostic. Though within nemastomatines wing-like penial structures occur in different genera (Martens, 2006; Schönhofer & Martens, 2012), this structure is unique and remarkable by its size and thin but robust hyaline appearance. Another genital character is also characteristic, the short glans penis. Generally, the proximal part of the glans is differentiated by the insertion of the penial tendons (Martens, 1976). These extend from the two basal muscles through the truncus to the glans. The glans is recognizable by the sparse but obvious presence of robust spicules. A similar short glans is also characteristic of the genus *Sinostoma* Martens, 2016; in that genus it is thicker and the stylus is rather short. *Sinostoma* also represents an East Palaearctic genus in southwestern China, the easternmost one in the Nemastomatinae.

Both genera may represent a common isolated evolutionary line within the Nemastomatinae. *Starengovia* is unique by its broad foliate alate distal part of the truncus penis (Snegovaya, 2010) which is lacking in *Sinostoma*. In an evolutionary tree based on molecular genetics as

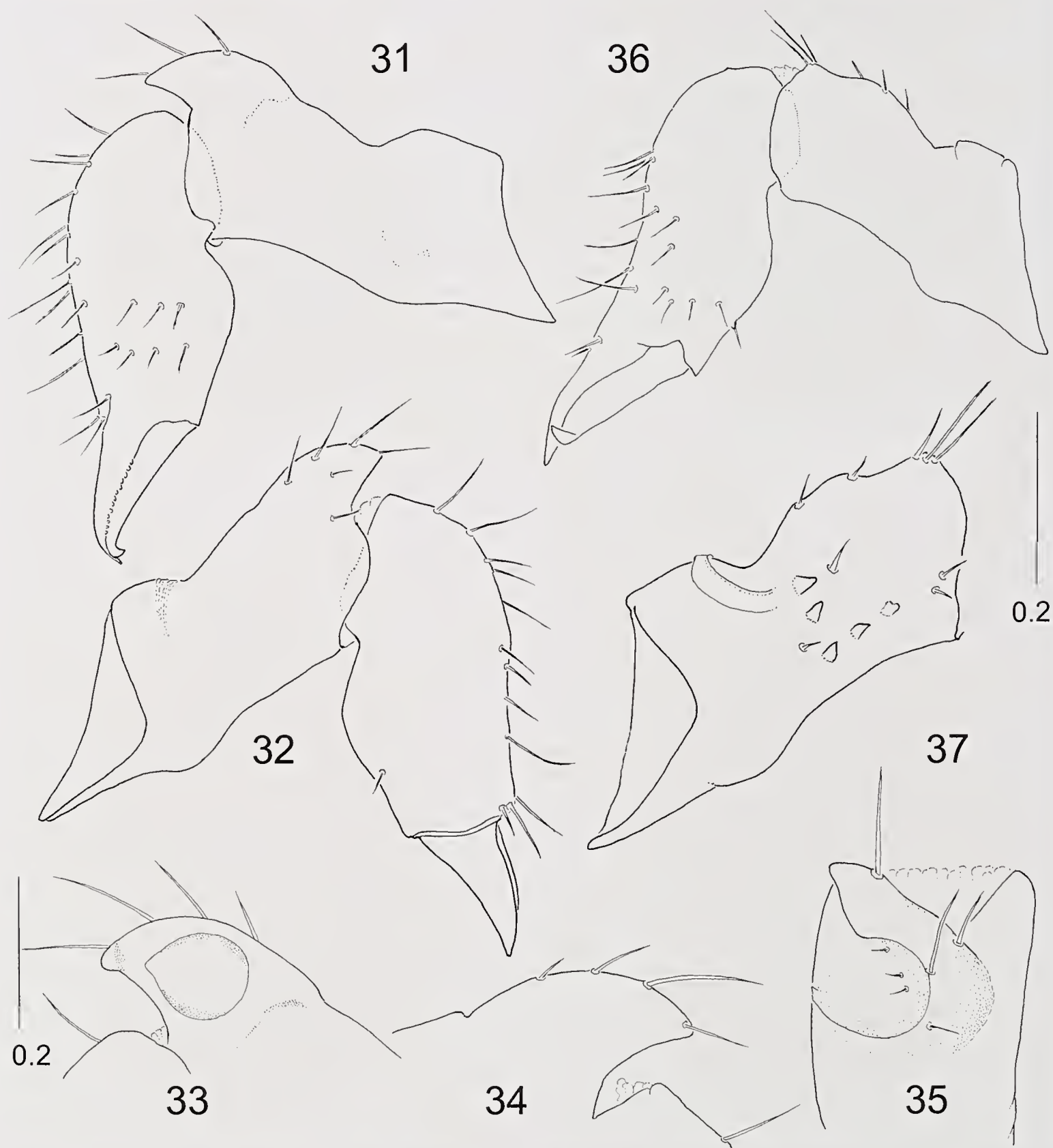




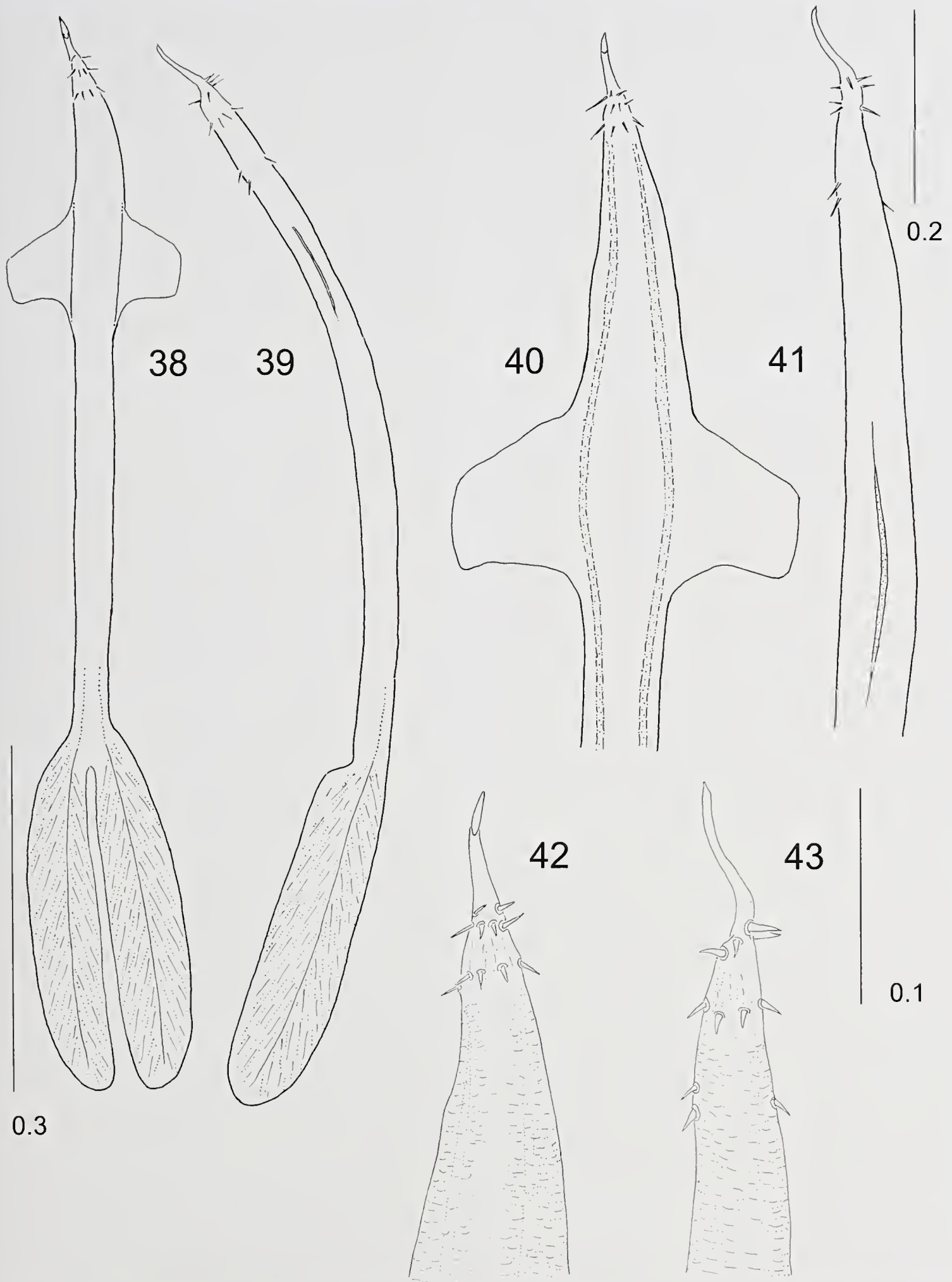
Figs 27-30. *Starengovia ivanloebli* sp. n. (27) Body of male in dorsal view. (28) Same in ventral view. (29) Body of female in dorsal view. (30) Same in ventral view. Scale: 0.5 mm.

published by Schönhofer & Martens (2012) *Starengovia* appears close to the basis of the tree. Unexpectedly, the genus *Mitostoma* Roewer, 1951, with a highly complicated male genital morphology, forms the sister group to all other nemastomatine genera screened so far. A bowl-like medial excavation of the cheliceral apophysis in males, a quite distinct character, is present in several nemastomatine genera and may have developed

independently several times. This is to be inferred from the placement of the relevant genera on the molecular-based tree (Schönhofer & Martens, 2012). *Nemastomella* Mello-Leitão, 1936 and *Mediostoma* Kratochvíl, 1958, two of the genera screened so far, are not closely related. They are restricted to the Iberian Peninsula, and range from the Balkans to the Caucasus, respectively. The very similar apophysis form in *Sinostoma* and *Starengovia*



Figs 31-37. *Starengovia ivanloebli* sp. n. (31) Right chelicera of male in prolateral view. (32) Same in retrolateral view. (33) Cheliceral apophysis in prolateral view. (34) Same in retrolateral view. (35) Same in dorsal view. (36) Entire female chelicera in prolateral view. (37) Basal article of female chelicera in retrolateral view. Scale: 0.2 mm (Figs 31-32, 36-37; Figs 33-35).



Figs 38-43. *Starengovia ivanloebli* sp. n., male genital morphology. (38) Truncus penis in ventral view. (39) Same in lateral view. (40) Distal part of truncus penis in ventral view. (41) Same in lateral view. (42) Glans penis in ventral view. (43) Same in lateral view. Scales: 0.3 mm (Figs 38-39); 0.2 mm (Figs 40-41); 0.1 mm (Figs 42-43).

may indicate a close relationship in accordance with the common occurrence at the eastern margin of the subfamily distribution. However, very different male genital characters of *Starengovia* and *Sinostoma* contradict this. Generally, the position of extrusion areas for the secretion on the male cheliceral apophysis differs among species and strongly varies among genera of nemastomatines. The secretion plays a role during courtship (Martens, 1969; Martens & Schawaller, 1977). Thus, alongside male genital morphology, the shape of this apophysis and the structure of the internal gland, which discharges its secretion via the cheliceral apophysis (Martens & Schawaller, 1977) plays a major role in systematics of Nemastomatinae.

### Biogeography

Beside *Sinostoma yunnanicum* Martens, 2016 of southwestern China, the two *Starengovia* species are the easternmost representatives of Nemastomatinae. The nemastomatine locality nearest to the localities of the two *Starengovia* species lies in the Central Asian Tadjik Pamir. There occurs "*Mediostoma*" *pamiricum* Staręga, 1986, apparently a rather localized endemic, known from only a single locality. This species, too, may belong to *Starengovia*. The easternmost *Mediostoma* species are known from the Caucasus and from northern Iran (Martens, 2006); occurrences further east are not likely. In addition, the illustration of the dorsal side of *M. pamiricum* by Staręga (1986) corresponds well with the two *Starengovia* species by possessing short to medium-sized peg-like para-median tubercles and lines of anvil-shaped denticles on scutal areas, the latter being most prominent on the prosoma (Fig. 6B).

The Pakistan localities of *S. ivanloebli* sp. n. reduce the distance to the *Sinostoma* population in Yunnan, China to about 2700 km. Despite intensive sampling of small soil arthropods by researchers of the Geneva Natural History Museum and of the (former) Mainz Institute of Zoology in many parts of the western and central Himalayas, no nemastomatids turned up except for the isolated Pakistan locations. The only previous record of nemastomatids on the Indian Subcontinent was presented by Roewer (1959), but that is false (Schönhofer, 2013). Though more Nemastomatinae species will hopefully be discovered in China, the group seems to be rare and local there, probably confined to (already rare) primeval montane forests, and the only species known today may represent a relict (Martens, 2016).

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## An annotated list of the Diplopoda described by Aloïs Humbert alone and with Henri de Saussure, and the Diplopoda from Saussure's Mexico expedition

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**Abstract:** Aloïs Humbert and Henri de Saussure described 70 species of millipede based primarily on specimens collected on their respective expeditions, but including some other holdings of the Muséum d'histoire naturelle de Genève, and 52 species based on specimens borrowed from the Naturhistorisches Museum Wien. These species are listed alphabetically; the type specimens identified in the collections of both museums are enumerated and their state of preservation noted, the whereabouts of type specimens identified in other institutions are discussed and the currently valid combination is given for each species where this has been established.

**Keywords:** Millipedes - Geneva - Vienna - Antilles - Cuba - Sri Lanka - type-catalogue.

### INTRODUCTION

The early Diplopoda collections of the Muséum d'histoire naturelle de Genève (MHNG) were greatly enriched by the material brought back from the expeditions of Henri de Saussure to Mexico and the Antilles in 1854-1856 and of Aloïs Humbert to Sri Lanka (then Ceylon) in 1858-1860.

Saussure published two papers (Saussure, 1859a, b) with very cursory descriptions of the specimens he collected during his expedition, followed by a monograph (Saussure, 1860) with more extended descriptions and in some cases more details about the number of specimens and the type localities. He was the first myriapod expert to collect in the American tropics (Hoffman, 1999), although some of the specimens he described from there were collected by others, notably François Sumichrast, a Swiss naturalist who had accompanied Saussure on his expedition and chosen to remain in Mexico (Hollier & Hollier, 2012).

Humbert (1865) produced a monograph of the myriapods of Sri Lanka which was notable for its "superior lithographic figures of genitalia" (Hoffman, 2009: 102). The two men collaborated on further publications on myriapods, principally of the Americas. Three papers (Humbert & Saussure, 1869a, b, 1870) with very short species descriptions were followed by a monograph which gave more details for at least some of the species (Saussure & Humbert, 1872). Two of these papers

(Humbert & Saussure, 1869b, 1870) are largely based on specimens then in the Naturhistorisches Museum Wien (NHMW) and include many South American species not revisited in the monograph.

Humbert's final publication on the group was posthumous (Humbert, 1893); it was only partially complete and was prepared for publication by Saussure (with a significant contribution from Leo Zehntner, who matched the illustrations to the slide preparations of Humbert and produced some missing illustrations).

Saussure returned to the Diplopoda late in his career, perhaps as a result of Humbert's unfinished study, and together with Zehntner published on the fauna of Madagascar. The Madagascan species are discussed in a separate publication (Hollier & Wesener, 2017).

These publications did not designate types, and the specimens were not labelled as such. Specimens of species considered to be in synonymy were placed under the name thought to be correct, usually with no indication of their original placement. The type specimens of many of the species described by Humbert and Saussure were revised by Jean Carl, curator of Arthropods at the MHNG and a prolific taxonomist of Diplopoda. Carl described and illustrated the taxonomically important features of many of Humbert and Saussure's species. Although he often mentioned he had studied one of the specimens used for the original description, he did not designate lectotypes and it is not always clear from his comments how many type specimens were then available to him.

More recently, Richard Hoffman identified many type specimens in the MHNG collection and designated a number of lectotypes, particularly of the American species. William Keeton and Jean-Paul Mauriès also revised some of the specimens in the MHNG.

The nomenclature of this list follows Hoffman (1999) for the North American millipede fauna. For the other species more limited checklists like Krabbe (1982), Marek *et al.* (2003), Jeekel (2001a, b, c, 2006, 2007), de Zoysa *et al.* (2016) and Wesener (2016) have been followed. In some cases other references are cited for the combination used. Nevertheless, some of the names remain *incertae sedis*, and in these cases the original combination is used as a place holder.

## ARRANGEMENT AND FORMAT

The species are listed alphabetically. The format for each is:

*specific epithet* Author, publication: page [*Original generic placement*].

Provenance as given in the original description, depository. Type series.

Subsequent revision of the type material. Number of specimens in the MHNG, label data of type specimens.

Other information.

*Currently valid combination (or placeholder name)*

The following abbreviations are used in the list:

BMNH Natural History Museum, London

MHNG Muséum d'histoire naturelle de Genève

MNHN Muséum national d'Histoire naturelle, Paris

NHMW Naturhistorisches Museum Wien

ZMHB Museum für Naturkunde, Berlin

## CATALOGUE

*acolhuus* Humbert & Saussure, 1869a: 150 [*Polydesmus (Fontaria)*].

Mexico temperata. Unspecified number of ♂ and ♀.

Saussure & Humbert (1872) gave a more detailed redescription. They stated that they had eight ♂ and seven ♀ from “Moyoapan et Sierra de Agua, près Orizaba” but it is not clear whether this refers to the original series or to a variety described just before this information was given. The MHNG collection has a card-mounted ♂ and at least eight specimens (or parts of specimens) in alcohol (loose in two jars) under the name *Fontania acolhuus*. The dry specimen is accompanied by a glass vial containing a dry pair of gonopods secured by a pin through the cork stopper. The dry specimen is labelled “Sierra de Agua” and the jars containing the specimens in alcohol are labelled “S<sup>t</sup> Cruz, Mexique” and “S<sup>ta</sup> Cruz Mexique.” The labels in both jars indicate type material; the dried specimen is also part of the type series. Hoffman

(1970: 159) designated one of the ♂ as a lectotype, put in a separate vial in the jar with the label “Lectotype!” There is a ♂ paralectotype in the NHMW (Inventory number 3348, Acquisition number 1866.I.A).

*Rhysodesmus acolhuus* (Humbert & Saussure, 1869)

*acutus* Humbert & Saussure, 1870: 176 [*Spirostreptus*]. Brasilia. Unspecified series.

Saussure & Humbert (1872) gave a more detailed redescription of the ♂ only, and the type locality as “Nouvelle-Grenade”. No specimens found in the MHNG. The NHMW contains a ♂ type specimen broken into three parts with the locality “New Grenada”, donated by E. Friedrichsthal (Inventory number 2165, Acquisition number 1866.I.51). The Acquisition Register shows that this specimen was part of a lot of two individuals that were described as two species by Humbert & Saussure, and it is therefore the holotype. The “New Grenada” on the data label probably refers to San Juan de Nicaragua, where Friedrichsthal disembarked in 1839 (Fischer-Westhauser, 2007; Stagl, 2003). Hoffman (1999: 36) suggested that the original placement of this species in the genus *Spirostreptus* was a *lapsus calami* and that it was considered by the authors to belong to the genus *Spirobolus*. This generic placement was formalised by Bollman (1893: 60).

*Spirobolus acutus* (Humbert & Saussure, 1870)

*aduncus* Saussure & Humbert, 1872: 158 [*Polydesmus (Rhachidomorpha)*].

New replacement name for *P. uncinatus* Humbert & Saussure, 1869a, a junior homonym of *P. uncinatus* Peters, 1864. The MHNG collection contains one ♂ specimen in alcohol under the name *Rhachidomorpha uncinata*, labelled as a type. The specimen is in fragments and lacks a data label, but was transferred from the dry collection and is presumably a syntype that had been placed in the collection before the name was changed. The MHNG also has two broken specimens in alcohol under the name *Rhachidomorpha adunca*, also labelled as types.

*Rhachidomorpha adunca* (Saussure & Humbert, 1872)

*angulatus* Saussure, 1860: 336-337, fig. 25 [*Eurydesmus*]. Selon toute probabilité, le Brésil. Unspecified number of ♀.

The pagination of the publication is faulty and reads 536-537. Saussure & Humbert (1872) gave the locality as “République Argentine” and indicated that the original description was based on a single dried specimen. The MHNG collection contains two ♂ specimens labelled “Amérique mérid.” in alcohol, with a broken pair of gonopods in a separate vial, under the name *Eurydesmus angulatus*. One of these is presumably the specimen used by Carl (1903) to describe and illustrate the gonopod. The whereabouts of the ♀ holotype is unknown. The NHMW collection includes a ♀ specimen from Rio de Janeiro



determined by Humbert & Saussure as *E. angulatus* (Inventory number 3288, Acquisition number 1866.1.8); according to a label in the jar this specimen was subsequently identified as *E. zebratus* (Gervais, 1836) by Hoffman in 1980.

*Eurydesmus angulatus* Saussure, 1860

***annectens*** Humbert & Saussure, 1869b: 677-678 [*Polydesmus (Stenonia)*].

Les Moluques (Musée de Genève). Unspecified number of ♂ and ♀.

Carl (1902) described and illustrated the gonopod based on an "Original exemplar." The MHNG collection contains three card-mounted specimens and one in alcohol under the name *Platyrrhachus annectens* used by Carl. The one ♂ and two ♀ card-mounted specimens each have a label with the sex, "Odontodesmus annectens" and "Moluques" on the pin but there are three different abbreviations for the authors. The specimen in alcohol has a similar label but in a different handwriting, and is indicated to be a type. These specimens are obviously syntypes. An undated label placed with the specimen in alcohol by Hoffman indicates that he thought it belonged to the genus *Psaphodesmus*, but this opinion was not published. The generic placement is uncertain.

'*Polydesmus*' *annectens* Humbert & Saussure, 1869

***arboreus*** Saussure, 1859b: 331 [*Julus*].

St. Thomas. Unspecified series.

Saussure (1860) stated that he had many specimens of both sexes, and that they were common on St. Thomas, where they were found climbing on trees or curled among the roots. The MHNG collection contains one ♂ and three ♀ in alcohol labelled as types under the name *Anadenobolus arboreus*. There are also numerous specimens in two jars under the name *Rhinocricus arboreus*, but these were collected after the publication of the original description and therefore cannot be types. The specimens under *Anadenobolus* each have the label "St. Thomas, Antilles" and are syntypes, notwithstanding the holotype and paratype labels. There are further syntypes in the ZMHB (Mortiz & Fischer, 1975; ZMB211, erroneously referred to as the holotype) and in the MNHN (MY4381) according to their online database.

*Anadenobolus arboreus arboreus* (Saussure, 1859)

***aztecus*** Humbert & Saussure, 1869a: 149 [*Cyclodesmus*].

Cordillera mexicana. More than one ♂.

Saussure & Humbert (1872) gave a more detailed redescription of the ♂ without mentioning the ♀ characters. Carl (1902) illustrated the gonopod based on an "Original exemplar." The MHNG collection contains one specimen under the name *Cyclodesmus aztecus* [sic]. There is no data label but the identification labels in the jar have "Mexique" written on them. The handwriting of one of these labels indicates that this was the specimen studied by Carl and it is therefore a syntype.

*Cyclodesmus aztecus* Humbert & Saussure, 1869

***aztecus*** Saussure, 1859b: 331 [*Julus*].

Cordova au Mexique. Unspecified series.

Saussure (1860) gave a much more detailed redescription of both sexes. He stated that he had many specimens from "les parties chaudes du Mexique, à Vera Cruz, à Cordova, à Orizaba etc." Carl (1919) described and illustrated the gonopods. The MHNG collection contains three ♂ and two ♀ card-mounted specimens and one ♀ directly pinned under the name *Spirobolus aztecus* and many specimens in alcohol in three jars under the name *Rhinocricus aztecus*. The three dry ♂ each have the label "Mexique, Voyage de Saussure," two of the ♀ are labelled "Mexique, V<sup>g</sup>e de Saussure" and the third is labelled "Orizava [sic] Mexique, V<sup>g</sup>e de Saussure." These are all syntypes. One of the jars containing two ♂ specimens in alcohol has the label "Spirobolus aztecus Sss, type, Mexique, Sumichrast." The second, labelled "Holotypus" contains around twenty broken specimens without a contemporary data label. The third contains around eight broken specimens and is labelled "Spirobolus aztecus Sauss., Mexique (Sumichrast)." It is likely that all of these are syntypes. There are further syntypes in the ZMHB (Moritz & Fischer, 1975; ZMB209) and in the MNHN (MY305, MY4328) according to their online database.

*Anadenobolus aztecus* (Saussure, 1859)

***aztecus*** Saussure, 1859a: 324 [*Polydesmus (Leptodesmus)*].

Plateau du Mexique. Unspecified series.

Saussure (1860) gave a much more detailed description of both sexes. He stated that he had taken it "à plusieurs reprises sur le plateau de Puebla" adding "Un grand individu mâle a été pris sur les Flancs du Pic d'Orizaba, mais d'autres individus proviennent du volcan de Tuxtla, d'un climat tempéré." Carl (1903) illustrated the gonopod, mentioning an "Original exemplar" from Puebla. The MHNG collection contains a ♂ and a ♀ labelled as types in alcohol under the name *Neoleptodesmus aztecus* and two specimens in alcohol labelled as a type under the name *Polydesmus aztecus*. The first two specimens, which have been transferred from the dry collection, have the data labels "Puebla, Mexique, M H de Saussure" and are clearly part of the type series. The other two have the data label "Potrero, Mexico, Sumichrast" and are probably specimens sent to Saussure subsequently to the expeditions and are not part of the type series collected by Saussure. Hoffman (1999: 424) designated the ♂ from Puebla as the lectotype. There is a paralectotype in the ZMHB (Moritz & Fischer, 1978; ZMB207).

*Neoleptodesmus aztecus* (Saussure, 1859)

***butaviue*** Humbert & Saussure, 1869b: 688-689 [*Polydesmus (Strongylosoma)*].

Java, Batavia, Ida Pfeiffer (Musée de Vienne). Unspecified number of ♂.

No specimens found in the MHNG. There is one ♂

type specimen in the NHMW (Inventory number 2116, Acquisition number 1866.I.314). The Acquisition Register shows that the lot contained only one specimen, so this can be considered the holotype. Attems (1898) referred to the poor condition of this type which is broken but retains one of the gonopods. The generic placement follows Jeekel (1979).

*Sundanina bataviae* (Humbert & Saussure, 1869)

**brandti** Humbert, 1865: 38-39, pl. 3, fig. 15, pl. 5, fig. 15 [*Sphaeropoens*].

Peradenia près Kandy. Unspecified number of ♂ and ♀. The MHNG collection contains two pinned specimens and two specimens in alcohol under the name *Sphaeropoens brandtii*, and seven specimens loose in a jar in alcohol under the name *Arthrosphaera brandti*. One of the pinned specimens has the label “Peradenia, Ceylan, Voyage Humbert,” the other lacks a label (Fig. 1). The specimens in alcohol under the name *S. brandti* have identification labels with “Ceylan, Voy. Humbert” and are accompanied by two vials, one containing a telopod and the other one of the second pair of legs of a ♀. The specimens placed under *S. bandtii* and *S. brandti* are syntypes. The



Fig. 1. A syntype of *Arthrosphaera brandti* (Humbert, 1865) (photo P. Schwendinger).

specimens in alcohol under *A. brandti* were collected by Bugnion in 1912 and are therefore not part of the type series. The generic placement follows Wesener (2016).

*Arthrosphaera brandti* (Humbert, 1865)

**brotii** Humbert 1893: 70-74, pl. 10, fig. 15(1-6), pl. 14, fig. 8 [*Julus*].

Petit Salève; Bois d'Yvres; Pitons; sommet des Voirons; Reponsoir; Louèche [sic] (Valais); Sevrier. Many ♂ and ♀. The MHNG collection contains many specimens in alcohol under the name *Cylindroiulus brotii*. None can be identified as syntypes, having been collected after the publication of the original description. The whereabouts of the type material is unknown.

*Cylindroiulus brotii* (Humbert, 1893)

**caicarae** Humbert & Saussure, 1870: 174 [*Spirostreptus*]. Brasilia. Unspecified series.

Saussure & Humbert (1872) gave a more detailed redescription of the ♀ only, identified the type locality Caicara and stated that the specimen(s) had been collected by Natterer. No specimens found in the MHNG. There is one ♀ type specimen collected by Natterer in the NHMW (Inventory number 2439, Acquisition number 1866.I.47). The Acquisition Register shows that the lot contained only one specimen, so this can be considered the holotype. The locality probably refers to a fazenda on the Paraguay River where Natterer stayed between October 1825 and June 1826 (Schmutzer, 2007). The generic placement is uncertain.

'*Spirostreptus*' *caicarae* Humbert & Saussure, 1870

**californicus** Humbert & Saussure, 1870: 177 [*Spirostreptus*].

California. Unspecified number of ♂.

Saussure & Humbert (1872) gave a more detailed redescription, implying that they only had one specimen. No specimens found in the MHNG. There is a ♂ type specimen, collected in California by Parreyss, in the NHMW (Inventory number 2168, Acquisition number 1866.I.43). The Acquisition Register shows that the lot contained only one specimen, so this can be considered the holotype. Hoffman (1999: 36) considered that the placement of this species as a member of the genus *Spirostreptus* rather than *Spirobohus* in the original description was probably a *lapsus calami*.

A junior synonym of *Tylobolus uncigerus* (Wood, 1864)

**carneus** Saussure, 1859a: 324 [*Polydesmus* (*Leptodesmus*)].

Brésil. Unspecified series.

Saussure (1860) implied that the original description was based on a single ♂ specimen from Bahia in Brazil, although the phrasing is ambiguous because it refers to an illustration. Saussure & Humbert (1872) described the ♀, giving the locality as Rio de Janeiro. Carl (1903) stated that he studied two ♂ “Originalexamplare,” describing

and illustrating the gonopod. The MHNG collection has two specimens in alcohol under the name *Leptodesmus carneus*, with a vial containing part of the head of a third specimen, a gnathochilarium, a pair of gonopods and a ♀ second pair of legs. Although there are no original data labels, these are presumably the syntypes referred to by Carl. The NHMW collection contains a non-type ♀ specimen collected by Tóth in 1864 in Rio de Janeiro (Inventory number 3292, Acquisition number 1866.I.140) and identified by Humbert and Saussure. This specimen was presumably the one used for the description of the ♀ in Humbert & Saussure (1872). *L. carneus* was designated the type species of *Leptodesmus* by Pocock (1909: 162), but the genus is poorly defined (Hoffman, 2012).

*Leptodesmus carneus* Saussure, 1859

***carolinensis*** Saussure, 1859a: 325 [*Polydesmus (Paradesmus)*].

Caroline du Sud. Unspecified series.

Saussure (1860) gives a much more detailed redescription which mentions both sexes. Saussure & Humbert (1872) considered the name to be a junior synonym of *P. erythropygus* Brandt, 1839. Carl (1903) described and illustrated the gonopod of an “Original exemplar” of *P. carolinensis* under the name *Euryurus erythropygus*. The MHNG collection has two card-mounted specimens under the name *Pachyurus carolinensis*. One is a ♂ labelled “Caroline S., Etats Unis” the other is ♀ and unlabelled. Hoffman refers to a ♂ holotype in the MHNG but because the original series was unspecified and the redescription covers both sexes, these specimens should be considered syntypes. There is a further syntype in the ZMHB (Moritz & Fischer, 1978; ZMB206, erroneously referred to as the holotype).

*Euryurus carolinensis* (Saussure, 1859)

***chichimecus*** Saussure, 1859b: 331 [*Julus*].

Mexique, Cordova. Unspecified series.

Saussure (1860) gave a more detailed redescription of the ♀, indicating that he had more than one specimen and stating that he had not found the ♂. The MHNG collection contains a directly pinned ♀ specimen under the name *Spiroboldus chichimecus* and a ♀ in alcohol under the name *Rhinocricus chichimecus*. The dry specimen, which has a card mount under the middle of the body, is labelled “Mexique, Voyage de Saussure.” The specimen in alcohol does not have a data label, but has “Mexique” on the identification labels. Both specimens are presumably syntypes. The status of the specimen in alcohol is less certain because it could have been acquired with the ♂ specimen in alcohol which was once placed under this name, presumably after the original description was published, and was subsequently identified by Carl as *A. zapotecus*. There is a syntype in the MNHN (MY4384) according to their online database.

*Anadenobolus chichimecus* (Saussure, 1859)

***cinctus*** Humbert & Saussure, 1870: 174-175 [*Spirostreptus*].

Rio. Unspecified series.

Saussure & Humbert (1872) gave a more detailed redescription of the ♀ only. No specimens found in the MHNG. The NHMW contains a single broken ♀ type specimen collected in Rio by Frauenfeld (Inventory number 2440, Acquisition number 1866.I.5). The Acquisition Register shows that the lot contained only one specimen, so this can be considered the holotype. The generic placement is uncertain.

*Spirostreptus cinctus* Humbert & Saussure, 1870

***cingalensis*** Humbert, 1865: 32-34, pl. 3, fig. 13 [*Polydesmus (Strongylosoma)*].

Pundel-Oya Valley. One ♀.

No specimens found in the MHNG. The whereabouts of the holotype is unknown. The generic placement follows de Zoysa *et al.* (2016).

*Singhalorthomorpha cingalensis* Humbert, 1865

***clarazianus*** Humbert & Saussure, 1869a: 152 [*Polydesmus (Odontotropis)*].

Ager argentinus. Unspecified series.

Saussure & Humbert (1872) gave a more detailed redescription and stated that the material was collected by Georges Claraz. The MHNG collection contains three specimens in alcohol, in two jars, under the name *Odontotropis clarazianus*. The label in the first jar reads “Odontotropis clarazianus Sauss., TYPE, La Plata, M<sup>r</sup> Claraz.” Although the word type has been added to the label in pencil as an afterthought, it indicates that the specimen is a syntype. A label in the other jar indicates that the two specimens it contains were identified by Carl and are therefore probably not syntypes. The generic placement follows Hoffman (1981).

*Odontopeltis clarazianus* (Humbert & Saussure, 1869)

***cluniculus*** Humbert & Saussure, 1870: 174 [*Spirostreptus*].

Brasilia. Unspecified series.

Saussure & Humbert (1872) gave a more detailed redescription, the type locality “Rio Negro” and noted that the specimen(s) had been collected by Natterer. No specimens found in the MHNG. The NHMW contains two ♀ syntypes collected by Natterer (Inventory numbers 2437 and 2438, Acquisition numbers 1866.I.49 and 1866.I.45 respectively).

*Orthoporus cluniculus* (Humbert & Saussure, 1870)

***coarctatus*** Saussure, 1860: 297-298, fig. 18 [*Polydesmus*].

Cayenne. Unspecified number of ♂ and ♀.

Saussure questioned the locality labels because he considered the specimens to be very similar to *P. beaumontii* Lcguillou, 1841, described from Java. The MHNG collection contains many specimens in alcohol, including some studied by Saussure, but none could be

identified as syntypes. The NHMW collection includes a specimen collected by Ida Pfeiffer in Borneo and identified as this species by Humbert & Saussure (Inventory number 3503, Acquisition number 1866.I.135). This species is of Asian origin, but now found throughout the tropics. The whereabouts of the syntypes is unknown.

*Asiomorpha coarctata* (Saussure, 1860)

**coccineus** Humbert & Saussure, 1869a: 152 [*Polydesmus* (*Tropisoma*)].

Cordillera orientalis mexicana. Unspecified number of ♂ and ♀.

Saussure & Humbert (1872) gave a more detailed redescription, the locality "Orizaba" and the information that they had 22 individuals collected by Sumichrast. Carl (1903) illustrated the gonopod on the basis of an "Originalexemplar." The MHNG collection contains one ♂ and two ♀ in alcohol, under the name *Strongylosoma coccinea*, that are labelled as types. The specimens have been transferred from the dry collection and although they do not have data labels they are clearly syntypes. The NHMW contains two ♀ syntypes (one incomplete) donated by Humbert & Saussure (Inventory number 3421, Acquisition number 1866.I.E).

*Acutangulus coccineus* (Humbert & Saussure, 1869)

**cognatus** Humbert, 1865: 22-23, pl. 2, fig. 6 [*Polydesmus*]. Peradenia près Kandy; Pundel-Oya Valley. Unspecified series.

Carl (1932) illustrated the antenna and gonopod but stated that he could not find Humbert's type. The MHNG collection contains the dissected parts studied by Carl in alcohol under the name *Lankadesmus cognatus*. The type material is apparently lost.

*Lankadesmus cognatus* (Humbert, 1865)

**consobrinus** Humbert & Saussure, 1870: 174 [*Spirostreptus*].

Brasilia. Unspecified series.

Saussure & Humbert (1872) gave a more detailed redescription of only the ♀, and the type locality as "Colombie." No specimens found in the MHNG. The NHMW contains one ♀ syntype collected by Sulkowski in 1847 in Columbia (Inventory number 2441, Acquisition number 1866.I.61). The Acquisition Register indicates that the original lot contained two specimens collected in 1847 by Sulkowsky in Columbia; the whereabouts of the other syntype is unknown. The generic placement is uncertain.

'*Spirostreptus*' *consobrinus* Humbert & Saussure, 1870

**consobrinus** Saussure, 1859a: 322 [*Polydesmus* (*Fontaria*)].

Plateau du Mexique. Unspecified series.

Saussure (1860) gave a more detailed description of both sexes, but he implied that the original description was based on the ♂ only. He stated that he frequently

took both sexes together under stones, "dans toutes les terres froides du Mexique, dans l'Anahuac, au pic d'Orizaba etc." Although Hoffman (1999) stated that the whereabouts of the type specimens was unknown and that he had not seen them in the MHNG, the collection has three card-mounted specimens under the name *Fontaria consobrinus*. There is also a vial containing a damaged pair of gonopods secured by a pin through the cork stopper. The two ♂ and one ♀ each have only "Mexique" on the label and all are in poor condition, but there is no reason not to think that the ♂ at least are syntypes.

*Rhysodesmus consobrinus* (Saussure, 1859)

**couloni** Humbert & Saussure, 1869a: 151 [*Polydesmus* (*Oxyurus*)].

Cuba. Unspecified number of ♂ and ♀.

Saussure & Humbert (1872) gave a more detailed redescription. Carl (1903) refers to "Originalexemplare" in his discussion of this species. The MHNG collection has two card-mounted specimens under the name *Leptodesmus couloni*. Both the ♂ and the ♀ specimens are badly damaged. They both have the data label "Oxyurus Couloni Humb. et Sauss., Cuba," apparently in Humbert's handwriting, and are syntypes. Hoffman (1999) refers to a ♂ holotype in the MHNG without justification.

*Amphelictogon couloni* (Humbert & Saussure, 1869)

**crassicornis** Humbert & Saussure, 1870: 177 [*Spirostreptus*].

Nova-Granada. Unspecified series.

Saussure & Humbert (1872) gave a more detailed redescription of the ♂ only, and stated that the specimen(s) had been collected by Natterer. No specimens found in the MHNG. There is one broken ♂ type specimen collected by Friedrichsthal in the NHMW (Inventory number 2167, Acquisition number 1866.I.51a). The Acquisition Register shows that this specimen was part of a lot of two individuals that were described as two species by Humbert & Saussure, and it is therefore the holotype. The "New Grenada" on the data label probably refers to San Juan de Nicaragua, where Friedrichsthal disembarked in 1839 (Fischer-Westhauser, 2007; Stagl, 2003). Hoffman (1999: 36) suggested that the placement of this species in the genus *Spirostreptus* in the original description was a *lapsus calami* and that it was considered by the authors to belong to the genus *Spirobolus*. This generic placement was formalised by Bollman (1893: 60).

*Spirostreptus crassicornis* (Humbert & Saussure, 1870)

**crebristriatus** Humbert, 1865: 55-56, pl. 5, fig. 24 [*Spirobolus*].

Peradenia. Two ♂.

The MHNG collection contains fragments of two specimens in alcohol under the name *Spirobolus crebristriatus*. A label in the jar reads "Spirobolus

*crebrestriatus* Humb., (type) Peradenia, Ceylan” indicating that the specimens are syntypes. The generic placement is uncertain; here we follow Jeekel (2001c).

*Cingalobolus crebrestriatus* (Humbert, 1865)

***cultratus*** Humbert & Saussure, 1870: 175 [*Spirostreptus*].  
Brasilia. Unspecified series.

Saussure & Humbert (1872) gave a more detailed redescription, stating that the original description was based on three fragments of a ♂ collected by Natterer. No specimens found in the MHNG. The holotype is in the NHMW (Inventory number 2523/2532, Acquisition number 1866.I.92). The specimen was reviewed by Hoffman, who illustrated the head and left gonopod (Hoffman, 1968a). This specimen has two inventory numbers because it was also described as *Alogostreptus nattereri* Attems, 1950, making the latter a junior synonym of *U. cultratus* (Humbert & Saussure, 1870).

*Urostreptus cultratus* (Humbert & Saussure, 1870)

***cyaneus*** Saussure, 1859a: 327 [*Strongylodesmus*].

Régions tempérées du Mexique. Unspecified series.

Saussure (1860) gave a more detailed redescription of the ♂ without mentioning the ♀, and indicated that he had several specimens. Carl (1903) described and illustrated the gonopod, referring to more than one ♂ “Original exemplare.” The MHNG collection has five ♂ specimens labelled as types in alcohol under the name *Strongylodesmus cyaneus*. All are broken, some have the data label “Orizaba, Mexique, M H de Saussure” and others are without data labels, but are presumably syntypes. Some more recently collected specimens are also present. Hoffman (1999) refers to a ♂ holotype in the MHNG without justification.

*Strongylodesmus cyaneus* Saussure, 1859

***cyprius*** Humbert & Saussure, 1869a: 684-685 [*Polydesmus (Oxyurus)*].

Chypre, Kotschy (Musée de Vienne). Unspecified number of ♂ and ♀.

Attems (1898) redescribed the species based on type specimens in the NHMW. The MHNG has one specimen in alcohol under the name *Leptodesmus cyprius*. A note in the jar reads “Polydesmus cyprius Sss. & H. (Type) Chypre, Mus. Vienne”, indicating that it is a syntype. The NHMW contains fragments of at least six syntypes, including one pair of gonopods *in situ* and one pair in a glass vial (Inventory number 2024, Acquisition number 1866.I.152). Hoffman (1968b) illustrated the gonopods of a syntype in the NHMW.

*Melaphe cypria* (Humbert & Saussure, 1869)

***decolor*** Humbert & Saussure, 1870: 173 [*Polydesmus (Oxyurus)*].

Brasilia. Unspecified number of ♀.

Saussure & Humbert (1872) gave a more detailed redescription, noting that the specimen(s) had been

collected by Natterer. No specimens found in the MHNG. The NHMW contains one broken ♀ (Inventory number 3295, Acquisition number 1866.I.137a). According to the Acquisition Register, *P. decolor* and *P. nattereri* were described from lot 137 which comprised only two specimens, specimen 3295 can therefore be considered the holotype. Although Attems (1898: 383) placed this species in the genus *Leptodesmus*, the generic placement remains uncertain and the genus *Leptodesmus* is poorly defined (Hoffman, 2012).

*'Polydesmus' decolor* (Humbert & Saussure, 1870)

***domingensis*** Saussure & Humbert, 1872: 176 [*Spirobolus*].

Substitute name for *Julus haitensis* Saussure, 1860 (the two specimens described by Saussure as *Julus haitensis* Gervais, 1847 were in fact a different species). The MHNG collection has one ♂ syntype in alcohol under the name *Alcimobolus domingensis*, erroneously labelled as the holotype by Mauriès in 1980. The whereabouts of the second syntype is unknown.

*Alcimobolus domingensis* (Saussure & Humbert, 1872)

***filicornis*** Saussure, 1859b: 332 [*Julus*].

Vera-Cruz. Unspecified series.

Saussure (1860) gave a more detailed description of the ♀ without mentioning the ♂ or the number of specimens. Saussure & Humbert (1872) gave a description of the ♂, stating that they had received a number of specimens of both sexes from Cuernavaca. The MHNG collection includes one card-mounted ♂ under the name *Paraiulus filicornis*, and a ♀ specimen in alcohol under the name *Julus filicornis*. The specimen in alcohol is labelled “Cuernavaca” while the dry specimen is labelled “Vera Cruz, Mexique, M<sup>r</sup> de Saussure.” The specimen from Cuernavaca is presumably the one received after the publication of the description and not part of the type series. The specimen from Vera Cruz could be part of the type series but the original description appears to have been based on only the ♀ characters and so its status is dubious. Hoffman (1999) regarded the generic position as uncertain.

*'Julus' filicornis* Saussure, 1859

***fraternus*** Saussure, 1860: 374, fig. 40 [*Julus*].

Yautepec dans les terres chaudes de la province de Mexico. One ♀.

The MHNG collection contains one card-mounted ♀ under the name *Spirostreptus fraternus*. It is labelled “Atihuayan, Mexique, M H de Saussure” and matches the rough measurements given in the original description. This specimen is presumably the holotype. There is a ♂ specimen in alcohol under the same name, but the identification is given with a question mark so it cannot be part of the type series.

*Orthoporus fraternus* (Saussure, 1860)

**fraternus** Saussure, 1859a: 322-323 [*Polydesmus* (*Fontaria*)].

Côte orientale du Mexique. Unspecified number of ♂ and ♀.

Saussure (1860) stated that he had four ♂ and three ♀, collected “dans les vallées du versant oriental de la Cordillère”. The MHNG has two ♂ and two ♀ in the dry collection under the name *Fontaria fraternus*. One ♂ and the two ♀ have the data label “Cordova, Mexique, M H de Saussure,” the other ♂ has “Pic Orizaba, Mexique, M H de Saussure.” There is also a glass vial containing a pair of gonopods secured by a pin through the cork stopper. All are part of the type series; the ♂ from Cordova was designated as the lectotype by Hoffman (1970: 155). There is a paralectotype in the ZMHB (Moritz & Fischer, 1978; ZMB202).

*Rhysodesmus fraternus* (Saussure, 1859)

**frauenfeldianus** Humbert & Saussure, 1870: 172 [*Polydesmus* (*Oxyurus*)].

Nova Granada. Unspecified number of ♀.

Saussure & Humbert (1872) gave a more detailed redescription. No specimens found in the MHNG or in the NHMW. The whereabouts of the type specimen(s) is unknown.

*Chondrodesmus frauenfeldianus* (Humbert & Saussure, 1870)

**gracilipes** Humbert & Saussure, 1870: 172 [*Polydesmus* (*Oxyurus*)].

Brasilia. Unspecified number of ♀.

Saussure & Humbert (1872) gave a more detailed redescription, stating that the specimen had been donated to the NHMW by Archduke Maximilian. No specimens were found in the MHNG. The NHMW contains a number of fragments, probably all from one ♀ type specimen (Inventory number 2612, Acquisition number 1866.I.146). The Acquisition Register shows that the lot contained only one specimen, so this can be considered the holotype. Attems (1898) redescrbed the species based on this ♀ type specimen, and placed the species in the genus *Odontopeltis*. This placement was later rejected by Pena-Barbosa *et al.* (2013) and the actual generic position is uncertain.

'*Polydesmus*' *gracilipes* Humbert & Saussure, 1870

**gracilis** Humbert & Saussure, 1869a: 149 [*Sphaeriodesmus*].

Cordillera mexicana. Unspecified series.

Saussure & Humbert (1872) gave a more detailed redescription (explicitly stating that there was more than one specimen) and a more precise type locality “Cordillère oriental, Moyoapan.” No specimens found in the MHNG. The whereabouts of the type specimens is unknown.

*Cyliomis gracilis* (Humbert & Saussure, 1869)

**granosus** Humbert & Saussure, 1869b: 674 [*Polydesmus* (*Pachyurus*)].

Les Moluques (Musée de Genève). Unspecified number of ♀.

The MHNG has one card-mounted ♀ and one ♂ in alcohol under the name *Pachyurus granosus*. The ♀ has the label “Pachyurus granosus ♀ H. et S. Moluques” and is a syntype. The ♂ is in fragments. A typed label in the vial reads “Pachyurus granosus Sauss. ♂ TYPUS, ex. Mus. Genf, Moluques.” The original description only treats the ♀ and so the type status of this specimen is dubious.

*Polylepis granosus* (Humbert & Saussure, 1869)

**granulosus** Saussure, 1859a: 323 [*Polydesmus* (*Leptodesmus*)].

Cordova au Mexique. Unspecified series.

Saussure (1860: 325) placed this name in the synonymy of *P. toltecus* Saussure, 1859 (and noted that it was a junior homonym of *P. granulosus* Palissot de Beauvoir, 1805), and indicated that the original description was based on the ♀. No specimens are placed under this name in the MHNG but the ♀ in alcohol placed under the name *P. tolteca* could be a syntype, although this seems unlikely.

A junior synonym of *Rhysodesmus toltecus* (Saussure, 1859)

**haastii** Humbert & Saussure, 1869b: 683-684 [*Polydesmus* (*Oxyurus*)].

Auckland, Waikato River, Nouvelle Zélande (Musée de Vienne, Voyage Novara). Unspecified number of ♀.

No specimens found in the MHNG. The NHMW contains one broken ♀ syntype (Inventory number 3811, Acquisition number 1866.I.22). Johns (1964: 41) refers to a ♀ specimen in the NHMW as the holotype, which can be regarded as a lectotype designation by holotype assumption. The Acquisition Register gives a more detailed locality “Waikato River/Tauperi” showing that the specimen was collected during the Novara’s stay in Auckland in 1858 (Scherzer, 1862).

*Pseudoprionopeltis haastii* (Humbert & Saussure, 1869)

**haitensis** Saussure, 1860: 363-364 [*Jnhis*].

Ile de St-Domingue. Two ♂.

The specimens were first ascribed to *J. haitensis* Gervais, 1847 but were recognized by Saussure & Humbert (1872: 176) to be a distinct species and the species was given the new replacement name *Spirobolus domingensis*. The pagination of the publication is faulty, and reads 563-564. The MHNG collection has one ♂ syntype in alcohol under the name *Alcimobolus domingensis*, erroneously labelled as the holotype by Mauriès in 1980. The whereabouts of the second syntype is unknown.

*Alcimobolus domingensis* (Saussure & Humbert, 1872)

**hamifer** Humbert, 1865: 52-53, pl. 4, fig. 22, pl. 5, fig. 22 [*Spirostreptus*].

Ceylan (Peradenia?). Unspecified number of ♀.

The MHNG collection contains two specimens in alcohol in separate jars. One jar contains a broken ♀ specimen, with the main parts of the body in one vial and the second pair of legs in another. A label in the jar reads “*Spirostreptus hamifer* Humb. Type, Ceylan Voyage Humbert” indicating that it is a syntype. The second jar has a label indicating that the specimen was collected by Schneider, and it is therefore not a syntype.

*Harpurostreptus hamifer* (Humbert, 1865)

**heteropygus** Humbert & Saussure, 1869a: 154 [*Spirobolus*].

Mexico temperata. Unspecified number of ♂ and ♀.

Saussure & Humbert (1872) gave a more detailed redescription of the ♂ only and the type locality “Cuernavaca.” No specimens found in the MHNG. The whereabouts of the type specimens is unknown.

*Centrelus heteropygus* (Humbert & Saussure, 1869)

**hochstetterii** Humbert & Saussure, 1869b: 690-691 [*Polydesmus (Icosidesmus)*].

Auckland, Nouvelle-Zélande (Musée de Vienne, Voyage Novara). Unspecified series.

Attems (1899) redescribed the species based on type specimens in the NHMW. Carl (1902) gave a detailed redescription based on a type specimens in the MHNG and illustrated the gonopod. The MHNG collection contains two ♂ specimens in alcohol under the name *Icosidesmus hochstetteri*. The labels in the jar indicate that the specimens came from the NHMW and are types. Johns (1964: 6) designated one of the specimens (identified by a label in the vial containing the specimen) as lectotype. The NHMW houses two ♂ specimens from the type series (Inventory number 3823, Acquisition number 1866.I.10b), rather than the three reported by Johns (1964).

*Icosidesmus hochstetteri* Humbert & Saussure, 1869

**humbertiana** Saussure in Humbert, 1893: 89, pl. 14, fig. 13 [*Glomeris*].

Pitons, Mont Salève. Based on a coloured drawing by Humbert.

The MHNG collection contains two specimens under this name. They were collected on the Salève by Zehntner and are not part of the type series because Saussure stated that the type specimen had been lost and that he described it based on the colour pattern illustrated by Humbert. Hoess & Scholl (2001) discussed the confusion surrounding patterned *Glomeris*, and demonstrated that recent specimens of patterned *Glomeris* from Mont Salève belonged to *G. connexa*.

A junior synonym of *Glomeris connexa* C. L. Koch, 1847

**ignobilis** Humbert & Saussure, 1870: 177 [*Spirostreptus*]. America borealis. Unspecified number of ♂.

Saussure & Humbert (1872) gave a more detailed redescription, and indicated that they had two specimens. No specimens found in the MHNG or in the NHMW. Hoffman (1999) stated that the holotype (actually a syntype) was in the NHMW. Although it appears in the acquisitions register (Acquisition number 1866.I.42), the specimen is apparently lost.

A junior synonym of *Narceus annularis* (Rafinesque, 1829)

**inermis** Humbert, 1865: 39-41, pl. 3, fig. 16 [*Sphaeropoeus*].

Peradenia. Unspecified number of ♂ and ♀.

Humbert mentioned a series of varieties from several localities, but did not name them. The MHNG contains one card-mounted and four directly pinned specimens under the name *Sphaeropoeus inermis*, and four specimens in alcohol under the name *Arthrophaera inermis*. The card-mounted specimen and one of the pinned specimens each have the label “Peradenia, Ceylon, Voyage Humbert.” Two of the pinned specimens have the label “Pundal O Vall., Ceylan, Voyage Humbert.” The other pinned specimen lacks a data label. The specimens in alcohol are in two vials, each with the label “*Sphaeropoeus inermis* Humb., Ceylan, Voy. Humbert”; these specimens were revised by Thomas Wesener in 2008. All are syntypes.

*Arthrophaera inermis* (Humbert, 1865)

**inornatus** Humbert, 1865: 30-31, pl. 3, fig. 11 [*Polydesmus*].

Peradenia. One ♂.

No specimens found in the MHNG. The whereabouts of the holotype is unknown. The generic placement follows de Zoysa *et al.* (2016).

*Anoplodesmus inornatus* (Humbert, 1865)

**insignis** Saussure, 1859b: 332 [*Julus*].

La Plata. Unspecified number of ♂.

Saussure (1860) stated that he had two specimens, one of them damaged. The MHNG collection contains one ♂ in alcohol under the name *Pelmatojulus insignis*. The specimen, which has been transferred from the dry collection and is in fragments, is labelled “La Plata, M Melly” and as holotype. The latter label is erroneous and the specimen is a syntype.

*Pelmatojulus insignis* (Saussure, 1859)

**insularis** Humbert & Saussure, 1869b: 678-680 [*Polydesmus*].

Les Moluques (Musée de Genève). Unspecified number of ♀.

Although the original description refers to the specimen(s) as ♀, Carl (1902) illustrated the gonopod based on what he stated was an “Original exemplar.” The MHNG collection contains one card-mounted specimen

under the name *Platyrrhachus insularis* used by Carl. It is labelled “P. insularis, Sauss & H, Moluques” and is presumably a syntype.

*Psaphodesmus insularis* (Humbert & Saussure, 1869)

**intermedius** Humbert & Saussure, 1869a: 151-152 [*Polydesmus* (*Oxyurus*)].

Cordillera orientalis mexicana. Unspecified number of ♂.

Saussure & Humbert (1872) gave a more detailed redescription and the type locality as Orizaba. Carl (1903) placed this name in the synonymy of *P. sumichrasti* having examined the gonopod, but Hoffman (1999) revalidated the name. The MHNG collection contains one ♂ in alcohol, under the name *Polydesmus intermedius*, labelled as a type. The specimen has been transferred from the dry collection and is a syntype.

*Neoleptodesmus intermedius* (Humbert & Saussure, 1869).

**javanus** Saussure, 1859a: 324-325 [*Polydesmus* (*Leptodesmus*)].

L'île de Java. Unspecified series.

Carl (1902) redescribed the species, illustrating the gonopod, on the basis of a single ♂ “Original exemplar.” The MHNG collection contains one card-mounted specimen under the name *Platyrrhachus javanus*, the name used by Carl. The specimen is labelled “Java, M Melly” and should be regarded as the lectotype, designated by holotype assumption by Carl (1902: 656) who clearly stated that he had the one “Original exemplar.” The generic placement is uncertain; here we follow Carl (1902).

*Platyrrhachus javanus* (Saussure, 1859)

**kandyanus** Humbert, 1865: 49-50, pl. 4, fig. 20, pl. 5, fig. 20 [*Spirostreptus*].

Peradenia près Kandy. One ♂ and two ♀.

The MHNG collection contains one ♂ and three ♀ in alcohol under the name *Spirostreptus kandyanus*. As mentioned in the original description, the ♀ are paler and smaller than the ♂ (the third ♀, not mentioned in the description, is even smaller than those described). Humbert explicitly based the description solely on the ♂, adding that the ♀ specimens were found with it. de Zoysa *et al.* (2016) erroneously placed this name as a junior synonym of *Thyropygus allevatus* (Karsch, 1881), citing Hoffman (1982). However, in this publication Hoffman (1982: 36) revised specimens from Thailand identified as *S. kandyanus* by Daday, and identified them as *T. allevatus*, but his mention of “*Spirostreptus kandyanus* (sensu Daday nec. Humbert, 1866 [sic])” clearly did not bring Humbert’s species into question. The generic placement is uncertain, and the genus *Spirostreptus* probably does not occur in Sri Lanka (de Zoysa *et al.*, 2017).

*'Spirostreptus' kandyanus* Humbert, 1865

**kelaarti** Humbert, 1865: 23-25, pl. 2, fig. 7 [*Polydesmus*]. Trincomalie. Unspecified series.

Humbert mentioned a number of varieties, but did not name them. Carl (1902) made reference to “die kleinsten Original exemplare”. Carl (1932) discussed the variation in the species. The MHNG collection contains three card-mounted specimens and three in alcohol under the name *Prionopeltis kelaarti*. The dry specimens are each labelled “Ceylan, V<sup>g</sup>e Humbert” while the jar contains the label “Polydesmus kelaarti Humb. (Type) Peradenia, Ceylan, Voyage Humbert.” The gonopods of one of the specimens in alcohol, identified by a label “Gonopodes” in the vial, were illustrated by Carl (1932: 464, figs 65-67) as the “Type”. Although the locality given for the alcohol specimens does not match the one in the original description, all of these specimens are probably syntypes. There are many other specimens in alcohol under the name *Anoplodesmus kelaarti* but these were collected by Carl after the publication of the original description and are therefore not syntypes. The generic placement follows de Zoysa *et al.* (2016).

*Chondromorpha kelaarti* (Humbert, 1865)

**lankaensis** Humbert, 1865: 50-52, pl. 4, fig. 21, pl. 5, fig. 21 [*Spirostreptus*].

Trincomalie. Two ♂ and two ♀.

Carl (1917) illustrated the posterior gonopod of the “type.” The MHNG contains five specimens in alcohol in three jars under the name *Spirostreptus lankaensis* and five specimens in alcohol together in one jar under the name *Ktenostreptus lankaensis*. The first jar contains two specimens and the label “*Spirostreptus lankaensis* Humb. (type) Trincomalie, Voy. Humbert.” The second jar contains one specimen and the label “*Spirostreptus lankaensis* Humb. (type) Trincomalie, Voy. Humbert.” These three specimens are clearly syntypes, and the jars have type labels on them. The third jar contains two specimens and a vial with a pair of gonopods, with the label “*Spirostreptus lankaensis* Humb. Ceylan coll. Schneider” while the fourth jar with five specimens has the label “*Spirostreptus* (*Ktenostreptus*) *lankaensis* Humb. Ceylan, Bugnion.” These seven specimens are not syntypes. Given the dissection, Carl presumably studied the specimens collected by Schneider.

*Ktenostreptus lankaensis* (Humbert, 1865)

**laticaudatus** Humbert & Saussure, 1870: 175-176 [*Spirostreptus*].

Brasilia. Unspecified series.

Saussure & Humbert (1872) gave a more detailed redescription of the ♂ only, stating that the specimen(s) had been collected by Natterer. No specimens found in the MHNG. The NHMW contains a single ♂ type specimen with the gonopods intact (Inventory number 2166, Acquisition number 1866.I.50) collected by Natterer. The Acquisition Register shows that the lot contained only one specimen, so this can be considered



the holotype. Hoffman (1999: 36) considered the original placement of this species in the genus *Spirostreptus* instead of *Spirobolus* was a *lapsus calami*. The generic placement is uncertain.

'*Spirostreptus*' *laticaudatus* Humbert & Saussure, 1870

*layardi* Humbert, 1865: 28-30, pl. 3, fig. 10 [*Polydesmus*].  
Peradenia près Kandy. Unspecified number of ♀.

No specimens found in the MHNG. The whereabouts of the type material is unknown.

*Anoploidesmus layardi* (Humbert, 1865)

*limax* Saussure, 1859a: 322 [*Polydesmus* (*Fontaria*)].

Terres chaudes du Mexique. Unspecified series.

Saussure (1860) stated that he had two ♂ and three ♀, and gave Cordova and San-Andrès-Tuxtla as localities. The MHNG collection has two ♂, one card-mounted and one in alcohol, under the name *Fontaria limax*. The dry ♂ has the data label "Cordova, Mexique" and is accompanied by a vial containing a broken pair of gonopods secured by a pin through the cork stopper. The ♂ in alcohol has the data label "Tuxtlan [sic], Mexique." Both are part of the type series. Hoffman (1966: 10) designated the ♂ which was transferred from the dry collection to alcohol, as the lectotype. There is a further paralectotype in the ZMHB (Moritz & Fischer, 1978; ZMB196).

A junior synonym of *Rhysodesmus dasyptus* (Gervais, 1847)

*lunelii* Humbert, 1865: 47-49, pl. 4, fig. 19 [*Spirostreptus*].

Putlam, côte occidentale de Ceylan. One ♂.

Carl (1917) re-illustrated the gonopod of the type because Humbert's original figure was printed too small for some of the detail to be visible. The MHNG collection contains one ♂ specimen in alcohol under the name *Thyropygus luneli*. The specimen is in several pieces and there is a vial containing a pair of gonopods. A label in the jar reads "Thyropygus luneli (Humb.) type! Ceylon, A. Humbert" indicating that this is the holotype. The MNHN online database states that there is a type (MY4391) in their collection, but since they give the country of origin as India, this must be a mistake.

*Humbertostreptus lunelii* (Humbert, 1865)

*macilentus* Humbert, 1893: 10-14, pl. 2, fig. 2 (1-7) [*Polydesmus*].

[Environs de Genève]. Unspecified series.

Humbert gave a description of his specimens under the name *P. macilentus* C.L. Koch, 1844. Attems (1898: 446) recognized that Humbert's specimens were not of this species, but placed the name *P. macilentus* Humbert in the synonymy of *P. subintiger* Latzel, 1884 rather than replacing it. The MHNG contains some 40 specimens in alcohol, in three jars, under the name *Polydesmus subintiger macilentus*. Two jars contain a label reading "Polydesmus macilentus C.Koch (Type Humbert) env. Genève coll. Humbert", apparently in Carl's handwriting.

The first jar has a vial with some 15 ♀ specimens, the second a vial with some 10 ♂ and 15 ♀ specimens. The third jar contains one ♂ and three ♀ collected near Bex and they are not labelled as types.

A junior synonym of *Propolydesmus testaceus* (C.L. Koch, 1847)

*macrourus* Humbert & Saussure, 1870: 176 [*Spirostreptus*].

Brasilia. Unspecified series.

Saussure & Humbert (1872) gave a more detailed redescription of the ♂ only. No specimens found in the MHNG. Although there is a single type specimen listed in the NHMW Acquisition Register (Acquisition number 1866.I.104), the specimen is apparently lost. Hoffman (1999: 36) considered that the original placement of this species in the genus *Spirostreptus* instead of *Spirobolus* was probably a *lapsus calami*.

'*Spirostreptus*' *macrourus* Humbert & Saussure, 1870

*mayus* Saussure, 1859a: 322 [*Polydesmus* (*Fontaria*)].

Cordillère du Mexique. Unspecified series.

Saussure (1860: 323) placed this name in the synonymy of *P. toltecus* Saussure, 1859, and indicated that the original description was based only on the ♂. There are no specimens placed under this name in the MHNG. The ♂ specimen in alcohol placed under the name *P. toltecus* in the MHNG could be a syntype of *P. mayus* if Saussure (1860) was correct in stating that *P. toltecus* was described on the basis of ♀ material only.

A junior synonym of *Rhysodesmus toltecus* (Saussure, 1859)

*mexicana* Humbert & Saussure, 1869a: 155-156 [*Siphonophora*].

Mexico, Cordillera orientalis. Unspecified number of ♀. Saussure & Humbert (1872) gave a more detailed redescription and the locality "montagnes de la Sierra de Agua, près Orizaba." The MHNG contains fragments of an unknown number of specimens in alcohol under the name *Siphonophora mexicana*. There is no data label but the identification labels in the jar have "Mexique" written on them. The specimens are presumably syntypes. The NHMW contains a ♂ donated by Humbert and Saussure, which may be a syntype (Inventory number 2098, Acquisition number 1866.I.G).

*Linozonium mexicanum* (Humbert & Saussure, 1869)

*mexicanum* Humbert & Saussure, 1869a: 153 [*Craspedosoma*].

Mexico, Cordillera orientalis. Unspecified number of ♀. Saussure & Humbert (1872) gave a more detailed redescription. The MHNG collection contains one specimen in alcohol under the name *Craspedosoma mexicana*. There is no data label but the identification labels in the jar have "Mexique" written on them. Hoffman (1999) refers to the specimen as holotype

but the type series was not specified and it should be considered a syntype.

*Cleidogona mexicana* (Humbert & Saussure, 1869)

**mexicanus** Saussure, 1859b: 328-329 [*Glomeridesmus*]. Mexique. Unspecified number of ♂ and ♀.

Saussure (1860) states that the specimens came from "Cordova, zone chaude du Mexique".

Carl (1902) illustrated the gonopod. The MHNG collection contains three specimens in alcohol (in two jars) and parts of at least five card-mounted or pinned specimens under the name *Sphaeridesmus mexicanus*. The pinned specimens are broken, and some parts that have been secondarily card-mounted are not necessarily all from the same specimen. The ♂ specimen studied by Carl is in alcohol and labelled as a type with a locality label in the jar reading "Pic d'Orizaba, H. de Sss". Among the pinned specimens there are a ♂ and part of a ♀ labelled "Cordova, Mexique, M H de Saussure" which are clearly syntypes. The other specimens were collected by Sumichrast or have illegible labels and are less certainly syntypes. There is also a syntype in the ZMHB (Moritz & Fischer, 1978; ZMB213).

*Sphaeridesmus mexicanus* (Saussure, 1859)

**mexicanus** Saussure, 1859b: 332 [*Julus*].

Mexique. Unspecified series.

Saussure (1860) gave a more detailed redescription of both sexes, indicating that he had many specimens from numerous localities. Carl (1919) described and illustrated the gonopods. The MHNG collection contains four card-mounted ♂ specimens, eight card-mounted ♀ specimens and one ♂ specimen in alcohol under the name *Spirobolus mexicanus*. The card-mounted specimens have labels indicating that they were collected on Saussure's expedition (one ♀ lacks a label). The specimen in alcohol was collected by Sumichrast, labelled as a type and is the one studied by Carl. All these specimens are syntypes. There are further syntypes in the ZMHB (Moritz & Fischer, 1975; ZMB210) and in the MNHN (MY3487) according to their online database.

*Hiltonius mexicanus* (Saussure, 1859)

**mexicanus** Saussure, 1859b: 328 [*Oniscodesmus*].

Mexique. Unspecified series.

Saussure (1860) stated that the specimen(s) came from the "parties chaudes du Mexique (Cordova)." The MHNG collection has one card-mounted ♀ and one ♂ in alcohol under the name *Oniscodesmus mexicanus*. Both are labelled "Cordova, Mexique, M H de Saussure" and are from the type series. Hoffman (1979a: 5) designated the ♂, which was transferred to alcohol from the dry collection, as lectotype.

*Cyphodesmus mexicanus* (Saussure, 1859)

**mexicanus** Humbert & Saussure, 1869a: 156 [*Platydesmus*].

Mexico, Cordillera orientalis. Unspecified series.

Saussure & Humbert (1872) gave a more detailed redescription, giving the type locality "Sierra de Agua" and mentioning nine ♂ specimens. The MHNG collection has four card-mounted specimens. The two largest specimens, mounted on the same card, have the locality "Mexiq." written on the identification label, and "A." written at the lower right corner of the card. Another specimen has an identification label without locality and the last specimen has no labels but "A." written in the lower right corner of the card. There is no reason to suppose that they are not all syntypes. There is also a ♀ syntype in the NHMW (Inventory number 2099, Acquisition number 1866.I.D)

*Platydesmus mexicanus* Humbert & Saussure, 1869

**mexicanus** Saussure, 1859a: 327 [*Stenodesmus*].

Terres chaudes du Mexique. Unspecified number of ♂ and ♀.

Saussure (1860) gave a more detailed description and the type locality as Cordova. Carl (1903) stated that the dry ♂ type specimen was so badly damaged that he could only examine the last segment of the gonopod. The MHNG collection has one card-mounted ♀ under the name *Stenodesmus mexicanus*. It is labelled "t.c. [terres chaudes], Mexique" and the anterior part of the body is missing. This specimen is clearly a syntype. The remains of the ♂ syntype studied by Carl are apparently lost.

*Stenodesmus mexicanus* Saussure, 1859

**modestus** Humbert, 1865: 53-54, pl. 5, fig. 23 [*Spirostreptus*].

Peradenia. Two ♀.

No specimens found in the MHNG. The whereabouts of the syntypes is unknown. The generic placement of the species is uncertain.

'*Spirostreptus*' *modestus* Humbert, 1865

**montezumae** Saussure, 1859b: 330 [*Julus*].

Vera-Cruz. Unspecified series.

Saussure (1860) gave a more detailed redescription of both sexes. The MHNG collection contains a ♂ in alcohol under the name *Orthoporus montezumae* and a ♀ in alcohol under the name *Spirostreptus montezumae*. The ♂ is labelled as holotype but because the type series was unspecified it should be considered as a syntype. The ♀ is identified as *montezumae* var. and may not be a syntype. There is a further syntype in the MNHN (MY4388) according to their online database.

*Orthoporus montezumae* (Saussure, 1859)

**montezumae** Saussure, 1859a: 323 [*Polydesmus* (*Fontaria*)].

Versant orientale de la Cordillière du Mexique. Unspecified series.

Saussure (1860) gave a much more detailed redescription of both sexes, and stated that it was common around Mirador and Cordova, and that he took specimens in

many localities between 1000 and 7000 feet in altitude. The MHNG has one ♂, one ♀ and a badly damaged specimen in the dry collection and a further ♀ specimen in alcohol, all under the name *Fontaria montezumae*. The data labels of the dry specimens read “Puebla, Mexique” with only that of the ♀ having Saussure’s name on the label. There is also a glass vial containing a dry pair of gonopods secured through the cork stopper. The ♀ in alcohol has the data label “Moyoapan”. These are all part of the type series. The ♂ was designated as lectotype by Hoffman (1999: 348). There is a further paralectotype in the ZMHB (Moritz & Fischer, 1978; ZMB203).

*Rhysodesmus montezumae* (Saussure, 1859)

*mystecus* Saussure, 1860: 369-370, fig. 36 [*Julus*].

Régions tempérées du Mexique, Oaxaca. Unspecified number of ♂ and ♀.

Carl (1919) described and illustrated the gonopods. The MHNG collection contains one ♂ specimen in alcohol under the name *Messicobolus mystecus*. It is labelled “t. c. Mexique” and is accompanied by a glass vial containing a pair of gonopods with the label “*Messicobolus tepanacus* Sauss. = *mystecus* Sauss voir Carl 1919, métatype ♂, Gonopodes postérieures.” This specimen is the one referred to by Carl (1919: 387) as having been labelled “tepanacus” and it is not a syntype. The whereabouts of the type specimens is unknown.

*Messicobolus mystecus* (Saussure, 1860)

*mystecus* Humbert & Saussure, 1869a: 150 [*Polydesmus* (*Fontaria*)].

Mexico temperata. Unspecified number of ♂ and ♀.

Saussure & Humbert (1872) gave a more detailed redescription and gave the locality “Cordillère orientale, région moyenne”. The MHNG collection contains two specimens in alcohol under the name *Fontaria mystecus*. There is no data label but the identification labels in the jar have “Mexique” written on them. One of these labels reads “*Polydesmus mystecus* Sss et H., Type, Mexique”, indicating that the specimens are syntypes.

*Rhysodesmus mystecus* (Humbert & Saussure, 1869)

*nahuus* Humbert & Saussure, 1869a: 150-151 [*Polydesmus* (*Fontaria*)].

Mexico temperata. Unspecified number of ♂ and ♀.

Saussure & Humbert (1872) gave a more detailed redescription, the locality “Cordillère orientale” and stated that they had one ♂ and seven ♀. The MHNG collection contains one specimen in alcohol under the name *Fontaria nahua*. There is no data label but the identification labels in the jar have “Mexique” or “Cordova” written on them. One of these labels reads “*Polydesmus nahua* Sss et H. (type) Cordova” indicating that it is a syntype. There is one broken ♀ syntype in the NHMW (Inventory number 3333, Acquisition number 1866.I.B) donated by Humbert and Saussure. The whereabouts of the other syntypes is unknown.

*Rhysodesmus nahuus* (Humbert & Saussure, 1869)

*nahuus* Humbert & Saussure, 1869a: 154 [*Spirobolus*]. Mexico, Cordillera orientalis. Unspecified number of ♂ and ♀.

Saussure & Humbert (1872) gave a more detailed redescription, the type locality “Sierra de Moyoapan” and indicated that they had three ♂ and three ♀. Carl (1919) redescribed the species and illustrated the gonopods. The MHNG collection contains parts of at least seven specimens in alcohol under the name *Chelogonobolus nahuus*. The specimens are in two vials and a third vial contains a damaged pair of gonopods. There is no data label but there is a label indicating that the specimens were studied by Carl for the 1919 publication and therefore include syntypes.

*Chelogonobolus nahuus* (Humbert & Saussure, 1869)

*nattereri* Humbert & Saussure, 1870: 173 [*Polydesmus* (*Oxyurus*)].

Brasilia. Unspecified number of ♀.

Saussure & Humbert (1872) gave a more detailed redescription. No specimens found in the MHNG. The NHMW contains one ♀ (Inventory number 3296, Acquisition number 1866.I.137b). According to the Acquisition Register, *P. decolor* and *P. nattereri* were described from lot 137 which comprised only two specimens; this specimen is therefore the holotype. The generic placement is uncertain and the genus *Leptodesmus* remains poorly defined (Hoffman, 2012).

*Leptodesmus nattereri* (Humbert & Saussure, 1870)

*nattereri* Humbert & Saussure, 1870: 176 [*Spirostreptus*]. Brasilia. Unspecified series.

Saussure & Humbert (1872) gave a more detailed redescription of the ♂ only, the type locality as Caicara and stated that the specimen(s) had been collected by Natterer. No specimens found in the MHNG. The NHMW contains a single ♂ syntype collected by Natterer (Inventory number 2171, Acquisition number 1866.I.48). The locality probably refers to a fazenda by the Paraguay River where Natterer stayed between October 1825 and June 1826 (Schmutzer, 2007). Hoffman (1999: 36) considered the original placement of this species in the genus *Spirostreptus* instead of *Spirobolus* a probable *lapsus calami*. The generic placement follows Marek *et al.* (2003).

*Rhinocricus nattereri* (Humbert & Saussure, 1870)

*nietanus* Saussure, 1860: 365-366, fig. 33 [*Julus*].

Mexique, près de Cuernavaca. Unspecified number of ♂. The pagination of the publication is faulty and reads 565-566. Saussure & Humbert (1872) implied that the original description was based on one immature specimen, stating that they had subsequently received adults of both sexes collected by Matija Botteri. Carl (1919) described and illustrated the gonopod of Saussure’s specimen. The MHNG contains five specimens in alcohol in two jars under the name *Saussurobolus nietanus*. One jar contains

the ♂ specimen studied by Carl. The specimen is in a vial with the label “Atlhuayan, Mexique” and another vial contains a broken pair of gonopods. The jar is labelled “Holotypus” but the specimen should be considered a syntype because the original description did not clearly define the type series. The specimens in the second jar are in fragments and have three identification labels with “Mexico” or “Mexique” as the locality, one indicating only ♂ while the other two read “♂♀ type!” These specimens may be syntypes but it is more likely that the ♀ is part of the material collected by Botteri.

*Centrelius nietanns* (Saussure, 1860)

**novarae** Humbert & Saussure, 1869b: 689-690 [*Polydesmms*].

Auckland, Nouvelle-Zélande (Musée de Vienne, Voyage Novara). Unspecified number of ♂ and ♀.

Attems (1898) redescribed the species in more detail, using type specimens in the NHMW. The MHNG collection contains one ♂ specimen in alcohol under the name *Strongylosoma novarae*. A label in the jar reads “Strongylosoma novarae H. u S., Nouv. Zealand, Mus. Vienne” indicating that it is part of the type series. Rowe & Sierwald (2006: 535) designated a ♂ specimen in the NHMW as the lectotype and a ♀ specimen as a paralectotype (Inventory number 3426/3). There are also five other specimens (Inventory number 3426/1). The Acquisition number for all three lots is 1866.I.10a, even though only six specimens were sent to Humbert and Saussure, and these were identified as belonging to two species. This is the type species of the genus *Akamptogomis* Attems, 1914.

*Akamptogomis novarae* (Humbert & Saussure, 1869)

**olmecus** Humbert & Saussure, 1869a: 155 [*Parajulus*]. Mexico, Cordillera orientalis. Unspecified number of ♂ and ♀.

Saussure & Humbert (1872) gave a more detailed redescription, the type locality Moyoapan and stated that they had six ♂ and eight ♀. The MHNG collection contains 3 ♂ and parts of at least 6 ♀ in alcohol, in three jars. The ♂ lectotype, designated by Mauriès (1972: 160), is in one jar, two ♂ and five ♀ labelled as paralectotypes are in the second, while fragments of ♀ are in the third. According to notes in the jars, the lectotype and paralectotypes were transferred from the dry collection by Mauriès in 1971.

*Parajulus olmecus* Humbert & Saussure, 1869

**orizabae** Humbert & Saussure, 1869a: 151 [*Polydesmms* (*Oxyrnus*)].

Mexico, Orizaba. Unspecified number of ♀.

Saussure & Humbert (1872) gave a more detailed redescription. The MHNG collection contains one ♀ in alcohol under the name *Rhysodesmms orizabae*, labelled as a type. The specimen has been transferred from the dry collection and the original identification and locality

label is illegible. Hoffman labelled this specimen as the holotype, but since the type series was not specified it should be considered a syntype.

*Neoleptodesmus orizabae* (Humbert & Saussure, 1869)

**otomitus** Saussure, 1859b: 330 [*Julus*].

Mexique. Unspecified series.

Saussure (1860) gave a more detailed redescription of the ♀, stating that he had eight specimens, all ♀. He gave a number of localities: “Cordova, Vera Cruz, San-Andres-Tuxtla – Oaxaca?” The MHNG collection contains one specimen in alcohol under the name *Julus otomitus*. The specimen has been transferred from the dry collection and the original label is illegible. A more recent label states that the specimen was identified as the type of *Orthoporus otomitus* by Hoffman in 1975. This specimen is a syntype. There is a syntype in the ZMHB (Moritz & Fischer, 1974; ZMB212, erroneously referred to as the holotype). A specimen in the NHMW collection (Inventory number 2445, Acquisition number 1866.I.H) donated by Humbert & Saussure is probably another syntype. The NHMW collection also contains a ♂ collected by Friedrichsthal in “Nova Grenada” (Inventory number 2444, Acquisition number 1866.I.51c) and fragments of three ♀ collected by Scherzer in “Central America” (Inventory number 3043, Acquisition number 1866.I.119) which were identified as this species by Humbert & Saussure.

*Orthoporus otomitus* (Saussure, 1859)

**otomitus** Saussure, 1859a: 322 [*Polydesmms* (*Fontaria*)]. Plateau du Mexique. Unspecified series.

Saussure (1860) gave a more detailed description of both sexes, although based on apparently immature specimens. The MHNG collection has two dry specimens under the name *Fontaria otomitus*. One is card-mounted and has the label “♀ Puebla, Mexique, M H de Saussure,” the other is directly pinned with a small piece of card supporting the centre of the specimen and is unlabelled. Hoffman (1999) stated that he had only found one immature ♂ in the MHNG, it is unclear whether this refers to the unlabelled specimen. Both specimens are presumably syntypes.

*Rhysodesmms otomitus* (Saussure, 1859)

**paraensis** Humbert & Saussure, 1870: 176 [*Spirostreptus*]. Para. Unspecified series.

Saussure & Humbert (1872) gave a more detailed redescription of both sexes. No specimens found in the MHNG. The acquisitions register of the NHMW lists a single specimen (Acquisition number 1866.I.38) but no specimen can be located in the collection; the type material appears to be lost. Hoffman (1999: 36) considered that the original placement of this species as a member of the genus *Spirostreptus* rather than *Spirobolus* was probably a *lapsus calami*.

*Rhinocricus paraensis* (Humbert & Saussure, 1870)

*persicus* Humbert & Saussure, 1869b: 687-688 [*Polydesmus* (*Strongylosoma*)].

Perse, Kotschy (Musée de Vienne). Unspecified series.

Attems (1898) redescribed this species and noted that the type specimens in the NHMW were in very bad condition and might not be useful. No specimens found in the MHNG. The NHMW contains six presumed syntypes, all of them broken but including a fragment with a pair of gonopods *in situ* (Inventory number 3574, Acquisition number 1866.I.215). The Acquisition Register lists the localities as “Karak insul” (Kharg Island) and “Sin. Pers.” but only enumerates five specimens.

*Tetrarthrosoma persicuum* (Humbert & Saussure, 1869)

*pfeifferae* Humbert & Saussure, 1869b: 680-681 [*Polydesmus* (*Stenonia*)].

Batavia, Ida Pfeiffer (Musée de Vienne). Unspecified number of ♂.

Attems (1899) redescribed this species but did not explicitly refer to type specimens in the NHMW. No specimens found in the MHNG. The NHMW contains a single broken ♂ type specimen (Inventory number 2117, Acquisition number 1866.I.172). The Acquisition Register shows that the lot contained only one specimen, so this can be considered the holotype. The generic placement follows Jeckel (2007).

*Gigantorhacus pfeifferae* (Humbert & Saussure, 1869)

*picteti* Saussure, 1859a: 325-326 [*Polydesmus* (*Paradesmus*)].

Terres chaudes du Mexique. Unspecified series.

Saussure (1860) placed this name in the synonymy of *P. klugii* Brandt, 1839. He stated that the latter species is abundant and that he collected it “à Cordova, à Orizaba, à Panuco et sur tout le versant oriental du plateau”. Hoffman (1999: 389) erroneously assumed that the localities given by Saussure for the distribution of *P. klugii* referred to *P. picteti* whereas Saussure (1860: 294) implied that a single ♀ specimen served for the original description. The MHNG collection contains 14 card-mounted specimens under the name *Pachyurus klugii*. No specimen can be identified as the type of *P. picteti* from the labels, but one fits the size given in the original description and most of the characters described by Saussure (1860: 295), and it may be the holotype.

A junior synonym of *Anplinus klugii* (Brandt, 1839)

*picteti* Humbert, 1865: 59-61, pl. 5, fig. 26 [*Siphonophora*].

Montagnes qui dominant Peradenia (sous les écorces).

One ♂ and two ♀.

The MHNG collection has two card-mounted ♀ and one ♂ in alcohol under the name *Siphonophora picteti*. The jar holding the ♂ contains the label “Siphonophora Picteti Humb., (Type), Peradenia Ceylon, Voy. Humb.” indicating that it is a syntype. One of the dry ♀ has the data label “Peradenia, Ceylan, V<sup>ge</sup> Humbert,” the other lacks a data label but the species name label in the box

has “Ceylan” written in the lower left corner. The jar is labelled as holotype but all three specimens are syntypes. *Pterozoniium picteti* (Humbert, 1865)

*sallei* Saussure, 1860: 300-301, fig. 8 [*Polydesmus*].

Antilles, Saint-Domingue, leg. Sallé. Unspecified number of ♀.

The MHNG collection has a card-mounted ♀ specimen and a ♂ in alcohol under the name *Leptodesmus sallei*. The ♂ is from Haiti, but the ♀ has the data label “S<sup>t</sup> Domingue, Antilles, M H de Saussure” and is a syntype. Hoffman (1999) refers to this specimen as the holotype without justification. The generic placement follows Pérez-Asso (2010).

*Beatadesmus sallei* (Saussure, 1860)

*saussurei* Humbert, 1865: 26-27, pl. 2, fig. 8 [*Polydesmus*].

Peradenia près Kandy. Unspecified number of ♂ and ♀ (several samples).

The MHNG collection contains one card-mounted ♂ and two specimens in alcohol in separate jars under the name *Prionopeltis saussurei*. The dry specimen is labelled “P<sup>er</sup>adenia, Ceylan, V<sup>ge</sup> Humbert.” Both of the specimens in alcohol have a label in the jar that reads “Polydesmus saussurei Humb. (Type) Peradenia, Ceylan, Voyage Humbert.” One of the specimens in alcohol is broken into many pieces. All three are syntypes. There are also specimens collected by Carl under this name in the MHNG; these were collected after the publication of the original description and are not syntypes. The generic placement follows de Zoysa *et al.* (2016).

*Anoploidesmus saussurei* (Humbert, 1865)

*simillinus* Humbert & Saussure, 1869a: 150 [*Polydesmus* (*Fontaria*)].

Mexico temperata. Unspecified series (more than one individual).

Saussure & Humbert (1872) gave a more detailed redescription, and mentioned the locality “Cordillère orientale; Santa Cruz près Orizaba”, noting that the species was found under the bark of trees. The MHNG collection has six card-mounted specimens under the name *Fontaria simillina*. Two ♂ specimens mounted on the same card have the label “5d” while four smaller specimens, all mounted on the same card, have the label “5c”. There is also a glass vial with a dry pair of gonopods secured by a pin through the cork stopper. Hoffman (1966: 16) designated the smaller ♂ (mounted legs-up) as lectotype, as indicated by the word “Lectotype” handwritten on the card at the rear of the specimen.

*Stenodesmus simillinus* (Humbert & Saussure, 1869)

*simplex* Humbert, 1865: 34-35, pl. 3, fig. 14 [*Polydesmus* (*Strongylosoma*)].

Pundel-Oya Valley. Unspecified series.

Carl (1932) gave a new illustration of the gonopod,

without stating that it came from the type. The MHNG collection contains the gonopod studied by Carl, stored in alcohol under the name *Orthomorpha (Kalorthomorpha) simplex*. An undated label in the jar indicates that Hoffman identified these as part of the type; given that the type series was undefined, it is a syntype. The generic placement follows de Zoysa *et al.* (2016).

*Anoplodesmus simplex* (Humbert, 1865)

*skinneri* Humbert, 1865: 31-32, pl. 3, fig. 12 [*Polydesmus (Strongylosoma)*].

Peradenia. Unspecified series.

In the comparison with *P. cingalensis*, Humbert implied that he only had ♂ specimen(s). No specimens found in the MHNG. The whereabouts of the type material is unknown. The generic placement follows de Zoysa *et al.* (2016).

*Singhalorthomorpha skinneri* (Humbert, 1865)

*strangulatus* Humbert & Saussure, 1870: 175 [*Spirostreptus*].

Brasilia. Unspecified series.

Saussure & Humbert (1872) gave a more detailed redescription, indicated the type locality as Mato Grosso and stated that they had two ♀ specimens. The MHNG collection contains one ♂ specimen in alcohol under the name *Spirostreptus strangulatus*. The specimen is in a vial and there is a pair of gonopods in a second vial. A label in the jar reads “*Spirostreptus strangulatus* Sss. et H., Brésil Mus. Vienne” indicating that it could be a syntype. Another label, dated 1960, states that Hoffman designated the specimen as lectotype, but this designation does not appear to have been published, possibly because the sex of the specimen makes its status as a syntype questionable. There is one broken ♀ syntype in the NHMW (Inventory number 2443, Acquisition number 1866.I.79). The Acquisition Register indicates that this lot comprised two specimens collected by Natterer, who was active in the Mato Grosso between 1823 and 1829. An undated label in the jar indicates that Hoffman considered the species to belong to the genus *Pseudonannolene*.

‘*Spirostreptus*’ *strangulatus* Humbert & Saussure, 1870

*subterraneus* Saussure, 1859a: 323-324 [*Polydesmus (Leptodesmus)*].

Profondeur des grandes cavernes de l’île de Cuba. Unspecified number of ♂ and ♀.

Saussure (1860) stated that he had numerous specimens and gave a more precise locality; “grotte de Cotilla, à dix lieues de la Havane,” to which he added in a footnote “et je crois aussi dans celle de Matanzas.” Carl (1903: 551-552) described the gonopod based on one of the “Original exemplare.” The MHNG collection contains two ♂ and two ♀ card-mounted specimens under the name *Leptodesmus subterraneus*, all of them damaged. Each has the data label “Grottes de Cuba, M H de

Saussure” and they are all syntypes. Hoffman (1999) refers to a ♂ holotype in the MHNG without justification. There are three further syntypes in the ZMHB (Moritz & Fischer, 1978; ZMB208).

*Amphelictogon subterraneus subterraneus* (Saussure, 1859)

*sumichrasti* Humbert & Saussure, 1869a: 151 [*Polydesmus (Oxyurus)*].

Cordillera mexicana orientalis. Unspecified series.

Saussure & Humbert (1872) gave a more detailed redescription and the type locality Orizaba. The specimens were collected by Sumichrast. Carl (1903) illustrated the gonopod based on one of the “Original exemplare” from Orizaba. The MHNG collection contains parts of at least two ♂ in alcohol under the name *Polydesmus sumichrasti*, at least one specimen having been transferred from the dry collection according to a label left in the box. One tube contains three vials, one with a broken body, one with a single gonopod and one with two loose segments. The second tube contains a vial with a broken pair of gonopods and an identification label in Carl’s handwriting. The third tube contains body fragments lacking the head and a label indicating that Keeton-Brown had identified it as *Neoleptodesmus* sp. in 1970. These are presumably all part of the type series. Hoffman (1999) refers to a ♂ holotype in the MHNG without justification.

*Neoleptodesmus sumichrasti* (Humbert & Saussure, 1869).

*syriacus* Humbert & Saussure, 1869b: 686-687 [*Polydesmus (Strongylosoma)*].

Syrie, Gödl (Musée de Vienne). Unspecified number of ♂ and ♀.

Attems (1898) redescribed the species and examined the type specimens, which were stated to be in poor condition. The MHNG collection contains a number of specimens in alcohol identified as *Tetrathrosoma syriacum*, but these were collected in the 1970s and are therefore not types. There are six potential syntypes in the NHMW (Inventory number 3576, Acquisition number 1866.I.83). The Acquisition Register states that four specimens collected by Gödel in 1853 were sent to Humbert. It is probable that the other specimens were collected by Edmund Boissier (a Genevan botanist who collected many specimens for Saussure in “Syria” and “Asia Minor”) and are part of the type series used in the original description even if they were not part of the original loan. Rudolf Oskar Gödel-Lannoy was consul-general in Beirut from 1850 to 1855 (Hamernik, 2006) and the type locality could therefore be Beirut.

*Tetrathrosoma syriacum syriacum* (Humbert & Saussure, 1869)

*syriacus* Saussure, 1859b: 329-330 [*Julus*].

Syrie, Edmond Boissier. Unspecified number of ♀.

The MHNG collection contains one ♀ in alcohol

under the name *Julus syriacus*. The specimen has been transferred from the dry collection and is labelled “Syrie, Voyage Boissier.” The jar has a holotype label, but the series was unspecified and the specimen should be considered a syntype.

*Archispirostreptus syriacus* (Saussure, 1859)

*taprobanensis* Humbert, 1865: 56-57, pl. 5, fig. 25 [*Spirobolus*].

Peradenia. Unspecified series.

The MHNG collection contains one specimen in alcohol under the name *Spirobolus taprobanensis*. A label in the jar reads “*Spirobolus taprobanensis* Humb., type, Peradenia Ceylan” indicating that it is a syntype. The generic placement is uncertain and here we follow the suggestion of Jeekel (2001c).

*Cingalobolus taprobanensis* (Humbert, 1865)

*tarascus* Saussure, 1860: 377-378, fig. 52 [*Julus*].

Les montagnes du Mexique. One ♀.

Saussure (1860: 378) stated “j’ai trouvé l’individu qui sert de type à cette espèce dans les montagnes du district d’Anganguo (Mechoacan), à une altitude de 9000 pieds”. No specimens found in the MHNG collection. The whereabouts of the holotype is unknown. The generic placement is uncertain.

*‘Julus’ tarascus* Saussure, 1860

*tarascus* Saussure, 1860: 327, fig. 24 [*Polydesmus* (*Rhachidomorpha*)].

Zone chaude du Mexique, Cordova. Unspecified series.

The MHNG collection contains parts of at least one ♂ specimen in alcohol under the name *Polydesmus tarascus*. At least one specimen has been transferred from the dry collection according to a label left in the box. One tube contains two vials, one with body fragments and the other with a pair of gonopods. A second tube contains a vial with body fragments. Both tubes have identification labels and it is not clear if they are different specimens, although the fact that there are two old data labels of the kind used in the dry collection reading “Cordova, Mexique, M H de Saussure” might indicate that there were two. The jar is labelled “Holotypus”, but since the type series was unspecified, the contents should be considered as syntype(s).

*Rhachidomorpha tarascus* Saussure, 1860

*tepanecus* Saussure, 1859b: 332 [*Julus*].

Cordova au Mexique. Unspecified series.

Saussure (1860) gave a more detailed redescription of the ♀ without mentioning the ♂ and without indicating the number of specimens. The MHNG collection contains one card-mounted ♀ specimen under the name *Spirobolus tepanacus* and two ♀ in alcohol in separate jars under the name *Messicobolus tepanaca*. The card-mounted specimen is labelled “Mexique, V<sup>se</sup> de Saussure” and fits the rough measurements given in the description.

One jar contains the label “*Spirobolus tepanacus* Sauss. type ♀, Santa Cruz, Sumichrast” and has been labelled as holotype. The other has only the locality “Mexique” on the old identification labels in the jar, but according to a label dated 2000, H. v. d. Merwe determined that the specimen is not in the same genus. The card-mounted specimen and that labelled as holotype are both syntypes. *Messicobolus tepanacus* (Saussure, 1859)

*tepanecus* Saussure, 1859a: 321 [*Polydesmus* (*Fontaria*)].  
Des terres chaudes du Mexique. Unspecified series.

Saussure (1860) gave a more detailed redescription of the ♂ without mentioning the ♀, and gave Cordova as the type locality. Saussure & Humbert (1872) described the ♀ on the basis of five specimens from Moyoapan and Santa Cruz, but these are not syntypes (and may not be conspecific). The MHNG collection has five dry specimens under the name *Fontaria tepanecus*, the ♂ having the data label “Cordova, Mexique, M H de Saussure.” There is also a tube containing a dry pair of gonopods secured by a pin through the cork stopper. These are all part of the type series. Hoffman (1970: 155) refers to a ♂ specimen in the MHNG collection as the holotype, which can be considered a lectotype designation by holotype assumption, particularly because the specimen has the label “Lectotype sig. Hoffman ’60.” *Rhysodesmus tepanecus* (Saussure, 1859)

*teres* Humbert & Saussure, 1870: 175 [*Spirostreptus*].

Brasilia. Unspecified series.

Saussure & Humbert (1872) gave a more detailed redescription of the ♀ only, stating that the specimen(s) had been collected by Natterer. No specimens found in the MHNG. There is one dissected ♂ type specimen in the NHMW (Inventory number 2442, Acquisition number 1866.I.46) collected by Natterer. The Acquisition Register shows that the lot contained only one specimen, so this can be considered the holotype. The sex given in the redescription is either an error or they used a different specimen, the whereabouts of which is unknown. The generic placement is uncertain.

*‘Spirostreptus’ teres* Humbert & Saussure, 1870.

*thwaitesii* Humbert, 1865: 27-28, pl. 2, fig. 9 [*Polydesmus*].

Peradenia. Unspecified series.

The MHNG collection contains one card-mounted ♂ specimen under the name *Prionopeltis thwaitesii*. It is labelled “Peradenia, Ceylan, V<sup>se</sup> Humbert” and is obviously one of the “Original exemplare” referred to by Carl (1902). The whereabouts of the other syntypes is unknown. The generic placement follows de Zoysa *et al.* (2016).

*Anoplodesmus thwaitesii* (Humbert, 1865)

*toltecus* Saussure, 1859b: 331 [*Julus*].

Mexique. Unspecified series.

Saussure (1860) indicated that he had more than one specimen, without mentioning their sex, and gave the locality “terres chaudes du Mexique, Cordova”. Carl (1919) described and illustrated the gonopods. The MHNG collection contains one ♂ in alcohol under the name *Rhinocricus toltecus*. The specimen is accompanied by a glass vial containing a pair of gonopods. There is a green label in the jar with “toltecus Sauss. Mexique” and a label in the vial with “Rhinocricus toltecus Sss, type! Gonopodes” in Carl’s handwriting. Because the type series was unspecified, Carl’s (1919: 381) identification of this specimen as the type constitutes an inadvertent lectotype designation.

*Anadenobolus toltecus* (Saussure, 1859)

**toltecus** Saussure, 1859a: 322 [*Polydesmus* (*Fontaria*)]. Cordova au Mexique. Unspecified series.

Saussure (1860) gave a more detailed redescription of both sexes, but indicated that the original description was based only on the ♀. The ♂ description could have been based on the specimen(s) that furnished the description of *P. mayus* Saussure 1859a, which he had placed in the synonymy of *P. toltecus* (Saussure, 1860: 325). The MHNG collection has parts of what appear to be one ♂ and one ♀ in alcohol under the name *Polydesmus toltecus*. The fragments are separated in five vials in the same jar. The ♀ specimen, which has been transferred from the dry collection, is labelled “Cordova, Mexique” and is probably a syntype of *P. toltecus*. The ♂ is unlabeled and could be a syntype of *P. mayus*.

*Rhysodesmus toltecus* (Saussure, 1859)

**totonacus** Saussure, 1860: 361, fig. 31 [*Julus*].

Mexique, Oaxaca. Unspecified number of ♂ and ♀.

The pagination of the publication is faulty and reads 561. Carl (1919) described and illustrated the gonopods. The MHNG collection contains two card-mounted specimens under the name *Spirobolus totonacus*. Both specimens have larger, secondary card mounts placed under the originals, and are accompanied by glass vials containing a pair of dry gonopods secured on pins through the cork stoppers. One of the dry specimens is labelled “Mexique” and “totonacus per expl. = zapotecus”, the latter written by Carl in pencil. The other lacks a data label but has “Mexique” written on the species name label pinned in the box. It bears a label “cet expl. doit être le véritable totonacus” written in pencil by Carl. Although Carl (1919: 381) identified the latter specimen as the holotype, the original description included both sexes and this does not qualify as an inadvertent lectotype designation. There is a further syntype in the MNHN (MY4396) according to their online database.

*Anadenobolus totonacus* (Saussure, 1860)

**totonacus** Saussure, 1859a: 321 [*Polydesmus* (*Fontaria*)]. Pic d’Orizaba, Mexique. Unspecified series.

Saussure (1860) gave a more detailed redescription of

the ♂ without mentioning the ♀, but implying that he had more than one specimen. The MHNG contains one card-mounted ♂ under the name *Fontaria totonacus*. The data label reads “Pic d’Orizaba, Mexique.” There is also a glass vial containing only unidentifiable dry fragments secured by a pin through the cork stopper. Hoffman (1999: 325) designated this specimen as lectotype, suggesting that another syntype (now to be considered as a paralectotype) might be in the BMNH.

*Rhysodesmus totonacus* (Saussure, 1859)

**tzendalus** Saussure, 1860: 370-371, fig. 37 [*Julus*].

Régions tempérées du Mexique, Oaxaca. Unspecified number of ♀.

The MHNG collection contains two specimens in alcohol under the name *Spirobolus tzendalus*, both broken. There is no data label but the identification labels in the jar have “Mexique” written on them. Hoffman (1999) speculated that the types may be lost because Carl did not revise the species, but since Carl was primarily focusing on illustrating the gonopods, he has very likely ignored the female type specimens, which are presumably also syntypes. There is a further syntype in the MNHN (MY4397) according to their online database.

*Messicobolus tzendalus* (Saussure)

**uncinatus** Humbert & Saussure, 1869a: 152 [*Polydesmus* (*Rachidomorpha*)].

Mexico, Cordillera orientalis. Unspecified number of ♂ and ♀.

Saussure & Humbert (1872) gave a more detailed redescription and the localities “Monte Azul, Cerro de Azeamela, Sierra de Agua, dans la Cordillère orientale.” They also noted that the species lived under the bark of pines. Carl (1903) illustrated the gonopod, although it is not clear which specimen(s) he studied. The MHNG collection contains one ♂ specimen in alcohol under the name *Rhachidomorpha uncinata* labelled as a type. The specimen is in fragments and lacks a data label. It was transferred from the dry collection and is presumably a syntype that had been placed in the collection before Saussure & Humbert (1872: 158) replaced the name with *Polydesmus* (*Rachidomorpha*) *aduncus* because it was a junior homonym of *P. uncinatus* Peters, 1864. There are also two broken specimens in alcohol under the name *Rhachidomorpha adunca*, also labelled as types.

*Rhachidomorpha adunca* Saussure & Humbert, 1872 (New replacement name)

**unicolor** Humbert, 1893: 41-42, pl. vi, fig. 1-6 [*Atractosoma*].

Mont Salève. One ♀ and several juveniles.

No specimens found in the MHNG. The whereabouts of the syntypes is unknown. The species was treated as *incertae sedis* by Brölemann (1935: 305).

*Atractosoma unicolor* Humbert, 1893



*vermiformis* Saussure, 1859a: 326 [*Polydesmus (Strongylosoma)*].

Terres chaudes du Mexique. Unspecified series.

Saussure (1860) stated that he had several ♀ specimens, and gave the locality as “terres chaudes du versant oriental de la Cordillère”. The MHNG collection contains a card-mounted ♀ under the name *Leptodesmus vermiformis*. It has the data label “Cordova, Mexique, M H de Saussure” and is almost certainly a syntype.

*Neoleptodesmus vermiformis* (Saussure, 1859)

*vicinus* Saussure, 1859a: 322 [*Polydesmus (Fontaria)*].

Plateau du Mexique. Unspecified series.

Saussure (1860) gave a more detailed redescription of both sexes, stating that he had eleven specimens. He gave the distribution as “les terres froides du Mexique, le plateau de l’Anahuac; toutefois on l’a pris aussi à Oaxaca.” Hoffman (1999) stated that he had not found this species in the MHNG, but the collection has three dry specimens under the name *Fontaria vicinus*. One card-mounted specimen is labelled “Puebla, Mexique” and the other “Mexique,” the latter is badly broken. There is a broken dry specimen in a glass tube containing a locality label “Puebla, Mexique” and secured by a pin through the cork stopper. There is also a glass vial with a pair of dry gonopods secured by a pin through the cork stopper. There is no reason to suppose that these are not syntypes. There is a further syntype in the ZMHB (Moritz & Fischer, 1978; ZMB204).

*Rhysodesmus vicinus* (Saussure, 1859)

*viridis* Saussure, 1859a: 326 [*Polydesmus (Rhachis)*].

Mexique, Tuxtla. Unspecified series.

Saussure (1860) gave a more detailed redescription of the ♂ without mentioning the ♀, but indicating that he had more than one specimen. The MHNG has two ♂ specimens in alcohol, labelled as types, under the name *Rhachis viridis*. These specimens have been transferred from the dry collection; both have the data label “Tuxtlan [sic], Mexique, M H de Saussure” and are obviously syntypes. Hoffman (1999) noted that a specimen in the NHMW, studied by Attems (1898), may also be a syntype. This specimen (Inventory number 8961, Acquisition number 1883.II.1), which was collected by Sumichrast and sold to the NHMW by Bilimek in 1883, is not part of the type series. This specimen, a ♂ lacking the gonopods, is probably associated with a microscopic preparation carrying gonopods, labelled as *Rhachis viridis* but without locality data, which might have been used by Attems (1898: 196, plate 4).

*Rhachodesmus viridis* (Saussure, 1859)

*woodi* Humbert & Saussure, 1870: 177 [*Spirostreptus*].

America borealis, Saint-Louis. Unspecified number of ♂.

Saussure & Humbert (1872) gave a more detailed redescription. No specimens found in the MHNG. There are two specimens in the NHMW. One, a dissected ♂ in

alcohol with the gonopods in a vial (Inventory number 2069, Acquisition number 1866.I.52), has the entry in the Acquisition Register “*Spirobol. Woodi* HBS. (Hekl) Amerika/St. Louis 1 [specimen].” The other ♂, also identified by Humbert and Saussure, has a separate entry (Inventory number 2170, Acquisition number 1866.I.82) and has the locality data “America borealis”. It is not clear whether the specimens are syntypes (interpreting “America borealis” and “St Louis” as the localities of the two specimens) or whether the first is the holotype. Hoffman (1999: 36) considered that the original placement of this species as a member of the genus *Spirostreptus* rather than *Spirobolus* was probably a *lapsus calami*, an inference supported by the Acquisition Register entry.

A junior synonym of *Narceus americanus* (Palisot de Beauvois, 1817)

*woodianus* Humbert & Saussure, 1869a: 152 [*Polydesmus (Scytonotus)*]

Mexico, Cordillera orientalis. Unspecified number of ♂ and ♀.

Saussure & Humbert (1872) gave a more detailed redescription and the localities Orizaba and Moyoapan. They also stated that they had 22 specimens collected by Sumichrast. The MHNG collection has ten card-mounted specimens under the name *Peridontodesmus woodianus*. One specimen has the label “Orizaba, Mexique, env. Sumichrast.” Six smaller specimens mounted on one card have the label “3a”; they are badly damaged. Two specimens mounted on one card also have the label “3a.” There is one unlabelled specimen. Although only one specimen is labelled with the type locality and collector, it seems probable that all of these specimens are syntypes. *Peridontodesmus woodianus* (Humbert & Saussure, 1869)

*zapotecus* Saussure, 1860: 359-361, fig. 30 [*Julus*].

Parties chaudes du Mexique. Unspecified number of ♂ and ♀.

The pagination of the publication is faulty and reads 559-561. Carl (1919) described and illustrated the gonopods using Saussure’s specimens. The MHNG collection contains one card-mounted specimen under the name *Spirobolus zapotecus* and a ♂ in alcohol under the name *Rhinocricus zapotecus*. The dry specimen is labelled “Mexique” and is presumably a syntype. The specimen in alcohol is broken and the gonopods are separated in a vial. It has a label in Carl’s handwriting “cet expl. était étiquetté chichimecus mais il est identique à zapotecus type. Saussure n’a pas eu le ♂ de chichimecus.” It is therefore not a syntype of *J. zapotecus*.

*Anadenobolus zapotecus* (Saussure, 1860)

*zapotecus* Saussure, 1860: 314-315, fig. 11 [*Polydesmus*].

Régions chaudes du Mexique, San-Andrés-Tuxtla etc. Unspecified number of ♂ and ♀.

The MHNG collection has one ♀ in the dry collection under the name *Fontaria zapotecus*, with the data label “Tuztlant [sic], Mexique, M H de Saussure” and there is no reason to doubt that it is a syntype despite Hoffman’s statement (1999: 353) that he could not find any type specimens in the MHNG.

*Rhysodesmus zapotecus* (Saussure, 1860)

*zelebori* Humbert & Saussure, 1870: 173 [*Polydesmus* (*Oxyurus*)].

Brasilia merid. Unspecified series.

Saussure & Humbert (1872) gave a more detailed redescription and the locality Rio de Janeiro. No specimens found in the MHNG. There is a broken ♂ syntype with a single gonopod in a vial in the NHMW (Inventory number 3321, Acquisition number 1866.I.6a) (Fig. 2). According to the Acquisition Register the locality is Rio de Janeiro. The generic placement is unclear, and Hoffman, 1979b did not include this species in *Leptodesmus*.

*Leptodesmus zelebori* (Humbert & Saussure, 1870)



Fig. 2. A syntype of *Leptodesmus zelebori*. (A) Head and anterior body rings (B) Ventral view of gonopod. (photos O. Macek/N. Akkari)

*zendalus* Humbert & Saussure, 1869a: 150 [*Polydesmus* (*Fontaria*)].

Mexico orientalis. Unspecified number of ♂ and ♀.

Saussure & Humbert (1872) gave a more detailed redescription, and the locality “Cordillère orientale.” The MHNG collection has one ♂ and one ♀ in alcohol under the name *Fontaria zendala*, and labelled as types. The data label in the jar reads “Moyoapan, Mexique”. The ♂ was designated as lectotype by Hoffman (1970: 157). *Rhysodesmus zendalus* (Humbert & Saussure, 1869)

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## New and rare species of *Holoparasitus* Oudemans, 1936 (Acari, Gamasida, Parasitidae) from the Athias-Henriot Collection

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**Abstract:** Five new species, *Holoparasitus madridensis*, *H. rondai*, *H. aquilinus*, *H. paralawrencei* and *H. floriformis* are described. Some characteristics of *H. lawrencei* Hyatt, 1987 are redescribed and a new species group, the *lawrencei*-group is established. New locality records for *H. maritimus* Hyatt, 1987 are given.

**Keywords:** Acari - Parasitidae - *Holoparasitus* - taxonomy - new records.

### INTRODUCTION

The Parasitidae material deposited in the Muséum d'histoire naturelle (MHNG) of Geneva, which includes the large collection of the well known acarologist C. Athias-Henriot, is surprisingly diverse and rich, especially in the genera *Holoparasitus* Oudemans, 1936, *Leptogamasus* Trägårdh, 1936 and *Pergamasus* Berlese, 1904.

The genus *Holoparasitus* now includes a total of 55 species, mainly from the Palearctic region (Witalinski, 2017a). Only 41 species were attributed to 7 groups of species and their characteristics analyzed by different authors. One of the most important characteristics, which separate these groups into two categories, is the presence or absence of an excipulum (an oval pattern on sternal cuticle, between coxa II and III) in the male. The species groups with an excipulum are: the *calcaratus*-group (Hyatt, 1987; Witalinski & Skorupski, 2002) with 7 species, the *peraltus*-group (Witalinski & Skorupski, 2003) and the *leuisphaericus*-group (Witalinski, 2006) both with 2 species.

The others species groups are: the *annulus*-group (Juvara-Bals & Witalinski, 2006) with 2 species, the *caesus*-group (Juvara-Bals, 1975) with 4 species, the *crassisetosus*-group (Witalinski, 2017a) with 3 species and the *mallorcae*-group (Juvara-Bals, 1975; Juvara-Bals & Witalinski, 2000; Juvara-Bals, 2008) with 21 species. Concerning the other taxa, more revisions will be necessary to include them in species groups.

This paper continues with the description of new species from soil and leaf litter in west Mediterranean countries (Juvara-Bals & Witalinski, 2000; Juvara-Bals &

Witalinski, 2006; Juvara-Bals, 2008). The new species, *Holoparasitus madridensis* sp. nov., *H. rondai* sp. nov., *H. aquilinus* sp. nov., belong to the *mallorcae* group. The new species *H. paralawrencei* from northern Spain and *H. lawrencei* from Great Britain are here placed in a new species group. *Holoparasitus floriformis* sp. nov. has peculiar morphological characteristics and cannot be included in any of the established species groups. The geographical distribution of *H. maritimus* Hyatt, 1987, described and previously known from Great Britain, is here also reported from Spain.

A better knowledge of the species in this genus would allow us to better understand their phylogenetic relationship and to re-evaluate the species groups. The key to the species of the genus *Holoparasitus* was recently published by W. Witalinski (2017b).

### MATERIAL AND METHODS

The material studied here is mostly part of the Athias-Henriot Collection, deposited in the Muséum d'histoire naturelle de Genève (MHNG) except for specimens of *H. lawrencei*, deposited in the Natural History Museum, London (NHML). In the majority of cases the specimens of *Holoparasitus*, examined in this paper from both collections, are in poor condition on permanent slides, so that some characteristics cannot be properly observed. The morphological terminology is based on Evans & Till (1979), the system of setal notation for the idiosoma follows that of Lindquist & Evans (1965) and Lindquist (1994). The following abbreviations are used: *hyp.*-hypostomatal setae, *pc.*-palpcoxal setae.

The measurements and indices characterizing females and males are those established by Juvara-Bals (2008). Morphometrics seem to be useful to separate closely related species. The length of the peritrematal groove, the length of tarsus I and IV give us information about the size of the mite, especially when mounted on permanent slides. Length and width of the mites are given only for two species kept in alcohol and earlier macerated in lactic acid, so that the size of the mite is indicative. The following measurements were also taken: epigynium height (h) represents the midline from the tip of the shield to the posterior margin and the basal width (b) is the length of its posterior margin; ratio h/b refers to the proportion between these two features of the epigynium; setae distance *st-st'* was measured between the two setae of pair *st* on the sternal shield. The setae on the idiosoma are simple, so that only their length (when possible) from the insertion to their tip, is given. Measurements in micrometers are specified after each presentation of a structure. I do not use standard characteristics, e.g. as female chelicera. The reasons for this are explained in the revisions of Micherdzinski (1969) and Hyatt (1987). Locality references, in the text, composed of initials followed by a number, refer to the Athias-Henriot collection. All the material, except the specimens of *H. lawrencei* was sampled by Prof. Herbert Franz.

## TAXONOMY

### Genus *Holoparasitus* Oudemans, 1936 *mallorcae* species group

#### *Holoparasitus madridensis* sp. nov.

Fig. 1

**Holotype:** Male; Spain, El Prado, surroundings of Madrid, sifting leaf litter under *Quercus ilex* L.; 5.02.1951 (Sp. 13).

**Paratypes:** 2 males and 5 females; with the same data as for the holotype.

**Other material examined:** 4 males, 4 females, 1DN; Spain, El Prado, surrounding of Madrid, sifting leaf litter under bushes of *Quercus ilex* L.; 05.02.1951 (Sp. 8). – 1 male, 14 females; Spain, El Prado, surrounding of Madrid, swampy soil near a spring, sifting litter of *Scirpus* sp.; 05.02. 1951 (Sp. 11). – 3 males, 3 females; Spain, surrounding of Torrelodones, north of Madrid, forest soil under *Quercus ilex* L.; 06.07.1952 (Sp. 93).

**Diagnosis:** Male palptrochanter with sharp protuberance situated between slightly pilose seta *v1* and thicker pilose seta *v2*; this character associated with elongated corniculi carrying a small protuberance in their distal part. Female endogynium cup-shaped, with two short protrusions on posterior margin; epigynium with ovoidal, subapical structure and with sharp triangular apex.

**Etymology:** The species name, a Latinized adjective, refers to the city of Madrid in the surroundings of which the species was sampled.

**Description of male:** Idiosoma well sclerotized, yellow-brown-colored; its length 648-672, width 388-456. Dimensions of setae: on podonotum *j1* = 36, *r5* = 48, others about 24; opisthonotal setae short 12-18. Length of peritrematal shield 197-205.

**Ventral idiosoma:** Genital lamina in a shallow concavity; anterior margin of genital lamina with truncated central prong and two lateral triangular extensions, microsclerite trapezoidal (Fig. 1B). Sternogenital shield reticulated, gland pore *gv1* present, length of sternal setae 42 to 48; gland pore *gv2* simple; 8-9 pairs of opisthogastric setae, their length 36 to 42.

**Gnathosoma:** Gnathotectum trispinate, with large median prong and tiny lateral ones (Fig. 1E). Corniculi elongated, with small protuberance in their distal third (Fig. 1D). Hypognathal groove with 8-10 slightly denticulate rows; length of simple setae: *hyp.1* = 36, *hyp.2* = 43, *hyp.3* = 24, *pc.* = 42-48. Palptrochanter with setae *v1* slightly pilose, *v2* barbed and with a small, sharp protuberance located between these setae (Fig. 1C). Chelicera (Fig. 1F): fixed digit straight, with 2-3 small denticles above and under pilus dentilis; movable digit 78 long, with 4-5 denticles on inner margin; spermatodactyl slightly arched; arthrodistal brush small.

**Legs:** Coxa II with a group of six denticles and an isolated basal one (Fig. 1L). Spurs of legs II illustrated in Fig. 1A: short rounded apophysis and axillary process, ellipsoidal apophysis located on anterior margin of genual segment, tibial apophysis rectangular, its anterior margin indented. Measurements: tarsus I = 156-168; tarsus IV = 170-180.

**Description of female:** Idiosoma well sclerotized, yellow-brown-colored; its length 648-672 and its width 432-456. Dimensions of some podonotal setae: *j1* = 38, *r5* = 54; opisthonotal setae 12. Length of peritrematal shield 206-209.

**Ventral idiosoma:** Presternal plate ribbon-like, serrated, with median constriction; sternal shield reticulated, *gv1* situated near setae *st3*, sternal setae simple, their length ranging from 42 to 48. (Fig. 1G). Paragynial shield with rounded posterolateral protrusions, metagynial shield ellipsoidal (Fig. 1I). Epigynium with sharp triangular apex, its length 48-54; subapical structure discoidal (Fig. 1H).

Endogynium cup-like, with two conical protrusions on its posterior margin; their height 24-30 and their basal distance 4-5 (Fig. 1J-K). Gland pore *gv2* simple. Eight pairs of simple opisthogastric setae, their length 24 to 30. Adanal and postanal setae simple and short (12 long). Measurements: Sternal shield: *st1-st1'* = 50-60, *st2-st2'* = 80-96, *st3-st3'* = 108-117. Epigynium: height = 144-156, basal width = 168-180, h/b = 0.85-0.86.

**Gnathosoma:** Gnathotectum trispinate, its central prong sharply pointed (Fig. 1N). Corniculi conical, hypognathal

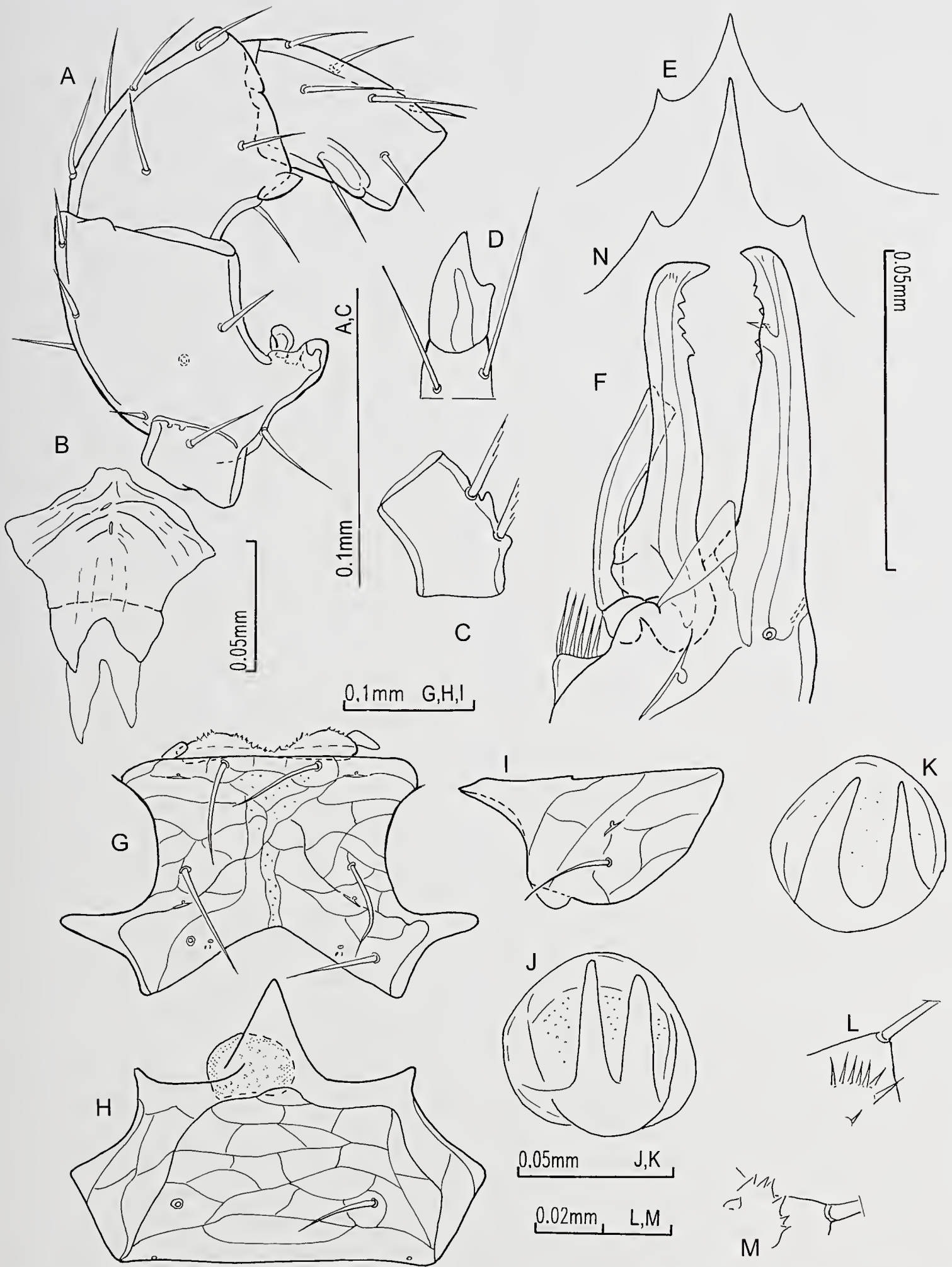


Fig 1. *Holoparasitus madridensis* sp. nov., male (A-F, M), female (G-L, N). (A) Femur, genu, tibia of leg II. (B) Genital lamina. (C) Palptrochanter. (D) Corniculus. (E-N) Gnathotectum. (F) Chelicera, anti-axial view. (G) Presternal plate and sternal shield. (H) Epigynum. (I) Paragynium. (J-K) Endogynium. (L-M) Group of denticles on coxa II.

groove with 8 rows of denticles, last 3 oligodenticulated. Hypostomatic setae simple, palpcoxal setae pilose; their length *hyp.1* = 36, *hyp.2* = 30, *hyp.3* = 24, *pc.* = 48. Length of movable digit of chelicera 84. Palptrochanter with small protuberances between pilose seta *v2* and simple seta *v1*.

*Legs*: Coxa II with a group of six short denticles (Fig. 1M). Tarsus I = 163-168; tarsus IV = 180-205.

**Remarks:** *Holoparasitus madridensis* sp. nov. is most closely related to the species in which males are characterized by a trispinate gnathotectum with a slender prong and two similar short lateral spines, and by a chelicera having denticles on the inner margin of both digits and a slightly curved spermatodactyl. These are: *H. mallorcae* Juvara-Bals, 1975 and *H. vaucheri* Juvara-Bals, 2008 from Algeria and *H. mahnerti* Juvara-Bals, 2008 from Morocco. The new species is distinguished by the shape of its corniculus, the sharp protuberance, between setae *v1* and *v2* on palptrochanter and the slightly arched spermatodactyl. Females differ from other species with two protrusions on the posterior margin of the endogynium (*H. mallorcae*, *H. vaucheri*, *H. gibber* Juvara-Bals & Witalinski, 2000) by the two protrusions being short and straight, the endogynial sac without denticles and the subapical epigynial structure formed like an ovoid disc.

#### *Holoparasitus rondai* sp. nov.

Fig. 2

**Holotype:** Male; Spain, Sierra de Ronda, Monte Arastepa, Prov. Andalusia, sifting of leaf litter and humus under bushes of *Quercus ilex* L. and *Crataegus* sp., alt. 1100 m; 26.02.1951 (Sp. 34).

**Paratypes:** 10 males and 17 females, 1 DN; same data as for holotype.

**Other material examined:** 2 males, 3 females; same locality as types, sifting of turf soil, alt. 1400 m (Sp. 37).

**Diagnosis:** Male characterized by trispinate gnathotectum with a straight line between central prong and lateral spines and by tibia II with an ovoid and large apophysis. Female distinguished by epigynium with a subapical structure extending slightly beyond lateral margin of apex, its posterior side denticulate.

**Etymology:** The name is derived from the mountain Sierra de Ronda where the species was found.

**Description of male:** Length of idiosoma 624-650, width around 360. Cuticle well sclerotized, yellow-brown; length of some podonotal setae: *j1* = 36, *j2* = 48, *s1* = 24, *z2* = 36 others 25 to 30; opisthonotal setae from 14 to 16; length of peritrematal shield 210-228.

*Ventral idiosoma:* Sternogenital shield reticulated,

without any pattern. Genital lamina with large triangular central process and rounded corners. Length of peritrematal shield = 210-228.

*Gnathosoma:* Gnathotectum trifold, with triangular, slender central prong and two little lateral spines (Fig. 2D). Hypognathal groove with 10 fine denticulated rows, hypostomatic setae simple, palpcoxal setae pilose, their length *hyp.1* = 42, *hyp.2* = 48, *hyp.3* = 24, *pc.* = 48. Corniculi conical, with protuberance in proximal half (Fig. 2E). Palptrochanter with seta *v1* barbed and *v2* slightly pilose; between them a flat protuberance (Fig. 2C).

*Chelicera* (Fig. 2A): Fixed digit slender its apex slightly curved, two little teeth above and below pilus dentilis. Movable digit with two denticles and a tooth at end of spermatotrema. Medium-sized brush-like process on arthrodial membrane (Fig. 2B).

*Legs:* Armature of leg II as in Fig. 2F: truncated femoral apophysis and rounded axillary process both ending on same level. Trapezoidal apophysis located near distal genual margin. Oval tibial apophysis large. On coxa II a ridge of 9 denticles. Measurements: tarsus I = 175-182; tarsus IV = 184-192.

**Description of female:** Length of idiosoma 720-745. Podonotal setae simple, *j1* = 48, others 24-42 long; opisthonotal setae short (18). Peritrematal shield 222-240 long.

*Ventral idiosoma:* Presternal plate denticulate, narrowed medially. Sternal shield with one dotted stripe medially; gland pore *gv1* located under *st3*, near posterior margin (Fig. 2G). Epigynium with pyramidal apex; subapical epigynial structure with lateral sides smooth and its center denticulated (Fig. 2H). Paragynial shield with ellipsoidal posterior protrusions, metagynial sclerite elongated (Fig. 2I). Endogynium cup-shaped, with two protrusions curved inwards; lateral walls of some specimens armed with 1 to 3 spines (Fig. 2J-K). Eight pairs of ventral setae, on opisthogaster, their length 42 to 60. Gland pore *gv2* simple. Measurements: sternal shield: *st1-st1'* = 54-57, *st2-st2'* = 85-93, *st3-st3'* = 110-120; length of sternal setae *st1* = 54-60, *st2* = 90-96, *st3* = 110-120; *h* = 96-97. Epigynium: height = 144-146, basal width = 180-192, *h/b* = 0.75-0.83.

*Gnathosoma:* Gnathotectum trispinate, with central prong long (Fig. 2L). Hypognathal groove with 10 rows of fine denticles; hypostomatic setae simple (*hyp.1*, *hyp.2* = 48, *hyp.3* = 24), palpcoxal pilose (48-54). Corniculi conical. Palptrochanter with seta *v1* barbed and seta *v2* slightly pilose.

*Legs:* Coxa II with an anterolateral ridge of 9 denticles. Tarsus I = 180-197; tarsus IV = 204-209.

**Remarks:** The most easily recognized features, which distinguished the male of *H. rondai* sp. nov. from the other species of the *mallorcae*-group, are the big oval apophysis (78 long) on tibia II, the characteristics of the chelicera and those of the trochanter of the pedipalp.



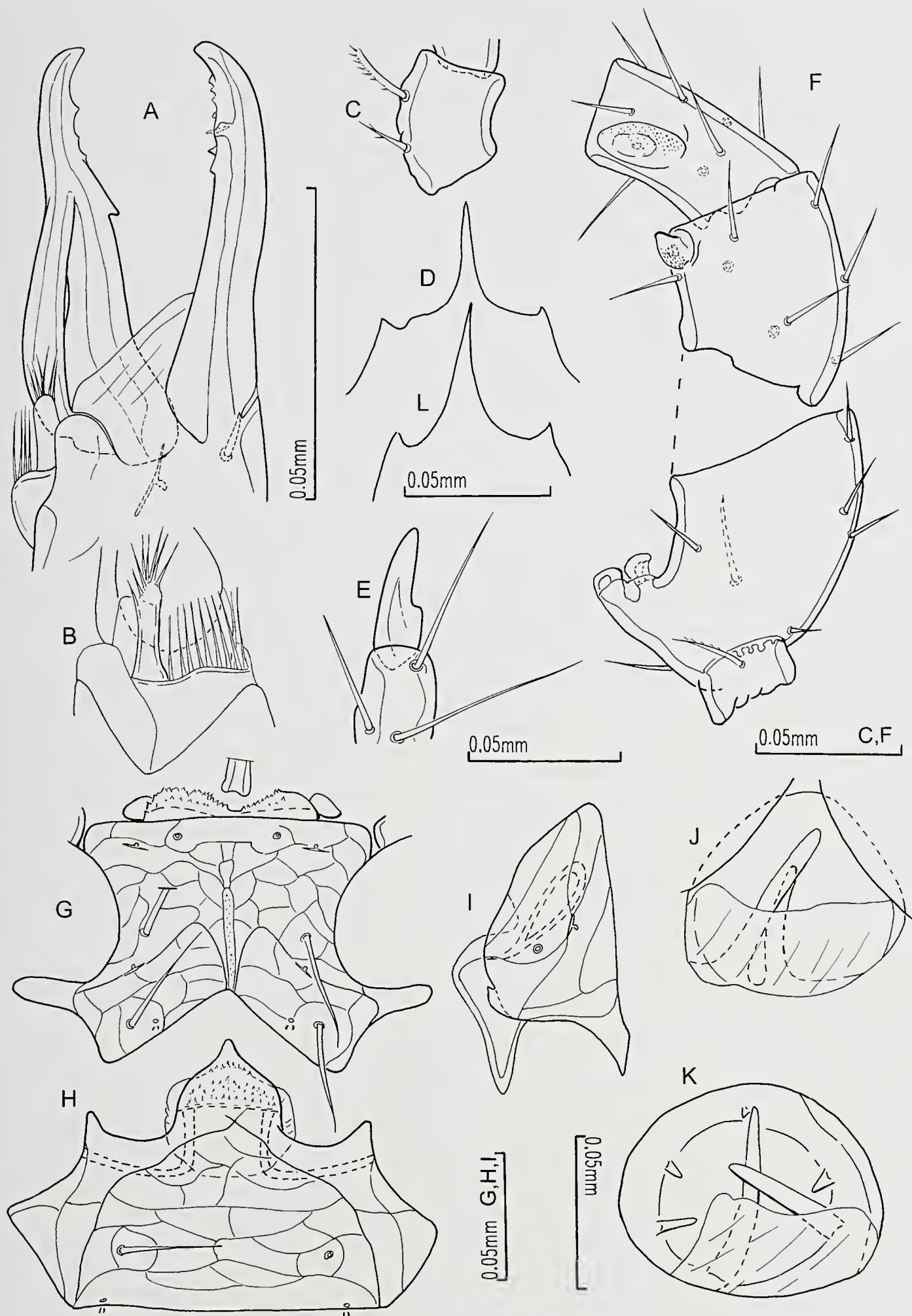


Fig 2. *Holoparasitus rondai* sp. nov., male (A-F), female (G-L). (A) Chelicera, paraxial view. (B) Arthroal membrane with brush-like process. (C) Palptrochanter. (D, L) Gnathotectum. (E) Corniculus. (F) Femur, genu tibia of leg II. (G) Presternal plate and sternal shield. (H) Epigynum. (I) Paragynium. (J-K) Endogynium.

The female is similar to the females of the *mallorcae*-group by having a cup-shaped endogynium with two protrusions on its posterior margin (sometimes with denticles on lateral walls) and a trispinate gnathotectum. This is particularly visible in *H. mallorcae*, *H. vancheri*, *H. ellipticus* Juvara-Bals & Witalinski, 2000 and *H. gibber*.

The form of the endogynial protrusions (curved inwards) as well as characteristics of the epigynial apex make the female of *H. rondai* sp. nov. easily distinguishable.

***Holoparasitus aquilinus* sp. nov.**

Fig. 3

**Holotype:** Male; Morocco, Monte Lachab (Lechhab) near Beni Bajale (Beni Bejalle)-Beni Bouchaib, west Rif, near a spring, alt. 1700 m, leaf litter from *Quercus ilex* L.; 2.04.1959 (Sp. 656).

**Paratype:** 1 female; same data as for holotype.

**Diagnosis:** Chelicera of male apex with movable digit hooked; fixed digit slightly curved, with 6-7 denticles, spermatodactyl arched. Epigynium with a long triangular apex and 2 spine-like lateral prongs; subapical epigynial structure a large slightly denticulate strip.

**Etymology:** The species name is a Latin cognomen derived from “*aquila*” = eagle, meaning “the eagle-like”, and refers to the shape of the apex of the movable digit of the male chelicera being hooked like the beak of an eagle.

**Description of male:** Length of squashed idiosoma 600-624. Dimensions of some podonatal setae: *jl* = 30 others 24; opisthonatal setae very short, 6-7 long. Length of peritrematal shield 192-204.

**Ventral idiosoma:** Sternogenital shield reticulated. Genital lamina with anterior margin rounded and with subgenital sclerite rectangular (Fig. 3C). Length of *st1* = 36. Distance between setae: *st1-st1'* = 72, *st2-st2'* = 84, *st3-st3'* = 96, *st4-st4'* = 66. Gland pore *gv1* and *gv2* simple.

**Gnathosoma:** Gnathotectum trispinate, with a large triangular central prong, with rounded apex and two tiny lateral spines (Fig. 3E). Corniculi conical, with small, sharp protuberance situated medially (Fig. 3B). Palptrochanter without protuberance, setae *v1* and *v2* pilose. Hypognathal groove with 4 large, non-denticulate rows. Chelicera (Fig. 3A): straight fixed digit with 1 denticle above pilus dentilis and 6 more below it; movable digit (96 long) with hooked apex, 4 denticles and a tooth on internal margin; arm of spermatodactyl arched; arthrodiol membrane with short brush-like process.

**Legs:** Coxa II with a fan-shaped ridge of 7-9 tiny denticles located anterolaterally (Fig. 3F). Leg II armed as follows (Fig. 3D): rounded femoral apophysis and

oval, inward bent axillary process, their apices at same level; between them a small protuberance. Triangular genual spur located near distal margin of the segment. Rectangular tibial apophysis 30 long, its apex slightly concave. Measurements: tarsus I = 156; tarsus IV = 144.

**Description of female:** Length of squashed dorsal idiosoma 672. Length of some setae: on podonotum *jl* = 25, *r1* = 12, others 36; opisthonotum with tiny setae, their length 6-12. Length of peritrematal shield 221.

**Ventral idiosoma:** Presternal plate serrated. Sternal shield reticulated, gland pore *gv1* under seta *st3* on posterior margin; length of sternal setae 48-50 (Fig. 3G). Paragynial shield with small rounded posterior protrusions and metagynial sclerite ellipsoidal (Fig. 3I). Epigynium: anterior margin with two lateral spines and long median apex (90 long); subapical structure a basal slightly denticulate strip (Fig. 3H). Gland pore *gv2* simple. Endogynium: a simple oval cup covered by a hyaline membrane and two rounded protrusions (Fig. 3J). Measurements: epigynium: height = 180, basal width = 192; h/b = 0.94;

**Gnathosoma:** Only the following character discernible: palptrochanter without protuberance between simple *v1* and pilose *v2*

**Legs:** Length of tarsus I and IV = 180 long.

**Remarks:** I examined only a female and a male, both not in very good condition, but the main features which distinguish the new species from others in the *mallorcae*-group could be properly observed. The female of *H. aquilinus* sp. nov. can be distinguished by the long triangular apex on the anterior margin of the epigynium and by the endogynium being a simple, oval cup. The male is easily recognizable by the shape of the chelicera. More material will be necessary in order to discern other characters especially those of the endogynium.

***H. maritimus* Hyatt, 1987**

**Material examined**

*Spain*

1 female; Prov. Pontevedra, Cuesta del Ralo Salcedo, sifting leaves under bushes near old *Quercus* sp. tree; 1.07.1952 (Sp. 121). – 4 females, 3 males; Isla Estela, Enterra near Bayona, grassland; 2.08.1956 (Sp. 474). – 1 male; Monte Ferro, near Bayona, grassland; 3.08.1956 (Sp. 478). – 2 females, 1 male; Isla de Onc, humid turfs near a spring; 4.08.1956 (Sp. 484). – 2 females, 1 male, idem, from moss; (Sp. 122). – 1 female, 1DN; Prov. Ourense, Montes del Invernadero near Verin, Sierra de San Mamed near Campo de Buceros, soil near a rivulet; 24.07.1955 (Sp. 408). – 2 females, 1 male; Prov. Galicia, Sierra de Fontefria near Caniza, under *Quercus robur*; 31.07.1956 (Sp. 471). – 1 female; Brana de Bruins, near Santiago de Compostela, moss from a small peat bog;

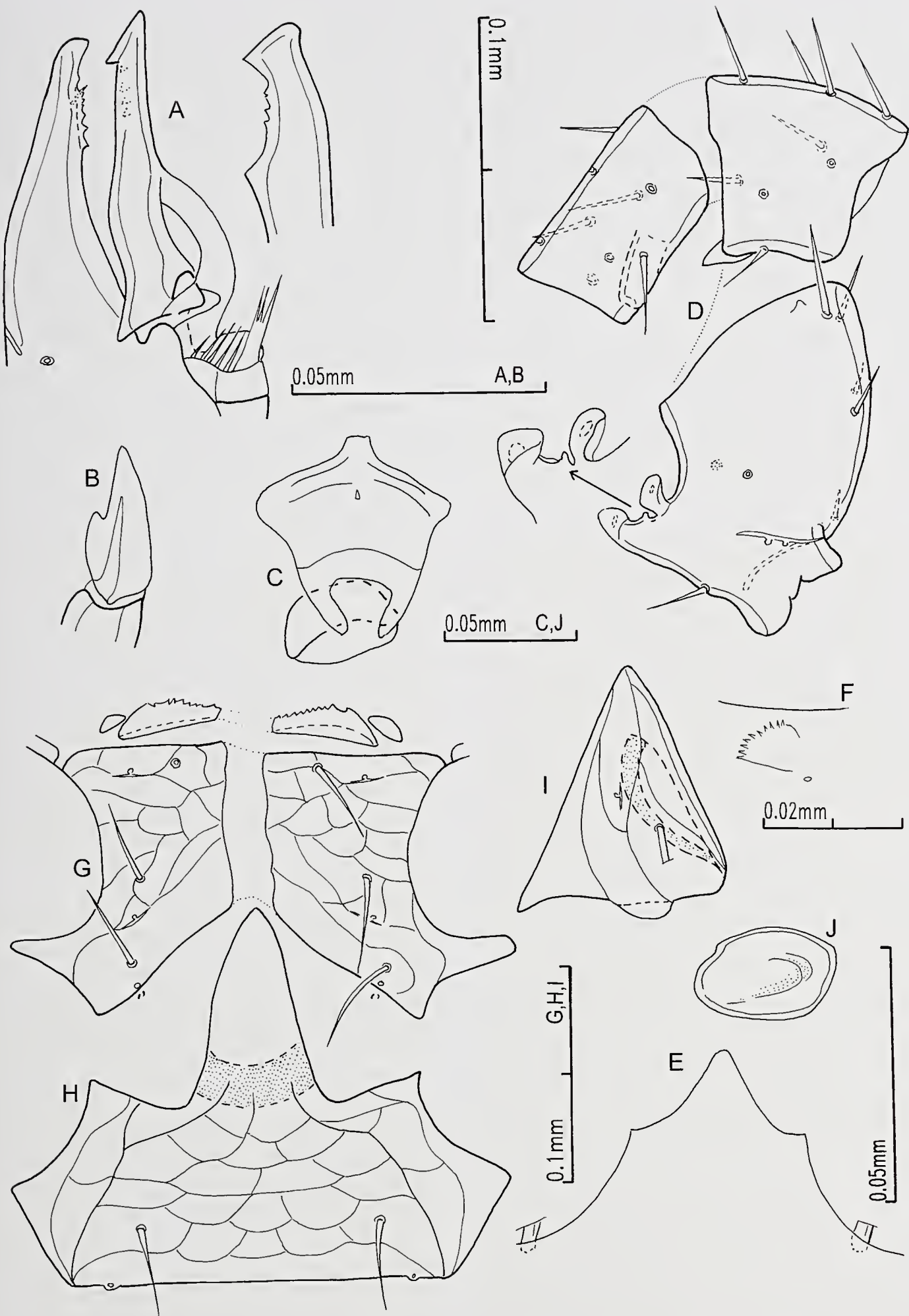


Fig 3. *Holoparasitus aquilinus* sp. nov., male (A-F), female (G-J). (A) Chelicera, antiaxial view. (B) Corniculus. (C) Genital lamina. (D) Femur, genu, tibia of leg II. (E) Gnathotectum. (F) Group of denticles on coxa II. (G) Presternal plate and sternal shield. (H) Epigynum. (I) Paragynium. (J) Endogynium.

4.08.1956 (Sp. 497). – 6 females, 3 males; Prov. Leon, Rio Duerna valley, near Molina Ferrada, leaf litter under bushes of *Quercus pyrenaica* and *Erica arborea*; 10.08.1957 (Sp. 567). – 1 female, 1 male; idem, leaf litter under *Quercus toza* near a rivulet; 10.08.1957 (Sp. 568). – 5 females, 3 males; Principado de Asturias, El Fito, west of Aviles, Oviedo, leaf litter under *Betula* sp., *Alnus* sp., *Quercus* sp.; 16.08.1957 (Sp. 587). – 1 female; Prov. Jaen, Sierra de Cazorlas, near Pantano el Tranco, leaf litter in maquis; 22.04.1963 (Sp. 945). – 1 male; Tenerife, Anaga, road to Pico del Ingles, leaf litter in laurel forest; 8.04.1965 (Sp. 1038).

#### Portugal

2 females; Madeira, south slope under Rabaçal, leaf litter under mimosa tree; 30.03.1967 (Sp. 1138). – 1 female; Ribeiro Grande and Ribeiro Bonito, leaf litter in laurel forest; 7.04.1967 (Sp. 1148-1151). – 1 female, 2 males; Queimadas near Santana, leaf litter of laurel tree; 1.04.1967 (Sp. 1141). – 1 female, 1 male; Acha das Areias, under la Boca de Encumeada; 5.04.1967 (Sp. 1146).

**Remarks:** *Holoparasitus maritimus* was described from Great Britain the type locality is Cornwall-Kelsey “from thrift *Armeria maritima*, on cliffs” (Hyatt, 1987). The species was also sampled in Scotland (Inner Hebrides) and in the Channel Islands (Jersey) from mossy turf, seaweed and beach grass. In the Athias-Henriot Collection I identified *H. maritimus* predominantly from different places and biotopes in the north-west and east of Spain (Prov. Pontevedra, Ourense, Galicia, Leon and the Principado de Asturias), as well as from the islands of Madeira and Tenerife. The distribution of these species seems to be linked to the sea shore and to the European Atlantic coast. Unexpectedly, I found *H. maritimus* also in one sample (Sp. 945) from the Sierra de Cazorla in the south of Spain. For a meaningful discussion of the distribution of this species more samples from other countries in Europe are necessary. *Holoparasitus maritimus* is easily recognizable by the following characteristics: the cuticle of the podonotum is medially strongly granular, the gnathotectum triangular, with a granular cuticle; the female has a simple cup-like endogynium with two lateral protrusions, a mucronate epigynial apex and a particular ornamentation of the sternal shield.

#### *lawrencei* species group

**Remarks:** *Holoparasitus lawrencei* and *H. paralawrencei* sp. nov. cannot be included in any of the previously known species-groups which lack an excipulum. Therefore these two species are placed in a new species group which is close to *caesus*-group and has a similar pattern of reticulation on the ventral idiosoma in male and female. Other similarities between both groups are the characteristics of the fixed digit of

the male chelicera which has only 1 or 2 denticles in *H. tberculatus* Juvara-Bals, 1975 and is indented in *H. fortunatus* Juvara-Bals, 1975. Both species groups differ in the armature of leg II, in features of palpfemur and palpgenual, and in characters of the epi- and endogynium in females. Only the particular characters of this group are mentioned.

**Diagnosis:** *Both sexes:* Gnathotectum trispinate, with central prong long and lateral prongs tiny; on ventral idiosoma gland pore *gv1* simple and *gv2* double on an unmodified cuticle.

*Male:* Gnathosoma without lateral incisions under setae *hyp.2*; corniculi conical; chelicera with fixed digit edentate and mobile digit without or with 1 or 2 denticles. Genital lamina without subgenital microsclerites. Ventral idiosoma reticulated, with one conspicuous line delimiting a slightly raised central part between *st1* and *st2* and a second less noticeable line between *st3* and *st4*. Armature of leg II: rounded femoral apophysis and trapezoidal process with their apices at the same level; ellipsoidal genual apophysis near anterior margin of the segment; large triangular or rounded (40 long) tibial apophysis.

*Female:* Presternal plate slightly denticulate, lateral platelets free; sternal shield reticulated, with a pair of lines starting between coxa II and III and running towards the middle of the shield where they join (*H. paralawrencei* sp. nov.) or not (*H. lawrencei*). Apex of epigynium mucronate, subapical epigynial structure trapezoidal, with small membranous wings. Endogynium a big sack with ventrally two spherical protuberances continued dorsally by two elongated and denticulate structures. Endogynium covered with a fine membrane.

**Distribution and remarks:** *Holoparasitus lawrencei* was recorded from Great Britain and Ireland (Hyatt, 1987). *Holoparasitus paralawrencei* sp. nov. was sampled by Prof. H. Franz in the north-west of Spain. In the Athias-Henriot Collection I identified other specimens from the north of Spain: Prov. Ourense (Sp. 408), Prov. Pontevedra (Sp. 483), and the Principado de Asturias (Sp. 498). The characteristics of the Spanish specimens are closed to those of *H. lawrencei* and *H. paralawrencei* sp. nov. Unfortunately not enough material is available to identify them properly.

**Species included:** *Holoparasitus lawrencei* Hyatt, 1987 and *H. paralawrencei* sp. nov.

#### *Holoparasitus lawrencei* Hyatt, 1987

Figs 4, 6E

**Material examined:** NHML 1984.12.4.-1; holotype; female; England, Cornwall-Hayle, from dry, light, leaf-litter; 24.5.1975; leg P. N. Lawrence. – NHML 1925.6.24.584; paratype; female; England, Lincolnshire,

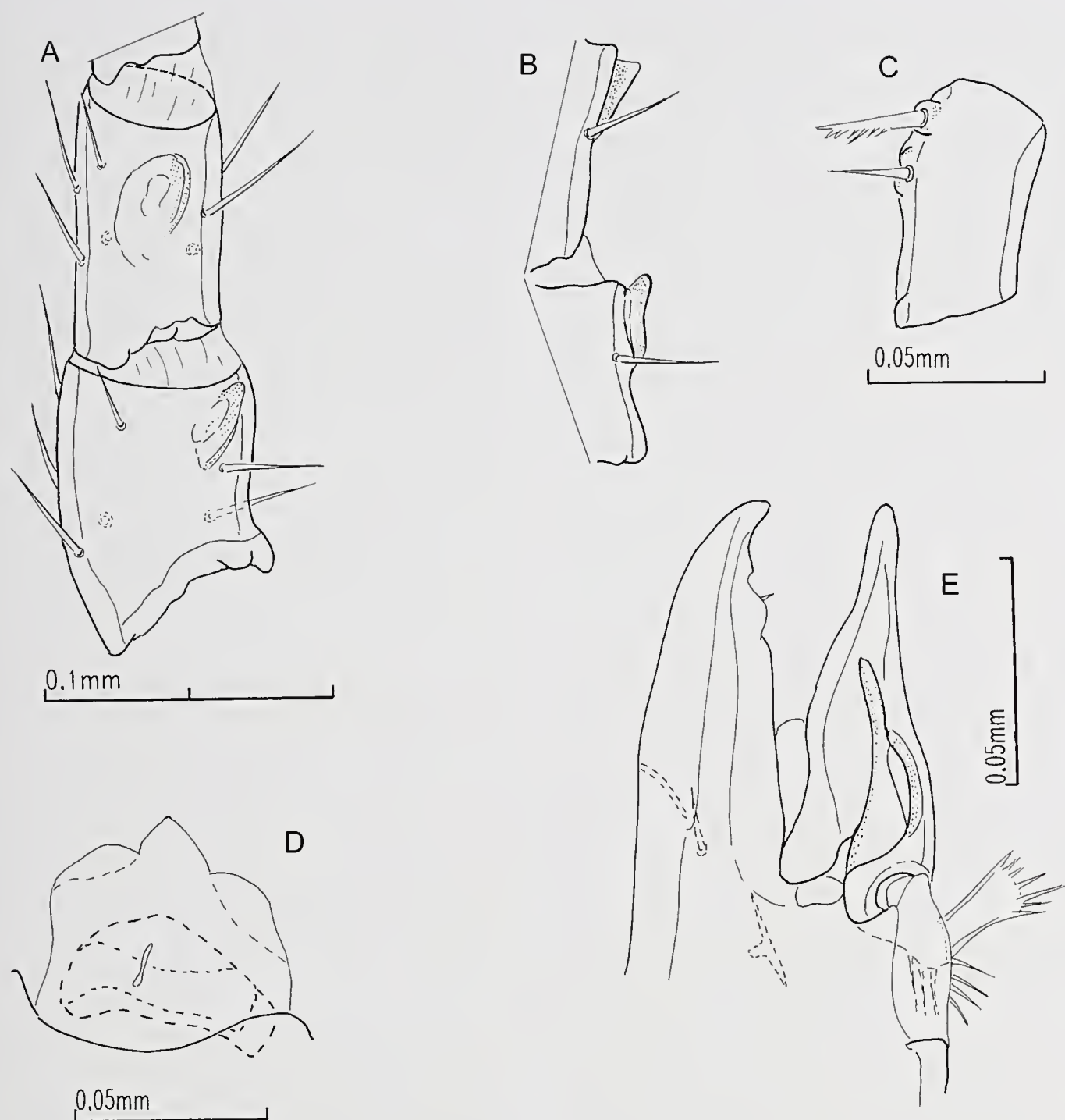


Fig 4. *Holoparasitus lawrencei* Hyatt, 1987, male. (A-B) Genual and tibial apophysis of leg II, ventral and lateral view. (C) Palptrochanter. (D) Genital lamina. (E) Chelicera, paraxial view.

no locality, no habitat data, 1900, leg. C. F. George. – NHML 1984.12.4.-3; paratype; male; United Kingdom, Isle of Wight, no habitat data; April 1948; leg T. A. Lloyd. – NHML 1984.12.4-2; paratype; male; Norfolk-Blackborough, with no habitat data; 25.2.1969; leg. A. Reeve.

**Redescription of male:** Length of idiosoma 780-840, width 550-610 (Hyatt, 1987). Genital lamina with a triangular apex instead of a bifid one (Fig. 4D). Length of simple hypognathal setae: *hyp.1*, *hyp.2* = 54-61, *hyp.3* = 38; *pc. pilose* = 66. Trochanter of pedipalp with a small protuberance between *v1* and *v2* (Fig. 4C).

Armature of leg II shown in Fig. 4A-B. Gland pore *gv2* double, situated behind coxa IV. Measurements (of 2 specimens): tarsus I = 192-206; tarsus IV = 240-250.

**Redescription of female:** Endogynium formed by a very big, oval and denticulate sack. Ventrally a central protrusion flanked by two rounded sacks and covered by a wrinkled membrane on posterior margin. Dorsally two very big structures filled with prominent denticles (Fig. 6E). Measurements: epigynium: height = 184-192, basal width = 228; h/b = 0.82-0.84. Sternal shield: *st1-st1'* = 62, *st2-st2'* = 108, *st3-st3'* = 139; *st1* = 54, *st2* = 60, *st3* = 66. Tarsus I = 187-192; tarsus IV = 240.

**Remarks:** The holotype and the paratypes examined correspond well with the original description of Hyatt. I here illustrate the endogynium, the armature of leg II and add some measurements. In the original description (Hyatt, 1987: fig. 11E) the movable digit of the female chelicera was drawn with 4-5 denticles, but in the holo- and paratypes studied I observed only 3 denticles. The other paratypes were not available in the NHML collection. *Holoparasitus lawrencei* was described by Hyatt (1987) from Great Britain; the type locality is Hayle in Cornwall. He identified specimens of this species from England (10 places), Scotland (2 localities), Wales and Ireland. All the specimens, except

the holotype, were considered as paratypes (20 males, 15 females). Unfortunately not all of the paratypes are deposited in the collection of the NHML so that the variability of the morphological characters of this species cannot be evaluated.

***Holoparasitus paralawrencei* sp. nov.**

Figs 5, 6 A-D, F

**Holotype:** slide M753 in MHNG arthropoda collection; male; Spain, Prov. Pontevedra, road from Gondomar to Tui, Sierra Grova, near Bayona, leaf litter under *Quercus* sp.; 5.08.1956 (Sp. 485).

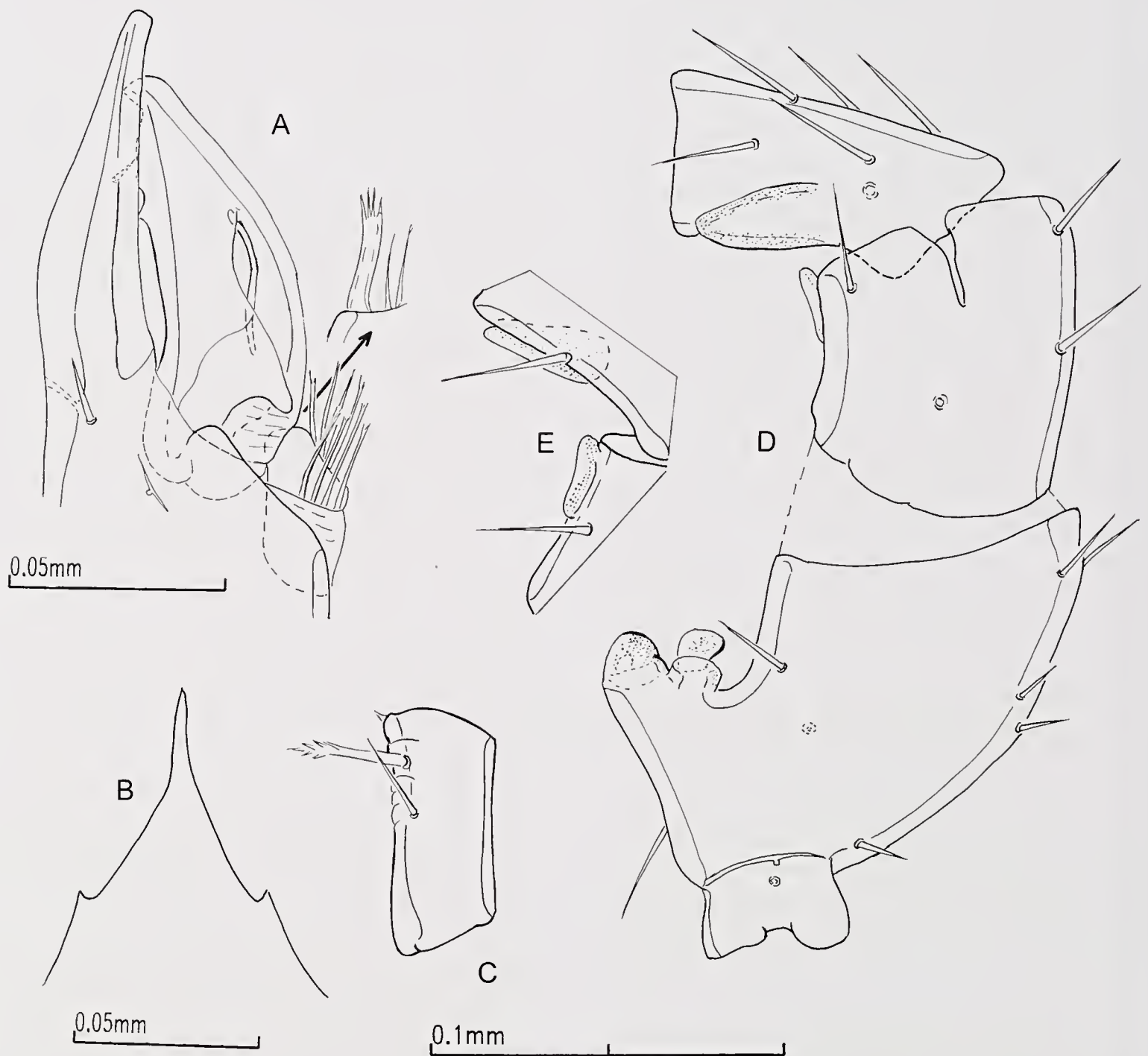


Fig 5. *Holoparasitus paralawrencei* sp. nov., male. (A) Chelicera, anti-axial view. (B) Gnathotectum. (C) Palptrochanter. (D) Femur, genu and tibia of leg II, anterolateral view. (E) Genu and tibial apophysis, posterolateral view.

**Paratypes:** 4 males, 3 females; same data as for holotype.

**Diagnosis:** Male chelicera with fixed digit straight and toothless, movable digit with 1-2 tiny denticles. Female endogynium a big sack with two rounded, slightly denticulate formations ventrally, each of them continued dorsally by a long peculiar structure with denticles apically and 1 or 2 teeth medially.

**Etymology:** The species name refers to similarities between the new species and *H. lawrencei*.

**Description of male:** Length of dorsal idiosoma 720-790, cuticle brownish red; podonotal setae:  $j1 = 42$ , others 36-42 long, opisthonotal setae shorter 12-18 long. Length of peritrematal shield 252-257.

**Ventral idiosoma:** Genital lamina with a trapezoidal central prong and rounded lateral corners. Sternogenital region reticulated, slightly raised between setae  $st1$  and  $st2$ , with two conspicuous lines in its central part (Fig. 6F). Gland pore  $gv1$  present, gland pore  $gv2$  double. Length of sternal setae:  $st1 = 48$ ,  $st2 = 50-54$ ,  $st3 = 48$ ,  $st4 = 55$ ; length of opisthogastric setae 36.

**Gnathosoma:** Gnathotectum trispinate, its central prong long and sharply pointed (Fig. 5B). Palptrochanter with simple seta  $v1$  and pilose seta  $v2$  (Fig. 5C). Corniculi conical. Hypognathal groove with 10 denticulate rows. Palpcoxal setae pilose (60 long), hypostomatic setae simple, their length 54-66. Incisions absent in cuticle behind hypostomatic setae. Chelicera (Fig. 5A): Fixed digit straight, pilus dentilis situated medially on a toothless inner margin. Movable digit with 1-2 small teeth. Arthrodistal membrane with a small brush-like process.

**Legs:** Coxa II with a ridge of 7-10 denticles. Armature of legs II as in Fig. 5D-E: rounded femoral apophysis and trapezoidal axillary process; ellipsoidal genual apophysis located near anterior margin of segment; large triangular medially apophysis situated on tibia, its length 42. Measurements: tarsus I = 192-206; tarsus IV = 216-233.

**Description of female:** Idiosoma 840 long, cuticle brownish-red well sclerotized. Length of peritrematal shield 266.

**Ventral idiosoma:** Presternal plate slightly denticulate. Sternal shield, reticulated, with a pair of lines passing under pores  $iv2$  and joining in center of shield (Fig. 6A);  $gv1$  situated below setae  $st3$ . Sternal setae simple, their length around 65, only  $st2$  longer, 72-79. Paragynial shield with a small rounded postero-lateral protrusion; metagynial shield elongated. Epigynium reticulated, with mucronate apex and rectangular subapical structure with small rounded membranous wings (Fig. 6B-B'). Setae  $st5$  simple, 66 long. Endogynium (Fig. 6C-D) a big sack, covered at its base with a fine, pleated cuticle, formed by 2 rounded and slightly denticulate protuberances located ventrally and by 2 elongated structures with denticles on their tips situated dorsally. Opisthogaster with 9 pairs of

setae, their length around 50. Gland pore  $gv2$  with one opening and 2 glands. Measurements: Distance between sternal setae:  $st1-st1' = 66$ ;  $st2-st2' = 96-108$ ;  $st3-st3' = 122-132$ ; epigynium: length = 168, basis = 233,  $h/b = 0.72$ ; tarsus I = 204; tarsus IV = 228-233.

**Gnathosoma:** Gnathotectum similar to that of male, trispinate with a longer central prong. Hypognathal groove with 9-10 fine denticulate rows. Length of hypognathal setae:  $hyp.1, hyp.2 = 50$ ;  $hyp.3 = 24$ ;  $pc. = 54$ . Chelicera with movable digit (120 long) with 3 denticles and fixed digit with 2 denticles above pilus dentilis and 2 denticles below it.

**Remarks:** The new species found in the north of Spain is very similar to *H. lawrencei*. Females of *H. paralaurencei* sp. nov. differ from those of *H. lawrencei* in the following characteristics: the structure of the endogynium, the anterior margin of the epigynium which has a mucronate apex and the proportion of this shield ( $h/b = 0.72$  versus 0.84). The two noticeable lines on the sternal shield are joined in the middle in *H. paralaurencei* sp. nov. but not in *H. lawrencei*. The male of the new species has 1 or 2 small teeth on the movable digit of the chelicera which is without teeth in *H. lawrencei*. The size of the Spanish specimens is smaller than those of the British specimens.

#### **Species-group *incertae sedis*** ***Holoparasitus floriformis* sp. nov.**

Figs 7- 8

**Holotype:** slide D768 in MHNG arthropoda collection; male; Spain, Roncesvalles, Prov. Navarra, road towards Burguete (the Pyrenees), litter of beech forest, alt. 949 m; 5.08.1955 (Sp. 429).

**Paratypes:** 4 females; same data as for holotype.

**Diagnosis:** Long corniculi of male reaching level of seta  $v2$ , movable digit of the chelicera stout and with an axe-shaped apex; femur of leg II with a long, curved femoral apophysis and with a big, oval axillary process. Presternal plate of female without denticles; epigynium very long  $h/b = 1$ ; endogynium a sack with its opening surrounded with petal-like structures.

**Etymology:** The species name refers to the unique flower-shape (Latin: *flos* = flower) of the endogynium.

**Description of male:** Sclerocuticle of dorsal idiosoma with a simple reticulation, colour yellowish brown. Setae simple, their length on opisthonotum 12-15. Length of peritrematal shield 220.

**Ventral idiosoma:** Genital lamina with rounded angles; central prong absent (Fig. 7D). Sclerocuticle reticulated, without strongly procurved line or excipulum. All setae simple. Gland pore  $gv1$  and  $gv2$  simple. Eight pairs of setae on opisthogaster, their length about 24.

**Gnathosoma:** Gnathotectum trispinate (Fig. 8H). Corniculi straight and long (48 long), reaching setae  $v2$ , with

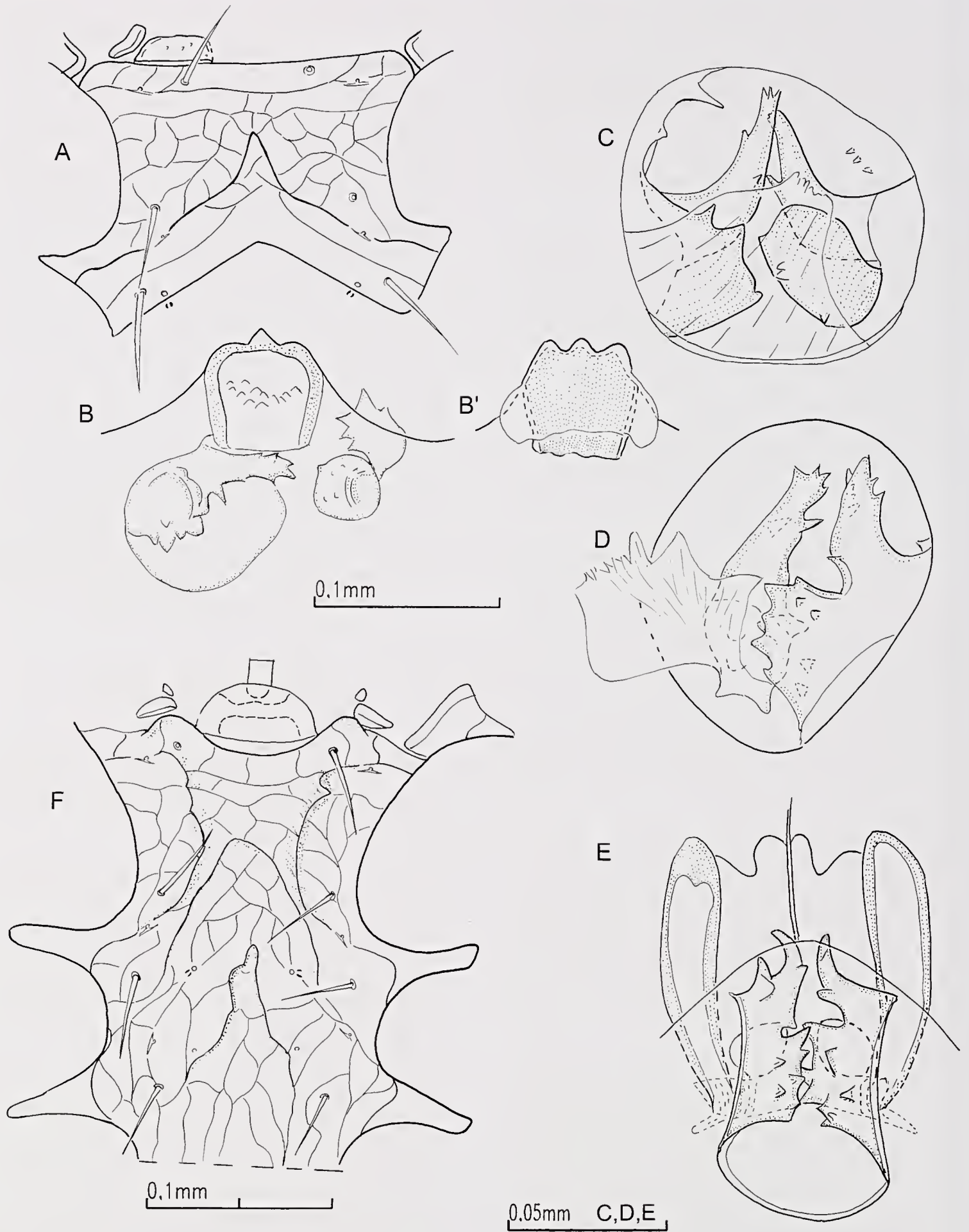


Fig 6. *Holoparasitus paralarrencei* sp. nov., female (A-D), male (F) and *Holoparasitus lawrencei* Hyatt, 1987, female (E). (A) Presternal plate and sternal shield. (B) Apex of epigynum and endogynium, ventral view. (B') Apex of epigynum, dorsal view. (C-D) Endogynium, ventral and (E) dorsal view. (F) Sternal shield and genital lamina.



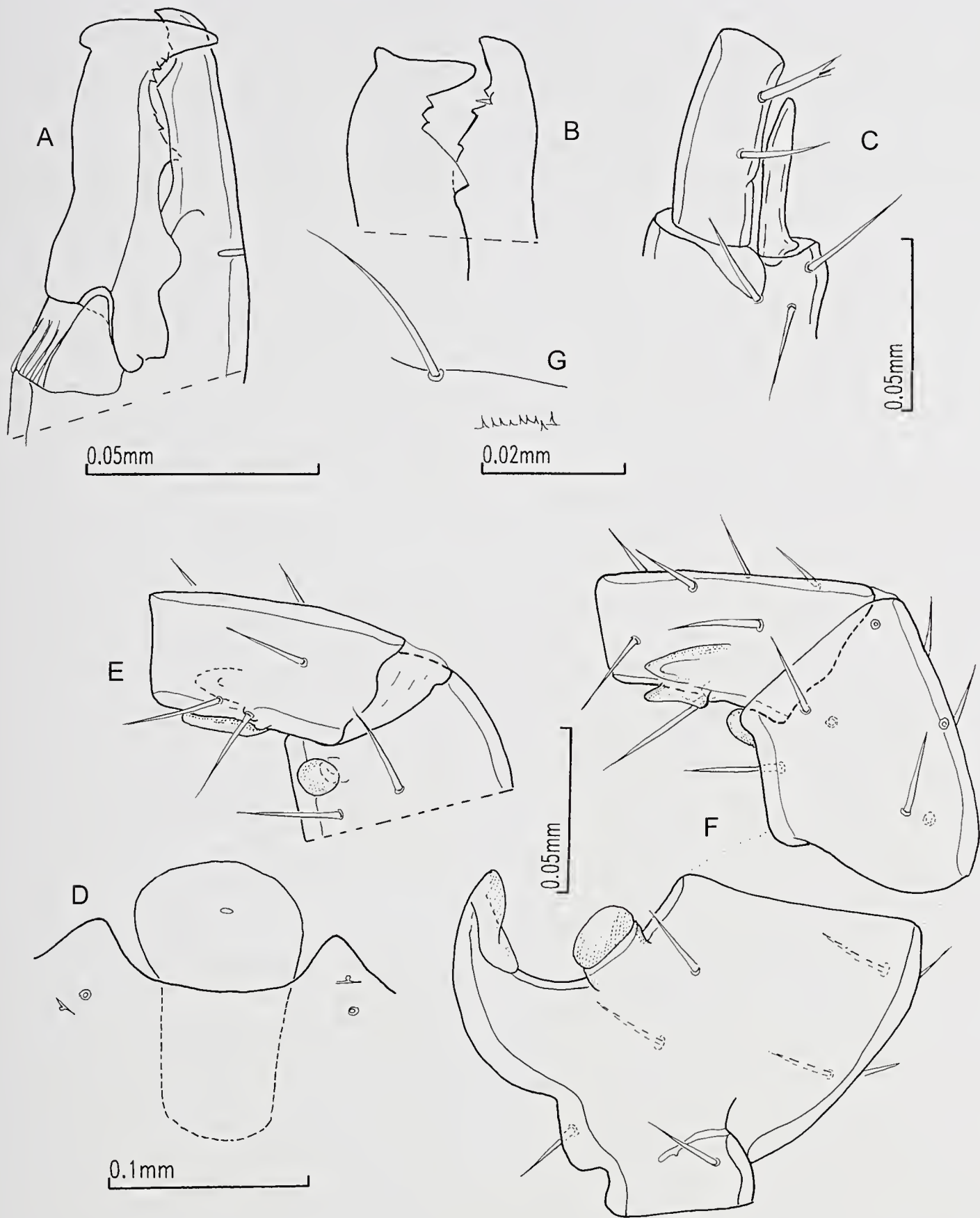


Fig 7. *Holoparasitus floriformis* sp. nov., male (A-F), female (G). (A-B) Chelicera. (C) Palptrochanter and corniculus. (D) Genital lamina. (E) Genual and tibial apophysis of leg II, anterolateral view. (F) Femur, genu, tibia, posterolateral view. (G) Denticulate ridge on coxa II.

a small protuberance at their base (Fig. 7C). Length of simple hypognathal setae: *hyp.1* = 36, *hyp.2* = 30, *hyp.3* = 24, *pc.* = 42. Palptrochanter with pilose *v2* and simple *v1*. Chelicera (Fig. 7A-B): movable digit large (84 long), its apex like a sharp axe and its inner margin denticulate; fixed digit with slightly curved apex and its inner margin with 1 denticle above pilus dentilis and 3 below it.

*Legs*: Armature of leg II as shown in Fig. 7E-F: long,

curved femoral apophysis and large, oval axillary process; rounded apophysis situated on distal margin of genual segment; tibia with two apophyses, one triangular the other elliptical, both situated medially. Measurements: tarsus I = 163; tarsus IV = 156.

**Description of female:** Idiosoma well sclerotized, **colour** yellowish brown. All setae simple, length of podonotal setae: *jl* = 36, *sl* = 18, others 24; length of

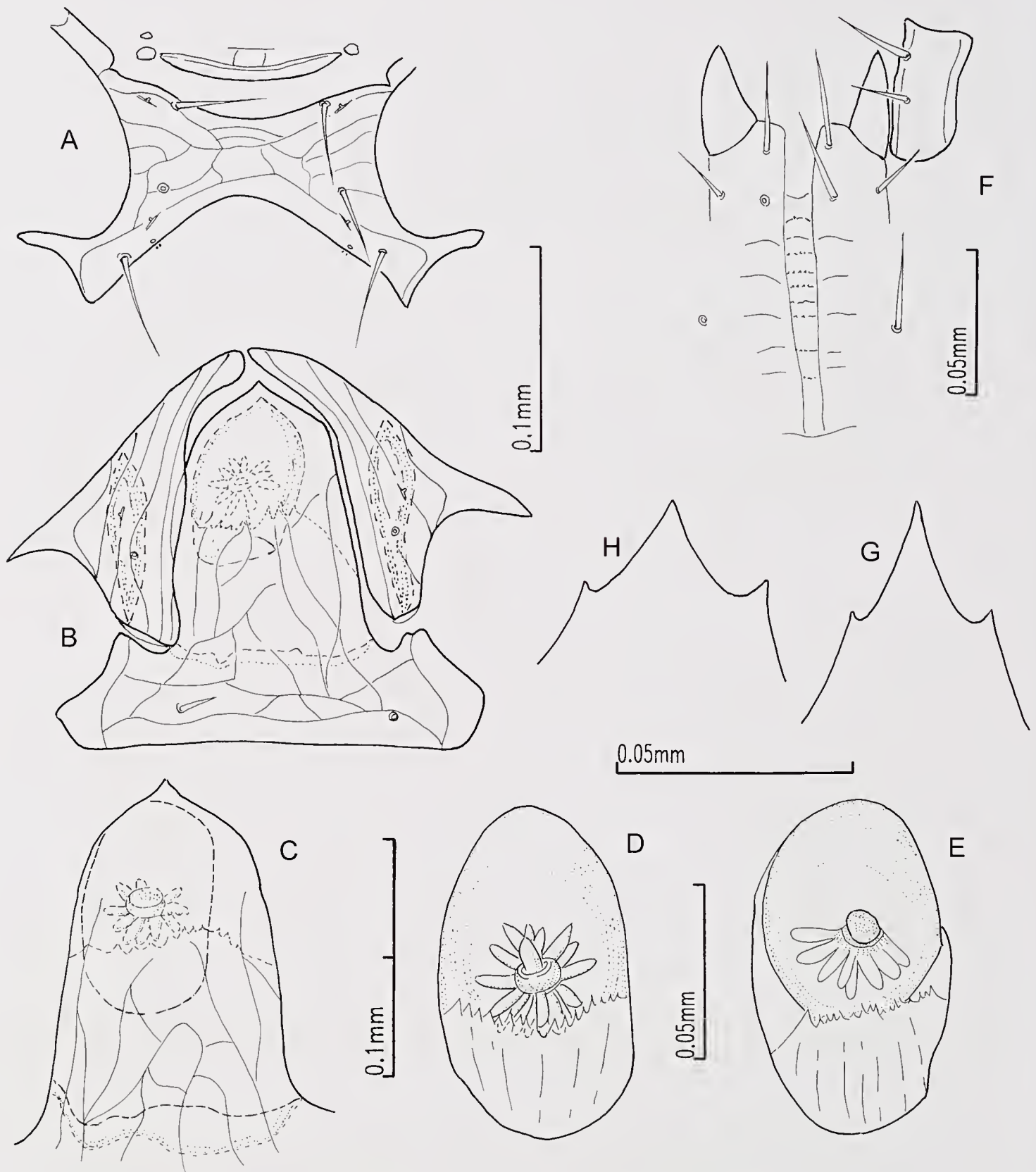


Fig 8. *Holoparasitus floriformis* sp. nov., female (A-G), male (H). (A) Presternal plate and sternal shield. (B) Paragynia and epigynum. (C) Apex of epigynum. (D-E) Endogynium. (F) Gnathosoma and palptrochanter, ventral view. (G-H) Gnathotectum.

opisthonotal setae 12-18. Length of peritrematal shield about 230.

*Ventral idiosoma*: (Fig. 8A-B). Presternal plate ribbon-like, without denticles. Sternal shield reticulated; length of sternal setae:  $st1 = 48$ ,  $st2 = 42$ ,  $st3 = 54$ . Gland pore  $gv1$  situated medially on posterior margin (Fig. 8A). Paragynial shield reticulated, stretched out around lateral margin of epigynium; posterior paragynial protrusion small and rounded; metagynial sclerite elliptical (Fig. 8B). Epigynium as long as its width at base. Apex elongated, anteriorly with a triangular apex and a slightly sclerotized subapical structure (Fig. 8C). Setae  $st5$  short (20-24). Endogynium a big sack with its opening surrounded by structures shaped like petals, all covered by a thin membrane with a denticulate anterior margin (Fig. 8D- E). Gland pore  $gv2$  simple. Opisthogaster with 8-9 pairs of setae, their length:  $ZV4 = 30$ ,  $JV5 = 18$ , others 24-30. Measurements: distance between sternal setae:  $st1-st1' = 72$ ,  $st2-st2' = 96$ ,  $st3-st3' = 110-132$ ; height of sternal shield = 36; epigynium: height = 187-192, basal width = 180-192,  $h/b = 1-1.10$ ;

*Gnathosoma*: Gnathotectum trispinate (Fig. 8G). Corniculi conical. Hypognathal groove with 9-10 rows, most of them oligodent; hypostomatic setae simple, their length  $hyp.1$ ,  $hyp.2 = 30$ ;  $hyp.3 = 24$ ;  $pc. = 42$  (Fig. 8F). Movable and fixed digit of chelicera 84 long.

*Legs*: Coxa II with a ridge of 8 denticles (Fig. 7G). Length of tarsus I = 150-156 and tarsus IV = 156-161.

**Remarks:** The new species can be easily distinguished from all the known species of *Holoparasitus* by the particular characteristics of the endo- and epigynium of the female and by those of the chelicera of the male.

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## On the Auguste Forel ant collection in the Naturmuseum Solothurn, Switzerland: current state and illustrated type catalogue (Hymenoptera, Formicidae)

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**Abstract:** A collection of 457 specimens of Formicidae in 195 taxa from all over the World donated by Auguste Forel has been conserved since 1901 at the Naturmuseum Solothurn, Switzerland (NMSO). Hardly noticed by the scientific community, the collection includes 40 syntypes of 16 species and subspecies, and five paralectotypes from two species. To spread this knowledge, and to encourage the inclusion of the Formicidae collection in future taxonomic studies, all species from the collection are listed, and the types are catalogued and imaged.

**Keywords:** Formicidae, museum collection, type specimens, taxonomy, Auguste Forel, Solothurn, Switzerland.

### INTRODUCTION

Auguste Forel (1848-1931) had been a passionate myrmecologist since his childhood. Born in Switzerland near Morges in the canton of Vaud he completed his medical studies in the year 1871 in Zurich. After a short stay in Vienna, where he deepened his knowledge in the field of neuroanatomy and neuropsychiatry, he passed the cantonal medical examination in Lausanne one year later. In 1873 Forel moved to Munich, where he intensively worked on his anatomical studies of the human brain (Parent, 2003) as well as on the Swiss ant fauna, crowned with his extensive work “*Les fourmis de la Suisse*” (Forel, 1874). From 1879 to 1898 he was director at the Burghölzli asylum in Zurich, and professor of psychiatry at the University of Zurich. Auguste Forel travelled a lot, and in 1889 and 1893 went on journeys to Tunisia and Algeria, in 1891 to Bulgaria (Forel, 1892b), and in the last years of his working career and after his retirement, he intensified travelling and visited Colombia in 1896, the United States and Canada in 1899, Eastern Europe and Russia in 1902, Egypt, Algeria, Tunisia, Italy in 1908, and in the following year he travelled from the Balkans to Greece and Turkey (Parent, 2003; Banani, 2005). After having suffered a stroke with partial paralysis in 1912 Forel was forced to stop his excursions.

In 1922 the main collection of Auguste Forel was sold to the Muséum d’histoire naturelle de Genève (MHNG). Apart from that collection doublets were given in 1923/1924 to the Zoological Museum Berlin, and a specific Swiss collection is conserved since the same date in the Musée de zoologie de Lausanne

(MZL). A small overview collection remained in the possession of Forel’s family (Horn & Kahle, 1935) and is conserved, presumably entirely, since 1981 also in the MZL (teste A. Freitag). In 1911 Forel visited the Zoologische Staatssammlung München (ZSM) (at that time Königlich Zoologisches Museum München) where he determined and described Formicidae, which was not mentioned by Horn & Kahle (1935). A series of types are therefore also at the ZSM (Merta, 1999). Similarly at the Naturhistorisches Museum der Burgergemeinde Bern (NMBE), not mentioned either in Horn & Kahle (1935), part of the Forel collection is conserved since 1911, comprising ant species from all over the World and syntype specimens. Interestingly, in the extensive online catalogue on biographies of entomologists of the Senckenberg Deutsches Entomologisches Institut, Müncheberg (SDEI Senckenberg, 2015) the Forel collection at the Naturmuseum Solothurn (NMSO) is mentioned.

Bloch (1940) provided an overview on all 457 specimens (from 174 species out of 64 genera at that time) of the Forel collection from localities all over the World conserved at the Naturmuseum Solothurn. The collection was first mentioned by Bloch (1911), where Forel himself is mentioned as donator of the collection. This was part of a common effort to contribute to the growing museum collection supported by other contemporaries (as Paul Born, Arnold Wullschlegel, E. Christ, Wilhelm Roos, Eduard Von Jenner, Fritz Rohr, Karl Ris, Emile Frey-Gessner, M. Bcdot) under the lead of August Rätzer. At the NMSO the Forel collection is registered under the number “E. K. [Eingangskatalog = accessions catalogue]

112” and is indicated as a donation dating back to 27th December 1901, long before his main collection was sold to the MHNG.

In the meantime the collection, formerly housed in an external depot, remained unexplored and unfortunately single specimens were destroyed by feeding of carpet beetles (Dermestidae). These damages – if relevant, e.g. not only single legs or antennae are missing – are reported in the following. The re-examination of species described (and mostly collected) by Forel, and comparisons with the very helpful AntWeb (2016) – where all historical literature is available – resulted in the discovery of syntype specimens. These were not yet adequately labelled and hence not recognisable as types at first sight. The knowledge of the existence of this ant collection at the NMSO is important for future taxonomic examinations. Therefore these specimens are listed and pictured in the following.

The determinations are those of Forel himself. Therefore, difficult genera and species-groups with subsequent new discoveries and/or species that have been split in the meantime should be carefully revised by any interested myrmecologist; a necessity which should be emphasized with this present contribution.

## MATERIAL AND METHODS

Photos were taken with a 3.15-megapixel digital camera (ProgRes CT3) on a stereomicroscope (Nikon SMZ 1000) for the ant specimens, and a digital camera (Canon G 11) for the labels. Series of images were captured with ProgRes Capture Pro 2.8.8 for Windows and stacked with the freely available CombineZP Image Stacking Software by Alan Hadley.

Additional remarks and corrections to label data are set in square brackets [ ], mistakes by Bloch (1940) are additionally highlighted by a preceding asterisk at the beginning of the square brackets [\*]. Specimens from different localities are separated by a dash (—). The original combination used on the labels in the Forel collection to every species is given in curly brackets { }. All specimens of the Forel collection are registered in the database of the NMSO and these data are available on request for further investigations. The Forel collection at the NMSO is conserved in three regular sized insect boxes (51 x 42 x 6 cm). As a peculiarity, but usual at that time, only the first specimen of a series of separately pinned specimens is provided with a label.

## ABBREVIATIONS

MHNG Muséum d’histoire naturelle de Genève (Switzerland)  
 NHMW Naturhistorisches Museum Wien (Austria)  
 NMBE Naturhistorisches Museum der Burgergemeinde Bern (Switzerland)

NMSO Naturmuseum Solothurn (Switzerland)

ZSM Zoologische Staatssammlung München (Germany)

## RESULTS

### Corrections, damaged and lost specimens

From the originally 457 specimens of the Forel collection, currently 426 from 195 taxa are still present in the collection of the NMSO (Appendix 1). Corrections as well as indications about damages or lost specimens are given for the 41 species below. 40 specimens are damaged and a few are lost. Bloch’s paper (1940) contained a number of mistakes which are shown and corrected here under the respective species (ordered in alphabetical order):

- *Acromyrmex disciger* (Mayr, 1887) {*Atta* (*Acromyrmex*) *discigera*} 2 ♀ Blumenau [Brasilia] [leg.] Möller [head of one ♀ is lost].
- *Aplaeogaster gibbosa* (Latreille, 1798) 3 ♀ Souk Ahras [\*Algeria; not Persia as in Bloch (1940)].
- *A. treatae* Forel, 1886 2 ♀ Tyorn 3400 “[feet] W.B. [has to be in the USA] 23.VII. [leg.] Forel.
- *Camponotus cruentatus* (Latreille, 1802) 3 ♀ près Montpellier, sous pierre [under stone] [one worker is heavily damaged; gaster, one leg and part of the head capsule are missing].
- *C. maculatus* (Fabricius, 1782) 3 ♀ Moyanga [=Moronga] Madagascar [the gaster of one of the workers is lost].
- *Cyphomyrmex rimosus* (Spinola, 1851) 3 ♀, 1 ♀ St. Vincent [São Vicente, Brasil] [of the ♀ only head and mesosoma are left].
- *Dolichoderus quadripunctatus* (Linné, 1771) 2 ♀ Vaux [the head of one is missing].
- *Dorylus helvolus* (Linnaeus, 1764) 3 ♀ Basutoland [today Lesotho] 14.VI. [\*not 1914, as the collection dates back to 1901] [leg.] Wroughton.
- *Eciton carolinense* Emery, 1894 3 ♀ Faisons [=Faison] N. C. [North Carolina, USA] ds.[dans] tronc [in (tree) trunk].
- *E. hamatum* (Fabricius, 1782) 3 ♀ Bonda Columbia [leg.] Forel [one specimen without head].
- *Forelius maccooki* (McCook, 1880) 2 ♀ Austin Texas [collector illegible] [\*no locality was given by Bloch (1940)].
- *Formica pallidefulva* Latreille, 1802 3 ♀ V...mera [illegible] Morganton [several localities in the USA are possible] N....trnc à mat [illegible] [one ♀ is lost].
- *F. rubicunda* Emery, 1893 {*F. sanguinea rubicunda* Emery, 1893} 2 ♀ Tyson N.C. [North Carolina] coll. excl. *subsericea* 20.VII. [collected from *Formica subsericea* Say, 1836; provenance unclear according to Bloch (1940)].
- *Formicoxenus nitidulus* (Nylander, 1846) 1 ♀ luz. Ural geb. [Ural mountains ?].

- *Goniomma hispanicum* (André, 1883) 2 ♀ Camargue [\*France; instead of unknown locality in Bloch (1940)] [leg.] Forel.
- *Harpegnathos saltator cruentatus* (Smith, 1858) {*H. cruentatus*} 1 ♀ Kanara [\*India; instead of “Kanada” in Bloch (1940)] [leg.] Bell 8. [18]66.
- *Iridomyrmex purpureus* (Smith, 1858): 2 ♀ Mackay, Queensland [Australia] [leg.] Turner [gasters of both specimens are missing].
- *Lasius alienus* (Foerster, 1850) 2 ♀ : Adelsberg [not specified if in Germany or Austria; several localities are possible; one ♀ is partly destroyed, gaster and two legs remain].
- *L. emarginatus* (Olivier, 1792) 3 ♀ : Adelsberg [same as above: not specified if in Germany or Austria; several localities are possible] 21.IX. [the head of one specimen is lost].
- *L. flavus* (Fabricius, 1782) 2 ♂, 1 ♀ Fisibach [canton AG, Switzerland] 7.VIII. [both ♂ are lost]. — 3 ♀ Fisibach.
- *L. umbratus* (Nylander, 1846) 2 ♂, 1 ♀ Burghölzli [Zurich] 30.IX. [one ♂ is lost]. — 2 ♀ : München [Bayern, Germany].
- *Leptogenys processionalis* (Jerdon, 1851) {*L. ocellifera* (Roger, 1861)} 3 ♀ [\*instead of no sex indicated] India, Ceylon.
- *Liometopum microcephalum* (Panzer, 1798) 2 ♀ : Sare-Mussa [Bulgarien; the head of one specimen is lost].
- *Manica rubida* (Latreille, 1802) {*Myrmica*} 1 ♀, 1 ♀ Murgthal [Murgtal near Quarten canton SG, Switzerland] 9.IV. [both specimens almost destroyed].
- *Messor arenarius* (Fabricius, 1787) 2 ♀ [both severely damaged] Gabès [Tunisia] [leg.] Forel.
- *M. barbarus* (Linné, 1767) 1 ♀ Perrégaux [\*today Mohammadia; not Perrigana as given by Bloch (1940)] Algérie 29.III. — 3 ♀ [one ♀ is completely destroyed] Laverdure [today Mechroha] Algérie, [leg.] Forel.
- *M. structor* (Latreille, 1798) 1 ♀, 2 ♀ [\*not 3 ♀ as mentioned in Bloch (1940); and additionally 4 plant seeds glued on the edges of a label] Miramar Baléares [Spain; not Switzerland as interpreted by Bloch (1940)].
- *Myrmica lobicornis* Nylander, 1846 3 ♀ Elinine Vrh [\*Rilo-Dagh mountains, Bulgaria; not “Schweizer Alpen” as mentioned by Bloch (1940)].
- *M. nigrocincta* Smith, 1858 1 ♀ : Zullusland [Australia] [whole specimen lost; labels still present in the box].
- *M. rubra* (Linné, 1758) {*M. laevinodis* Nylander, 1846} 1 ♀, 3 ♀ Bali – Effendi [=Aféndis, Crete, Greece] [the ♀ is completely destroyed].
- *M. ruginodis* Nylander, 1846 3 ♀ [one ♀ is completely destroyed] Rilo mo...otis [\*illegible, most probably Rilo mountains; Bulgaria instead of “In der ganzen Schweiz” (Bloch 1940)].
- *M. rugulosa* Nylander, 1849 3 ♀ Murg [near Quarten canton SG]; [one ♀ completely destroyed, another one partly destroyed].
- *M. scabrinodis* Nylander, 1846 2 ♂, 1 ♀ and 1 ♀ [without head] Vaux [near Morges] 8.VIII. — 1 ♀ : Vaux [near Morges] [the ♀ and one ♂ are completely destroyed].
- *M. sulcinodis* Nylander, 1846 3 ♀, 1 ♀ [\*not only 3 ♀ as mentioned in Bloch (1940)]: Schluderbach [=Carbonin, Italian; South Tirol] [1 ♀ is completely destroyed].
- *Pheidole megacephala* (Fabricius, 1793) 1 ♀ Manà Prov. Rio [Brasilia] [leg.] Göldi. — 2 ♀ : Madcira [Portugal] [leg.] Schmitz [one of them is completely destroyed]. — 1 ♀ Nosibé [Madagascar] [leg.] Völtzkow.
- *P. pallidula* (Nylander, 1849) 1 ♂ Ghadame [=Ghadamès, Lybia] (Ali). — 2 ♀, 1 ♀ Onsernonc [\*canton of Ticino, Switzerland; not mentioned in Bloch (1940)] [one ♀ is almost destroyed (gaster remaining), and parts of the gaster of the second one are missing]. — 2 ♀ : Algier [leg.] Moser. 1 ♀ [only gaster plus postpetiolus and petiolus are remaining] Tebessa [leg.] Forel.
- *Tapinoma erraticum* (Latreille, 1798) 1 ♂ Vaux. — 1 ♀ Horgen 1.VII. — 2 ♀ Vaux [gasters of both workers are missing].
- *Tennothorax recedens* (Nylander, 1856) 2 ♀ [\*not *suberis* Forel, 1894 as mentioned in Bloch (1940)] parc près Montpellier.
- *T. tuberum* (Fabricius, 1775) 3 ♀, 1 ♂ [1 ♀ and the ♂ are destroyed] Salève [France, near Geneva] 6.VI.
- *T. unifasciatus* (Latreille, 1798) 3 ♀ [where one ♀ is destroyed and another one heavily damaged (head missing)] Vaux [above Morges, Switzerland].
- *Tetramorium guineense* (Bernard, 1953) {*T. guineensis* (Fabricius, 1775)} 1 ♀ [completely destroyed] MacKay Queensland [Australia] 107 (Tarus) [?].

#### Annotated and illustrated catalogue of type specimens

In the following, 40 syntype specimens from 16 species and subspecies, 5 paralectotypes from two species and three former syntypes from a mixed type series are listed. Label data are mentioned verbatim in quotation marks. All type specimens were not yet marked or labelled as type specimens and hence difficult or not at all recognizable as such. Photos of the specimens and its original labels are given (Figs 1A-4S), and are available on request as maximally resolved images for scientific purposes. The types belong to species and subspecies published by Forel in the years 1887, 1890, 1892a, b, 1894a, b, 1899, 1901, and 1902. All species were compared with the original descriptions and – if type specimens were available – with AntWeb (2016). Details given in the descriptions, when necessary, are provided and additional references are included under



Fig. 1. Syntypes ♀ dorsal/lateral views. (A) *Strongylognathus huberi* Forel, 1874. (B) *Myrmica smythiesii* Forel, 1902. (C) *Monomorium indicum* Forel, 1902. (D) *Messor lobicornis* Forel, 1894. (E) *Camponotus bugnioni* Forel, 1899. (F) *Monomorium smithii* Forel, 1892. (G) *Temnothorax algiricus trabutii* (Forel, 1894). Scale bars 1 mm.



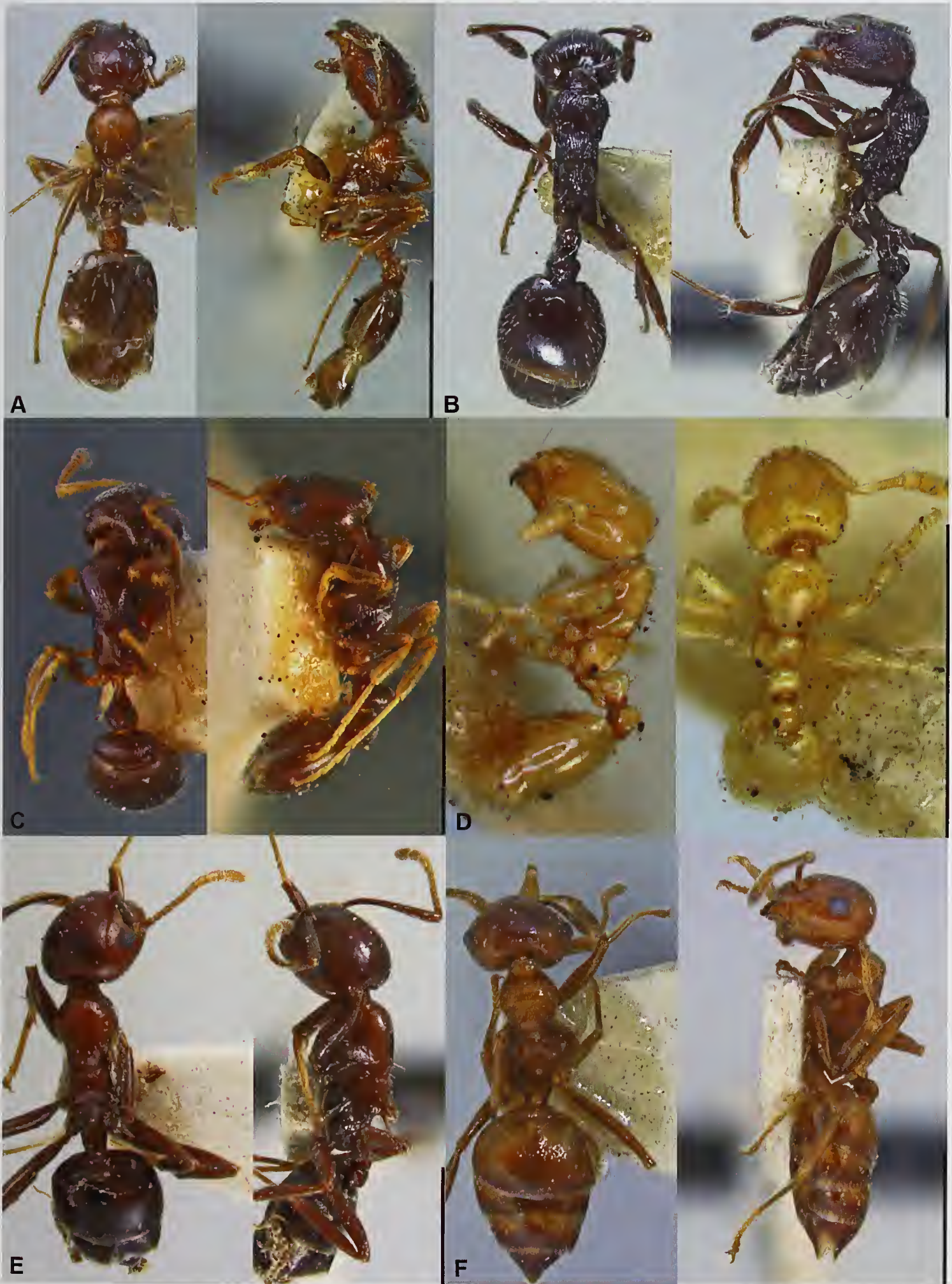


Fig. 2. Syntypes ♀ dorsal/lateral views. (A) *Temnothorax delaparti* (Forel, 1890). (B) *T. oraniensis* (Forel, 1894). (C) *Cardiocondyla stambuloffii* Forel, 1892. (D) *Solenopsis latro* Forel, 1894. (E) *Crematogaster ranavalonae* Forel, 1887. (F) Paralectotype of *C. daisyi* Forel, 1901. Scale bars 1 mm.



Fig. 3. (A) Paralectotype ♀ dorsal/lateral of *Pogonomyrmex mayri* Forel, 1899. (B) ♀ dorsal/lateral of *Azteca velox* Forel, 1899. (C) Syntypes ♀ of *A. delpini antillana* Forel, 1899. (D) *Lasius myops* Forel, 1894. (E) *Cataglyphis savignyi* (Dufour, 1862). (F) *Camponotus alii* Forel, 1890. Scale bars 1 mm.

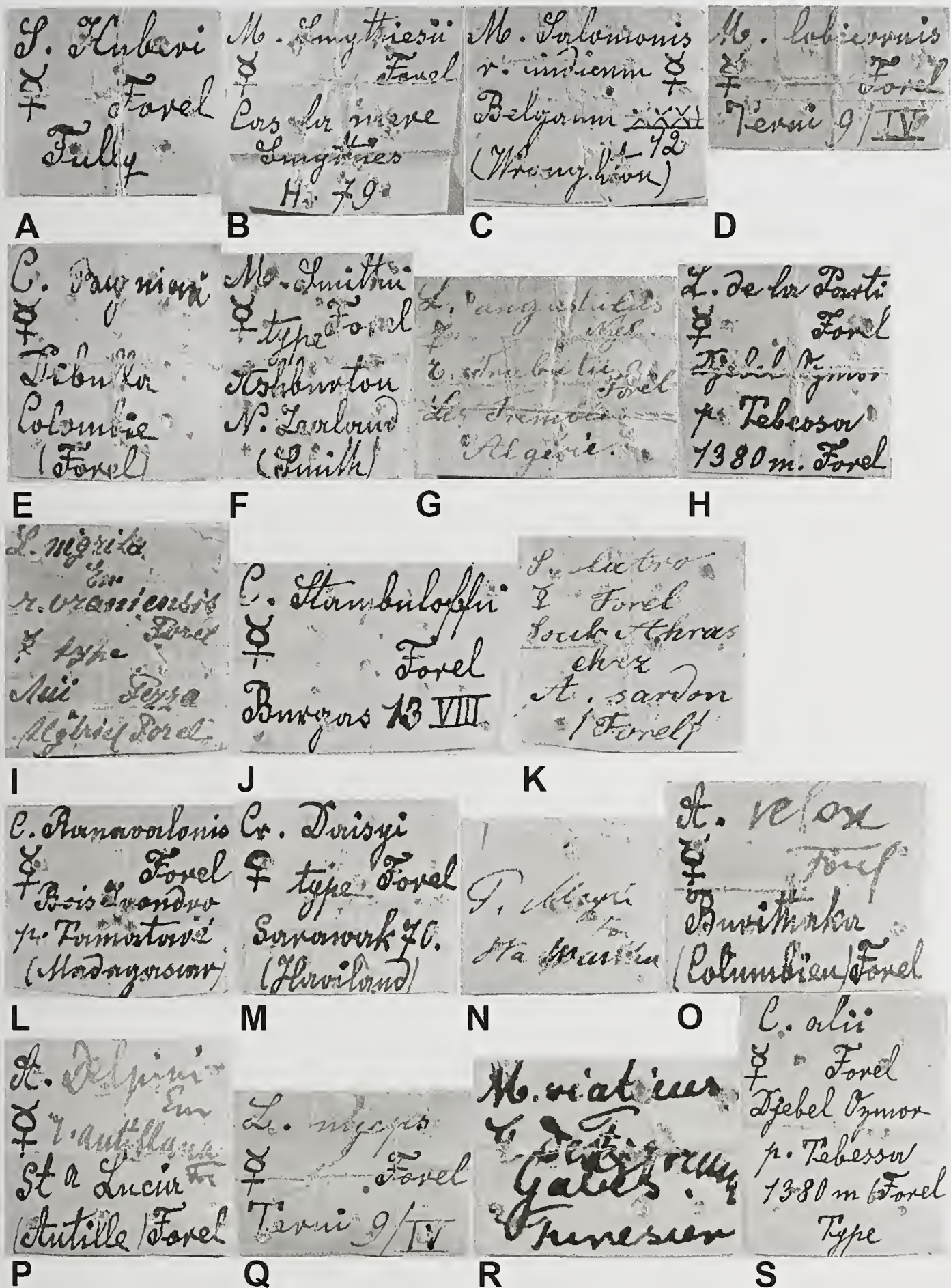


Fig. 4. Original labels of 16 syntypes and 2 paralectotypes. (A) *Strongylognathus huberi* Forel, 1874. (B) *Myrmica smythiesii* Forel, 1902. (C) *Monomorium indicum* Forel, 1902. (D) *Messor lobicornis* Forel, 1894. (E) *Cauponotus bugnioni* Forel, 1899. (F) *Monomorium smithii* Forel, 1892. (G) *Temnothorax algiricus trabuttii* (Forel, 1894). (H) *Temnothorax delaparti* (Forel, 1890). (I) *T. oraniensis* (Forel, 1894). (J) *Cardiocondyla stambuloffii* Forel, 1892. (K) *Solenopsis latro* Forel, 1894. (L) *Crematogaster ranavaloniae* Forel, 1887. (M) *C. daisyi* Forel, 1901. (N) *Pogonomyrmex mayri* Forel, 1899. (O) *Azteca velox* Forel, 1899. (P) *A. delpini antillana* Forel, 1899. (Q) *Lasius myops* Forel, 1894. (R) *Cataglyphis savignyi* (Dufour, 1862). (S) *Camponotus alii* Forel, 1890.

the respective species (listed here in alphabetical order within the respective subfamilies):

### Dolichoderinae

*Azteca aurita* Emery, 1893 {*A. lacrymosa* Forel, 1899} 3 ancient syntypes of a mixed type series (♂), which have lost their syntypical status: “*A. lacrymosa* ♂ Forel type Esperanza, Colombie ([leg. ] Forel) ...arton [illegible]”. Longino (2007) revised the *Azteca aurita*-species group, and designated lectotypes. The syntype series is a mixed one and consists of two species: *Azteca pilosula* Forel, 1899 and *A. aurita*, to which the Columbian specimens are assigned nowadays.

*A. delpini antillana* Forel, 1899 (Figs 3C, 4P) 3 syntypes (♂): “*A. Delpini* Sm r. [race] *antillana* For ♀ Sta Lucia (Antille) [leg.] Forel”. The locality fits perfectly with the description by Forel (1899: 111): “Hab. [Habitat] Antilles, St. Lucia (Forel)”.

*A. velox* Forel, 1899 (Figs 3B, 4O) 3 ♂): “*A. velox* Forel ♀ Burithaka (Columbien) [=Buritaca, Colombia] [leg.] Forel”. Forel (1899) mentioned his (re-)description: “...Colombie, pied de la Sierra Nevada (Forel)” which fits well with the label’s locality, located north of the Sierra Nevada de Santa Marta. However, *A. velox* is a replacement name for *A. coeruleipennis* var. *fasciata* Pergande, 1896, based on homonymy. Hence Forel’s specimens of *A. velox* are not syntypes, but are included and illustrated here to avoid misinterpretations.

### Formicinae

*Camponotus alii* Forel, 1890 (Figs 3F, 4S) 3 syntypes (♂): “*C. alii* ♂ Forel Djebel Ozmor p. Tebessa, 1380 m (Forel) Type”. The label data corresponds perfectly with the original description by Forel (1890: LXIII) where he stated: “Forêts de pins du Djébel Ozmor près Tébessa de 1100 à 1300 mètres...”.

*C. bugnioni* Forel, 1899 (Figs 1E, 4E) 3 syntypes (♂): “*C. Bugnioni* ♂ Dibulla, Colombie (Forel)”. Fits perfectly with the indicated type locality-area given by Forel (1899: 131): “Hab. [Habitat] Colombie, forêts du pied de la Sierra Nevada de Santa Marta, de Dibulla à Santa Marta.”

*Cataglyphis savignyi* (Dufour, 1862) {*Myrmecocystus viaticus desertorum* Forel, 1894} (Figs 3E, 4R) 2 syntypes (♂): “*M. viaticus* v. *desertorum* Gabès, Tunesien”. Forel (1894b) mentioned Gabès as the locality of *C. desertorum*, described as n. v. [nouvelle variété]. However, *C. desertorum* is at present a junior synonym of *C. savignyi*.

*Lasius nyops* Forel, 1894 (Figs 3D, 4Q) 2 syntypes (♂): “*L. nyops* ♂ Forel Terni [Algeria; not Umbria as mentioned by Bloch 1940] 9.IV.” One of the – originally three – ♂ is lost. The locality fits with the description (Forel, 1894a: 12), where he indicated: “Vallon près de Terni à plus de 1400 mètres d’élévation, sous les pierres, dans les lieux boisés.” Furthermore, Forel’s journey to

Algeria was undertaken from 27th March to 19th April 1893, which corresponds with the given collection date (9th April).

### Myrmicinae

*Cardiocondyla stambuloffii* Forel, 1892 (Figs 2C, 4J) 3 syntypes (♂): “*C. Stambuloffii* Forel ♀ Burgas [Bulgaria] 13. VIII”. The type locality and the time fit perfectly with Forel (1892b), who gave Burgas, Anchialo and Sozopolis as localities and 13th to 16th August 1891 as time frame of his excursion.

*Crematogaster daisyi* Forel, 1901 (Figs 2F, 4M) 4 paralectotypes (3 ♂, 1 ♀) [\*not 4 ♀ as mentioned by Bloch (1940)] : “*Cr. Daisyi* Forel ♀ type Sarawak 76. [1876 ?] Haviland [=Borneo]”. As a lectotype and paralectotypes have been designated very recently by Hosoishi (2015), these formerly syntype specimens are paralectotypes according to article 73.2.2. of the ICZN (2016).

*C. ranavalonae* Forel, 1887 [\*not *ranovalonae* (sic!) as cited by Bloch (1940)] (Figs 2E, 4L) 3 syntypes (♂): “*C. ranavalonis* [sic!] Forel ♀ Bois Ivondro p. [près] Tamatavé (Madagascar)”. The locality corresponds perfectly with the one given by Forel (1887: 389).

*Messor lobicornis* Forel, 1894 (Figs 1D, 4D) 1 syntype (♂): “Terni [\*Algeria, Tlemcen; not Umbrien as mentioned by Bloch (1940)] 9.IV”. Forel (1894a: 32) gives the locality as follows: Caravansérail d’Aïn Ghoraba, près de Terni, dans une prairie. The label is identical with the one pictured from another syntype from the Forel collection of the MHNG on AntWeb (2016).

*Monomorium indicum* Forel, 1902 (Figs 1C, 4C) 3 syntypes (♂): “*M. Salomonis* r. [race] *indicum* ♀ Belgaum [=Belagavi, Karnataka, India] XXXI.12 (Wroughton)”. Although Forel (1902: 213) does not give any localities under *indicum*, he mentions “Belgaum” and the collector (Wroughton) under the species described above in the text (which is *Monomorium dichroum* Forel, 1902). Therefore it seems logical that *M. indicum* was collected at the same locality as *M. dichroum*, and therefore the locality on the label is the type locality, and that the present specimens belong to the syntype series.

*M. smithii* Forel, 1892 (Figs 1F, 4F) 3 syntypes (♂): “*M. Smithii* ♀ Type Forel, Ashburton N. Zealand (Smith)”. The label data of the syntypes fits perfectly with the locality given by Forel (1892a: 13), where he mentions “Ashburton, Neu-Seeland [New Zealand] (W. W. Smith)”.

*Myrmica smythiesii* Forel, 1902 (Figs 1B, 4B) 2 syntypes (♂): “*M. Smythiesii* ♀ Forel Cas ha mere [Cashmere] Smythies H. [18]79.” Forel (1902: 227) wrote in the description: “Diverses localités de l’Himalaya, de 7000’ à 12000’ [feet] (Smythies).” This includes the present indication. Furthermore the specimen was collected by Smythies himself while he travelled in the Himalayas.

*Pogonomyrmex mayri* Forel, 1899 (Figs 3A, 4N) 1 paralectotype (♂): “Sta. Martha [Santa Marta,

Colombia]”. Johnson (2015) designated the lectotype and paralectotypes based on syntypes examined at the NHMW.

***Solenopsis latro* Forel, 1894** (Figs 2D, 4K) 3 **syntypes** (♀): “*S. latro* ♀ Forel Souk Ahras [Algeria] chez *A. [Aphaenogaster] sardoa* (Forel)”. In his description Forel (1894a: 21) gives the same data: “Souk Ahras (Algérie orientale), en nid double avec l’*Aphaenogaster sardoa*.”.

***Strongylognathus huberi* Forel, 1874** (Figs 1A, 4A) 2 **syntypes** (♀): “*S. huberi* ♀ Fully” [Switzerland, canton Valais]; 1 ♀ “*Str. huberi* ♀ Type Fully 28.VIII”. Forel (1874) mentioned that both males and females, were unknown to him when describing *S. huberi*. Therefore, the single female – although marked with the word “Type” – obviously does not belong to the syntype series. The label of the workers fits perfectly with further syntype specimens shown on AntWeb (2016).

***Tennothorax algiricus trabutii* (Forel, 1894)** (Figs 1G, 4G) {*Leptothorax angustulus* r. [race] *trabutii* Forel, 1894} 2 **syntypes** (♀): “*L. angustulus* Nyl. ♀ r. [race] *Trabutii* [sic!] Forel Les Trembles Algérie”. The given locality fits perfectly with the indications by Forel (1894a: 37–38): “Tas de bois et de racines d’arbustes à Tlemcen, Terni, les Trembles, Hammam bou Hadjar.”

***T. delaparti* (Forel, 1890)** {*Leptothorax*} (Figs 2A, 4H) 2 **syntypes** (♀): “*L. de la Parti* Forel ♀ Djebel Ozmor p. [près] Tebessa 1380 m. [Algeria] Forel”. Fits perfectly with the description (Forel, 1890: LXXIV), where he stated: “Sommet du Djébel Ozmor (1380 mètres), près de Tebessa (Algérie)...”.

***T. oraniensis* (Forel, 1894)** {*Leptothorax nigrata* r. [race] *oraniensis*} (Figs 2B, 4I) 3 **syntypes** (♀): “*L. nigrata* r. [race] *oraniensis* Forel ♀ type Aïn Fezza Algérie (Forel)”. Fits perfectly with the indications in the description (Forel, 1894a: 35): “Franchetti, Aïn Fezza, Tlemcen, en fourmilières fort populeuses, situées sous les pierres des prairies un peu, mais pas trop rocailleuses. A Aïn Fezza, j’en ai trouvé plusieurs fourmilières dans une prairie située à côté de la gare.”

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**Appendix 1.** All 426 Formicidae from the Auguste Forel collection at the NMSO are listed with given locality, canton (for Swiss localities), states/nations, the year they were collected (if given), the numbers of specimens (m = males; q = queens; w = workers), the collector (leg.) and the presence of type specimens.

subfamily/genus/species	locality	canton	state	year	m	q	w	leg	types
<b>Dolichoderinae</b>									
<i>Azteca aurita</i>	Esperanza		Colombia		-	-	3	A. Forel	3 ancient syntypes (mixed type series)
<i>Azteca delpini antillana</i>			Santa Lucia		-	-	3	A. Forel	3 syntypes
<i>Azteca instabilis</i>	Buritaca (=Burithaka)		Colombia		-	-	2	A. Forel	
<i>Azteca velox</i>	Buritaca (=Burithaka)		Colombia		-	-	3	A. Forel	
<i>Bothriomyrmex meridionalis</i>	Mont Salève		France		-	-	3	A. Forel	
<i>Dolichoderus hispinosus</i>			Costa Rica		-	-	2	A. Forel	
<i>Dolichoderus decollatus</i>	Rio Frio		Colombia		-	-	2	A. Forel	
<i>Dolichoderus quadripunctatus</i>	Genève	GE	Switzerland		-	-	3	Frey-Gessner	
<i>Dolichoderus quadripunctatus</i>	Vaux-sur-Morges	VD	Switzerland		-	-	2	A. Forel	
<i>Forelius maccooki</i>	Austin (Texas)		USA		-	-	2		
<i>Iridomyrmex purpureus</i>	Mackay (Queensland)		Australia		-	-	2	A. Forel	
<i>Liometopum microcephalum</i>	Veselie (=Sare-Mussa)		Bulgaria		-	-	2	A. Forel	
<i>Tapinoma erraticum</i>	Vaux-sur-Morges	VD	Switzerland		-	-	2	A. Forel	
<i>Tapinoma erraticum</i>	Vaux-sur-Morges	VD	Switzerland		1	-	-	A. Forel	
<i>Tapinoma erraticum</i>	Mohammadia (=Perrégaux)		Algeria		2	-	-		
<i>Tapinoma erraticum</i>	Horgen	ZH	Switzerland		-	1	-	A. Forel	
<i>Tapinoma nigerrimum</i>	"Sudeuropa"				-	-	2	A. Forel	
<i>Tapinoma nigerrimum</i>	Sfax		Tunesia		-	1	-	A. Forel	
<b>Dorylinae</b>									
<i>Aenictus fergusonii</i>			India		-	-	2	A. Forel	
<i>Dorylus fuscipennis</i>	Aburi (Fisch)		Ghana		-	-	3		
<i>Dorylus helvolus</i>			Lesotho (Basutoland)		-	-	3	Wroughton	
<i>Eciton carolinense</i>	Faison, North Carolina		USA		-	-	3		
<i>Eciton hamatum</i>	Bonda		Colombia		-	-	3	A. Forel	
<i>Labidus coecus</i>	St. Catharina		Brasil		-	-	3		
<i>Labidus praedator</i>	Naranjo		Colombia		-	-	2	A. Forel	
<b>Ectatomminae</b>									
<i>Ectatomma ruidum</i>	Don Diego		Colombia		-	-	3	A. Forel	
<i>Rhytidoponera metallica</i>	#		Australia		-	-	1		
<b>Formicinae</b>									
<i>Camponotus aethiops</i>	Vaux-sur-Morges	VD	Switzerland		1	-	-	A. Forel	
<i>Camponotus aethiops</i>	Ajaccio (Korsika)		France		-	-	1	Bugnion	
<i>Camponotus aethiops</i>	Sofia		Bulgaria		1	-	2		
<i>Camponotus alii</i>	Djebel Ozmor, Tebessa		Algeria		-	-	3	A. Forel	3 syntypes
<i>Camponotus bugnioni</i>	Dibulla		Colombia		-	-	3	A. Forel	3 syntypes
<i>Camponotus cruentatus</i>	Montpellier (Hérault)		France		-	-	3	A. Forel	
<i>Camponotus foreli</i>	Mohammadia (=Perrégaux)		Algeria		-	-	3	A. Forel	

subfamily/genus/species	locality	canton	state	year	m	q	w	leg	types
<i>Camponotus herculeanus</i>	Uctliberg (Uto)	ZH	Switzerland		1	-	1	A. Forel	
<i>Camponotus lateralis</i>	Vaux-sur-Morges	VD	Switzerland		-	-	3	A. Forel	
<i>Camponotus lateralis</i>	Marseille, St. Loup		France		-	-	3	A. Forel	
<i>Camponotus ligniperda</i>			Switzerland		-	1	-	A. Forel	
<i>Camponotus ligniperda</i>	Vaux-sur-Morges	VD	Switzerland		-	-	1	A. Forel	
<i>Camponotus ligniperda</i>	Langnau am Albis	ZH	Switzerland		1	-	-	A. Forel	
<i>Camponotus maculatus</i>	Morongang (=Moyanga)		Madagascar		-	-	3		
<i>Camponotus massiliensis</i>	Marseille		France		-	-	3	A. Forel	
<i>Camponotus micans</i>	Soussa (=Susa)		Lybia		-	-	3	A. Forel	
<i>Camponotus oasium</i>	Ghadame (=Ghadamès)		Lybia		-	-	2	Ali	
<i>Camponotus sylvaticus</i>	Marseille, St. Loup		France		-	-	3		
<i>Camponotus sylvaticus</i>	Tebessa		Algeria		-	-	3	A. Forel	
<i>Camponotus vagus</i>			Bulgaria		-	1	-		
<i>Camponotus vagus</i>	Veselie (=Sare-Mussa)		Bulgaria		-	-	2		
<i>Cataglyphis albicans</i>	Soussa (=Susa)		Lybia		-	-	2	A. Forel	
<i>Cataglyphis bicolor</i>	Ghardimaon		Tunesia		-	-	2	A. Forel	
<i>Cataglyphis bombycina</i>	Ghadame (=Ghadamès)		Lybia		-	-	2	Ali	
<i>Cataglyphis cursor</i>	Montpellier (Hérault)		France		-	-	2	A. Forel	
<i>Cataglyphis savignyi</i>	Gabes		Tunesia		-	-	2	A. Forel	2 syntypes
<i>Formica cinerea</i>	Branson (Fully)	VS	Switzerland		-	-	2	A. Forel	
<i>Formica exsecta</i>	Mustad		Norway		-	-	2		
<i>Formica exsecta</i>	Mustad		Norway		-	1	-		
<i>Formica exsectoides</i>			USA		-	-	3	A. Forel	
<i>Formica exsectoides</i>	Worcester, Massachusetts		USA	1899	1	-	-		
<i>Formica fusca(-group)</i>	Stavanger		Norway		-	-	2	A. Forel	
<i>Formica fusca(-group)</i>	Zürich	ZH	Switzerland		-	1	-	A. Forel	
<i>Formica gagates</i>	Wien		Austria		-	-	2		
<i>Formica integra</i>	Washington		USA		-	-	3		
<i>Formica pallidefulva</i>	Morganton (State unknown)		USA		-	-	2	A. Forel	
<i>Formica pratensis</i>	Quarten, Quinten	SG	Switzerland		1	-	-		
<i>Formica pratensis</i>	Quarten, Quinten	SG	Switzerland		-	-	1		
<i>Formica pratensis</i>	München (Bayern)		Germany		-	-	2		
<i>Formica pressilabris</i>	Vaux-sur-Morges	VD	Switzerland		1	-	3	A. Forel	
<i>Formica rufa(-group)</i>	Horgen	ZH	Switzerland	1891	1	-	-		
<i>Formica rufa(-group)</i>	Fisibach	AG	Switzerland		-	-	2		
<i>Formica rufa(-group)</i>	Schliersee, Bayern		Germany		-	-	3		
<i>Formica rufibarbis</i>	Kashmir		India	1872	-	-	2		
<i>Formica sanguinea</i>	Rilo (Rila-mountains)		Bulgaria		-	1	-		
<i>Formica sanguinea</i>	Vallombrosa, Florenz		Italien		-	-	2		
<i>Lasius alienus</i>	Adelsberg (Krain)				-	-	2		
<i>Lasius brunneus</i>	Himalaja		Nepal	1860	-	-	2	Smythies	
<i>Lasius emarginatus</i>	Adelsberg (Krain)				-	-	3		
<i>Lasius flavus</i>	Fisibach	AG	Switzerland		-	-	3		
<i>Lasius flavus</i>	Fisibach	AG	Switzerland		-	1	-		

subfamily/genus/species	locality	canton	state	year	m	q	w	leg	types
<i>Lasius fuliginosus</i>	Drôme		France		-	-	2	A. Forel	
<i>Lasius fuliginosus</i>	Zürich	ZH	Switzerland		1	-	-		
<i>Lasius mixtus</i>	Morges	VD	Switzerland		-	1	-	A. Forel	
<i>Lasius mixtus</i>	Quarten, Quinten	SG	Switzerland		-	-	3	A. Forel	
<i>Lasius myops</i>	Terni		Algeria		-	-	2	A. Forel	2 syntypes
<i>Lasius niger</i>	Zürich	ZH	Switzerland		-	1	-	A. Forel	
<i>Lasius niger</i>	Madeira		Portugal		-	-	3	Schmitz	
<i>Lasius umbratus</i>	München (Bayern)		Germany		-	-	2		
<i>Lasius umbratus</i>	Zürich, Burghölzli	ZH	Switzerland		-	1	-	A. Forel	
<i>Lasius umbratus</i>	Zürich, Burghölzli	ZH	Switzerland		1	-	-	A. Forel	
<i>Lepisiota frauenfeldi</i>	Meseheria, Djebel Autar		Algeria		-	-	3	A. Forel	
<i>Oecophylla smaragdina</i>	Delagoa (Bay; =Maputo-Bucht)		Mozambique		-	-	2		
<i>Polyergus rufescens</i>	Vaux-sur-Morges	VD	Switzerland		1	1	3	A. Forel	
<i>Polyrhachis abdominalis</i>	Sumatra		Indonesia		-	-	1	Moesch	
<i>Polyrhachis bihamata</i>	Bingham		Burma		-	-	2		
<i>Polyrhachis dives</i>	Assam		India	1860	-	-	2	Smythies	
<i>Proformica nasuta</i>	Dubnitza		Bulgaria		-	-	1		
<b>Myrmicinae</b>									
<i>Acromyrmex disciger</i>	Blumenau		Brasil		-	-	2	Möller	
<i>Acromyrmex niger</i>	Rio de Janeiro		Brasil		-	-	3	Göldi	
<i>Acromyrmex octospinosus</i>	Don Diego		Colombia		-	-	2	A. Forel	
<i>Aphaenogaster fulva</i>	Baltimore		USA		-	1	2	A. Forel	
<i>Aphaenogaster gibbosa</i>	Souk Ahras		Algeria		-	-	3	A. Forel	
<i>Aphaenogaster lamellidens</i>	Faison, North Carolina		USA		-	-	2		
<i>Aphaenogaster pallida</i>	Les Trembles		Algeria		-	-	2	A. Forel	
<i>Aphaenogaster sardoa</i>	Meehroha (=Laverdure)		Algeria		-	-	2	A. Forel	
<i>Aphaenogaster subterranea</i>	Sliven		Bulgaria		-	-	1	A. Forel	
<i>Aphaenogaster subterranea</i>	Neapel, Capodimonte		Italien	1866	1	-	-	A. Forel	
<i>Aphaenogaster swammerdami</i>	Nosibé		Madagasear		-	-	1	Völtzkow	
<i>Aphaenogaster tennesseensis</i>	New Hampshire		USA		-	-	1		
<i>Aphaenogaster testacopilosa</i>	Tunis		Tunesia		-	-	2	A. Forel	
<i>Aphaenogaster treatae</i>	AA Fundort unbekannt				-	-	2	A. Forel	
<i>Apterostigma pilosum</i>	Santa Catharina		Brasil		-	-	2	Möller	
<i>Atta cephalotes</i>			Costa Riea		-	-	3	Tonduz	
<i>Atta lacvigata</i>	San Antonio		Colombia		-	-	3	A. Forel	
<i>Atta sexdens</i>			Colombia		-	-	2	A. Forel	
<i>Atta tardigrada</i>	Black Mountain, North Carolina		USA		-	-	1	A. Forel	
<i>Cardiocondyla stambuloffii</i>	Burgas		Bulgaria		-	-	3	A. Forel	3 syntypes
<i>Carcara diversa</i>			India		-	-	4		
<i>Cataulacus latus</i>	Kanara (SW India)		India		-	1	-	Wroughton	
<i>Cephalotes atratus</i>	Pará		Brasil		-	-	1	Göldi	
<i>Cephalotes umbraculatus</i>	Trinidad		Trinidad and Tobago		-	-	2	Urieh	



subfamily/genus/species	locality	canton	state	year	m	q	w	leg	types
<i>Crematogaster auberti</i>	Tilimsen (Tlemcen)		Algeria		-	-	2	A. Forel	
<i>Crematogaster daisyi</i>	Sarawak, Borneo		Indonesia		-	1	3		4 paralectotypes
<i>Crematogaster ranavalonae</i>	Ivondro, Tamatavé		Madagascar		-	-	3		3 syntypes
<i>Crematogaster rogenhoferi</i>	Poona		India		-	-	3	Wroughton	
<i>Crematogaster scutellaris</i>	Souk Ahras		Algeria		-	-	3	A. Forel	
<i>Crematogaster sordidula</i>	Marseille		France		-	-	3	A. Forel	
<i>Cyphomyrmex rimosus</i>	Sao Vicente		Brasil		-	1	3		
<i>Formicoxenus nitidulus</i>	Ural (Gebirge)		Russia		-	-	1	A. Forel	
<i>Goniomma hispanicum</i>	Camargue		France		-	-	2	A. Forel	
<i>Leptothorax accervorum</i>	Trient, La Forelaz	VS	Switzerland		-	-	3	A. Forel	
<i>Leptothorax muscorum</i>	Schluderbaeh (=Carbonin), Südtirol		Austria		-	-	3	A. Forel	
<i>Meranoplus bicolor</i>			India	1877	-	-	2	Rogers	
<i>Messor barbarus</i>	Mohammadia (=Perrégaux)		Algeria		-	1	-	A. Forel	
<i>Messor barbarus</i>	Meehroha (=Laverdure)		Algeria		-	-	3	A. Forel	
<i>Messor lobicornis</i>	Terni		Algeria		-	-	1	A. Forel	1 syntype
<i>Messor structor</i>	Miramar, Balearn		Spain		-	1	2	A. Forel	
<i>Monomorium antarcticum</i>	Ashburton		New Zealand	1891	-	-	2	Smith	
<i>Monomorium antarcticum</i>	Nordinsel		New Zealand		-	-	3	Brooks	
<i>Monomorium indicum</i>	Belgaum (=Belagavi, Karnataka)		India		-	-	3	Wroughton	3 syntypes
<i>Monomorium pharaonis</i>	Blumenau		Brasil		-	-	3	A. Forel	
<i>Monomorium smithii</i>	Ashburton		New Zealand		-	-	3	Smith	3 syntypes
<i>Myrmica lobicornis</i>	Elinine Vrh, Rilo Dagh		Bulgaria		-	-	3		
<i>Myrmica rubida</i>	Quarten, Murg	SG	Switzerland		-	1	1		
<i>Myrmica rubra</i>	AA Fundort unbekannt				-	-	3		
<i>Myrmica ruginodis</i>	Rilo (Rila-mountains)		Bulgaria		-	-	2		
<i>Myrmica rugulosa</i>	Quarten, Murg	SG	Switzerland		-	-	3	A. Forel	
<i>Myrmica scabrinodis</i>	Vaux-sur-Morges	VD	Switzerland		2	1	2	A. Forel	
<i>Myrmica smythiesii</i>	Kashmir		India	1879	-	-	2	Smythies	2 syntypes
<i>Myrmica sulcinodis</i>	Schluderbaeh (=Carbonin), Südtirol		Austria		-	1	3		
<i>Myrmecaria fodica</i>	Chennai (=Madras)		India		-	-	2	Rothney	
<i>Nylanderia steinheili</i>	Barranquilla		Colombia		-	-	1	A. Forel	
<i>Nylanderia steinheili</i>	Rio Frio		Colombia		-	-	3	A. Forel	
<i>Pheidole megacephala</i>	Mana, Rio		Brasil		-	-	1	Göldi	
<i>Pheidole megacephala</i>	Madeira		Portugal		-	-	2	Schmitz	
<i>Pheidole megacephala</i>	Nosibé		Madagascar		-	1	-	Völtzkow	
<i>Pheidole pallidula</i>	Algier		Algeria		-	-	2	Moser	
<i>Pheidole pallidula</i>	Valle Onsernone	TI	Switzerland		-	1	2	A. Forel	
<i>Pheidole pallidula</i>	Ghadame (=Ghadamès)		Libya		1	-	-	A. Forel	
<i>Pheidole pallidula</i>	Tebessa		Algeria		-	-	2	A. Forel	
<i>Pheidole praenusta</i>	Rio Frio		Colombia		-	-	2	A. Forel	
<i>Podomyrma gratioso</i>	Süd-Australia		Australia		-	-	1		
<i>Podomyrma laevifrons</i>	Queensland		Australia		-	-	1		

subfamily/genus/species	locality	canton	state	year	m	q	w	leg	types
<i>Pogonomyrmex badius</i>	Florida		USA		-	-	1		
<i>Pogonomyrmex mayri</i>	Santa Marta (=Martha)		Colombia		-	-	1		1 paralectotype
<i>Pseudomyrmex gracilis</i>	Tuis		Costa Rica	1868	-	-	1	Pillier	
<i>Pseudomyrmex termitarius</i>	San Antonio		Colombia		-	-	3	A. Forel	
<i>Solenopsis fugax</i>	Adelsberg, Erzgebirge (Sachsen)		Germany		-	-	3	A. Forel	
<i>Solenopsis geminata</i>	Odisha (=Orissa)		India	1864	-	-	3	A. Forel	
<i>Solenopsis latro</i>	Souk Ahras		Algeria		-	-	3	A. Forel	3 syntypes
<i>Strongylognathus huberi</i>	Fully	VS	Switzerland		-	1	-	A. Forel	
<i>Strongylognathus huberi</i>	Fully	VS	Switzerland		-	-	2	A. Forel	2 syntypes
<i>Strongylognathus testaceus</i>	Fribourg	FR	Switzerland		1	1	1		
<i>Temnothorax affinis</i>	Vaux-sur-Morges	VD	Switzerland		-	-	3	A. Forel	
<i>Temnothorax algiricus trabutii</i>	Les Trembles		Algeria		-	-	2	A. Forel	2 syntypes
<i>Temnothorax delaparti</i>	Djebel Ozmor, Tebessa		Algeria		-	-	2	A. Forel	2 syntypes
<i>Temnothorax nigriceps</i>	Elsass, Neuntelstein		Germany		-	-	3	A. Forel	
<i>Temnothorax nylanderi</i>	Sofia		Bulgaria		-	-	3	A. Forel	
<i>Temnothorax oraniensis</i>	Ain Fezza		Algeria		-	-	3	A. Forel	3 syntypes
<i>Temnothorax recedens</i>	Montpellier (Hérault), parc près de		France		-	-	2	A. Forel	
<i>Temnothorax rogeri</i>	Sliven		Bulgaria		-	-	1	A. Forel	
<i>Temnothorax rottenbergii</i>	Mechroha (=Laverdure)		Algeria		-	-	3	A. Forel	
<i>Temnothorax tuberculum</i>	Mont Salève		France		-	-	2	A. Forel	
<i>Temnothorax unifasciatus</i>	Vaux-sur-Morges	VD	Switzerland		-	-	2	A. Forel	
<i>Tetramorium caespitum</i>	Wien Leopoldsberg		Austria		-	-	3	A. Forel	
<i>Tetramorium sericeiventre</i>	Imérina, Camboné		Madagascar		-	-	3	A. Forel	
<i>Tetraponera rufonigra</i>	Dharamsala, Himachal Pradesh		India		-	-	2	Fulton	
<i>Trichomyrmex scabriceps</i>	Surat, Siwalli (Ost- India)		India		-	-	3	Roger	
<i>Xenomyrmex floridanus</i>	Faison, North Carolina		USA		-	-	3	A. Forel	
<b>Ponerinae</b>									
<i>Anochetus emarginatus</i>	Calabasso		Colombia		-	-	3	A. Forel	
<i>Anochetus inermis</i>	Trinidad		Trinidad and Tobago		-	-	1		
<i>Brachyponera lutea</i>	Ost Zullusland, Wiederkehr		Australia		-	-	1		
<i>Euponera stigma</i>	Naranjo		Colombia		-	-	1	A. Forel	
<i>Harpegnathos saltator cruentatus</i>	Kanara (SW India)		India	1866	-	-	1	Bell	
<i>Leptogenys processionalis</i>	Ceylon (Sri Lanka)		India		-	-	3		
<i>Odontomachus haematodus</i>	Sumatra		Indonesia		-	-	3	Tritöchler	
<i>Ponera coarctata</i>			Europe		-	-	1		

**Taxonomic revision of the genus *Sertularella* (Cnidaria: Hydrozoa)  
from southern South America and the subantarctic, with descriptions of five new species**

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**Abstract:** The hydroids belonging to the genus *Sertularella* Gray, 1848 from southern South America and the subantarctic are revised, based on both literature data and the reexamination of type specimens and additional material dealt with in earlier accounts. Thirty-two species are recognized as valid, of which five are new to science, namely *S. juanfernandezensis*, *S. oblonga*, *S. recta*, *S. robustissima*, and *S. subantarctica*. Modern redescriptions of *S. implexa* (Allman, 1888) and *S. novarae* Marktanner-Turneretscher, 1890 are provided. Additionally, it is demonstrated that *S. argentinica* El Beshbeeshy, 2011 and *S. jorgensis* El Beshbeeshy, 2011 are junior synonyms of *S. clausa* (Allman, 1888) and *S. valdiviae* Stechow, 1923, respectively. *Sertularella paessleri* Hartlaub, 1901 is assigned to the synonymy of *S. allmani* Hartlaub, 1901, *S. lagena* Allman, 1876 to that of *S. contorta* Kirchenpauer, 1884, *S. picta* (Meyen, 1834), *S. protecta* Hartlaub, 1901 and *S. margaritacea* Allman, 1885 to that of *S. gaudichaudi* (Lamouroux, 1824), *Sertularella uruguayensis* Mañé Garzón & Milstein, 1973 to that of *S. mediterranea* Hartlaub, 1901, and *S. striata* Stechow, 1923 to that of *S. patagonica* (d'Orbigny, 1842). Lectotypes are designated for *S. allmani*, *S. antarctica* Hartlaub, 1901, and *S. implexa*. A checklist of all species records from the study area, together with new identifications, is provided as an appendix.

**Keywords:** Chile - Argentina - Uruguay - subantarctic.

## INTRODUCTION

During the last decade, a rich hydroid material was collected from Chile in the frame of a series of expeditions carried out by the staff of the Huinay Scientific Field Station (HSFS) and the Instituto de Ciencias Marinas y Limnológicas (Universidad Austral de Chile, Valdivia), from Taltal, in the north, to the Strait of Magellan, in the south. Several papers, among which Galea (2007), Galea *et al.* (2007a, b; 2009), Galea & Schories (2012a) and Galea *et al.* (2014), resulted from the study of these collections, updating and clarifying earlier accounts by Philippi (1866), Ridley (1881), Jäderholm (1904), Hartlaub (1905) and Leloup (1974).

One of the most speciose genera present in these collections, *Sertularella* Gray, 1848, is – according to the literature – represented by 24 nominal species in Chile. Some of them have a much wider geographical distribution, and are equally found along the Argentine

Shelf (El Beshbeeshy, 2011), while some others extend well to the subantarctic. To verify the accuracy of earlier identifications provided for the Chilean members of the genus, it became necessary to reexamine the materials corresponding to all species created by El Beshbeeshy.

Moreover, since a rather restricted number of studies, some outdated according to the requirements of modern taxonomy, have been published (Allman, 1876, 1879, 1888; Blanco, 1963, 1967, 1968, 1974, 1976, 1982, 1984; Hartlaub, 1901, 1905; Jäderholm, 1903, 1905, 1910; Kirchenpauer, 1884; Ritchie, 1907; Stechow, 1923a, 1925; Vanhöffen, 1910), it became imperative to clarify the status of the various records of hydroids assignable to the genus *Sertularella*.

Among them, many nominal taxa belong to a group characterized by the unilateral arrangement of both hydrothecae and side branches along the stem, namely: *S. allmani* Hartlaub, 1901, *S. antarctica* Hartlaub,

1901, *S. contorta* Kirchenpauer, 1884, *S. gaudichaudi* (Lamouroux, 1824), *S. paessleri* Hartlaub, 1901, *S. picta* (Meyen, 1834), and *S. protecta* Hartlaub, 1901. As noted by El Beshbeeshy (2011), their taxonomic status, as well as their relationships, were often misunderstood, thus spreading confusion within the relevant literature.

To provide a comprehensive account on the taxonomy and species composition, all literature records from a large geographical area encompassing the coasts of Chile, Argentina, and Uruguay, as well as the subantarctic, are being reviewed herein. Literature records from the latter area include the Scotia Arc, the Falkland Is., Marion and Prince Edward Is., the French Southern and Antarctic Lands, and Macquarie I.

The gonothecae of many genera of thecate hydroids are important anatomical structures allowing reliable species identifications. There is a considerable uniformity in their morphology within the genus *Sertularella* in general, and among the species from the study area in particular (*cf.* literature cited above). Indeed, nearly all nominal species (exclusive of both *S. argentinica* El Beshbeeshy, 2011 and *S. valdiviae* Stechow, 1923b) have broadly ovoid, transversely ribbed gonothecae, provided distally with (generally) 4 spines. During this study, it became obvious that their structural homogeneity does not offer sufficient grounds for species separation, and thus their morphology is not always taken into consideration herein.

The colony structure, the habit of the stem, and the hydrothecal shape, however, represent the most reliable characters, and thus are used here to distinguish between species.

## MATERIAL AND METHODS

Sampling was done by scuba diving by three of us (VH, GF and DS). The material was collected during various “Huinay Fiordos” (HF) expeditions carried out by the HSFS staff, as well as by DS and his research team.

The collected specimens were fixed in 4% formalin in seawater. Observations were done on preserved material using the methods described in Galea (2007). Most samples were deposited in collections of the *Muséum d'Histoire Naturelle* of Geneva, Switzerland, whose catalogue numbers are indicated by MHNG-INVE-. Parts of the collected materials are also housed in the private collection of the senior author, and their corresponding registration numbers are indicated by HRG-.

Additional samples examined in the frame of this study were obtained from various European museums, and their registrations are indicated by numbers after the codes NHML (Natural History Museum, London, United Kingdom), NMSZ (National Museums Scotland, Edinburgh, United Kingdom), SMNH (*Naturhistoriska Riksmuseet*, Stockholm, Sweden), ZMB Cni (*Naturkundemuseum Berlin*, Germany), ZMH C (*Zoologisches Institut und zoologisches Museum der*

*Universität Hamburg*, Germany), and ZSM (*Zoologische Staatssammlung München*, Germany).

Comprehensive synonymies are generally given for the species records belonging exclusively to the study area; in only rare instances, significant records from outside this perimeter are provided. To facilitate comparisons between the species dealt with herein, all colony fragments and all hydrothecae are drawn to the same scale, respectively. The gonothecae are illustrated either for the new taxa described herein or some poorly-known species, while relevant bibliographical sources, including both descriptions and illustrations of them, are indicated for the remaining species, whenever these anatomical structures are known.

## TAXONOMY AND RESULTS

### Order Leptothecata Cornelius, 1992

### Family Sertularellidae Maronna *et al.*, 2016

### Genus *Sertularella* Gray, 1848

#### *Sertularella allmani* Hartlaub, 1901

Figs 1A, B, 2; Table 1

*Sertularella Allmani* Hartlaub, 1901: 81, pl. 5 figs 12, 13; pl. 6 figs 1, 8 (replacement name for *Sertularia secunda* Allman, 1888). – (?) Jäderholm, 1903: 283.

non *Sertularella Allmani*. – Jäderholm, 1905: 32, pl. 12 fig. 11 (= *Sertularella subantarctica* Galea, sp. nov.).

*Sertularella allmani*. – Hartlaub, 1905: 649, fig. O<sup>1</sup>. – Bedot, 1916: 199; 1918: 234. – Billard, 1924: 61. – El Beshbeeshy, 2011: 121, fig. 37F.

non *Sertularella allmani*. – Naumov & Stepanjants, 1962: 86 [= *Sertularella gaudichaudi* (Lamouroux, 1824)].

*Sertularia secunda* Allman, 1888: pl. 25 figs 2, 2a, 2b (replacement name for *Sertularia unilateralis* Allman, 1888: 53). – Vervoort, 1972: 108, fig. 33 (reexamination of holotype).

non *Sertularella secunda* Kirchenpauer, 1884: 50, pl. 15 figs 7, 7a [= *Symplectoscyphus secundus* (Kirchenpauer, 1884)].

*Sertularia unilateralis* Allman, 1888: 53 {non *Sertularia unilateralis* Lamouroux, 1824: 615, pl. 90 figs 1-3 [= *Symplectoscyphus unilateralis* (Lamouroux, 1824)]; non *Sertularia unilateralis* Allman, 1885: 139, pl. 13 figs 5-7 [= *Amphisbetia bispinosa* (Gray, 1843)]}.

(?) *Sertularella paessleri* Hartlaub, 1901: 80, pl. 6 figs 3, 19. – Hartlaub, 1905: 654, fig. S<sup>4</sup>.

*Sertularella mediterranea asymmetrica* Millard, 1958: 191, fig. 7B. – Millard, 1964: 45. – Millard, 1975: 295, fig. 96A [non *Sertularella mediterranea* Hartlaub, 1901].

*Sertularella antarctica*. – Blanco, 1963: 170, figs 5, 6. – Stepanjants, 1979: 84, pl. 15 fig. 3. – Blanco, 1994: 198. – Galea *et al.*, 2009: 7, figs 2J-N, 3A-B [non *Sertularella antarctica* Hartlaub, 1901].

**Material examined:** ZMH C04177; Chile, Región de Magallanes y de la Antártica Chilena, Isla Navarino, west of Puerto Pantalón del Oeste, ca. 12 m, coll. Michaelsen no. 180; 31.12.1892; several fertile

fragments (only part of the whole sample examined herein), up to 3.8 cm high, largest with accessory tubes on stem. There is obviously a crossing-out in the ZMH catalogue for this material: although it bears the official no. 180, it was indicated as no. 189 by Hartlaub (1901), as both share the same collection data. However, no. 189 corresponds to another specimen,

ZMH C04178, assignable to *S. picta* (Meyen, 1834). As indicated by Hartlaub, the material is well-preserved and fertile. Since the 2nd specimen (from Port Stanley, Falkland Is., coll. Paessler, 12.04.1893) on which *S. allmani* was equally based upon was destroyed during WWII (H. Roggenbuck, pers. comm.), the specimen ZMH C04177 is designated here as the lectotype of



Fig. 1. (A, B) *Sertularella allmani* Hartlaub, 1901. Two holotype slides of *Sertularia secunda* Allman, 1888 (= *Sertularia unilateralis* Allman, 1888). (C) *Sertularella blanconae* El Beshbeeshy, 2011, material identified as *S. gayi* (Lamouroux, 1821) by Jäderholm (1903). (D) *Sertularella clausa* (Allman, 1888), holotype slide. (E, F) *Sertularella contorta* Kirchenpauer, 1884 identified as *S. polyzonias* (Linnaeus, 1758) by Jäderholm (1910) (E) and *S. lagena* Allman, 1876 by Stechow (1925) (F), respectively. (G) Slide material studied by Jäderholm (1905), containing *S. contorta* (colony on the left-hand side) and *S. subantarctica* Galea, sp. nov. (colony on right-hand side), the latter identified by him as *S. allmani*. (H-K) *Sertularella gaudichaudi* (Lamouroux, 1824). Slide materials identified as *S. picta* (Meyen, 1834) (H), *S. antarctica* Hartlaub, 1901 (I) and *S. protecta* Hartlaub, 1901 (J) by Jäderholm (1903); as *S. protecta* by Stechow, according to Rees & Thursfield (1965) (K).

*S. allmani*. – NHML 1888.11.13.101; French Southern and Antarctic Lands, Kerguelen Is., ca. 36 m, coll. *Challenger*; holotype of *Sertularia secunda* Allman, 1888 (= *Sertularia unilateralis* Allman, 1888), three male colony fragments (3.0, 1.5 and 1 cm high) in ethanol, as well as two slides; one slide (Fig. 1B), labeled “type” contains a 1.1 cm high, fertile colony fragment, and bears the mention “Challenger Stat 149D, Kerguelen, Depth 20 faths, *Sertularia secunda* (*unilateralis*)”; the second slide (Fig. 1A) is a 1.7 cm high, fertile, branched colony fragment and bears the label “Challenger Coll., *Sertularella secunda* (Allman), Kerguelen (d. 20 fms), B. carm.”. – MHNG-INVE-62835; Chile, Región de los Lagos, south of Isla Yencouma (south Chiloé), -42.40958° -74.08353°, 8 m, coll. HSFS, HF6, lot A521; 24.02.2008; several stems up to 1.6 cm high bearing male gonothecae. – HRG-0637; Chile, Región de Magallanes y de la Antártica Chilena, Islotes Gemelos, -54.91942° -67.36308°, 13 m, coll. HSFS, HF9, lot C132; 15.12.2010; several stems up to 5 cm high, richly bearing either male or female gonothecae, the latter with acrocysts. – HRG-0314; Chile, Región de los Ríos, Corral, La Amistad

(San Carlos), -39.85744° -73.44024°, 5-10 m, coll. D. Schories, pooled lots 02 and 06; 26.05.2011; colony on seaweed, composed of many stems up to 4.3 cm high, bearing male gonothecae. – HRG-0634; Chile, Región de los Ríos, north of Corral, Chaihuin, -39.95730° -73.60245°, 6-12 m, coll. D. Schories; 27.10.2011; profuse colonies with up to 5 cm high stems, bearing either male or female gonothecae, the latter with acrocysts. – HRG-0644; Chile, Región de los Ríos, north of Corral, Chaihuin, -39.95730° -73.60245°, 6-12 m, coll. D. Schories; 27.10.2011; male colony on seaweed, composed of numerous stems up to 5 cm high. – HRG-0636; Chile, Región de los Ríos, Niebla, Bonifacio, -39.69002° -73.37940°, 10-15 m, coll. D. Schories; 09.10.2012; numerous colonies on seaweed, with up to 3.5 cm high stems, bearing either male or female gonothecae, the latter with acrocysts.

**Description:** Creeping, branching, anastomosing stolons giving rise to erect, bushy, irregularly-pinnate colonies, up to 6 cm high. Stems either mono- or lightly fascicled basally; in the first case, with 2-5 twists above origin from stolon. Both stems and branches divided into regularly-short, almost collinear internodes by

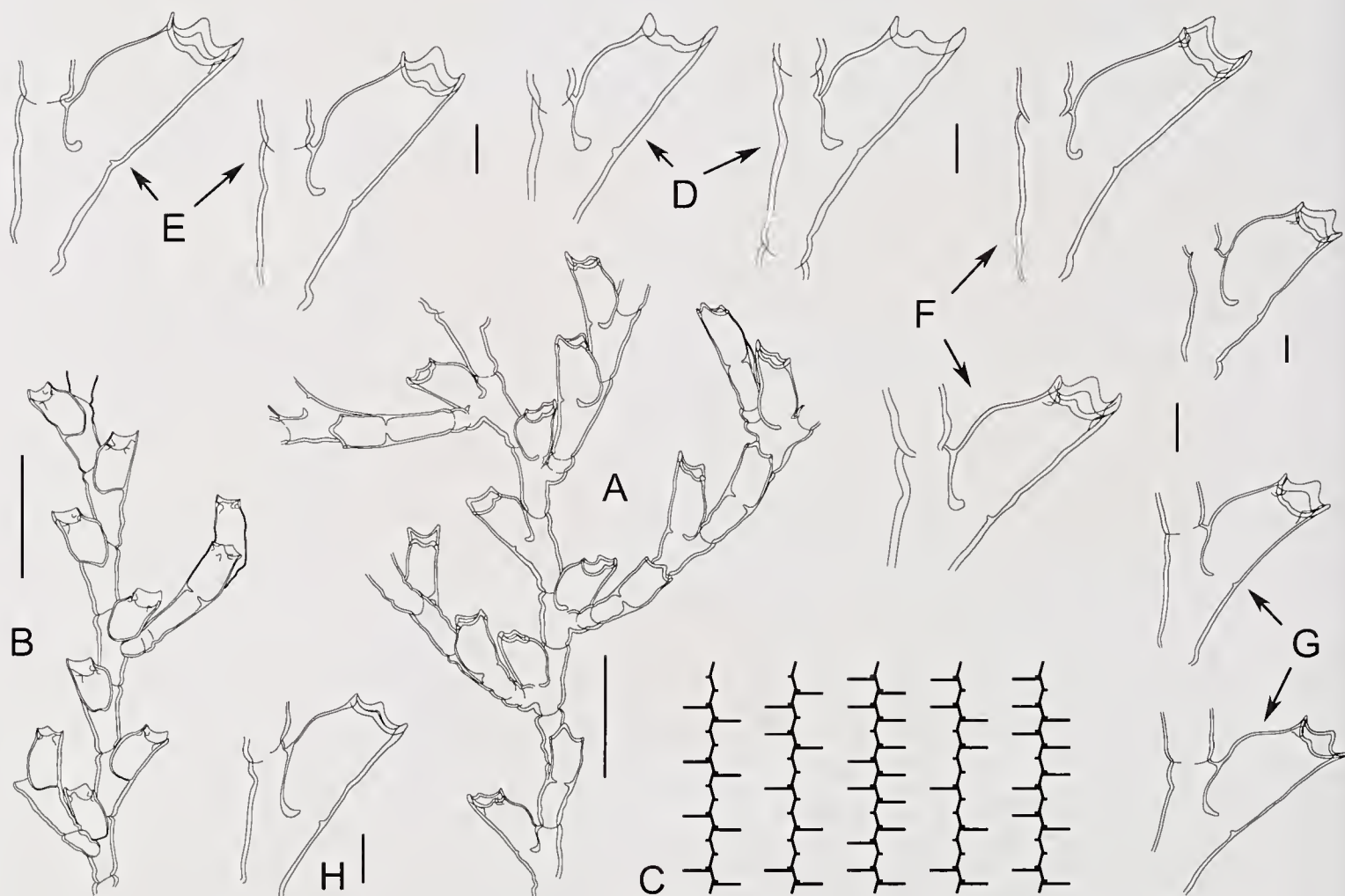


Fig. 2. *Sertularella allmani* Hartlaub, 1901. Colony fragments from lectotype (A) and material MHNG-INVE-62835 (B). Mode of branching (C). Hydrothecae from the lectotype of *S. allmani* (D), the holotype of *Sertularia secunda* Allman, 1888 (= *Sertularia unilateralis* Allman, 1888) (E, alcohol-preserved material; F, 2nd slide), and materials HRG-0314 (G), HRG-0637 (H) and HRG-0644 (I). Scale bars: 200  $\mu$ m (D-I), 1 mm (A, B).

means of deep, slightly oblique constrictions of the perisarc; the latter typically dark-brown at nodes, and almost transparent elsewhere; each internode with slight bulges at each end, and distally bearing a hydrotheca, or a hydrotheca and a lateral apophysis arising immediately from below its base. Hydrothecae, apophyses and side branches shifted on to one side of the colony at an acute angle, giving it two obvious, frontal and dorsal sides, respectively. Branching profuse, with a general, characteristic pattern: a couple of two consecutive, alternate side branches is separated from the next couple of branches by 1-2 (occasionally 0) internodes devoid of apophyses; occasionally, only one branch of a “pair” occurs (Fig. 2C); there are up to 3rd order branches. Hydrothecae biserial, alternate, flask-shaped, moderately-long, adnate for about 1/3rd of their length, distinctly swollen adaxially, narrowing below aperture; abaxial wall nearly straight, free adaxial wall sigmoid, convex for most of its length, becoming concave a short distance below the aperture; rim thickened, provided with four, unequal cusps (abaxial one conspicuously produced, adaxial one the shortest, and the laterals asymmetrical and of intermediate length, the “anterior” one comparatively shorter than its “posterior” counterpart); cusps separated by deep, rounded embayments; 3 internal, submarginal cusps (2 latero-adaxial, 1 abaxial), not always present; operculum composed of 4 triangular flaps forming a conical roof. Gonothecae borne on both stems and side branches, arising from below the hydrothecal bases; broadly ovoid, with 6-8 transverse ridges, not always distinct; distally a short neck provided with generally 4 (occasionally 2-5) blunt projections of perisarc

surrounding a central, rounded aperture; acrocysts in female. Perisarc of colonies either thin or thick.

**Dimensions:** See Table 1.

**Remarks:** When Allman (1888) realized that his *Sertularia unilateralis* (main text, p. 53) was a homonym (of *Sertularia unilateralis* Lamouroux, 1824 and *Sertularia unilateralis* Allman, 1885), he introduced the replacement name *Sertularia secunda* (legend of pl. 25, figs 2, 2a, 2b). However, Hartlaub (1901) correctly placed Allman’s species in the genus *Sertularella* Gray, 1848 and noted that, there, it becomes a junior synonym of *Sertularella secunda* Kirchenpaucr, 1884 (the latter is now assigned to the genus *Symplectoscyplus* Marktanner-Turneretscher, 1890). He therefore introduced a second replacement name, viz. *S. allmani*.

Calder (2015, p. 239, note 39), influenced by the opinion originally expressed by Vervoort (1972) and subsequently followed by Galea *et al.* (2009), decided to reject as invalid the binomen *Sertularia unilateralis* Allman, 1888 (a species of *Sertularella* Gray, 1843), its replacement name *Sertularia secunda* Allman, 1888 and, in turn, its replacement name *Sertularella allmani* Hartlaub, 1901, in the belief that all were synonyms of the frequently reported *Sertularella antarctica* Hartlaub, 1901 and its senior objective synonym *Sertularella unilateralis* Allman, 1876 (Calder, pers. comm.). However, in light of the present study, *S. allmani* is considered as a valid species, distinct from *S. antarctica* (see also remarks under the latter). Consequently, Calder’s (2015) suggestion, according to which a “case could be made (ICZN Art. 59.3.) for retention of

Table 1. Measurements of *Sertularella allmani* Hartlaub, 1901, in  $\mu\text{m}$ .

	El Beshbeeshy (2011), lectotype of <i>S. allmani</i> , ZMH C 04177	Galea <i>et al.</i> (2009), as <i>S. antarctica</i>	Present study (trophosome), Vervoort (1972, gonosome), type of <i>Sertularia secunda</i>	Millard (1958), as <i>S. mediterranea</i> v. <i>asymmetrica</i>
<b>Internode</b>				
- length	450-550	340-640	590-700	310-420
- diameter at node	127-150	125-205	170-180	90-130
<b>Hydrotheca</b>				
- free adaxial length	320-417	335-390	560-660	240-400
- adnate adaxial length	162-232	135-245	220-245	110-170
- abaxial length	504-603	390-540	720-745	330-540
- maximum width	278-330	275-360	350-390	220-290
- diameter at aperture	266-301	205-295	270-310	140-210
<b>Gonotheca</b>				
- total length	-	1805-2205	2200-2400	1080-1290 (♀)
- maximum width	-	995-1120	880-1100	750-890 (♀)

*Sertularella secunda* Allman, 1888 [sic!] as the valid name of the species”, resurfaces, but it appears today to not carry enough weight according to the requirements of the Code. Indeed, Art. 59.3. stipulates that *Sertularia secunda* Allman, 1888, as a junior secondary homonym of *Sertularella secunda* Kirchenpauer, 1884, and replaced before 1961, be permanently invalid unless the substitute name, *Sertularella allmani* Hartlaub, 1901, is not in use and the relevant taxa are no longer considered congeneric (*Sertularia secunda* Allman, 1888 belongs actually to *Sertularella* Gray, 1843, and *Sertularella secunda* Kirchenpauer, 1884 to *Symplectoscyphus* Marktanner-Turneretscher, 1890), in which case the junior homonym is not to be rejected on grounds of that replacement. In light of the synonymy given above, it appears that the binomen *S. allmani* was used more often than *S. secunda*. Consequently, Hartlaub’s (1901) *S. allmani* is retained as the valid name of the species.

The typical shape of the colonies of *S. allmani* is illustrated by Galea *et al.* (2014, pl. 3D, as *S. antarctica*), while several gonothecae are depicted by Galea *et al.* (2009, fig. 3B, as *S. antarctica*). The branching pattern in this species is irregularly pinnate. In some parts of very profuse colonies, nearly all internodes give rise to alternate side branches, although in more sparingly branched ones, there is a tendency to form groups of two consecutive, alternate side branches separated by 1-2 stem internodes devoid of apophyses. Occasionally, though not rarely, more irregular side branches, separated by a varied number of internodes with no apophyses, may arise successively on the same side of the stem.

In all specimens from Chile, the stems are monosiphonic in habit, and give rise to side branches of up to 3rd order. Polysiphonic stems were reported only in rare instances [Hartlaub 1901, as both *S. allmani* and *S. paessleri* (see below for the taxonomic status of the latter)]. The perisarc of the colonies (including the hydrothecae) may be either thin (as in the Chilean material) or thick (Hartlaub, 1901; Blanco, 1963, as *S. antarctica*). The hydrothecal margin is always thickened, and the abaxial marginal cusp is generally distinctly produced, though its length may vary among various colonies, or even within the same stem. The gonothecae of both sexes are either distinctly transversely ringed (e.g. HRG-0637, HRG-0644), or only wrinkled to nearly smooth (e.g. HRG-0634, HRG-0636). Material of *Sertularella paessleri* Hartlaub, 1901 is no longer extant in collections of ZMH (H. Roggenbuck, pers. comm.). However, Hartlaub emphasized the large size and the smooth appearance of the gonothecae in the obviously young colony available. Otherwise, the characters of the trophosome alone (branching almost regularly pinnate, with consecutive, alternate “pairs” of side branches separated by 2 internodes devoid of apophyses; invariably short internodes; short, adaxially-swollen hydrothecae shifted on to one side, and adnate for 1/3rd their length; abaxial cusp produced; rim thickened) agree well with the present concept of

*S. allmani*, including the presence of fascicled stems, as those observed in the lectotype, ZMH C04177.

The variety *asymmetrica*, created by Millard (1958) for a hydroid assigned to *S. mediterranea* Hartlaub, 1901, is likely conspecific with the present species. Although all her specimens were represented by small, unbranched stems, their microscopic structure displays all the distinctive characters of *S. allmani*, notably: short internodes, thick-walled hydrothecae conspicuously shifted on to one side of the stem, a produced abaxial cusp, the noteworthy asymmetry of the laterals, as well as the presence of 3 internal, submarginal cusps.

**Distribution:** Chile – Región de los Ríos [around Corral (Galea & Schories, 2012a, as *S. antarctica*)]; Región de los Lagos [south of Isla Grande de Chiloé (Galea *et al.*, 2009, as *S. antarctica*)]; Región de Magallanes y de la Antártica Chilena [west of Puerto Pantalón del Weste, Isla Navarino (Hartlaub, 1901; 1905); Islote Gemellos (present study); Magellan Strait (? Jäderholm, 1903)]. Argentina – Provincia de Santa Cruz [Punta Peñas, San Julián (Blanco, 1963; 1994, both as *S. antarctica*)]. Falkland Is. – Port Stanley (Hartlaub, 1901; 1905); Port Williams (Hartlaub, 1901; 1905, both as *S. paessleri*). French Southern and Antarctic Lands, Kerguelen Is. – off Accessible Bay [Allman 1888, as *Sertularia secunda* (= *Sertularia unilateralis*)]. South Africa – Millard (1958; 1964; 1975, all as *S. mediterranea* var. *asymmetrica*).

### *Sertularella antarctica* Hartlaub, 1901

Fig. 3A-G; Table 2

- Sertularella antarctica* Hartlaub, 1901: 82, pl. 6 figs 27, 28 (replacement name for *Sertularella unilateralis* Allman, 1876: 114). – (?) *p.p.* Jäderholm, 1903: 283. – Hartlaub, 1905: 650, fig. P<sup>1</sup>, Q<sup>1</sup>. – Bedot, 1916: 200; 1918: 235. – Billard, 1924: 61. – (?) Vervoort, 1972: 106, fig. 32. – El Beshbeeshy, 2011: 119, fig. 37D.
- non *Sertularella antarctica*. – *p.p.* Jäderholm, 1903: 283 [= *Sertularella gaudichaudi* (Lamouroux, 1824)]. – Jäderholm, 1905: 32, pl. 13 fig. 1 (= *Sertularella subantarctica* Galea, sp. nov.). – Blanco, 1963: 170, figs 5-6 (= *Sertularella allmani* Hartlaub, 1901).
- Sertularella unilateralis* Allman, 1876: 114. – Allman, 1879: 282, pl. 18 figs 10, 11. – Studer, 1879: 120. – Kirchenpauer, 1884: 40.
- non *Sertularia unilateralis* Lamouroux, 1824: 615, pl. 90 figs 1-3 [= *Symplectoscyphus unilateralis* (Lamouroux, 1824)].
- Sertularella allmani*. – (?) Nutting, 1904: 84, pl. 18 figs 3-6 [non *Sertularella allmani* Hartlaub, 1901].
- Sertularella gigantea*. – Billard, 1906: 12, fig. 4 [non *Sertularella gigantea* Mereschowsky, 1878].
- Sertularella ? lagena*. – Galea & Schories, 2012a: 41, fig. 4K-L [non *Sertularella lagena* Allman, 1876].
- Sertularella sanmatiasensis*. – (?) Peña Cantero, 2006: 939, fig. 3L. – (?) Peña Cantero & Gili, 2006: 767. – (?) Peña Cantero, 2008: 459, fig. 2C. – (?) Peña Cantero &



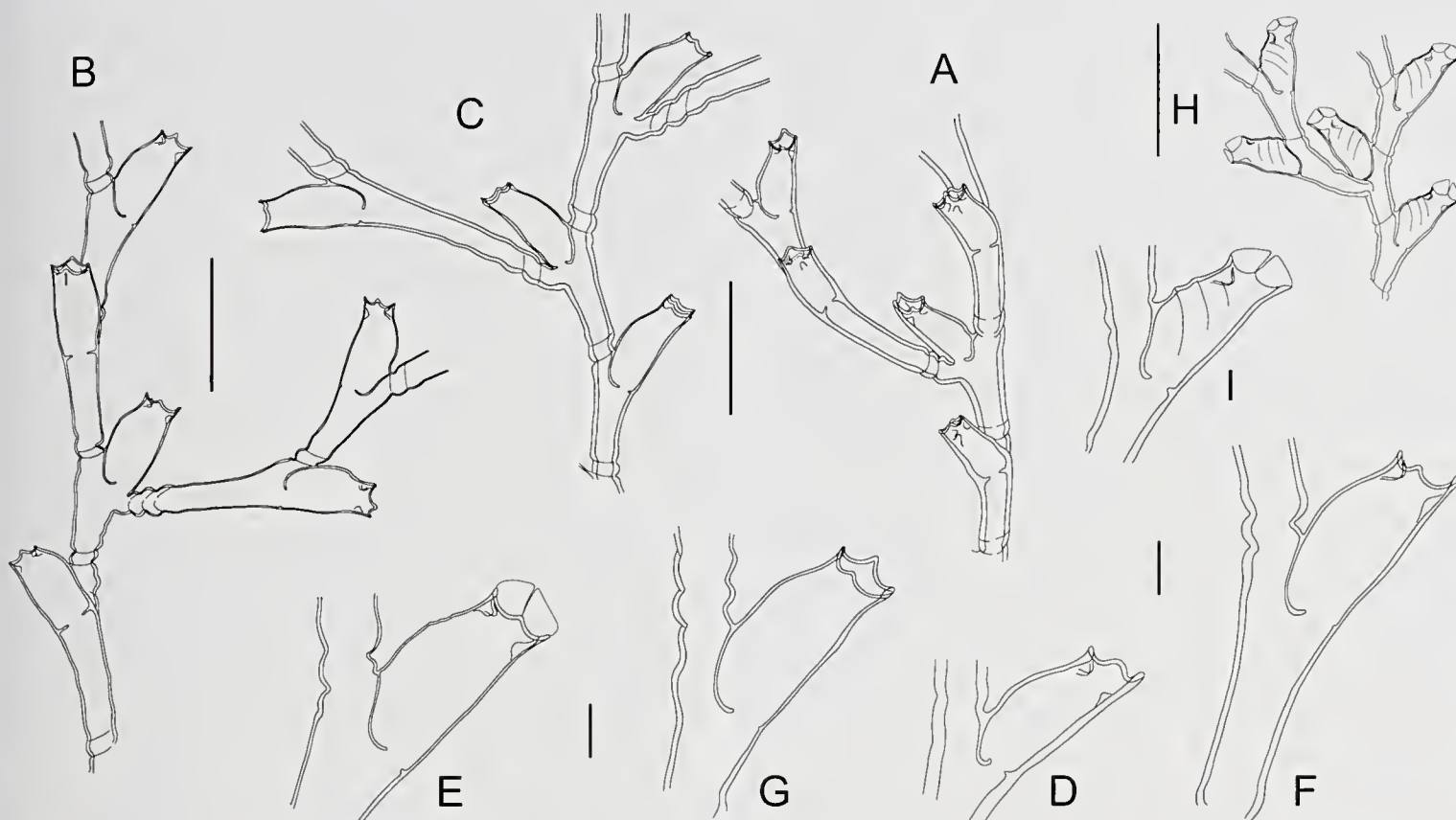


Fig. 3. (A-G) *Sertularella antarctica* Hartlaub, 1901. Colony fragments from lectotype (A), HRG-0290 (B) and HRG-0524 (C). Hydrothecae from lectotype (D), HRG-0290 (E), HRG-0524 (F) and HRG-0534 (G). (H, I) *Sertularella asymmetra* Galea & Schories, 2014. Portion of colony (H) and hydrotheca (I). Scale bars: 200  $\mu$ m (D-G, I), 1 mm (A-C, H).

Vervoort, 2009: 87, fig. 2B. – Peña Cantero, 2012: 858, fig. 4A; 2013: 130 [non *Sertularella sammatiasensis* El Beshbeeshy, 2011].

**Material examined:** ZMH C04161; Chilean-Argentinean border, Dungeness Point, beach, coll. Michaelsen no. 104; 15.10.1892; a few fragments (only a part of the whole sample examined herein), up to 2.2 cm high. According to Hartlaub (1901), this appears to be the sole material on which he based his species upon. As no holotype was designated by him, it is here regarded as the lectotype of *S. antarctica*. – ZMH C11879; FRV *Walther Herwig*, Argentine Shelf, no additional data; several sterile colony fragments, up to 5.2 cm high, with almost only the perisarc left, identified as *S. antarctica* Hartlaub, 1901. – MHNG-INVE-79773; Antarctica, King George I., Ras Tu,  $-62.22139^{\circ}$   $-58.88694^{\circ}$ , 15-20 m, coll. D. Schories, lot Ant. 12/2011; 21.02.2010; fully fertile (female) colony with stems up to 6.5 cm high. – MHNG-INVE-79776; Antarctica, King George I., Ras Tu,  $-62.22139^{\circ}$   $-58.88694^{\circ}$ , 15-20 m, coll. D. Schories, lot Ant. 03/2011; 21.02.2010; numerous stems and fragments up to 5.5 cm high, some bearing female gonothecae. – HRG-0534; Antarctica, King George I., Ras Tu,  $-62.22139^{\circ}$   $-58.88694^{\circ}$ , 10-40 m, coll. D. Schories, lot Ant. 08/2010; 12.02.2010; numerous stems and fragments, up to 4 cm high, one bearing a female gonotheca. – HRG-0290; Antarctica, Low I.,

$-63.43009^{\circ}$   $-62.2038^{\circ}$ , 82 m, coll. Bentart 2006, leg. A.L. Peña Cantero; 02.2006; numerous fertile stems, up to 9.5 cm high, sex could not be ascertained [part of the material from Stn. Low 44 studied by Peña Cantero (2013)]. – HRG-0362; Chile, Región de Magallanes y de la Antártica Chilena, Punta Arenas, Faro San Isidro,  $-53.78174^{\circ}$   $-70.97391^{\circ}$ , 40 m, coll. D. Schories, lot #25; 04.01.2011; three minute sterile stems [material assigned to *Sertularella ? lagena* Allman, 1876 by Galea & Schories (2012a)].

**Description:** Inspected colonies up to 9.5 cm high, arising from creeping, branching stolon. Stems monosiphonic, provided basally with 3-5 annuli above origin from stolon, then divided into uniform, moderately-long internodes by deep, oblique constrictions of perisarc slanting in alternate directions. A hydrotheca, or a hydrotheca and a short, lateral apophysis arising from below its base, confined to the distal end of each internode; proximally a couple of spiral twists (occasionally only one, or two incomplete), and distally a bulge. Hydrothecae, apophyses, and side branches shifted on to one side of the stem, at a wide angle, not giving the colony a markedly fronto-dorsal aspect. Branching pattern irregularly pinnate, with side branches originating every 0-18 stem hydrothecae, either alternately or many on the same side; up to 4th order branching; structure similar to that of stem; 1st internode with 2 (rarely 3) spiral twists basally, length

generally greater (occasionally shorter, or equal) than that of subsequent internodes. Hydrothecae long, flask-shaped, adnate for 1/3rd of their length to the corresponding internode, swollen adaxially at varied degrees; abaxial wall almost straight; free adaxial wall sigmoid, convex for most of its length, becoming concave immediately below aperture; aperture surrounded by 4 unequally-developed, triangular cusps: abaxial one produced, thought at varied degrees, adaxial the shortest, and the laterals asymmetrical; rim thickened, renovations occasional; 3 intrathecal, submarginal cusps (2 latero-adaxial, 1 abaxial), not always discernible; a 4-flapped operculum. Gonothecae borne on both stems and side branches, male similar to female; elongated-ovoid, walls transversely-wrinkled, especially on distal half, aperture mounted on short neck region and surrounded by generally 4 blunt cusps (up to 6 possible).

**Dimensions:** See Table 2.

**Remarks:** Hartlaub (1901) introduced the replacement name *Sertularella antarctica* for *Sertularella unilateralis* Allman, 1876 in order to avoid the secondary homonymy with *Sertularia unilateralis* Lamouroux, 1824, the latter considered by him as belonging to the group of 3-cusped *Sertularella* species (presently accepted as *Symplectoscyphus* Marktanner-Turneretscher, 1890).

Calder (2015, p. 239, note 39) expressed the view that Hartlaub's (1901) binomen "has been used only sparingly [...], and nomenclatural stability is not greatly threatened by adopting its senior synonym (*Sertularella unilateralis* Allman, 1876a) for the species". However, in light of the present study, his opinion changed (Calder, pers. comm.) taking into account that secondary homonymy no longer exists in the case of *S. unilateralis*, and the substitute name *S. antarctica* has come into rather frequent use for the species (ICZN Art. 59.3.).

Type material of *S. unilateralis* is likely no longer

extant in NHML (A. Cabrinovic, pers. comm.), and a comparison with the lectotype of *S. antarctica* is therefore impossible, leaving some doubts as to the conspecificity between these two nominal species. Indeed, the colony silhouette illustrated by Allman (1879, pl. 18 fig. 10) does not differ much from that of his *Sertularia secunda* (= *Sertularia unilateralis*) (Allman, 1888, pl. 25 figs 2, 2a) (= *S. allmani* Hartlaub, 1901, see previous species). El Beshbeeshy (2011) was right in stating that *S. allmani* and *S. antarctica* are two distinct, well-defined species. A contrary opinion was expressed earlier by Vervoort (1972), who founded his conclusion based exclusively on Hartlaub's (1901) accounts (p. 81 and 82, respectively), but not on the reexamination of the corresponding materials studied by the German author. This erroneous opinion was subsequently followed by Galea *et al.* (2009, as *S. antarctica*, p. 7 figs 2J-N, 3A-B) and Galea & Schories (2012a, as *S. antarctica*, p. 22, footnote 2, pl. 3D). However, the reexamination of the lectotypes of both *S. allmani* and *S. antarctica* for the purpose of the present study, leaves no doubts about the correctness of El Beshbeeshy's statement.

The typical shape of a colony of this species is illustrated in Galea & Schories (2012b, pl. 1R), while its gonothecae appear in the insert of the same plate, as well as in fig. 2S of the same paper.

The development of the perisarc in various colonies ranges from rather thin (*e.g.* HRG-0290, HRG-0405, HRG-0524, and HRG-0534) to exceedingly hypertrophied (*e.g.* ZMH C04161, ZMH C11879). The adaxial side of the hydrotheca is swollen at varied degrees but, generally, approaches an almost tubular shape; in some colonies, the hydrothecae are distinctly swollen, resembling those of *S. allmani* but, in this case, the colony shape is diagnostic. The hydrothecal rim is conspicuously thickened, though less so in younger thecae; renovations were observed in only several instances (Billard, 1906, as *S. gigantea*; specimen HRG-0524). The abaxial, marginal cusp is always produced, though at varied extents. On the other

Table 2. Measurements of *Sertularella antarctica* Hartlaub, 1901, in  $\mu\text{m}$ .

	El Beshbeeshy (2011)	Galea & Schories (2012b), as <i>S. gaudichaudi</i>	Billard (1906), as <i>S. gigantea</i>	Vervoort (1972)
<b>Internode</b>				
- length	498-846	730-1335	610-960	875-1210
- diameter at node	156-220	-	175-210	230-255
<b>Hydrotheca</b>				
- free adaxial length	324-346	470-570	525-610	460-485
- adnate adaxial length	145-232	320-375	260-315	270-285
- abaxial length	510-580	705-770	700-790	645-675
- maximum width	249-301	325-350	-	350-380
- diameter at aperture	179-255	255-295	ca. 260	245-270

hand, the submarginal, intrathecal projections of perisarc may be either absent or only lightly indicated (*e.g.* HRG-0534), present only on adaxial side (*e.g.* HRG-0405), or fully displayed (3 cusps, *e.g.* HRG-0290, ZMH C04161, ZMHC11879).

Type material of *Sertularella lagena* Allman, 1876, a poorly-described nominal species, obviously based on a young specimen, could not be located in collections of NHML (A. Cabrinovic, pers. comm.). However, the illustration provided by Allman (1879) places it closest to the present species, an opinion already expressed by Hartlaub (1901, p. 83, fig. 53; 1905, p. 647, figs M<sup>4</sup>-N<sup>4</sup>). The scarce material studied earlier by Galea & Schories (2012a), and provisionally assigned to *S. lagena*, was reexamined. It belongs to a very young colony whose stems do not exceed 5 internodes. Their hydrothecae are not obviously shifted unilaterally, and no intrathecal, submarginal cusps are present, although a careful inspection shows that the rims of some hydrothecae are slightly, but characteristically thickened. This, added to the typical shape and size of its internodes, suggests strong affinities with *S. antarctica*.

Through the courtesy of A.L. Peña Cantero, one of us (HRG) was able to examine a specimen from Low I., Antarctica (HRG-0290) identified by him as *S. sanmatiasensis* El Beshbeeshy, 2011 (Peña Cantero, 2013). In light of the present observations, there is no doubt that this material belongs to the present species. Consequently, it is assumed that at least some earlier records of El Beshbeeshy's species in the various papers (co)authored by Peña Cantero also belong to *S. antarctica*. However, since there are no formal descriptions of the materials involved and, occasionally, no illustrations of them, uncertainties subsist as to their real taxonomic statuses. In only rare instances (*e.g.* Peña Cantero, 2012), the morphology of both internodes (length, presence of proximal twists) and hydrothecae (thickened margin) leaves little doubt about the identity of the materials involved.

**Distribution:** Chile – Región de Magallanes y de la Antártica Chilena [(?) Isla Lennox, (?) Lennox Cove, and (?) Borgin Bay (Jäderholm, 1903); (?) Magellan Strait (Nutting, 1904, as *S. allmani*; Vervoort, 1972); south of Peninsula Brunswick (Galea & Schories, 2012a, as *S. ? lagena*)]. Chilean-Argentinean border – Dungeness Point (Hartlaub, 1901; 1905; El Beshbeeshy, 2011). Argentina – Provincia de Tierra del Fuego, Antártida e Islas del Atlántico Sur [(?) off the NE coast of Islas de los Estados (Vervoort, 1972)]. French Southern and Antarctic Lands, Kerguelen Is. – Swains Bay (Allman, 1876; 1879, both as *S. unilateralis*). Antarctica – Wandel I. (Billard, 1906, as *S. gigantea*), Bellingshausen Sea (Peña Cantero, 2012, as *S. sanmatiasensis*), Low I. (Peña Cantero, 2013, as *S. sanmatiasensis*), King George I. (Galea & Schories, 2012b, as *S. gaudichaudi*).

### *Sertularella asymmetra* Galea & Schories, 2014

Fig. 3H, I

*Sertularella asymmetra* Galea & Schories, 2014 in Galea *et al.*, 2014: 31, figs 6A-B, 7A.

**Material examined:** MHNG-INVE-86230; Chile, Región de los Ríos, Corral, Chaihuin/Huiro, -39.95000° -73.61667°, 10 m, coll. D. Schories, lot #05; 27.10.2011; a 4 cm high colony with female gonothecae (holotype). – MHNG-INVE-86231; Chile, Región de los Ríos, Corral, Chaihuin/Huiro, -39.95000° -73.61667°, 10 m, coll. D. Schories, lot #26; 03.10.2011; a 2.5 cm high colony with male gonothecae.

**Description:** Colonies arising from creeping, branching, anastomosing hydrorhiza. Stems erect, up to 4 cm high, monosiphonic, spirally-twisted above origin from stolon, then divided into short, slightly geniculate internodes by deep, oblique constrictions of the perisarc. Side branches arise irregularly from below the bases of stem hydrothecae, either laterally, or slightly displaced towards the front or the rear side of the colony; structure similar to that of stem. Hydrothecae biserial, alternate, fusiform, adnate for about 1/3rd their adaxial side to the corresponding internode; free adaxial wall swollen proximally, and provided with 2-3 weak, transverse ridges; abaxial wall with smooth perisarc, slightly concave proximally, becoming convex below the aperture; the latter facing upwards, and composed of four triangular cusps separated by shallow embayments, abaxial cusp produced; a 4-flapped operculum; three internal, submarginal cusps: 2 latero-adaxial and 1 abaxial. Gonothecae arising from below the hydrothecal bases; elongated-ovoid, walls more or less transversely ridged; male similar to female, though slenderer and longer; aperture surrounded by 3-4 perisarc projections in male and 5 in female; the latter producing 12-18 oocytes.

**Dimensions:** Internodes 560-730 µm long and 140-230 µm wide at nodes. Hydrothecal free adaxial length 285-355 µm, adnate adaxial length 230-280 µm, abaxial length 535-590 µm, maximum width 250-285 µm, diameter at aperture 230-240 µm. Length of the female gonotheca *ca.* 1695 µm, and of the male *ca.* 1890 µm; maximum width of the female gonotheca *ca.* 795 µm, and of the male *ca.* 710 µm.

**Remarks:** The gonothecae of this species are illustrated by Galea *et al.* (2014, fig. 7A).

**Distribution:** Chile – Región de los Ríos [Corral (Galea *et al.*, 2014)].

### *Sertularella blanconae* El Beshbeeshy, 2011

Figs 1C, 4A, C-H; Table 3

*Sertularella blanconae* El Beshbeeshy, 2011: 125, fig. 39. – Galea & Schories, 2012a: 37, fig. 3P-S. – Galea *et al.*, 2014: 32, pl. 3A, figs 6C, 7B.

*Sertularella geodiae*. – Blanco, 1976: 39, pl. 3 figs 7-8. – (?) Millard, 1977: 23, fig. 6E-F. – Blanco, 1994: 199 [non *Sertularella geodiae* Totton, 1930].

*Sertularella conica*. – Blanco, 1982: 154, figs 2-5. – Blanco, 1994: 198 [non *Sertularella conica* Allman, 1877].

*Sertularella Gayi*. – *p.p.* Jäderholm, 1903: 281 [non *Sertularella gayi* (Lamouroux, 1821)].

(?) *Sertularella gayi gayi*. – Vervoort, 1972: 116, fig. 36A, B [non *Sertularella gayi* (Lamouroux, 1821)].

(?) *Sertularella gayi* var. *gayi*. – Stepanjants, 1979: 87, pl. 16 fig. 4A, B [non *Sertularella gayi* (Lamouroux, 1821)].

**Material examined:** MHNG-INVE-86243; Chile, Región de Aysén, Isla Teresa, -44.95713° -73.79447°, 21.6 m, coll. HSFS, HF11, lot C234; 27.11.2011; a profuse, sterile colony with stems up to 16 cm high. – MHNG-INVE-86244; Chile, Región de Aysén, Isla Level, -44.47348° -74.20472°, 25 m, coll. HSFS, HF11, lot C128; 24.11.2011; a *ca.* 7 cm high, fragmentary

colony with male gonothecae. – HRG-0392; Chile, Región de Magallanes y de Antártica Chilena, Punta Arenas, Faro San Isidro, -53.78174° -70.97391°, 40 m, coll. D. Schories, lot #27; 04.01.2011; three sterile colony fragments 1.2-1.7 cm high. – HRG-0696; Chile, Región de Magallanes y de Antártica Chilena, Isla Santibañez, -54.91725° -68.36317°, 29 m, coll. HSFS, HF9, lot C247; 16.12.2010; very fragmented colony with lightly fascicled stems, some bearing spent gonothecae. – HRG-0694; Chile, Región de Aysén, southern exist of Canal Williams, -45.60103° -74.47819°, 8.9 m, coll. HSFS, HF11, lot C009; 19.11.2011; a profuse, *ca.* 8 cm high, sterile colony composed of several polysiphonic stems. – HRG-1168; Chile, Región de los Lagos, southern Chiloé, Isla Yencouma, -43.419316° -74.081766°, 10 m, coll. HSFS, HF22, lot #65; 18.01.2015; two profuse, *ca.* 7 cm high,

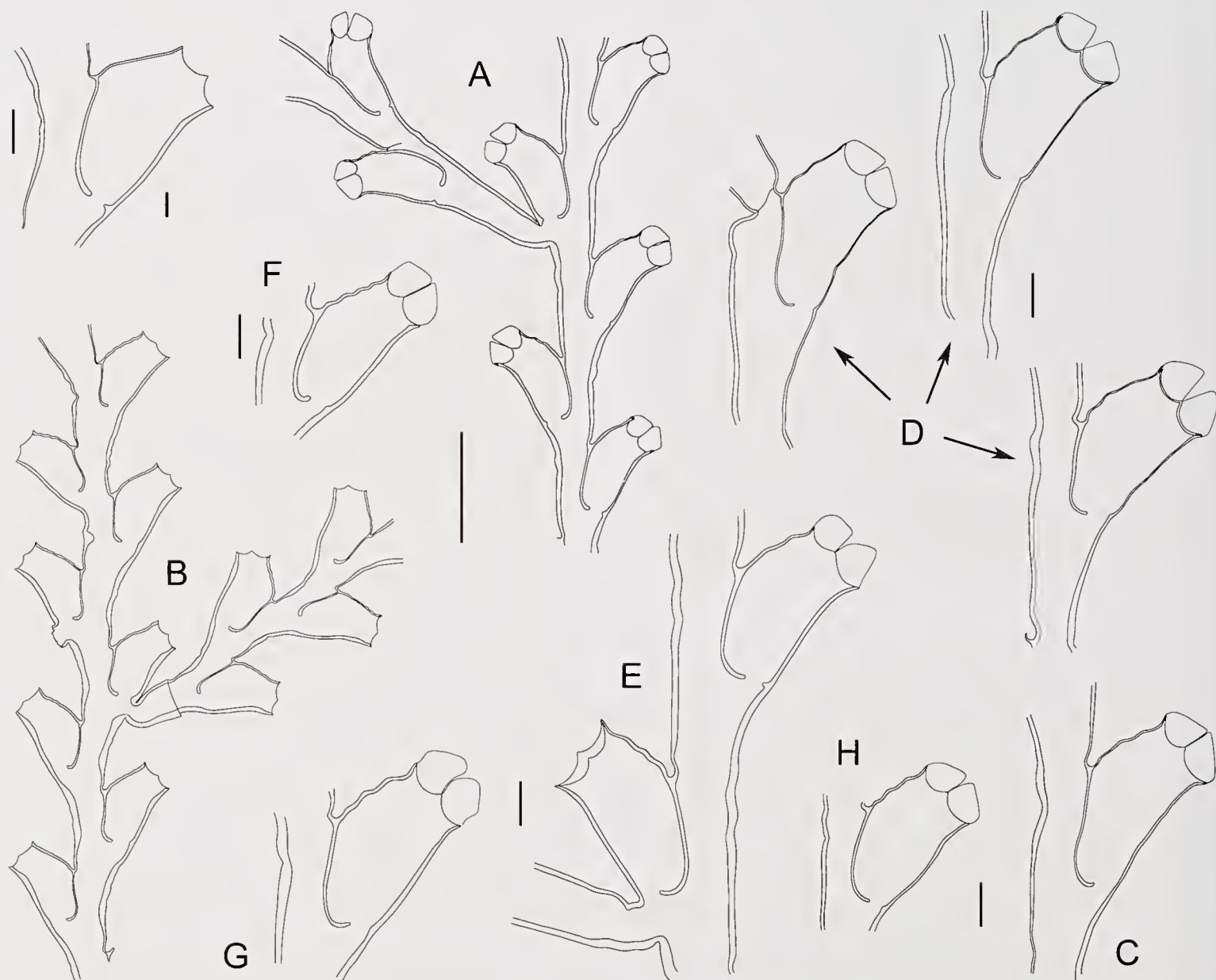


Fig. 4. *Sertularella blanconae* El Beshbeeshy, 2011. Portion of colony from MHNG-INVE-86243 (A), and comparison with sample HRG-0553 of *Sertularella gayi* (Lamouroux, 1821) (B). Hydrothecae from HRG-0696 (C), SMNH 123866 (D), Blanco (1976, as *S. geodiae*) (E), Blanco (1982, as *S. conica*) (F-H), and comparison with hydrotheca of *S. gayi* from sample HRG-1006 (I). Scale bars: 200 µm (C-I), 1 mm (A, B).

infertile colonies with polysiphonic stems. – SMNH 123866; Chile, Punta Arenas, coll. Swedish Tierra del Fuego Expedition 1895-1896; 05.12.1895; microslide (Fig. 1C) containing two sterile colony fragments, 2.0 and 2.3 cm high [material identified by Jäderholm (1903) as *S. gayi* (Lamouroux, 1821)].

**Comparison material:** HRG-1006; France, Roscoff, Trou aux Singes, 48.7961° -3.9708°, 72 m, leg. P. Schuchert; 08.09.2014; a 4.5 cm high, fertile colony of *Sertularella gayi* (Lamouroux, 1821). – HRG-0553; France, Brittany, depth unrecorded, coll. F. Ziemski; (day and month unavailable) 2011; a few infertile stems and fragments, up to 3.7 cm high, of *S. gayi*.

**Description:** Large, fan-shaped colonies, up to 16 cm high arising from broad, rhizoid stolon firmly attached to substrate; stems giving rise to irregularly-ramified side branches, up to the 3rd order; both stems and branches highly fasciated for most of their length; monosiphonic parts with regularly-pinnate structure. Both stems and branches divided into short, almost collinear internodes by means of weak, oblique constrictions of the perisarc. Each internode with a hydrotheca, or a hydrotheca and a short apophysis immediately below its base; apophyses alternate, arising generally every three hydrothecae. Hydrothecae biseriate, alternate, flask-shaped, adnate for about half their length; free adaxial wall slightly swollen and provided with 3-4 undulations, more prominent proximally, weaker distally, prolonged as inconspicuous transverse ridges at surface, not reaching the abaxial wall; the latter slightly concave to almost straight for most of its length, becoming convex below the aperture, surface smooth; aperture mounted on short, constricted neck region, expanding at rim; the latter with 4 pointed,

equal, triangular cusps separated by moderately-deep, rounded embayments; margin occasionally renovated; 4 triangular opercular flaps with concentric striae; no intrathecal, submarginal cusps. Gonothecae (only male known) elongated-ovoid, lateral walls with up to 8 transverse ridges, of which 5-6 distalmost are complete and prominent, while the remaining ones become obsolete towards the base; aperture borne on the summit of a short neck region, and is flanked by 4 blunt-ended projections of perisarc.

**Dimensions:** See Table 3.

**Remarks:** The typical shape of a well-developed colony is illustrated in Galea *et al.* (2014, pl. 3A), and a male gonotheca in fig. 7B of the same paper. This species has been previously confused with *S. gayi* (Lamouroux, 1821) by a number of authors (see synonymy). Their morphological differences are obvious by comparing Fig. 3A, C-H and Fig. 3B, I.

**Distribution:** Chile – Región de los Lagos [southern Chiloé (present study)]; Región de Aysén [Isla Level, Isla Teresa (Galea *et al.*, 2014); Canal Williams (present study)]; Región de Magallanes y de la Antártica Chilena [south of Peninsula Brunswick (Galea & Schories, 2012a); Isla Dawson and Punta Arenas (Jäderholm, 1903, as *S. gayi*); Isla Santibañez (present study)]. Tierra del Fuego, no exact locality (? Stepanjants, 1979, as *S. gayi* var. *gayi*). Argentina – Provincia del Chubut [(?) off Península Valdés (Vervoort, 1972, as *S. gayi* *gayi*), off Cabo Dos Bahías (Blanco, 1982; 1994, both as *S. conica*)]; Provincia de Santa Cruz [Puerto Deseado (Vervoort, 1972, as *S. gayi* *gayi*)]; Provincia de Tierra del Fuego, Antártida e Islas del Atlántico Sur [off the eastern entrance of the Magellan Strait (Blanco, 1976; 1994, both as *S. geodiae*); around Península Mitre

Table 3. Measurements of *Sertularella blanconae* El Beshbeeshy, 2011, in  $\mu\text{m}$ .

	El Beshbeeshy (2011)	Galea & Schories (2012a); present study	Blanco (1982), as <i>S. conica</i>	Millard (1977), as <i>S. geodiae</i>	Blanco (1976), as <i>S. geodiae</i>	Vervoort (1972), as <i>S. gayi</i> <i>gayi</i>
<b>Internode</b>						
- length	603-881	795-1095	720-1206	1010-1520	640-1288	1095-1175
- diameter at node	255-278	210-245	198-288	200-320	-	175-215
<b>Hydrotheca</b>						
- free adaxial length	371-464	410-495	324-612	460-600	368-386	405-420
- adnate adaxial length	417-533	440-475	360-620	490-610	386-478	495-500
- abaxial length	580-742	680-715	540-720	660-770	570-644	580-635
- maximum width	-	395-430	360-486	-	350-486	430-445
- diameter at aperture	301-464	335-370	288-360	350-400	294-368	325-350
<b>Gonotheca</b>						
- total length	-	1790-2300 (♂)	-	-	-	-
- maximum width	-	710-935 (♂)	-	-	-	-

(Blanco, 1982; 1994, both as *S. conica*); numerous scattered records from the Argentine Shelf between ca. 40°-54° S (El Beshbeeshy, 2011). Falkland Is. [(?) Stepanjants (1979, as *S. gayi* var. *gayi*); off the N coast (Blanco, 1982; 1994, both as *S. conica*); off the SE coast (El Beshbeeshy, 2011)]. (?) French Southern and Antarctic Lands – Crozet Shelf (Millard, 1977, as *S. geodiae*).

***Sertularella clausa* (Allman, 1888)**

Figs 1D, 5; Table 4

*Sertularia clausa* Allman, 1888: 54, pl. 25 figs 3, 3a. – Bedot, 1916: 219.

*Sertularella clausa*. – Nutting, 1904: 93, pl. 21 figs 3-4 (reexamination of the type). – Bedot, 1918: 236. – Milstein, 1976: 84, figs 24, 35.

non *Sertularella clausa*. – Fraser, 1938: 141, pl. 20 fig. 10; 1948: 241.



Fig. 5. *Sertularella clausa* (Allman, 1888). Colony fragments from holotype (A, B), and specimens ZMH C11882 (C) and C12145 (D) assigned to *S. argentinica* El Beshbeeshy, 2011. Hydrothecae from holotype (E), ZMH C11882 (F), ZMH C12145 (G, H), Blanco (1982, as *S. gayi* *gayi*) (I). Scale bars: 200 µm (E-I), 1 mm (A-D).

*Sertularella argentinica* El Beshbeeshy, 2011: 121, fig. 38 (**syn. nov.**). – Soto Àngel & Peña Cantero, 2015: 993, fig. 7A-B.

non *Sertularella argentinica*. – Galea, 2007: 59, fig. 14A-C. – Galea *et al.*, 2007c: 312, fig. 31 (= *Sertularella robustissima* Galea, Häussermann & Försterra, sp. nov.).

*Sertularella gayi gayi*. – Blanco, 1982: 157, figs 6-9 [non *Sertularella gayi* (Lamouroux, 1821)].

**Material examined:** NHML 1888.11.13.41; Uruguay, off Montevideo, *ca.* 1097 m; colony composed of *ca.* 15 sterile stems, up to 1.2 cm high, as well as a slide (now dried out, Fig. 1D) containing a *ca.* 1.5 cm high, branched colony fragment, labeled “Challenger Stat. 320, *Sertularia clausa*, type, Monte Video, Dcpth 600 faths”. – ZMH C11882; FRV *Walther Herwig*, Argentine Shelf, no additional data; several colony fragments, up to 2 cm high, at least one gonotheca, identified as *Sertularella argentinica* El Beshbeeshy, 2011. – ZMH C12145; FRV *Walther Herwig* 31, Stn. 676, Argentine Shelf, off Provincia del Chubut, -43.80500° -59.53333°, 570 m; 22.06.1976; fragmentary, fertile colony with monosiphonic stems, on axis of dead antipatharian [material studied by El Beshbeeshy (2011), as *S. argentinica*].

**Description:** Large, up to *ca.* 17 cm high, bushy, irregularly and much branched colonies with either mono- or reportedly polysiphonic stems. Monosiphonic parts divided into short, almost collinear, rather thick internodes, by means of oblique constrictions of the perisarc slanting in alternate directions, not always clearly demarcated; distally, a hydrotheca to each internode. Side branches originating not laterally, but in either front or rear side of the stem, from below the hydrothecal bases; 1st internode slightly longer than

subsequent ones; remainder of branches with similar structure as the stem; tips of branches commonly forming anastomoses with neighboring counterparts, resulting in much tangled, three-dimensional structure. Hydrothecae short, tronconical, adnate for slightly more than half their length to the corresponding internode; abaxial wall nearly straight to imperceptibly concave for most of its length, becoming convex below aperture; free adaxial wall slightly convex to nearly straight, surface smooth to wavy; rim with 4 short, triangular cusps separated by shallow embayments; renovations occasional; a 4-flapped operculum. Gonothecae borne on side branches, arising from below the hydrothecal bases; male similar to female; long, slender, tubular to spindle-shaped, tapering abruptly above origin, slightly constricted apically; lateral walls undulated; aperture distal, large, surrounded by 4 triangular cusps, and provided with a 4-flapped operculum.

**Dimensions:** See Table 4.

**Remarks:** Upon the comparison of the holotype of *S. clausa* with the Argentinean material assigned by El Beshbeeshy (2011) to his supposedly undescribed species, *S. argentinica*, it appears that both are indistinguishable morphologically (compare Figs 5A, B and 5C, D, as well as their respective measurements in Table 4). The former is an obviously young, sterile colony, with monosiphonic, unbranched or sparingly-branched stems, not surpassing 1.2 cm in height. Their mode of branching, with side branches arising in either the front or rear side of the stems, is peculiar and distinctive. Additionally, the frequent occurrence of terminal stolonization characterizes this species [present study; Blanco (1982, as *S. gayi gayi*)].

Table 4. Measurements of *Sertularella clausa* (Allman, 1888), in  $\mu\text{m}$ .

	Present study, holotype NHM 1888.11.13.41	El Beshbeeshy (2011), as <i>S. argentinica</i>	Soto Àngel & Peña Cantero (2015), as <i>S. argentinica</i>	Blanco (1982), as <i>S. gayi gayi</i>
<b>Internode</b>				
- length (in general)	710-1040	556-951	-	702-900
- length of 1st internode	1000-1190	-	-	-
- diameter at node	195-280	324-371	-	<i>ca.</i> 270
<b>Hydrotheca</b>				
- free adaxial length	255-305	232-301	255-280	220-270
- adnate adaxial length	330-365	301-395	290-330	330-460
- abaxial length	425-475	394-440	400-450	430-480
- maximum width	280-310	-	280-310	300-330
- diameter at aperture	215-260	208-255	220-240	220-260
<b>Gonotheca</b>				
- total length	-	1276-1858	-	-
- maximum width	-	324-417	-	-

**Distribution:** Uruguay – off Montevideo (Allman, 1888). Argentina – scattered records from the Argentine Shelf, between 40°-53°S (El Beshbeeshy, 2011, as *S. argentina*); Provincia de Tierra del Fuego, Antártida e Islas del Atlántico Sur [*ca.* 80 km off the northeastern coast of Isla de los Estados (Blanco, 1982, as *S. gayi gayi*)]. Burdwood Bank – Soto Ángel & Peña Cantero (2015, as *S. argentina*). Falkland Is. – off the SE coast (El Beshbeeshy, 2011, as *S. argentina*).

***Sertularella contorta* Kirchenpauer, 1884**

Figs 1E-G, 6, 7A-H; Table 5

*Sertularella contorta* Kirchenpauer, 1884: 39, pl. 15 figs 2, 2a. – *p.p.* Hartlaub, 1901: 83, pl. 4 fig. 26, pl. 6 figs 14-16 (reexamination of the cotype). – Nutting, 1904: 85, pl. 18 figs 7-9. – Hartlaub, 1905: 647. – Jäderholm, 1905: 31, pl. 12 figs 9-10. – Ritchie, 1907: 76. – Bedot, 1916: 202; 1918: 236. – Billard, 1924: 61. – *p.p.* Rees & Thursfield, 1965: 133.

(?) *Sertularella lagena* Allman, 1876: 114. – Allman, 1879: 283, text-fig. – Studer, 1879: 120. – Kirchenpauer, 1884: 40. – Bedot, 1912: 355; 1916: 207; 1918: 240. – Stechow, 1925: 475, fig. 34.

non *Sertularella ? lagena*. – Galea & Schories, 2012a: 41, fig. 4K-L (= *Sertularella antarctica* Hartlaub, 1901).

*Sertularella polyzonias*. – *p.p.* Jäderholm, 1910: 4. – *p.p.* Vanhöffen, 1910: 322 [non *Sertularella polyzonias* (Linnaeus, 1758)].

**Material examined:** NMSZ 1921.143.1351.C; Falkland Is., Cape Pembroke, coll. Scottish National Antarctic (*Scotia*) Expedition 1902-1904, shore; 01.1903-01.1904; a profuse, fertile (female) colony with numerous stems, up to 4.5 cm high, on pneumatocyst of *Macrocystis pyrifera* [material studied by Ritchie (1907), and listed by Rees & Thursfield (1965, p. 133)]. – NMSZ 1921.143.1351.D; Falkland Is., Cape Pembroke, coll. Scottish National Antarctic (*Scotia*) Expedition 1902-1904, shore; 01.1903-01.1904; a fertile (female) colony composed of several stems, up to 6 cm high, on *Macrocystis pyrifera* [material studied by Ritchie (1907), and listed by Rees & Thursfield (1965, p. 133)]. – SMNH 123884; Falkland Is., Port William, 5 m, Swedish Magellanic Expedition 1907-1909, coll. C. Skottsberg; 10.02.1908; microslide (Fig. 1E) containing several fragments (up to 1.3 cm high) of a fertile colony, assigned by Jäderholm (1910) to *Sertularella polyzonias* (Linnaeus, 1758). – SMNH 123851; Falkland Is., Port William, 40 m, coll. Swedish South Polar Expedition 1901-1903, Stn. 39; 04.07.1902; microslide (Fig. 1G) containing 2 species: 1) on the left-hand side, a *ca.* 2 cm high, fertile colony assigned to the present species by Jäderholm (1905), re-illustrated

herein in Fig. 6C, I; 2) on the right-hand side, two sterile colonies fragments, 1.3 and 1.5 cm high, assignable to *S. subantarctica* sp. nov. (see below), but identified by Jäderholm (1905) as *S. allmani* Hartlaub, 1901, and illustrated by him in his pl. 12 fig. 11, re-illustrated herein in Fig. 16K, O). – ZMB Cni945; French Southern and Antarctic Lands, Kerguelen Is., Observatory Bay, coll. Deutsche Südpolar (*Gauss*) Expedition 1901-1903; 15.02.1902; a sterile, fragmentary colony, 2.5 cm high [material studied by Vanhöffen (1910), as *S. polyzonias*]. – ZMN Cni620; French Southern and Antarctic Lands, Kerguelen Is., Port Gazelle, coll. Deutsche Tiefsee (*Valdivia*) Expedition 1898-1899; 28.12.1898; a fully fertile (male) colony, 2.5 cm high. – ZSM 20050442; French Southern and Antarctic Lands, Kerguelen Is., coll. Deutsche Tiefsee (*Valdivia*) Expedition 1898-1899, Stn. 160; 28.12.1898; microslide (Fig. 1F) containing two fertile (female) colony fragments, 9 and 13 mm high [material identified by Stechow (1925) as *S. lagena* Allman, 1876].

**Description:** Colonies erect, bushy, up to 6 cm high in inspected material (but up to 8 cm in the type), arising from dense mat of branching, intertwined stolonial fibers. Stems and basal parts of side branches either monosiphonic or fascicled in older colonies; divided into regular, slightly geniculate, rather short internodes by means of oblique constrictions of the perisarc; each internode with a couple of proximal twists, a distal swelling, and a hydrotheca, or a hydrotheca and a short, lateral apophysis below its base, confined to its distal part; branching pattern more or less regular, with generally every two consecutive apophysis-bearing internodes separated by a couple of internodes not supporting side branches; occasionally, only one apophysis-bearing internode is given off, instead of two consecutive ones, or successive apophysis-bearing internodes or couples of them are separated by 1 or 3 (instead of 2) internodes devoid of apophyses (Fig. 7A). Branching pattern of side branches similar to that of stem, though more irregular, with much spaced successive branchlets; proximal most internode generally slightly longer than subsequent ones, and provided with 2-3 spiral twists basally; branching up to at least 6th order. Basalmost side branches generally longer, hence more developed, than uppermost ones. Branches and hydrothecae shifted on to one side of the stem and forming an angle of less than 90°. Hydrothecae flask-shaped, distinctly swollen adaxially, adnate for about 1/3rd or less to corresponding internode; abaxial wall slightly concave to nearly straight for most of its length; free adaxial wall sigmoid, convex in middle; hydrotheca expanding below rim on

Fig. 6. *Sertularella contorta* Kirchenpauer, 1884 (part). Colony fragments from NMSZ 1921.143.1351.C (A), NMSZ 1921.143.1351.D (B), SMNH 123851 (C), SMNH 123884 (D) and ZSM 20050442 (E). Hydrothecae from NMSZ 1921.143.1351.C (F-H) and SMNH 123851 (I). Scale bars: 200 µm (F-I), 1 mm (A-E). ▶



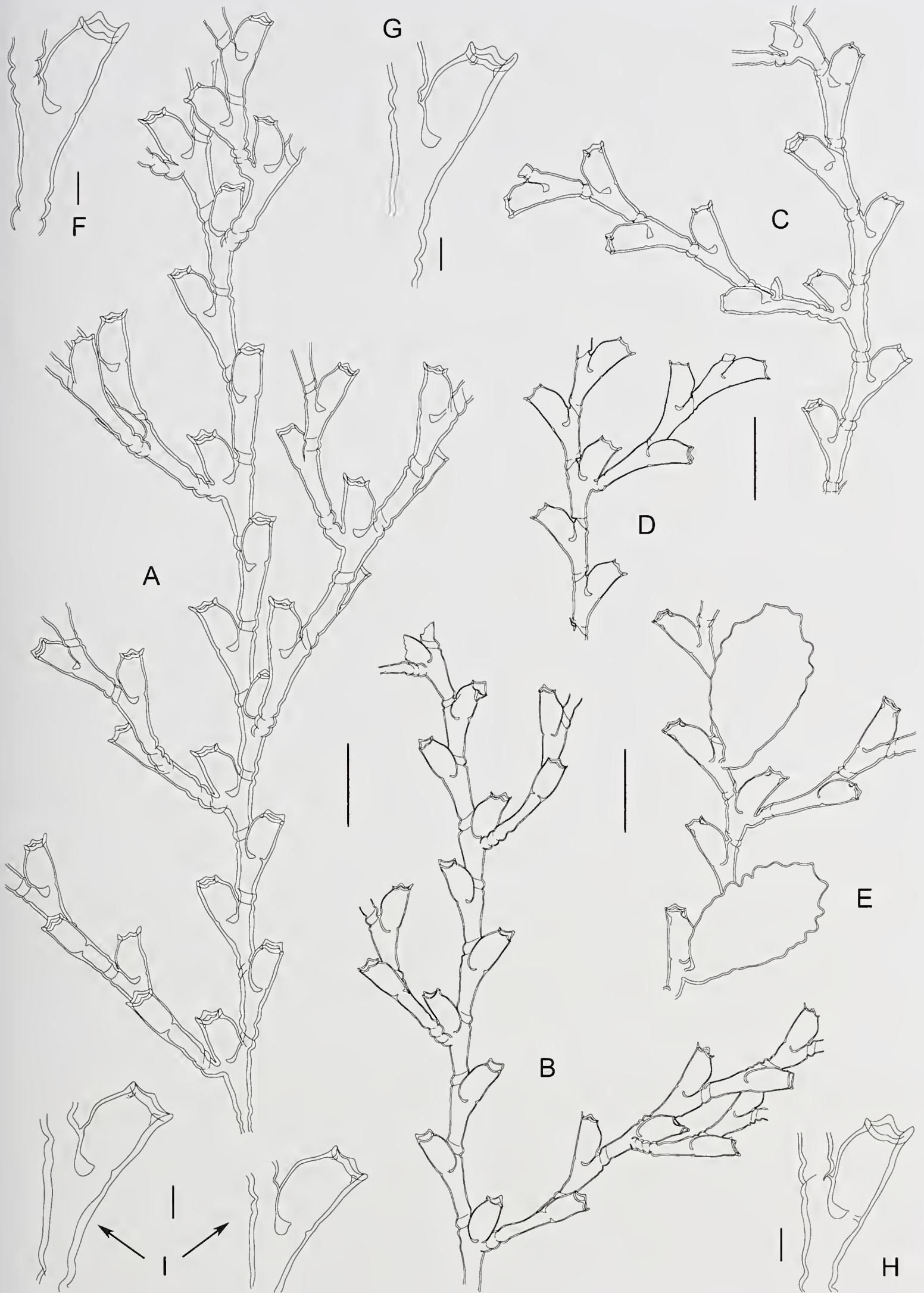




Fig. 7. (A-H) *Sertularella contorta* Kirchenpauer, 1884 (continued). Mode of branching (A). Hydrothecae from NMSZ 1921.143.1351.D (B), SMNH 123884 (C) and ZSM 20050442 (D). Gonothecae from NMSZ 1921.143.1351.C (E), NMSZ 1921.143.1351.D (F), SMNH 123851 (G) and SMNH 123884 (H). (I-L) *Sertularella cruzensis* El Beshbeeshy, 2011. Colony fragments from holotype (I) and Vervoort (1972, as *S. conica*) (J). Hydrothecae from the same sources (K and L, respectively). (M, N) *Sertularella curta* Galea & Schories, 2014. Portion of stem with basal part of a side branch from MHNG-INVE-86236 (M), and hydrotheca from HRG-0721 (N). Scale bars: 200  $\mu$ m (B-D, K, L, N), 500  $\mu$ m (E-H), 1 mm (I, J, M).

both ab- and adaxial sides; rim thickened, provided with 4 triangular cusps, of which the abaxial one is distinctly produced, and the laterals asymmetrical; three internal, submarginal cusps (2 latero-adaxial and 1 abaxial) of varied development, sometimes absent. Gonothecae arising from below the hydrothecal bases; male similar to female; broadly ovoid, tapering below, transversely wrinkled, distally with 4 short spines. The perisarc of the colony may be either thin or thick.

**Dimensions:** See Table 5.

**Remarks:** Although quite succinct, the description of *Sertularella contorta* given by Kirchenpauer (1884) does not allow an indisputable identification to be made in the absence of a reexamination of the type material (N.B.: this material could not be found in ZMB, where Kirchenpauer's "herbarium" was recently located; C. Lüter, pers. comm.). Some statements provided in the original account proved inaccurate, as for example the lack of unilateral arrangement of the hydrothecae, which was subsequently disputed by

Table 5. Measurements of *Sertularella contorta* Kirchenpauer, 1884, in  $\mu\text{m}$ .

	SMNH 123851, in Jäderholm (1905)	SMNH 123884, as <i>S. polyzonias</i> in Jäderholm (1910)	ZSM 20050442, as <i>S. lagena</i> in Stechow (1925)	NMSZ 1921.143.1351.C in Rees & Thursfield (1965)	NMSZ 1921.143.1351.D in Rees & Thursfield (1965)
<b>Internode</b>					
- length (in general)	725-955	615-895	550-945	675-1080	575-945
- length of 1st internode	800-1325	-	1310-1485	980-1350	860-1225
- diameter at node	140-230	145-190	140-185	140-230	140-210
<b>Hydrotheca</b>					
- free adaxial length	340-465	415-465	470-500	475-535	405-440
- adnate adaxial length	255-280	165-195	235-315	280-305	235-245
- abaxial length	415-500	490-520	635-730	535-635	525-585
- maximum width	325-385	290-300	335-365	365-420	285-315
- diameter at aperture	255-320	220-300	235-280	310-355	225-260
<b>Gonotheca</b>					
- total length	1655-1780 (♂ ?)	1520-1645	2035-2110 (♀)	1865-2050 (♀)	1695-1865 (♀)
- maximum width	735-920 (♂ ?)	780-980	1105-1200 (♀)	1055-1105 (♀)	905-1020 (♀)

Hartlaub (1901). The latter author reexamined the (then extant) cotype material, and provided more accurate details on its morphology, allowing a somehow easier identification of this species. The materials NMSZ 1921.143.1351.C&D assigned to *S. contorta* by Rees & Thursfield (1965), and reexamined here, agree with the available data on this species.

*Sertularella contorta* comes close to *S. gaudichaudi* (Lamouroux, 1824) through the shape (but not the size) of its internodes, and both the shape and size of its hydrothecae. Indeed, the length of the internodes in the later varies considerably (from short to exceedingly long), while it is uniformly short in the present species (this feature results also from Kirchenpauer's pl. 15 fig. 2). In addition, the mode of branching of *S. contorta* recalls that met with in *S. allmani* (with stem internodes devoid of lateral apophyses intercalating among those bearing these structures), while *S. gaudichaudi* exhibits a much denser branching pattern (with almost every stem internode bearing an apophysis supporting a branch). However, these differences should, perhaps, not be regarded as purely species-specific, especially given that a quite limited number of samples corresponding to both nominal species have been examined in the frame of the present study. Future collecting and molecular analyses are expected to clarify their relationships.

The Chilean material collected by Philippi and assigned by Hartlaub (1901) to the present species, although quite similar morphologically, should be better assigned to *S. gaudichaudi* (Lamouroux, 1824) owing to the presence of long stem internodes among the otherwise short ones (see remarks under the latter species).

**Distribution:** Falkland Is. (Kirchenpauer, 1884; Jäderholm, 1905; Ritchie, 1907; Jäderholm, 1910, as *S. polyzonias*). Le Maire Strait (Kirchenpauer, 1884). French Southern and Antarctic Lands – Kerguelen Is. (Allman, 1876; 1879, both as *S. lagena*; Vanhöffen, 1910, as *S. polyzonias*; Stechow, 1925, as *S. lagena*; present study).

### *Sertularella cruzensis* El Beshbeeshy, 2011

Fig. 7I-L; Table 6

*Sertularella cruzensis* El Beshbeeshy, 2011: 128, fig. 40.

*Sertularella grandensis* El Beshbeeshy, 2011: 20 [new name for Nutting's (1904, p. 79) record of *Sertularella conica* Allman, 1877; *nomen nudum*].

*Sertularella conica*. – *p.p.* Nutting, 1904: 79. – Vervoort, 1972: 123, fig. 38 [non *Sertularella conica* Allman, 1877].

**Material examined:** ZMH C11556; FRV *Walther Herwig*, Stn. 384, -39.93333° -57.18333°, 95 m; 19.07.1966; a 1.3 cm high sterile stem or branch fragment, with only the perisarc left (holotype).

**Description:** Colonies up to 3 cm high, composed of short, monosiphonic, sparingly-branched stems. Both stems and branches divided into rather short internodes delimited by oblique constrictions of perisarc slanting in alternate directions; a hydrotheca to the distal end of each internode; perisarc thick throughout the colony. Side branches, if present, arising laterally from below the bases of stem hydrothecae, and not branched further; 1st internode usually longer than subsequent ones. Hydrothecae biserial, alternate, strictly coplanar; large,

cylindrical, adnate for less than half their length to their corresponding internodes; slightly swollen basally, especially on adaxial side; abaxial wall almost straight for most of its length, slightly curving outwards below aperture; free adaxial wall wavy, with 3-5 undulations of the perisarc; aperture facing outwards, rim with 4 small, equally-developed, triangular cusps separated by shallow, semicircular embayments; margin usually renovated many times; a 4-flapped operculum, also renovated. Gonothecae unknown.

**Dimensions:** See Table 6.

**Remarks:** The description given above is based on the reexamination of the holotype, combined with the account of Vervoort (1972, as *S. conica*). The material from Albatross Stn. 2771 assigned to *S. conica* by Nutting (1904) was reexamined by Vervoort, and it is here included in the synonymy of the present species.

**Distribution:** Chile – Región de Magallanes y de la Antártica Chilena [Magellan Strait (Vervoort, 1972, as *S. conica*)]. Argentina – Provincia de Buenos Aires [off Bahía Blanca (Vervoort, 1972, as *S. conica*; El Beshbeeshy, 2011)]; Provincia de Santa Cruz [records from both off the eponymous city (Nutting, 1904, as *S. conica*) and the province's coast (Vervoort, 1972, as *S. conica*)]; Provincia de Tierra del Fuego, Antártida e Islas del Atlántico Sur [off the southern coast of the Península Mitre (Vervoort, 1972, as *S. conica*)]. Falkland Is. – off the northwest coast (Vervoort, 1972, as *S. conica*).

### *Sertularella curta* Galea & Schories, 2014

Fig. 7M, N

*Sertularella curta* Galea & Schories, 2014 in Galea *et al.*, 2014: 34, figs 6D-E, 7C.

*Sertularella geniculata*. – Leloup, 1974: 28, fig. 23 [non *Sertularella geniculata* Hincks, 1874 = *Sertularella tenella* (Alder, 1857)].

**Material examined:** MHNG-INVE-86236; Chile, Región de Antofagasta, Taltal, -25.38333° -70.51667°, 12-20 m, coll. D. Schories, lot #24; 24.04.2012; a 1.8 cm high, male colony (holotype). – MHNG-INVE-86237; Chile, Región de Antofagasta, Taltal, -25.38333° -70.51667°, 12-20 m, coll. D. Schories, lot #25; 22.04.2012; a 1.6 cm high, male colony (paratype).

**Description:** Colonies arising from creeping, branching stolon. Stems erect, up to 1.8 cm high, monosiphonic; basal part very short and ahydrothecate, either smooth or with up to 4 annuli; remainder of stem slightly geniculate, divided into short internodes by means of inconspicuous constrictions of the perisarc; a hydrotheca to the distal end of each internode. Side branches, when present (up to 3 per stem), short and arising irregularly from below a stem hydrotheca, either in front or the rear side of the colony; occasionally, the branches arise from within the stem hydrothecae; up to 2nd order branching observed. Hydrothecae biseriate, alternate, fusiform, adnate for about 2/3rd their length to the corresponding internode; free adaxial wall with about 3 transverse ridges prolonged abaxially; abaxial wall slightly concave, aperture expanding below rim, and perpendicular to long axis of the theca; margin with 4 equally-developed, triangular cusps separated by rounded, moderately-deep embayments; a 4-flapped operculum; 3 internal, submarginal cusps (2 latero-adaxial, 1 abaxial), not always noticeable. Gonothecae (only male known) originating from below the hydrothecal bases; ovoid-fusiform, walls with 6-7 transverse ridges, aperture surrounded by 4 perisarc projections.

**Dimensions:** Internodes 340-490 µm long and 170-210 µm wide at nodes. Hydrothecal free adaxial length 345-380 µm, adnate adaxial length 230-270 µm, abaxial length 485-515 µm, maximum width 250-270 µm, diameter at aperture 210-230 µm. Male gonotheca 1440-1660 µm long and 575-620 µm wide.

Table 6. Measurements of *Sertularella cruzensis* El Beshbeeshy, 2011, in µm.

	El Beshbeeshy, 2011	Vervoort (1972), as <i>S. conica</i> , Vema 16-39	Vervoort (1972), as <i>S. conica</i> , Vema 17-30
<b>Internode</b>			
- length	870-1067	ca. 1230	610-675
- diameter at node	208-272	ca. 200	190-255
<b>Hydrotheca</b>			
- free adaxial length	417-556	460-540	460-500
- adnate adaxial length	417-452	420-435	420-430
- abaxial length	603-788	ca 730	580-650
- maximum width	-	335-405	400-410
- diameter at aperture	295-382	285-325	300-405

**Remarks:** The gonotheca of this species is illustrated by Galea *et al.* (2014, fig. 7C).

**Distribution:** Chile – Región de Antofagasta [Bahía de Tocopilla (Leloup, 1974, as *S. geniculata*), Taltal (Galea *et al.*, 2014)].

***Sertularella curvitheca* Galea & Schories, 2012a**

Fig. 8A, B; Table 7

*Sertularella curvitheca* Galea & Schories, 2012a: 38, pl. 3E, fig. 4A-E.

*Sertularella gayi*. – Galea, 2007: 62. – Galea *et al.*, 2007b: 161. – Galea *et al.*, 2007c: 312 [non *Sertularella gayi* (Lamouroux, 1821)].

*Sertularella polyzonias*. – Leloup, 1974: 32, fig. 26. – Galea, 2007: 64, fig. 15A-D. – Galea *et al.*, 2007b: 161. – Galea *et al.*, 2007c: 312 [non *Sertularella polyzonias* (Linnaeus, 1758)].

**Material examined:** MHNG-INVE-79665; Chile, Región de los Lagos, Caleta la Arena, Caleta Yervas Buenas, -41.67263° -72.65650°, 20 m, coll. D. Schories, lot #05; 25.04.2007; colony composed of several profusely-branched, polysiphonic stems, up to 10 cm high, some bearing male gonothecae (holotype). – HRG-1178; Chile, Región de Aysén, Isla Waller, -46.7648° -75.2312°, 20 m, coll. HSFS, HF24, lot #128; 20.04.2015; three colonies with polysiphonic stems, 4.5, 5.8, and 7.0 cm high, the latter bearing a male gonotheca.

**Description:** Colonies erect, up to 10 cm high, arising from creeping, branching stolon. Stems either mono- or polysiphonic. Basal part of monosiphonic stems of varied length, not constricted above origin from stolon, ahydrothecate, with smooth perisarc; remainder of stem composed of a succession of moderately-

long, slightly geniculate internodes delimited by rather indistinct, oblique nodes sloping in alternate directions. A hydrotheca, or a hydrotheca and a short, lateral apophysis immediately below its base, confined to the distal end of each internode. Branching pattern alternate and coplanar, with generally 3 hydrothecae between successive side branches, but possibly 1 to 9; up to 3rd order branching observed; branches with similar structure as the stem, though 1st internode comparatively longer than subsequent ones. Hydrothecae tubular, distinctly curved outwards, adnate for about half their length to the corresponding internode; abaxial wall straight for 3/4th its length, conspicuously curved outwards below rim; free adaxial wall slightly convex, perisarc smooth to wavy, in the latter case provided with 2-3 indistinct undulations, more conspicuous proximally; hydrothecal aperture expanding just below rim; the latter provided with 4 acute cusps separated by moderately-deep, semi-circular embayments; operculum composed of 4 triangular flaps, with concentric, closely-set striae. Gonothecae arising from below the hydrothecal bases; male and female similar, though of slightly different size; broadly ovoid, with 6-7 transverse ribs, the 3-4 distalmost well-marked, becoming obsolete towards base; aperture mounted on short, terminal collar, truncate distally and provided with 4 blunt perisarc projections; female with acrocysts.

**Dimensions:** See Table 7.

**Remarks:** The typical shape of the colonies of this species is illustrated in Galea & Schories (2012a, pl. 3E, fig. 4A), and its gonothecae in both Galea (2007, fig. 15B, D) and Galea & Schories (2012a, fig. 4E).

**Distribution:** Chile – Región de los Lagos [Fjord Comau (Galea, 2007, as both *S. gayi* and *S. polyzonias*),

Table 7. Measurements of *Sertularella curvitheca* Galea & Schories, 2012a, in  $\mu\text{m}$ .

	Galea & Schories (2012a)	Galea (2007), as <i>S. polyzonias</i>
<b>Internode</b>		
- length (in general)	880-1320	1095-1305
- length of 1st internode	460-1930	-
- diameter at node	-	267-296
<b>Hydrotheca</b>		
- free adaxial length	410-450	412-577
- adnate adaxial length	375-495	467-522
- abaxial length	610-655	604-687
- maximum width	340-395	379-412
- diameter at aperture	290-325	330-357
<b>Gonotheca</b>		
- total length	2105-2520 (♀); 2215-2750 (♂)	1971-2183
- maximum width	810-915 (♀); 795-990 (♂)	732-901

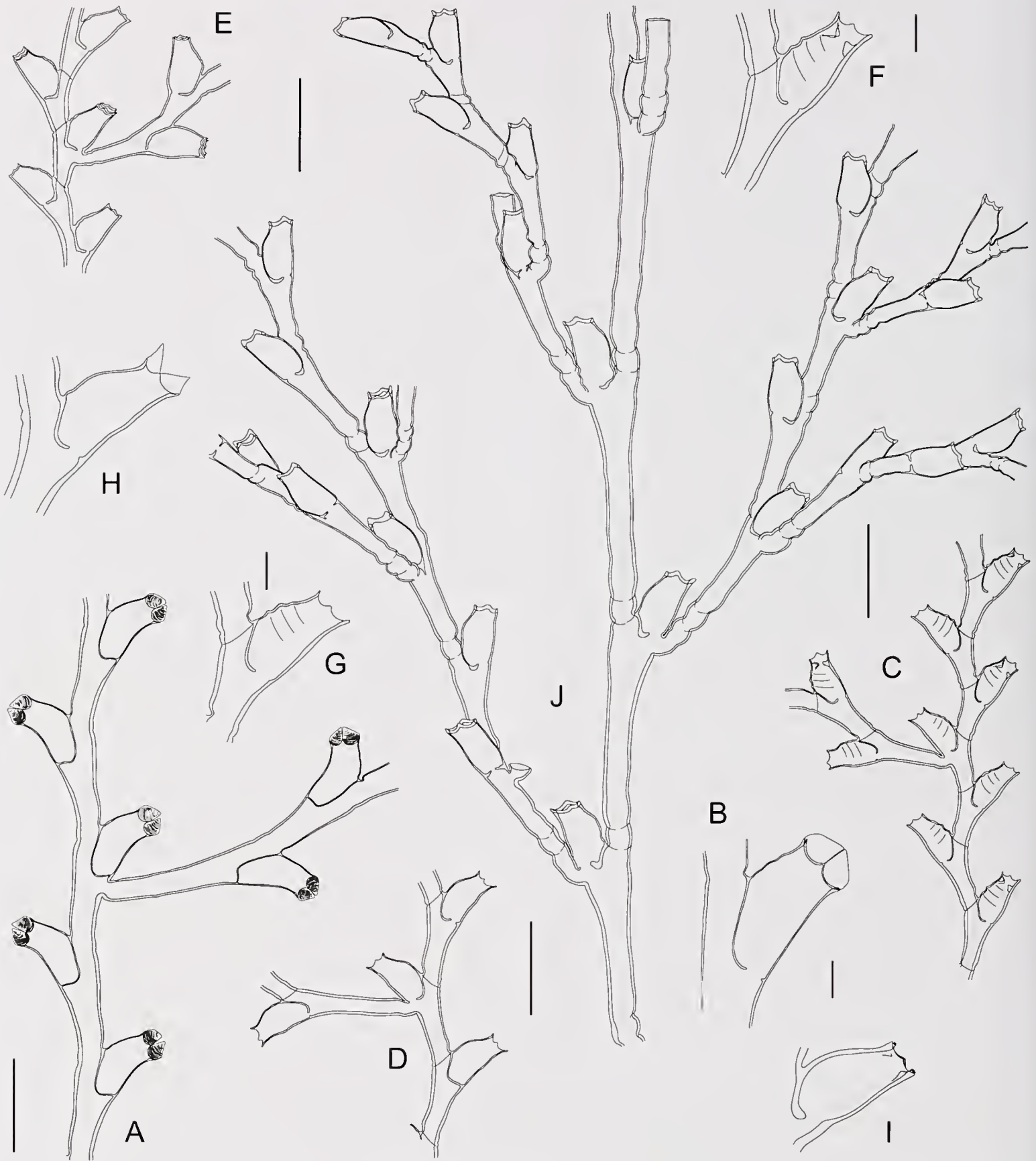


Fig. 8. (A, B) *Sertularella curvitheca* Galea & Schories, 2012a. Portion of colony from MHNG-INVE-79665 (A), and hydrotheca from HRG-1178 (B). (C-I) *Sertularella fuegonensis* El Beshbeeshy, 2011. Colony portions from ZMH C11884 (C), HRG-0009 (D) and Vervoort (1972, as *S. picta*) (E). Hydrothecae from ZMH C11884 (F, G), HRG-0009 (H) and Vervoort (1972, as *S. picta*) (I). (J): *Sertularella gaudichaudi* (Lamouroux, 1824) (part), colony fragment from ZMH C04172. Scale bars: 200  $\mu$ m (B, F-I), 1 mm (A, C-E, J).

Gulf of Ancud (Leloup, 1974, as *S. polyzonias*), Seno de Reloncaví (Galea & Schories, 2012a); Región de Aysén [Canal Puyuhuapi (Galea *et al.*, 2009, as *S. cf. gayi*); Isla Waller (present study)]; Región de Magallanes y de la Antártica Chilena [Canal Adalberto and Isla Camello (Galea, 2007, as *S. gayi*), Canal Fallos (Galea, 2007, as *S. polyzonias*)].

***Sertularella fuegonensis* El Beshbeeshy, 2011**

Fig. 8C-I; Table 8

*Sertularella fuegonensis* El Beshbeeshy, 2011: 131, fig. 41. – (?) Vervoort & Watson, 2003: 161, fig. 37A-B. – Galea, 2007: 60, fig. 14D-F. – Galea *et al.*, 2007c: 312, fig. 4A.

*Sertularella picta*. – Vervoort, 1972: 114, fig. 35A-B [non *Sertularella picta* (Meyen, 1834)].

non *Sertularella picta*. – Vervoort, 1972: 113, figs 34, 35C [= *Sertularella implexa* (Allman, 1888)].

**Material examined:** ZMH C11884; FRV *Walther Herwig*, Stn. 280, Argentine Shelf, off Provincia de Santa Cruz, -51.50000° -68.50000°; 11.02.1971; a few infertile stems, up to 2 cm high, with remains of coenosarc. – MHNG-INVE-53441; Chile, Región de Magallanes y de la Antártica Chilena, Canal Vicuña, -52.16222° -73.27617°, 15-25 m, coll. HSFS, HF3, lot #142; 06.03.2006; several sterile colony fragments, up to 6 cm high. – MHNG-INVE-53447; Chile, Región de Magallanes y de la Antártica Chilena, Canal Vicuña, -52.16222° -73.27617°, 15 m, coll. HSFS, HF3, lot #143; 06.03.2006; a colony, *ca.* 6 cm high, and smaller fragments, all sterile.

**Description:** Colonies much branched, with no definite main stems, arising from rhizoid stolon. Both stems and branches divided into moderately-long, geniculate internodes by means of weak, oblique constrictions of the perisarc, sloping in alternate directions; each internode with a distally-placed hydrotheca, or a hydrotheca and a lateral apophysis immediately below its basis; apophyses given off irregularly every

1-10 hydrothecae; side branches, up to the 3rd order, generally alternate and coplanar. Hydrothecae biserial, alternate, either coplanar or imperceptibly shifted on to one side of the stem; flask-shaped, adnate for 2/5th their adaxial length, constricted below aperture; free adaxial wall slightly sigmoid, surface either smooth or with 2-5 shallow wrinkles; 4 triangular, marginal cusps of unequal development (abaxial one the longest, adaxial one the shortest, and the two laterals of intermediate length), separated by rather deep, rounded embayments; occasionally 3 internal, submarginal cusps (2 latero-adaxial, 1 abaxial); renovations of the margin occur; 4 triangular opercular flaps. Gonothecae unknown.

**Dimensions:** See Table 8.

**Remarks:** The colony structure is illustrated by Galea (2007, fig. 14D). The free adaxial wall may be either smooth (Chilean material) or wrinkled (El Beshbeeshy, 2011), though colonies with hydrothecae exhibiting both situations may occur (*e.g.* Vervoort, 1972, fig. 35A, as *S. picta*). Intrathecal cusps occur variably among the hydrothecae of the same colony, with the abaxial one generally more conspicuous than the two latero-adaxial ones.

**Distribution:** Chile – Región de Magallanes y de la Antártica Chilena – Canal *Vicuña* (Galea, 2007). Argentina – scattered records from the Argentine Shelf between 41°-53° S (El Beshbeeshy, 2011); Provincia de Tierra del Fuego, Antártida e Islas del Atlántico Sur [off the northern coast of the tip of Península Mitre (Vervoort, 1972, as *S. picta*)]. (?) New Zealand (Vervoort & Watson, 2003).

***Sertularella gaudichaudi* (Lamouroux, 1824)**

Figs 1H-K, 8J, 9, 10; Tables 9, 10

*Sertularia gaudichaudi* Lamouroux, 1824: 615, pl. 90 figs 4, 5. – Van Praët, 1979: 901, fig. 47 (reexamination of schizoholotypes).

Table 8. Measurements of *Sertularella fuegonensis* El Beshbeeshy, 2011, in  $\mu\text{m}$ .

	El Beshbeeshy (2011)	Galea (2007)	Vervoort (1972), as <i>S. picta</i> (Vema 14-14)	Vervoort & Watson (2003)
<b>Internode</b>				
- length	452-556	449-646	475-540	820-1065
- diameter at node	145-185	208-230	<i>ca.</i> 175	130-165
<b>Hydrotheca</b>				
- free adaxial length	382-429	421-478	390-425	395-425
- adnate adaxial length	226-243	225-309	230-245	280-330
- abaxial length	417-493	506-601	420-485	510-575
- maximum width	-	309-348	310-325	295-330
- diameter at aperture	185-220	240-263	190-215	195-230

*Sertularella gaudichaudi*. – Bedot, 1905: 105. – Billard, 1909: 317, fig. 4A (reexamination of the holotype). – Bedot, 1910: 360; 1912: 354; 1916: 204; 1918: 238. – Billard, 1924: 61 (reexamination of the holotype). – Van Praët, 1979: 901, fig. 47. – Ramil *et al.*, 1992: 518, fig. 15 (reexamination of schizoholotypes).

non *Sertularella gaudichaudi*. – Cornelius, 1979: 282, fig. 20 [= *S. ellisii* (Deshayes & Milne-Edwards, 1836), *S. fusiformis* (Hincks, 1861), and *S. mediterranea* Hartlaub, 1901]. – García Corrales *et al.*, 1980: 30, fig. 10 [= *S. ellisii* (Deshayes & Milne-Edwards, 1836)]. – Gili *et al.*, 1989: 101, fig. 26B, C (= *S. cf. mediterranea* Hartlaub, 1901).

*Sertularella gaudichaudii*. – Kirchenpauer, 1884: 38 (incorrect subsequent spelling).

*Sertularia picta* Meyen, 1834: 201, pl. 34 figs 1-3 (**syn. nov.**). – Hartlaub, 1901: 77, pl. 5 fig. 14, pl. 6 figs 17, 18 & 20 (reexamination of the cotype). – Jäderholm, 1903: 282. – Nutting, 1904: 90, pl. 20 figs 5-7. – Bedot, 1905: 105; 1910: 361. – Hartlaub, 1905: 645, fig. L<sup>4</sup>. – Billard, 1922: 106, fig. 2B. – Stechow, 1923a: 187, fig. B<sup>1</sup> (reexamination of cotype). – Naumov & Stepanjants, 1962: 88. – Blanco, 1963: 175, figs 3-4. – (?) Millard 1971: 405, fig. 6A; 1977: 25, fig. 6A-D. – Blanco, 1994: 199. – Branch & Williams, 1993: 12, text-fig. – El Beshbeeshy, 2011: 138, fig. 44.

non *Sertularella picta*. – Blanco, 1967: 112, pl. 3 figs 1-7 (= *Sertularella mediterranea* Hartlaub, 1901). – Millard, 1971: 405, fig. 6B (= *S. subantarctica* Galea, sp. nov.). – Vervoort, 1972: 113, figs 34, 35C [= *Sertularella implexa* (Allman, 1888)]. – Vervoort, 1972: 114, fig. 35A, B (= *Sertularella fuegonensis* El Beshbeeshy, 2011).

*Sertularella protecta* p.p. Hartlaub, 1901: 79, pl. 6 figs 21-26 (**syn. nov.**). – Hartlaub, 1905: 652, fig. R<sup>4</sup>. – Billard, 1924: 62. – p.p. Jäderholm, 1903: 282. – Rees & Thursfield, 1965: 135.

(?) *Sertularella margaritacea* Allman, 1885: 133, pl. 7 figs 3, 4. – Nutting, 1904: 95, pl. 22 fig. 1. – Hartlaub, 1905: 657, fig. V<sup>4</sup>. – Bedot, 1916: 208; 1918: 240. – Billard, 1924: 60.

*Sertularella allmani*. – Naumov & Stepanjants, 1962: 86 (non *Sertularella allmani* Hartlaub, 1901).

*Sertularella antarctica*. – p.p. Jäderholm, 1903: 283 (non *Sertularella antarctica* Hartlaub, 1901).

*Sertularella contorta*. – p.p. Hartlaub, 1901: 83 (non *Sertularella contorta* Kirchenpauer, 1884).

*Sertularella polyzonias*. – p.p. Vanhöffen, 1910: 322 [non *Sertularella polyzonias* (Linnaeus, 1758)].

**Material examined:** ZMH C04172; Chile, Región de Magallanes y de la Antártica Chilena, Isla Lennox, coll. Michaelsen no. 181; 22.12.1892; fertile colony (stranded on beach) with multiple fascicled stems, up to ca. 7.5 cm high [material examined by Hartlaub (1901, p. 79) and assigned by him to *S. picta* (Meyen, 1834)]. – ZMH C04173; Chile, Región de Magallanes y de la Antártica Chilena, Lennox Cove, coll.

Michaelsen no. 182; 24.12.1892; fertile colony with multiple monosiphonic stems, up to 4 cm high, on kelp (type of *S. protecta* Hartlaub, 1901). – SMNH 123894; Chile, Región de Magallanes y de la Antártica Chilena, Lennox Cove, coll. Swedish Tierra del Fuego Expedition 1895-1896; 05.02.1896; microslide (Fig. 1J) containing 2 badly preserved, fertile colony fragments, both ca. 2.5 cm high [material identified by Jäderholm (1903) as *S. protecta* Hartlaub, 1901]. – SMNH 123881; Chile, Región de Magallanes y de la Antártica Chilena, Isla Lennox, 18-45 m, coll. Swedish Tierra del Fuego Expedition 1895-1896; 07.02.1896; microslide (Fig. 1H) containing 3 colony fragments 1.7-2.0 cm high, two of which bear gonothecae [material identified by Jäderholm (1903) as *S. picta* (Meyen, 1834)]; with small, epizootic colony of *Halecium annuliforme* Galea & Schories, 2012a, bearing an incipient gonophore of unassignable sex. – SMNH 123837; Chile, Región de Magallanes y de la Antártica Chilena, Isla Nueva, coll. Swedish Tierra del Fuego Expedition 1895-1896; 07.02.1896; microslide (Fig. 1I) containing a ca. 6 cm high, fertile colony fragment [material identified by Jäderholm (1903) as *S. antarctica* Hartlaub, 1901; a second identification, *contorta*, was subsequently added to the label]. – NMSZ 1959.33.472; Patagonia; microslide (Fig. 1K) comprising 2 colony fragments, 0.5 and 1.0 cm high, the largest bearing 2 gonothecae [material belonging to Ritchie's collection, identified by Stechow as *S. protecta* Hartlaub, 1901, and listed by Rees & Thursfield (1965, p. 135)]. – ZMB Cni1122; Chile, coll. Philippi, no additional data; a very fragmented, badly preserved fertile colony composed of numerous pieces up to 1.6 cm high, with fascicled portions of stem [material studied by Hartlaub (1901) and assigned by him to *S. contorta* Kirchenpauer, 1884]. – ZMB Cni946; French Southern and Antarctic Lands, Kerguelen Is., Royal Sound, coll. Deutsche Südpolar (*Gauss*) Expedition 1901-1903; 01.01.1902; a fully fertile (male) colony, 3 cm high [material studied by Vanhöffen (1910), as *S. polyzonias*].

**Description:** Slender, straggling, repeatedly branched, tangled colonies, up to 21 cm high, with mono- or polysiphonic stems and branches; these divided by oblique nodes into internodes of highly variable length, from short to exceedingly long and slender; each internode with a couple of spiral twists proximally, a hydrotheca distally, and a short, lateral apophysis below its base; apophyses alternate, supporting side branches with the same structure as the stem, though internodes generally shorter; first internode with 2-4 spiral twists basally. Side branches and hydrothecae shifted on to one side (“anterior”) of the colony, the two rows

Fig. 9. *Sertularella gaudichaudi* (Lamouroux, 1824) (continued). Colony fragments from proximal and distal parts of ZMH C04173 (A and B, respectively) and SMNH 123881 (C and D, respectively), and portion from ZMB Cni1122 (E). Hydrothecae from schizoholotype (F, after Ramil *et al.*, 1992), ZMH C04172 (G), ZMH C04173 (H), SMNH 123881 (I) and ZMB Cni1122 (J). Gonotheca from SMNH 123881 (K). Scale bars: 200 µm (F-J), 500 µm (K), 1 mm (A-E). ▶





forming a moderately wide angle. Hydrothecae short, flask-shaped, distinctly swollen adaxially; abaxial wall straight or nearly so; free adaxial wall convex for most of its length, becoming concave below aperture; margin with 4 short, triangular, unequally-developed cusps: abaxial one generally produced, occasionally less so; adaxial one the shortest; lateral ones asymmetrical, the “anterior” one comparatively shorter than “dorsal” one; rim generally thickened; internal, submarginal cusps of varied development: from absent, to 2 latero-adaxial, to a complete set of 3 (one abaxial and 2 latero-adaxial); a variously developed perisarc plug at the end of the adnate adaxial wall, forming an incomplete foramen for the passage of the hydranth. Gonothecae borne on both stems and branches; broadly ovoid, with 3-4 transverse ridges in distal half, smooth in the lower half; aperture on short collar surrounded by generally 4 blunt spines (occasionally 3-5).

**Dimensions:** See Table 9.

**Remarks:** The holotype colony of *Sertularia gaudichaudi*, stored in Caen, France, and reexamined earlier by Billard (1909; 1922), was lost during WWII (Redier, 1967). However, two schizoholotype slides (MNHN H.L. 615 & 616) were prepared by Billard from that colony (Van Praët, 1979), and were reexamined subsequently by Ramil *et al.* (1992). Unfortunately, those slides could not be located for the purpose of the present study (A. Andouche, *Muséum national d'Histoire naturelle*, Paris, pers. comm.). The cotype of *Sertularia picta* was reexamined by Hartlaub (1901) and Stechow (1920; 1923a), who provided additional information and more accurate illustrations.

The synonymy between these two nominal species was suspected by Meyen (1834), Kirchenpauer (1884), Hartlaub (1901; 1905), Bedot (1910), Billard (1909; 1910), and Galea & Schories (2012b). In contrast, Stechow (1920) and Billard (1922) provided arguments in favor of their specific separation, but their reliability could be contested in light of the new data available in the subsequent literature, and through the present observations. Stechow, who compared the redescription of *S. gaudichaudi* given by Billard (1909) with the cotype of *S. picta*, emphasized the following differences: 1) Lamouroux' species does not have hydrothecae with thickened rims, a statement invalidated later on by Billard (1922), who showed that this character is inconstant, an opinion equally shared by us; 2) the abaxial cusp is conspicuously produced in *S. picta*, although it is now recognized that its shape varies within the same colony (present study); 3) the gonothecae of *S. picta* have only wavy walls, while those of *S. gaudichaudi* are clearly transversely ringed, an argument not only contradicted by several observations (Blanco 1963; present study, material ZMH C04172), but also recognized as dependent on their state of maturation.

Billard (1922), for his part, emphasized the following distinguishing characters exhibited by *S. picta*: 1) the conspicuously hypertrophied abaxial hydrothecal cusp described by Stechow (1920), which is now recognized as a variable character; 2) the comparatively thickened hydrothecal rim, although the distalmost, youngest hydrothecae have evidently unthickened rims; 3) the more conspicuous internal, submarginal cusps, though it was demonstrated that this is an inconstant character (Blanco 1963); 4) the broad perisarc plug at the base of the hydrotheca, although obvious differences are seen in

Table 9. Measurements of *Sertularella gaudichaudi* (Lamouroux, 1824), in  $\mu\text{m}$ .

	Present study, SMNH 123881, as <i>S. picta</i> in Jäderholm (1903)	Blanco (1963), as <i>S. picta</i>	Millard (1977), as <i>S. picta</i>	El Beshbeeshy (2011), as <i>S. picta</i>
<b>Internode</b>				
- length	550-3990	1000-2500	770-1340	310-1617
- diameter at node	125-280	-	120-180	116-191
<b>Hydrotheca</b>				
- total length	-	684-741	-	-
- free adaxial length	390-405	-	400-510	301-475
- adnate adaxial length	220-235	-	240-350	162-232
- abaxial length	500-550	-	550-700	464-603
- maximum width	280-310	323-380	-	-
- diameter at aperture	200-235	228-281	200-260	185-266
<b>Gonotheca</b>				
- total length	1840-1900 (♀)	2200-2300	1500-2150	1856-2308
- maximum width	955-1030 (♀)	1050-1200	1300-1520	904-1032

the hydrothecae from various, or even the same, colonies (present study).

It appears, therefore, that none of the arguments provided by Stechow and Billard are reliable specific characters. In addition, a comparison of the available data (Table 10) and illustrations (Fig. 10) from various sources based on the examination of the types of both nominal species demonstrate, with little doubt, that they are coterminous, with Lamouroux's species having priority.

A typical, fully formed colony of *S. gaudichaudi* is illustrated by both Lamouroux (1824) and Billard (1922), while the gonotheca is depicted in a number of papers, e.g. Billard (1909), Stechow (1923a, as *S. picta*), Ramil *et al.* (1992), and El Beshbeeshy (2011, as *S. picta*). The habit of the stem varies in this species, and could be either monosiphonic (Blanco, 1963; El Beshbeeshy, 2011; specimen ZMH C04173 examined here) or polysiphonic (material ZMH C04172 examined here).

Type material of *S. protecta* [not designated by Hartlaub (1901), but indicated on the label of sample ZMH C04173] is characterized by: 1) the occurrence of long (up to 2 mm) internodes among the otherwise most numerous, much shorter stem internodes; 2) the profuse

branching, with almost every stem internode giving rise to a side branch, the latter alternate in position; 3) short and conspicuously adaxially-swollen hydrothecae. The perisarc of this material is comparatively hypertrophied with respect to that of sample ZMH C04172 assigned to *S. picta* by Hartlaub himself, giving the colony a more "peculiar", rigid appearance. The higher occurrence of short vs. long internodes does not justify the placement of this species close to *S. allmani* as suggested by Hartlaub, because long internodes have never been observed in the latter. On the contrary, their presence is a typical feature of *S. gaudichaudi*, and their length may reach as much as 4 mm (e.g. SMNH 123881 and 123894).

Two other specimens, one from Elizabeth I. (Magellan Strait) and the other from South Georgia were also assigned to *S. protecta* by Hartlaub. The former is possibly no longer extant in ZMH (H. Roggenbuck, pers. comm.) and, for the latter, there is no certainty whether it is the same specimen as ZMH C04384, now recognized as a distinct species, *S. subantarctica* Galea, sp. nov.

The Chilean material collected by Philippi and assigned by Hartlaub (1901, p. 83) to *S. contorta* Kirchenpauer, 1884 was reexamined, and should be better assigned

Table 10. Comparison of the available data on type materials of *S. gaudichaudi* (Lamouroux, 1824) and *S. picta* (Meyen, 1834). "B<sup>a</sup>" stands for Billard (1909), "B<sup>b</sup>" for Billard (1922), "B<sup>c</sup>." for Billard (1924), "H" for Hartlaub (1901), "L" for Lamouroux (1824), "M" for Meyen (1834), and "R" for Ramil *et al.* (1992).

	<i>Sertularella gaudichaudi</i> (Lamouroux, 1824)	<i>Sertularella picta</i> (Meyen, 1834)
<b>Origin of the specimens</b>	Vicinity of the Falkland Islands (L)	Eastern coast of Tierra del Fuego and the Falkland Islands (M).
<b>Colony structure</b>	Shrub-like, 1.5 to 2 inches high, with numerous alternate branches (L). Holotype 6.5 cm high, as high as broad, flabelliform, profusely and irregularly ramified (B <sup>b</sup> )	"6 to 8 inches, and over" (M). Growth very ample, reminiscent of <i>Obelia longissima</i> (H).
<b>Habit of the stem</b>	Lightly fascicled (B <sup>b</sup> )	Lightly fascicled (H).
<b>Color</b>	Greenish yellow to bluish green; hydranths pale blue (L)	"of a beautiful yellow, sometimes pale red" (M)
<b>Internodes</b>	Long, with the hydrothecae "very remote from each other" (L). Proximally with 1-2 annuli, not always distinct (B <sup>a</sup> ).	Typically very long, geniculate, strikingly resembling those of <i>S. gaudichaudi</i> (H).
<b>Branches</b>	With several annuli at origin from stem (B <sup>a</sup> ). Branchlets pinnately arranged, originating from below bases of successive hydrothecae, occasionally every 2-4 hydrothecae (B <sup>b</sup> ).	Each stem internode provides an origin for a side branch (H). Branches "strongly annulated" basally ( <i>i.e.</i> several annuli) (H).
<b>Hydrothecae</b>	Not in the same plane (B <sup>a</sup> , B <sup>b</sup> ), angle varying between 90-180° (B <sup>b</sup> ); adnate for 1/3rd, swollen adaxially, aperture on a constricted neck region, rim thickened though not always so (B <sup>b</sup> ); abcauline cusp produced; 3 internal, submarginal cusps (2 latero-adaxial, 1 abaxial) (B <sup>a</sup> , B <sup>b</sup> ), not always present (B <sup>c</sup> ).	Not in the same plane (H). Adnate for 1/3rd, swollen adaxially, rim thickened (H). Perisarc thickened (M).
<b>Gonothecae</b>	Profuse, nearly globular, walls transversely annulated in upper half (L, B <sup>a</sup> , B <sup>b</sup> ); aperture surrounded by 3-4 blunt cusps, indistinct in young thecae (B <sup>a</sup> , B <sup>b</sup> )	Wall annulated, with 4 apical projections (M), the latter not always obvious (H).



Fig. 10. Comparison of the type materials of *Sertularella gaudichaudi* (Lamouroux, 1824) (A-E) and *S. picta* (Meyen, 1834) (F-K) illustrated by various authors, as follows: Lamouroux (1824) (A, C), Meyen (1834) (F, H, I), Hartlaub (1901) (G, K), Billard (1909) (D), Billard (1922) (E) and Stechow (1923) (J).

to the present species. Indeed, quite long internodes (Fig. 9E) co-occur with otherwise uniformly short internodes in some stem fragments.

Billard (1924) reexamined the type of *Sertularella margaritacea* Allman, 1885 and noted the presence of a thickened hydrothecal rim, of a conspicuous abaxial cusp, as well as the apparent lack of internal, submarginal projections of the perisarc. In addition, the branching pattern illustrated in the original account (Allman, 1885, pl. 7 fig. 3) fits those provided by both Lamouroux (1824) and Billard (1922) for *S. gaudichaudi*. Although not evident from his pl. 7 fig. 4, Allman also stated that the hydrothecae of his species were “distant” and this is, indeed, noticeable on the lower part of the stem and a

couple of side branches, suggesting that both short and long internodes occur within the same colony, which is a character typically exhibited by *S. gaudichaudi*.

**Distribution:** Chile – Región de Magallanes y de la Antártica Chilena [Isla Navarino (Hartlaub, 1901; 1905, both as *S. picta*); Isla Lennox (Hartlaub, 1901; 1905, as both *S. picta* and *S. protecta*; Jäderholm, 1903, as *S. picta*); Lennox Cove (Hartlaub, 1901; Jäderholm, 1903; both as *S. protecta*); Cape Horn (Billard, 1922, as *S. picta*); Isla Nueva (Jäderholm, 1903, as *S. antarctica*); Magellan Strait (Allman, 1885, as *S. margaritacea*)]. Patagonia – no exact locality (Rees & Thursfield, 1965, as *S. protecta*). Argentina – scattered records from the Argentine Shelf between ca.

47° S and the east of Península Mitre (El Beshbecshy, 2011); Provincia del Chubut [Puerto Madryn (Blanco, 1963, as *S. picta*)]; Provincia de Tierra del Fuego, Antártida e Islas del Atlántico Sur [Isla de los Estados (Blanco, 1994, as *S. picta*); eastern coast of Tierra del Fuego (Meyen, 1834, as *S. picta*)]. Between Tierra del Fuego and the Falkland Is. (Naumov & Stepanjants, 1962, as *S. allmani*). Falkland Is. (Lamouroux, 1824; Meyen, 1834, as *S. picta*) and off their eastern coast (El Beshbeeshy, 2011). French Southern and Antarctic Lands – Kerguelen Is. (Vanhöffen, 1910, as *S. polyzonias*; Naumov & Stepanjants, 1962, as *S. picta*; Millard, 1977, as *S. picta*); Crozet Shelf (Millard, 1977, as *S. picta*). (?) South African Subantarctic Islands: Marion I. (Millard, 1971; Branch & Williams, 1993; both as *S. picta*), Prince Edward I. (Branch & Williams, 1993, as *S. picta*).

### *Sertularella geodia* Totton, 1930

Fig. 11A; Table 11

*Sertularella geodia* Totton, 1930: 196, text-fig. 43, pl. 3 figs 7-8.

non *Sertularella geodia*. – Vervoort, 1972: 120, fig. 37 (= ? *S. hermanosensis* El Beshbeeshy, 2011). – Blanco, 1976: 39, pl. 3 figs 7-8; 1994: 199 (= *Sertularella blanconae* El Beshbeeshy, 2011).

(?) *Sertularella geodia*. – ? Naumov & Stepanjants, 1962: 86, fig. 10 (incorrect subsequent spelling).

**Description:** Colonies up to 15 cm high, arising from large rooting masses; irregularly pinnate; stems and branches fascicled and well defined, divided into rather short, slightly geniculate internodes by means of oblique constrictions of the perisarc slanting in alternate directions; a hydrotheca to the distal end

of each internode. Side branches given off laterally from below the bases of stem hydrothecae; structure similar to that of stem. Hydrothecae biseriate, alternate, coplanar; large, flask-shaped, adnate for 3/5th their adaxial length, swollen adaxially; a typical notch at junction between proximal part of free adaxial wall with corresponding internode; abaxial wall slightly sigmoid (imperceptibly concave for most of its length, becoming suddenly convex below aperture); free adaxial wall with slight “shoulder” proximally, perisarc undulated; margin with 4 short, sharp, triangular cusps separated by very shallow, semicircular embayments; occasionally 3 submarginal, intrathecal projections of perisarc, 2 latero-adaxial, and one abaxial; a 4-flapped operculum. Gonothecae borne on both stem and side branches, arising from below the hydrothecal bases; elongated-ovoid, wall transversely-wrinkled, aperture surrounded by 3-4 apical cusps.

**Dimensions:** See Table 11.

**Remarks:** The description given above combines the original account with that provided by Vervoort & Watson (2003). As stated by these authors, *S. geodia* differs from *S. gayi* (Lamouroux, 1821) through its much larger hydrothecae, the occasional presence of submarginal cusps, and the apical part of its gonotheca. The typical shape of a colony fragment is illustrated by Totton (1930, pl. 3 fig. 8).

**Distribution:** (?) Chile – Región de Magallanes y de la Antártica Chilena [eastern coast of Tierra del Fuego (Naumov & Stepanjants, 1962, as *S. geodia*). New Zealand and New Caledonia (Vervoort & Watson, 2003).

Table 11. Measurements of *Sertularella geodia* Totton, 1930, in  $\mu\text{m}$ .

	Totton (1930)	Naumov & Stepanjants (1962), as <i>S. geodia</i>	Vervoort & Watson (2003)
<b>Internode</b>			
- length	1220-1390	750-950	-
- diameter at node	310-390	-	-
<b>Hydrotheca</b>			
- free adaxial length	470-550	350-500	540-575
- adnate adaxial length	680-760	550-650	705-770
- abaxial length	600-740	-	740-785
- maximum width	-	-	555-605
- diameter at aperture	380-400	330-450	375-425
<b>Gonotheca</b>			
- total length	2000-2040	-	-
- maximum width	890-1030	-	-

***Sertularella hermanosensis* El Beshbeeshy, 2011**

Figs 11B-G, 12A; Table 12

*Sertularella hermanosensis* El Beshbeeshy, 2011: 133, fig. 42.*Sertularella geodiae*. – p.p. Vervoort, 1972: 120, fig. 37. [non *Sertularella geodiae* Totton, 1930]

**Material examined:** ZMH C11885; FRV *Walther Herwig*, Argentine Shelf, no additional data; four sterile colony fragments 7.0-1.4 cm high, each bearing several hydrothecae, with only the perisarc left. – NHML 1888.11.13.42; between Cabo Virgenes, Argentina, and the Falkland Is., *Challenger* Stn. 314, ca. 128 m; 3 infertile colony fragments (6, 12 and 18 mm high) among the holotype of *Sertularella implexa* (Allman, 1888) (for more details, see under this species), and a microslide (Fig. 12A).

**Description:** Colonies composed of erect, monosiphonic, unbranched or sparingly-branched stems arising from stolonial fibers firmly adhering to substrate. Both stems and side branches divided into moderately long (though varied in length), imperceptibly geniculate to collinear internodes, by means of faint, oblique constrictions of the perisarc slanting in alternate directions. A hydrotheca to the distal end of each internode. Side branches generally arising from below the bases of every 3 stem hydrothecae by means of short, lateral apophyses. Hydrothecae biserial, alternate, coplanar; flask-shaped, adnate for slightly more than half their length to the corresponding internode, slightly tumid adaxially; abaxial wall straight to slightly concave proximally, suddenly becoming convex below aperture; free adaxial wall wavy to distinctly transversely-ridged, ridges occasionally reaching abaxial wall; aperture with 4 short, equal, triangular cusps, separated by shallow embayments; renovations occasional; a 4-flapped operculum. Gonothecae unknown.

**Dimensions:** See Table 12.

**Remarks:** According to El Beshbeeshy (2011), his species has hydrothecae with different forms, and this is also evident from his fig. 42. As not all his material was reinspected for the purpose of the present study, it is assumed that those differences could indicate the presence of a mix of species.

**Distribution:** Chile – Región de Magallanes y de la Antártica Chilena [Magellan Strait (Vervoort, 1972, as *S. geodiae*)]. Argentina – scattered records from the Patagonian Shelf, between ca. 41° S and Península Mitre (El Beshbeeshy, 2011). Elsewhere – between Cabo Virgenes, Argentina, and the Falkland Is.

[present study (material co-occurring with the type of *S. implexa*); El Beshbeeshy, 2011]; off the NE coast of Falkland Is. (El Beshbeeshy, 2011); a large perimeter including the Strait of Magellan, the Falkland Is., the Burdwood Bank, Isla de los Estados, and Cape Horn (Vervoort, 1972, as *S. geodiae*).

***Sertularella implexa* (Allman, 1888)**

Figs 12B, 13A-D; Table 13

*Sertularia implexa* p.p. Allman, 1888: 54, pl. 26 figs 1, 1a. – Hartlaub, 1901: 90. – Bedot, 1916: 223.non *Sertularella implexa*. – Galea & Schories, 2012a: 40, pl. 3 fig. 4F-J (= *Sertularella recta* Galea & Schories, sp. nov.)*Sertularella picta*. – Vervoort, 1972: 113, figs 34, 35C [non *Sertularella picta* (Meyen, 1834)].non *Sertularella picta*. – Vervoort, 1972: 114, fig. 35A-B [= *Sertularella fregonensis* El Beshbeeshy, 2011].

**Material examined:** NHML 1888.11.13.42; a vial containing numerous sterile colony fragments in alcohol (designated here as the lectotype of *S. implexa*), as well as two slides. One slide (Fig. 12A), marked as “type”, bears the label “Challenger Stat. 314, Falklands, Depth 70 faths, *Sertularia implexa*”, and contains a 1.1 cm high colony fragment bearing 3 side branches. This material clearly does not belong to Allman’s species; in addition, its hydrothecae were quite distorted upon squashing between slide and coverslip. The other slide (Fig. 12B), labeled “Challenger Coll., *Sertularia implexa*, bet. Cape Virgins & Falkland Is., 24” is a 1.6 cm high colony fragment bearing 5 side branches, and is in agreement with both the bulk of the alcohol-preserved material and Allman’s pl. 26 fig. 1A. This second slide is selected here as the paralectotype of *S. implexa*. Among the alcohol-preserved material, three colony fragments (6, 12 and 18 mm high) could be identified as *Sertularella hermanosensis* El Beshbeeshy, 2011, and are possibly conspecific with the material mounted in the “type” slide; they were transferred to a separate vial.

**Description:** Colonies growing in loosely entangled tufts, up to ca. 7.5 cm high; profusely and irregularly branched in all directions, with no definite main stems. Stems and side branches strictly monosiphonic, divided into long, slender internodes by means of oblique nodes; first internode with a proximal twist, and comparatively longer than subsequent ones; a hydrotheca, or a hydrotheca and a short apophysis arising laterally from below its base, confined to the distal part of each internode; hydrothecae in two alternate rows; rows

Fig. 11. (A) *Sertularella geodiae* Totton, 1930. Hydrothecae (modified after Totton 1930). (B-G) *Sertularella hermanosensis* El Beshbeeshy, 2011. Portions of colonies from ZMH C11885 (B), from material mixed with the holotype of *S. implexa* (Allman, 1888) (C), and after Vervoort (1972, as *S. geodiae*) (D). Hydrothecae from the same sources (E-G, respectively). Scale bars: 200 µm (A, E-G), 1 mm (B-D). ▶

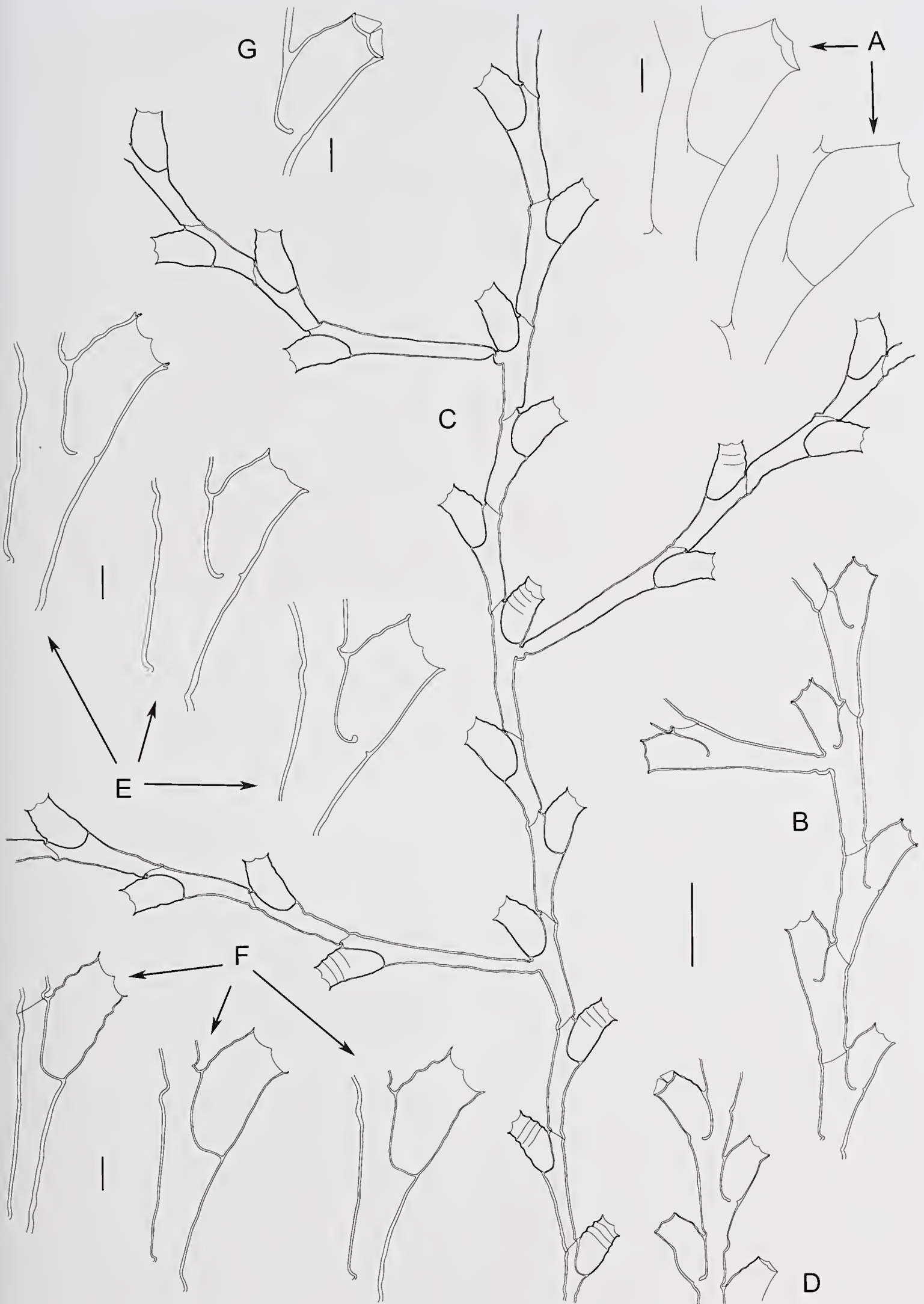


Table 12. Measurements of *Sertularella hermanosensis* El Beshbeeshy, 2011, in  $\mu\text{m}$ .

	El Beshbeeshy (2011)	Present study, in the cotype of <i>S. implexa</i>	Vervoort (1972), as <i>S. geodiae</i>
<b>Internode</b>			
- length	974-1229	1020-1385	1010-1350
- diameter at node	278-336	215-315	280-285
<b>Hydrotheca</b>			
- free adaxial length	394-487	385-450	405-485
- adnate adaxial length	498-556	440-475	515-540
- abaxial length	649-719	635-720	650-715
- maximum width	-	350-420	445-470
- diameter at aperture	348-365	320-370	350-365

Table 13. Measurements of *Sertularella implexa* (Allman, 1888), in  $\mu\text{m}$ .

	Present study, holotype NHM 1888.11.13.42	Vervoort (1972), as <i>S. picta</i> (Vema 18-16)
<b>Internode</b>		
- length (in general)	690-1155	580-675
- length of 1st internode	1655-2010	-
- diameter at node	160-180	110-135
<b>Hydrotheca</b>		
- free adaxial length	360-440	325-365
- adnate adaxial length	255-290	240-270
- abaxial length	560-595	515-565
- maximum width	275-310	270-310
- diameter at aperture	195-235	175-190
<b>Gonotheca</b>		
- total length	-	1485-1825
- maximum width	-	up to 810

coplanar or slightly shifted on to one side of the colony. Side branches originating every 1-14 hydrothecae; up to 3rd order branching observed. Hydrothecae long, adnate for 2/5th their length to the corresponding internode; swollen adaxially; perisarc either smooth or with 1-2 faint wrinkles forming shallow ridges not extending completely abaxially; abaxial wall nearly straight; abaxial cusp produced, remaining cusps triangular with rounded tips, separated by deep embayments; no intrathecal, submarginal projections of the perisarc. Gonothecae arising from below the hydrothecae; broadly ovoid, tapering below, distal half provided with ca. 6 transverse ridges; aperture on top, surrounded by 4 small cusps.

**Dimensions:** See Table 13.

**Remarks:** The typical silhouette of a colony is accurately depicted by Allman (1888) in his pl. 26 fig. 1. Part of Vervoort's (1972) material assigned to *S. picta* (Meyen, 1834), notably that from Vema 18-16 (described in detail), shows the following features: 1) the colony is bushy, composed of "irregularly intertwining, fine [...] repeatedly branched, side-branches"; 2) both the stems and branches are monosiphonic throughout; 3) the internodes are moderately long; 4) the hydrothecae are "arranged in two planes, that make a very obtuse angle"; 5) their free adaxial wall is "about 1.5-2 times the length of the fused part, [...] distinctly undulated, though the mode of development of the undulations is variable". Taken together, these represent distinctive features of *S. implexa*. Vervoort's material was fertile, and his



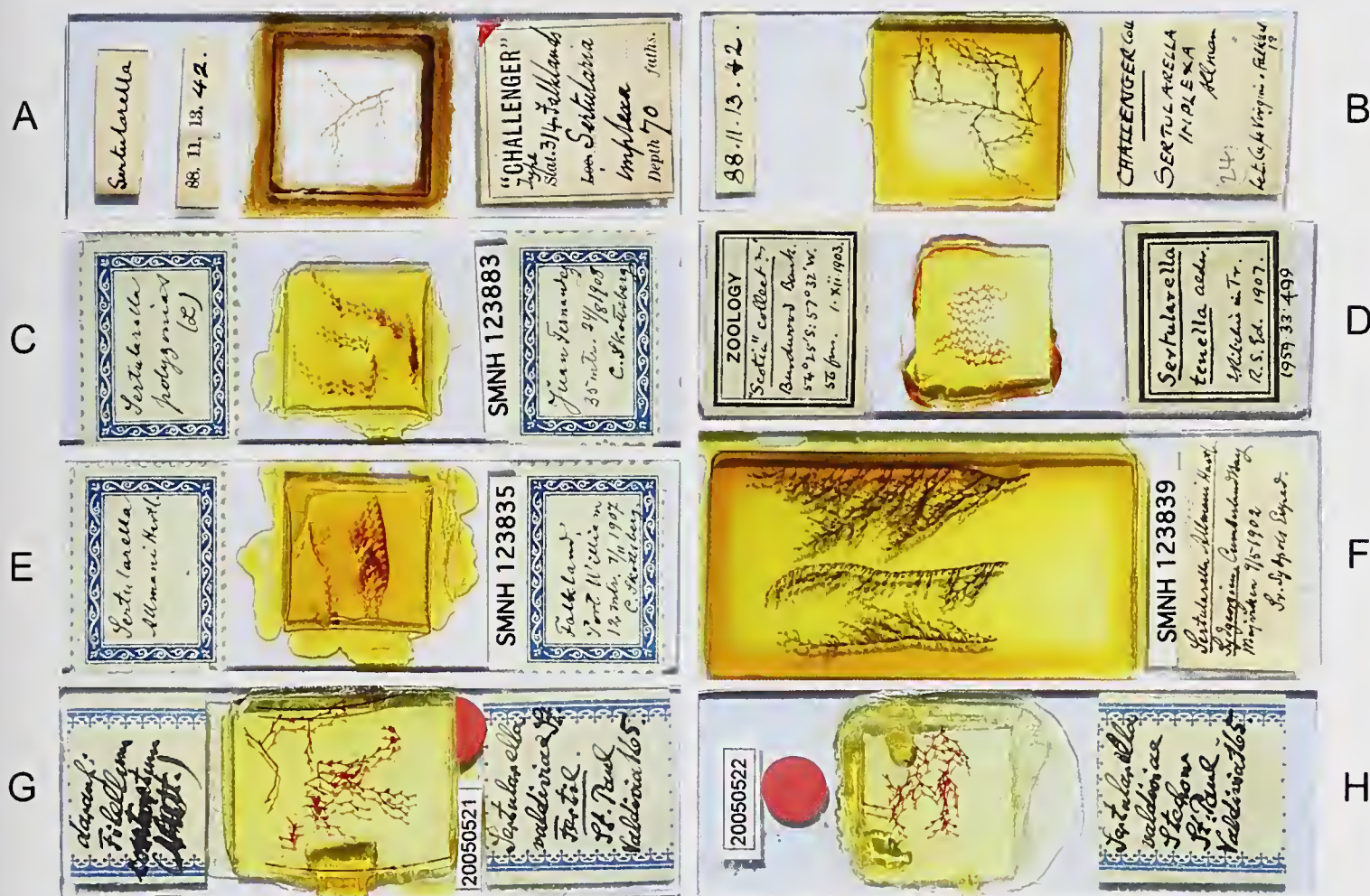


Fig. 12. (A) *Sertularella* (?) *hermanosensis* El Beshbeeshy, 2011. Likely a fragment of this species mounted on slide, as part of the type material of *S. implexa* (Allman, 1888). (B) *Sertularella implexa* (Allman, 1888), fragment from type colony mounted on slide. (C) *Sertularella juanfernandezensis* Galea, sp. nov., identified as *S. polyzonias* (Linnaeus, 1758) by Jäderholm (1910). (D) *Sertularella robusta* Coughtrey, 1876, identified as *S. tenella* (Alder, 1857) by Ritchie (1907). (E, F) *Sertularella subantarctica* Galea, sp. nov. Materials identified as *S. allmani* Hartlaub, 1901 by Jäderholm (1910, 1905) (E, F, respectively). (G, H) *Sertularella valdiviae* Stechov, 1923a, two slides prepared from type colony.

account represents the first description of the gonotheca of this species.

**Distribution:** Chile – Región de Magallanes y Antártica Chilena [off Isla Nueva (Vervoort, 1972, as *S. picta*)]. Argentina – Provincia de Santa Cruz [off Deseado (Vervoort, 1972, as *S. picta*)]; Provincia de Tierra del Fuego, Antártida e Islas del Atlántico Sur [off Isla de los Estados (Vervoort, 1972, as *S. picta*)]. Between Cabo Virgenes and the Falkland Is. (Allman, 1888).

***Sertularella juanfernandezensis* Galea, sp. nov.**

Figs 12C, 13E, F, H, I; Table 14

*Sertularella polyzonias*. – p.p. Jäderholm, 1910: 4. – p.p. Hartlaub, 1905: 655 [non *Sertularella polyzonias* (Linnaeus, 1758)].

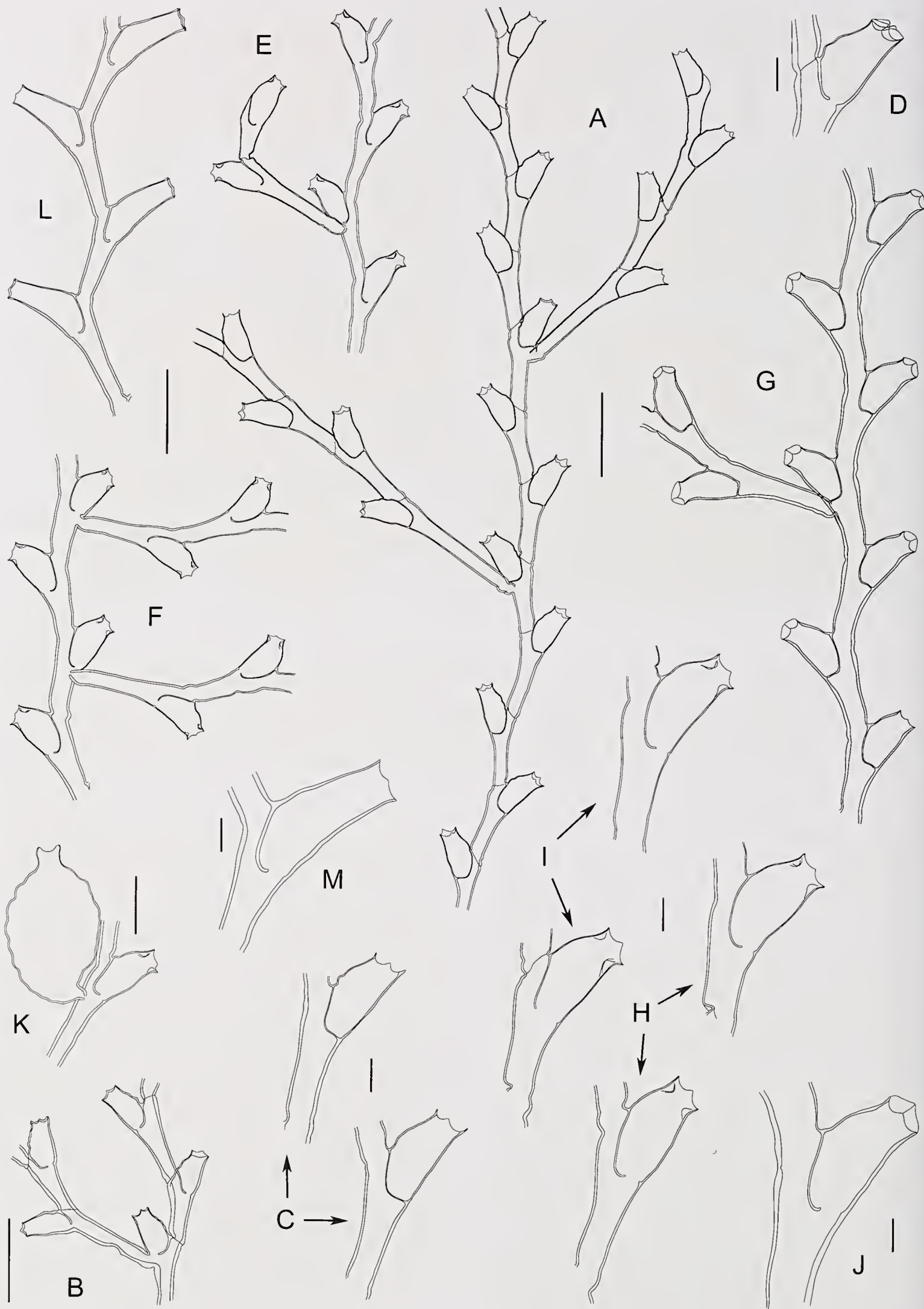
**Holotype material:** SMNH 123883; Chile, Juan Fernández archipelago, 35 m, Swedish Magellanic Expedition 1907-1909, coll. C. Skottsberg; 24.08.1908;

microslide (Fig. 12C) with three colony fragments 7-20 mm long, the largest bearing 4 gonothecae, the smallest unbranched, and the remaining two provided with two side branches each [material identified by Jäderholm (1910) as *S. polyzonias* (Linnaeus, 1758)].

**Paratype material:** ZMB Cni4421; Chile, Juan Fernández archipelago; coll. Plate, det. Hartlaub (1905, as *S. polyzonias*); a 3.8 cm high colony represented by a single, ramified, sterile stem.

**Comparison material:** HRG-0550; France, Brittany, depth unrecorded, coll. F. Ziemski; (day and month unavailable) 2011; numerous sterile, unbranched or sparingly-branched stems and fragments, up to 4.5 cm high, of *S. polyzonias*.

**Diagnosis:** Erect, coplanar colonies with monosiphonic, irregularly pinnate stems; internodes moderately-long, slightly geniculate; hydrothecae flask-shaped, decidedly facing outwards, adnate for half their length, free adaxial wall convex; gonothecae broadly ovoid,



transversely wrinkled, aperture mounted on constricted neck region, surrounded by 4 blunt spines.

**Etymology:** Named after its (presently known) area of occurrence.

**Description:** Colonies erect (though flaccid when out of liquid), up to 3.8 cm high, arising from creeping, branching stolon. Stems monosiphonic, unbranched; basal part of varied length (*ca.* 1.5 cm long in paratype) and ahydrothecate; above, divided into moderately-long, slightly geniculate internodes by means of oblique constrictions of the perisarc slanting in alternate directions; one hydrotheca confined to the distal end of each internode; side branches arising generally singly (occasionally in pairs) immediately below the base of a hydrotheca, either laterally or slightly shifted on to the front of stem, giving the colony a globally planar appearance; there are no distinct apophyses supporting the branches; 1-4 hydrothecae between successive side branches; branches not strictly alternate, several successive ones may be given off on same side of the stem; up to 2nd order branches observed; first internode comparatively longer than subsequent ones; remainder with structure similar to that of stem. Hydrothecae biseriata, alternate, flask-shaped, smooth-walled, adnate for half their length to the corresponding internode, with distinct outward bend; free adaxial wall convex for most of its length, slightly upturned distally; abaxial

wall concave for 3/4th its length, and distinctly convex below aperture; rim tilted away from stem/branches, and provided with 4 pointed, triangular cusps separated by moderately-deep embayments; a four-flapped operculum; three conspicuous internal, submarginal, lamellar projections of the perisarc, one abaxial and two latero-adaxial, the latter could be absent in distalmost, hence youngest, hydrothecae. Gonothecae arising laterally from the internodes, a short distance below the hydrothecal bases; broadly ovoid, transversely wrinkled (up to 6 distinct ridges in upper 2/3rd), tapering below into short, indistinct pedicel, distally bearing a constricted neck region on the top of which is found the aperture surrounded by 4 short, blunt spines; sex could not be ascertained, although a single, ovoid, central mass is carried on by the blastostyle.

**Dimensions:** See Table 14.

**Remarks:** This species has been incorrectly assigned to *Sertularella polyzonias* (Linnaeus, 1758) by both Hartlaub (1905) and Jäderholm (1910). Its morphological differences with the Linnean species are easily noted by comparing Fig. 13E, F and 13G, and Fig. 13H, I and 13J, respectively.

The hydrothecae of *S. juanfernandezensis* are very similar to those of a number of congeners, notably: 1) *S. arbuscula* (Lamouroux, 1816), but this species possesses very short internodes (Millard, 1957), and

Table 14. Measurements of *Sertularella juanfernandezensis* Galea, sp. nov., in  $\mu\text{m}$ .

	Present study, SMNH 123883	Present study, ZMB Cni4421
<b>Internode</b>		
- length (in general)	735-980	885-1165
- length of 1 <sup>st</sup> internode	1410-1570	1290-1765
- diameter at node	155-205	210-290
<b>Hydrotheca</b>		
- free adaxial length	375-450	360-420
- adnate adaxial length	355-400	400-450
- abaxial length	520-585	540-575
- maximum width	330-345	315-410
- diameter at aperture	225-255	220-260
<b>Gonotheca</b>		
- total length	1325-1350	-
- maximum width	860-885	-

Fig. 13. (A-D) *Sertularella implexa* (Allman, 1888). Colony fragments from holotype material (A) and Vervoort (1972, as *S. picta*) (B). Hydrothecae from the same sources (C and D, respectively). (E, F, H, I) *Sertularella juanfernandezensis* Galea, sp. nov. Portions of colonies from SMNH 123883 (E) and ZMB Cni4421 (F), and comparison with *S. polyzonias* (Linnaeus, 1758) HRG-0550 (G). Hydrothecae from the same sources (H, I and J, respectively). (L, M) *Sertularella leiocarpa* (Allman, 1888). Portion of colony (L) and hydrotheca (M) from HRG-1056. Scale bars: 200  $\mu\text{m}$  (C, D, H-J, M), 500  $\mu\text{m}$  (K), 1 mm (A, B, E-G, L).



its gonothecae are fusiform and, most often, smooth-walled (Millard 1975); 2) *S. crassiuscula* Bale, 1924, but this species has comparatively smaller hydrothecae, its internodes are very short, and its gonothecae are large and devoid of the distinctly constricted neck region met with in the present species (Bale, 1924; Ralph, 1961); 3) *S. falsa* Millard, 1957, but this species has relatively short internodes, there are 4 submarginal, intrathecal projections of the perisarc alternating with the hydrothecal cusps, and its gonothecae are spindle-shaped (Millard, 1957).

**Distribution:** Only known from Chile – Juan Fernandez archipelago (Hartlaub, 1905; Jäderholm, 1910).

### *Sertularella kerguelensis* Allman, 1876

*Sertularella kerguelensis* Allman, 1876: 113. – Studer, 1879: 120. – Kirchenpauer, 1884: 40.

**Description:** Stem monosiphonic, up to 2.5 cm high, profusely and irregularly branched. Internodes with shallow annulations basally, each bearing a hydrotheca distally; the latter somewhat tumid below, tapering distally, aperture slightly incurved adaxially. Gonothecae arising from below the hydrothecal bases, ovoid, transversely-ringed in upper half and becoming smooth towards the base; distally a short, tubular neck bearing apically an aperture surrounded by 4 perisarc projections.

**Remarks:** This species, succinctly described and not illustrated in the original account, is unrecognizable among its congeners recorded subsequently from Kerguelen, especially given that its type material could not be located in collections of NHML (A. Cabrinovic, pers. comm.). According to Allman (1876), it is

“nearly allied to *S. polyzonias*”, with which it has been synonymized later on (Allman, 1879). However, there are no relevant records of the Linnean species from the study area, as earlier assignments to it proved erroneous (see Appendix I).

Since the binomen *S. kerguelensis* has apparently not been used since 1899, it should be considered as a *nomen dubium*.

**Distribution:** French Southern and Antarctic Lands, Kerguelen Is. – Swains Bay (Allman, 1876).

### *Sertularella leiocarpa* (Allman, 1888)

Fig. 13L, M; Table 15

*Sertularia leiocarpa* Allman, 1888: 52, pl. 25 figs 1, 1a.

*Sertularella leiocarpa*. – Stechow, 1925: 477, fig. 35. – Galea, 2015: 9, fig. 3P.

**Material examined:** HRG-1056; Tristan da Cunha group of islands, E of Inaccessible I., -37.32000° 12.60000°, 160 m, coll. British Antarctic Survey, Stn. 80, lot DB12-0340; 24.05.2013; a *ca.* 5 cm high, sterile stem bearing a single side branch.

**Description:** Colonies up to *ca.* 7.5 cm high, arising from thin hydrorhizal fibers. Stems mono- or lightly polysiphonic basally, moderately stiff, giving rise to roughly alternate, coplanar side branches; stems and branches divided into moderately long, slender, geniculate internodes by means of indistinct oblique nodes; a hydrotheca confined to the distal end of each internode; side branches given off irregularly, directly (no apophyses present) and laterally from below a stem hydrotheca; up to 2nd order branches. Hydrothecae long, tubular, adnate for *ca.* 1/3rd their length to the corresponding internode, then curving gently outwards;

Table 15. Measurements of *Sertularella leiocarpa* (Allman, 1888), in  $\mu\text{m}$ .

	Stechow (1925)	Vervoort (1966), schizoholotype	Vervoort (1966), <i>Galathea</i> material	Gili <i>et al.</i> (1989)
<b>Internode</b>				
- length	-	1160-1880	1215-1350	800-1320
- diameter at node	300-470	240-260	150-300	150-180
<b>Hydrotheca</b>				
- free adaxial length	880-1040	800-860	675-900	480-600
- adnate adaxial length	560-620	400-560	410-450	-
- abaxial length	960-1200	1040-1120	745-850	660-720
- maximum width	480-500	480-500	310-500	-
- diameter at aperture	260-270	340-420	220-250	210-240
<b>Gonotheca</b>				
- total length	-	<i>ca.</i> 3260	-	1500-1650
- maximum width	-	<i>ca.</i> 1460	-	-

abaxial wall almost straight, free adaxial wall slightly convex proximally, then nearly straight for most of its length; aperture facing outwards, provided with 4 small, triangular cusps separated by very shallow embayments; usually without intrathecal, submarginal cusps, but occasionally 2-4 present, one below each embayment; a 4-flapped operculum. Gonothecae arising from the stem internodes at level of hydrothecal bases, on opposite side to hydrotheca; spindle-shaped, walls entirely smooth, apically 3-4 short spines.

**Dimensions:** See Table 15.

**Remarks:** The colony shape and the gonotheca are illustrated by both Allman (1888) and Millard (1975). Although generally absent, internal, submarginal hydrothecal cusps may occasionally occur (Vervoort, 1966; Gili *et al.*, 1989).

**Distribution:** Tristan da Cunha group of islands, Namibia, New Caledonia, New Zealand, as well as scattered records from the south and southeast Indian Ocean (Galea, 2015).

### *Sertularella mediterranea* Hartlaub, 1901

Fig. 14A-E; Table 16

*Sertularella mediterranea* Hartlaub, 1901: 86, pl. 5 figs 10-11, 15-16. – Genzano, 1990: 47, figs 13-15. – Blanco, 1994: 199. – Genzano & Zamponi, 2003: 308.

*Sertularella uruguayensis* Mañé Garzón & Milstein, 1973: 21, fig. 1 (**syn. nov.**). – Milstein, 1976: 85, figs 25, 28, 29, 36.

*Sertularella picta*. – Blanco, 1967: 112, pl. 3 figs 1-7 [non *Sertularella picta* (Meyen, 1834)].

**Material examined:** HRG-0001; France, La Ciotat, 43.174850° 5.611921°, 0.5 m, coll. H.R. Galea; 16.03.2003; male colony composed of numerous stems, up to 4 cm high.

**Description:** Stems erect, up to 1.5 cm high, monosiphonic, sparingly and irregularly branched. Internodes rather short, delimited by deep, oblique constrictions of the perisarc, basally with a more or less marked bulge; first internodes of side branches comparatively longer than subsequent ones, with 2-3 basal twists; distally a hydrotheca to each internode. Hydrothecae flask-shaped, adnate for less than half their length, swollen basally (notably on adaxial side), constricted below aperture; rim with 4 cusps, abaxial one conspicuously produced, adaxial one the shortest, and recurved outwards; rim not thickened; 3 internal, submarginal projections of perisarc (2 latero-adaxial, 1 abaxial). Gonothecae arising from below the hydrothecal bases, broadly ovoid, walls with 6-9 transverse ridges, aperture surrounded by 4 (rarely 5) pointed cusps.

**Dimensions:** See Table 16.

**Remarks:** The description given above is based on Argentinean material, and combines both Blanco's (1967, as *S. picta*) and Genzano's (1990) accounts. Blanco (1994) regarded her earlier record as conspecific with the present species, although El Beshbeeshy (2011) still believed that it belonged to Meyen's hydroid.

The occurrence of *S. mediterranea* Hartlaub, 1901 in Argentina is plausible, as additional remote records are, for instance, from South Africa (Millard, 1975).

There are no objective reasons to separate specifically *S. uruguayensis* Mañé Garzón & Milstein, 1973 from the

Table 16. Measurements of *Sertularella mediterranea* Hartlaub, 1901, in  $\mu\text{m}$ .

	Blanco (1967), as <i>S. picta</i>	Genzano (1990)	Mañé Garzón & Milstein (1973), as <i>S. uruguayensis</i>	Ramil <i>et al.</i> (1992)
<b>Internode</b>				
- length	330-680	505-632	450-640	504-561
- diameter at node	-	142-173	-	160-230
<b>Hydrotheca</b>				
- free adaxial side	280-310	316-348	280-400	375-432
- adnate adaxial side	230-270	221-237	170-270	317-360
- abaxial wall	480-530	474-584	450-650	590-662
- maximum width	220-280	189-253	270-300	-
- diameter at aperture	150-200	159-189	200-240	260-288
<b>Gonothecae</b>				
- total length	ca. 1250	790-835	?	1390-1780
- maximum width	ca. 480	-	?	680-870

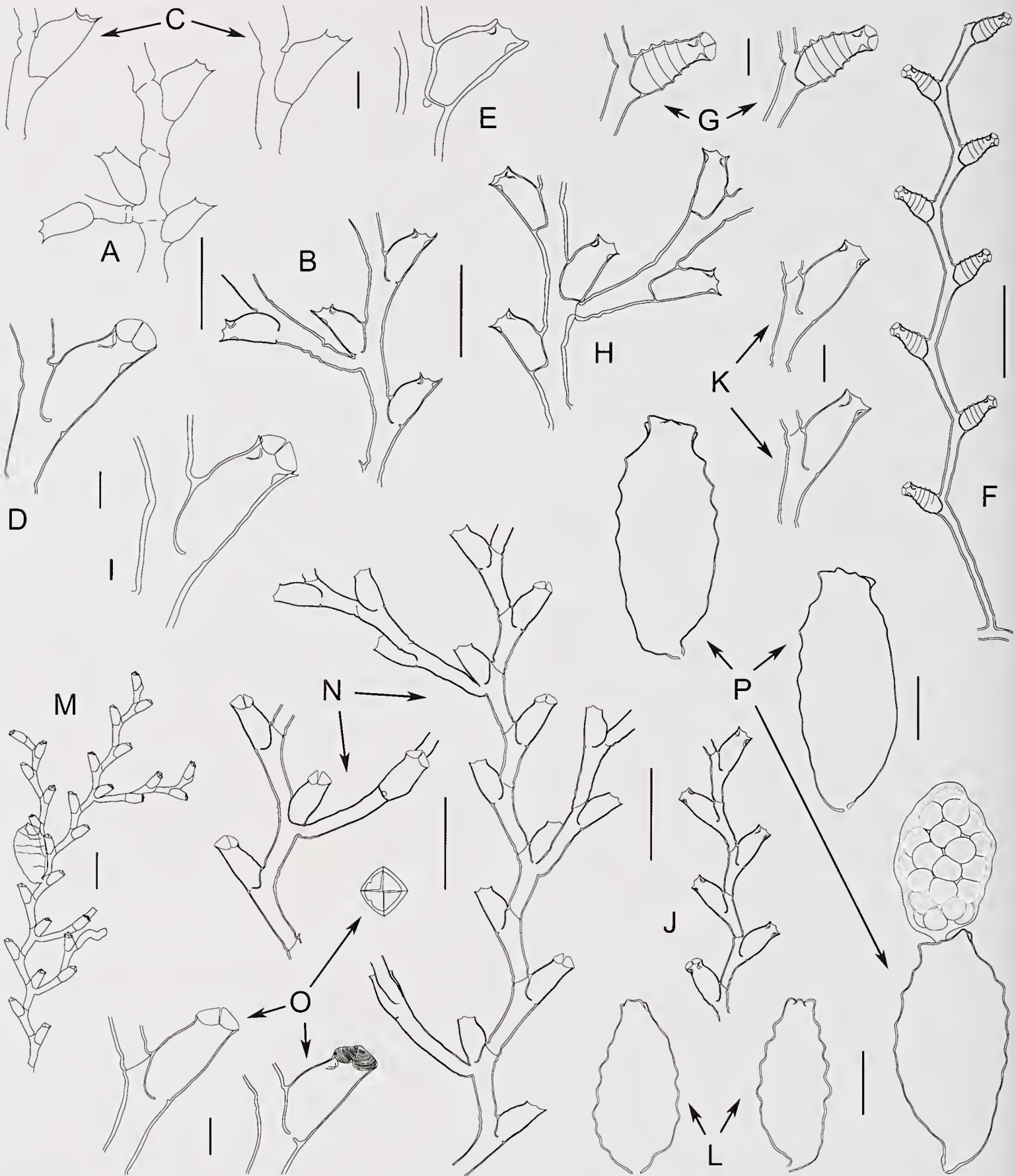


Fig. 14. (A-E) *Sertularella mediterranea* Hartlaub, 1901. Colony fragments after Genzano (1990) (A) and Mediterranean material HRG-0001 (B). Hydrothecae after Blanco [1967, as *S. picta* (Meyen, 1834)] (C), HRG-0001 (D), and Mañé Garzón & Milstein (1973, as *S. ruguayensis*) (E). (F, G) *Sertularella microtheca* Leloup, 1974. Portion of erect stem (F) and hydrothecae (G) from HRG-1095. (H, I) *Sertularella mixta* Galea & Schories, 2012a. Portion of colony from MHNG-INVE-79667 (H) and hydrotheca from HRG-0395 (I). (J-L) *Sertularella novarae* Marktanner-Turneretscher, 1890. Stem fragment (J), hydrothecae (K), and gonothecae (L) from sample ZMB Cni944. (M-P) *Sertularella oblonga* Galea, Häussermann & Försterra, sp. nov. Portions of colony (M, N), hydrothecae (O) and female gonothecae (P). Scale bars: 200  $\mu$ m (C-E, G, I, K, O), 500  $\mu$ m (L, P), 1 mm (A, B, F, H, J, M, N).

Argentinean hydroid. Both form colonies composed of short, erect, sparingly branched stems, their internodes are short, and each bears a flask-shaped hydrotheca, conspicuously swollen adaxially, and provided with a produced abaxial, marginal cusp, as well as with 3 internal, submarginal perisarc projections [Mañé Garzón & Milstein (1973); Genzano (1990)]. In addition, the measurements given by these authors for their respective materials are comparable (see Table 16 herein), and both originate from localities close to one another.

**Distribution:** Uruguay – Cabo Polonio (Mañé Garzón & Milstein, 1973, as *S. uruguayensis*). Argentina – Provincia de Buenos Aires [Mar del Plata (Blanco, 1967, as *S. picta*; Genzano 1990)]. Elsewhere – widely distributed in the Mediterranean and the eastern Atlantic, from Spitzbergen to South Africa (Ramil *et al.*, 1992).

### *Sertularella microtheca* Leloup, 1974

Fig. 14F, G; Table 17

*Sertularella microtheca* Leloup, 1974: 30, fig. 24.

*Sertularella robusta*. – *p.p.* Vervoort, 1972: 129, fig. 40B (non figs 40A, 41A = *S. robusta* Coughtrey, 1876). – *p.p.* El Beshbeeshy, 2011: 144, fig. 46E-H (non fig. 46A-D = *S. robusta*) [non *Sertularella robusta* Coughtrey, 1876].

**Material examined:** HRG-1095; Chile, Región de Aysén, southeastern point of Canal Ultima Esperanza, -45.97608° -74.01133°, 23 m, coll. HSFS, HF21, lot #216; 10.04.2014; small colony composed of several sterile stems, up to 1 cm high.

**Description:** Stolonal hydrothecae or short (up to 1 cm high), erect, unbranched or sparingly-branched stems,

arising from creeping, branching, filiform hydrorhiza. Stems and, when present, side branches divided into up to 10 exceedingly long, slender, geniculate internodes by means of indistinct, oblique constrictions of the perisarc; the latter relatively thick throughout the colony; side branches borne on short stem apophyses arising from below a hydrothecal base, apophyses displaced towards one side of the stem, not laterally and, consequently, not in the same plane; 1st internode of a side branch comparatively longer than subsequent ones; remainder of branch with same structure as the stem; no further branching observed. A hydrotheca confined to the distal end of each internode; fusiform, adnate for *ca.* 1/4th its length, transversely-ridged (generally 4, occasionally 5 ridges present), distally a short, smooth neck region; aperture with 4 pointed, triangular cusps separated by rather deep, semicircular embayments; 3 large, lamellar, submarginal, internal projections of perisarc (2 latero-adaxial, 1 abaxial); a 4-flapped operculum. Gonotheca stolonal, barrel-shaped, transversely ridged (with *ca.* 6 ridges), distally a neck region bearing apically an aperture surrounded by 4 spines.

**Dimensions:** See Table 17.

**Remarks:** The present material is composed of erect stems only, while Leloup (1974) reported the co-occurrence of stolonal hydrothecae within colonies otherwise comprising erect stems.

This species shows striking resemblances to *S. robusta* Coughtrey, 1876, a species with which it has been synonymized earlier (*e.g.* El Beshbeeshy, 2011; Galea, 2007). When colonies of both are examined side by side, obvious differences arise, such as: proportionally

Table 17. Measurements of *Sertularella microtheca* Leloup, 1974, in  $\mu\text{m}$ . \*The length of the hydrothecae given by Leloup (1974) is regarded as nearly the same as the length of their abaxial wall. •The size (810  $\mu\text{m}$ ) indicated by Vervoort (1972) for both the diameter of the basal part of the stems and the abaxial wall of the hydrotheca is obviously erroneous.

	Leloup (1974)	Present study	Vervoort (1972), as <i>S. robusta</i> (Vema 18-18)
<b>Internode</b>			
- length	-	675-920	<i>ca.</i> 1740
- diameter at node	-	85-115	(?)•
<b>Hydrotheca</b>			
- free adaxial length	-	350-385	<i>ca.</i> 270
- adnate adaxial length	-	150-180	<i>ca.</i> 215
- abaxial length	350-450*	415-425	(?)•
- maximum width	180-200	220-245	<i>ca.</i> 230
- diameter at aperture	100-140	145-155	<i>ca.</i> 110
<b>Gonotheca</b>			
- total length	< 280	-	-
- maximum width	< 220	-	-

longer and much slender internodes, as well as smaller and much slender hydrothecae in *S. microtheca*.

**Distribution:** Chile – Región de los Lagos [Canal Calbuco (Leloup, 1974)]; Región de Aysén [Canal Ultima Esperanza (present study)]. Argentina – Provincia de Santa Cruz [off Deseado (*p.p.* Vervoort, 1972, as *S. robusta*)].

***Sertularella mixta* Galea & Schories, 2012a**

Fig. 14H, I; Table 18

*Sertularella mixta* Galea & Schories, 2012a: 42, fig. 5A-G.

*Sertularella sanmatiasensis*. – Galea *et al.*, 2009: 12, fig. 3C-E [non *Sertularella sanmatiasensis* El Beshbeeshy, 2011].

*Sertularella ellisii* f. *lagenoides*. – Leloup, 1974: 28, fig. 22 [non *Sertularella ellisii* (Milne-Edwards, 1836); non *S. lagenoides* Stechow, 1919].

*Sertularella peregrina*. – Leloup, 1974: 31, fig. 25 [non *Sertularella peregrina* Bale, 1926].

**Material examined:** MHNG-INVE-79667; Chile, Región de Coquimbo, Punta Choros, Bajo Tiburon, -29.2551° -71.5265°, 17 m, coll. D. Schories, lot DS206; 01.11.2009; colony composed of numerous fertile and sterile stems (holotype). – HRG-0642; Chile, Región de los Ríos, north of Corral, Chaihuin, -39.95730° -73.60245°, 6-12 m, coll. D. Schories; 08.10.2012; four male stems 2.3-3.4 cm high. – HRG-0646; Chile, Región de los Ríos, north of Corral, Chaihuin, -39.95730° -73.60245°, 6-12 m, coll. D. Schories; 16.11.2011; female colony composed of numerous stems up to 2.5 cm high. – HRG-0332; Chile, Región de los Lagos, southern Chiloé, Punta Inio, -43.39300° -74.11769°, 15.6 m, coll. HSFS, HF6, lot A128; 22.02.2008; two female stems, 1.5 and 2.2 cm high.

**Description:** Colonies arising from creeping, branching, anastomosing hydrorhiza. Stems short, up to 2.8 cm high, monosiphonic, unbranched or sparingly-branched in one plane; basal part of varied length, though generally short, with a few twists above origin from stolon; remainder of stem composed of numerous short, almost collinear, hydrothecate internodes; the latter delimited by oblique nodes sloping in alternate directions. Side branches, when present, borne on short stem apophyses arising from below the bases of stem hydrothecae; occasionally, branches given off from within the hydrothecae; the latter tubular, slightly swollen basally, especially on adaxial side; adnate for about half their length to the corresponding internode; abaxial wall straight to slightly concave basally; aperture mounted on short neck region, expanding at rim; abcauline cusp slightly longer than the three others, though all relatively short, and separated by shallow, rounded embayments; three internal, submarginal perisarc projections (2 latero-adaxial, 1 abaxial). Gonothecae arising from below the hydrothecal bases;

ovoid, with several transverse ridges in upper half, much attenuated to absent in lower half; aperture mounted on short, quadrangular neck region, carrying four blunt projections of perisarc.

**Dimensions:** See Table 18.

**Remarks:** The gonothecae of this species are illustrated by both Galea *et al.* (2009, fig. 3E, as *S. sanmatiasensis*) and Galea & Schories (2012a, fig. 5F).

**Distribution:** Chile – Región de Coquimbo [Península de Coquimbo (Leloup, 1974, as *S. ellisii* f. *lagenoides*); vicinity of Punta de Choros (Galea & Schories, 2012a)]; Región de Bío-Bío [Bahía de Lota, Golfo de Arauco (Leloup, 1974, as *S. ellisii* f. *lagenoides*)]; Región de los Ríos [vicinity of Corral (present study)]; Región de los Lagos [south of Isla Grande de Chiloé (Galea *et al.*, 2009, as *S. sanmatiasensis*)]; Región de Aysén [Guaitecas Archipelago (Leloup, 1974, as *S. peregrina*)].

***Sertularella novarae* Marktanner-Turneretscher,**

1890

Fig. 14J-L; Table 19

*Sertularella novarae* Marktanner-Turneretscher, 1890: 226, pl. 4 figs 3, 3A, 3B. – Bedot, 1916: 208.

*Sertularella polyzonias*. – *p.p.* Vanhöffen, 1910: 322, fig. 39 [non *S. polyzonias* (Linnaeus, 1758)].

**Material examined:** ZMB Cni944; French Southern and Antarctic Lands, St. Paul I., coll. Deutsche Südpolar (*Gauss*) Expedition 1901-1903, stranded on beach; 26.03.1903; six stems and fragments, 0.5-1.4 cm high, of which four bear one gonotheca each [material studied by Vanhöffen (1910), as *S. polyzonias*].

**Description:** Upright, up to 2.5 cm high, monosiphonic, sparingly-branched stems arising from filamentous hydrorhiza; divided by faintly-indicated, oblique nodes into moderately-long, geniculate internodes with 1-2 basal twists and a hydrotheca distally; terminal stolonization occurs. Side branches arising irregularly from below the bases of stem hydrothecae, as well as from within their lumina; up to 2nd order branching, giving the colonies a somewhat bushy appearance. Hydrothecae biseriate, alternate, long, about 1/3rd adnate, tumid proximally, tapering distally, with 4 triangular marginal cusps separated by shallow embayments; 5 internal, submarginal cusps (2 latero-adaxial, 2 latero-abaxial, and 1 abaxial). Gonothecae arising from below the hydrothecal bases; elongated-ovoid, transversely wrinkled, tapering abruptly below into indistinct pedicel, aperture surrounded by 3-4 blunt, apical projections.

**Dimensions:** See Table 19.

**Remarks:** As noted by Vanhöffen (1910), there is no doubt that his material from St. Paul belongs to the present species. Indeed, both the measurements of the



Table 18. Measurements of *Sertularella mixta* Galea & Schories, 2012a, in  $\mu\text{m}$ .

	Galea <i>et al.</i> (2009), as <i>S. sanmatiasensis</i>	Galea & Schories (2012a)
<b>Internode</b>		
- length	540-790	745-1170
- diameter at node	210-280	240-320
<b>Hydrotheca</b>		
- free adaxial length	380-445	400-450
- adnate adaxial length	305-415	400-455
- abaxial length	630-690	670-725
- maximum width	315-380	330-355
- diameter at aperture	250-290	305-330
<b>Gonotheca</b>		
- total length	1770-1820 (♀)	1730-2105
- maximum width	840-930 (♀)	775-865

Table 19. Measurements of *Sertularella novarae* Marktanner-Turneretscher, 1890, in  $\mu\text{m}$ .

	Marktanner-Turneretscher (1890)	Vanhöffen (1910), as <i>S. polyzonias</i> (Linnaeus, 1758)	Present study, ZMB Cni944
<b>Internode</b>			
- length	920-1200	-	455-735
- diameter at node	-	-	110-140
<b>Hydrotheca</b>			
- total length	440-500	480-520	480-520
- free adaxial length	-	-	330-350
- adnate adaxial length	-	-	210-235
- abaxial length	-	-	455-485
- maximum width	210-260	240-260	230-255
- width at aperture	ca. 150	-	185-205
<b>Gonotheca</b>			
- total length	1500-1700	1500-1700	1350-1715
- maximum width	600-900	780-880	590-770

hydrothecae and the illustration provided by him are in agreement with the original account on this species. However, his specimens from Kerguelen, also assigned to it, were reexamined and proved to belong to both *S. contorta* Kirchenpauer, 1884 and *S. gaudichaudi* (Lamouroux, 1824) (see under these species).

Curiously, Vanhöffen overlooked the rather obvious specific differences between a number of closely-related subantarctic species [*viz.* *S. allmani* Hartlaub, 1901, *S. antarctica* Hartlaub, 1901, *S. contorta* Kirchenpauer, 1884, *S. novarae*, *S. paessleri* Hartlaub, 1901, *S. picta* (Meyen, 1834), and *S. protecta* Hartlaub, 1901], and

assigned them all to the synonymy of *S. polyzonias* (Linnaeus, 1758), a species not known to occur in the study area (see Appendix I).

As underlined by him, the present species is a true *Sertularella*, in possessing 4 hydrothecal cusps, not 3, as erroneously stated by Marktanner-Turneretscher (1890). A typical colony of this species is accurately illustrated by Vanhöffen (1910, p. 325, fig. 39).

**Distribution:** French Southern and Subantarctic Lands – St. Paul (Marktanner-Turneretscher, 1890; Vanhöffen, 1910, as *S. polyzonias*).

***Sertularella oblonga* Galea, Häussermann & Försterra, sp. nov.**

Fig. 14M-P

**Holotype material:** MHNG-INVE-97916; Chile, Región de Magallanes y de la Antártica Chilena, Isla Desolación, Cabo Pilar, -52.71578° -74.68245°, 10 m, coll. HSFS, HF26, lot #221; 21.09.2015; female colony composed of multiple, highly ramified stems, up to 2.8 cm high.

**Diagnosis:** Colonies with indistinct stems, divided subdichotomously several times. Internodes moderately-long, slender, geniculate. Hydrothecae adnate for 2/5th, almost tubular, tapering towards aperture, indistinctly swollen adaxially, abaxial cusp produced, two latero-adaxial, internal, submarginal cusps. Gonotheca elongated-ovoid, transversely wrinkled, aperture distal, surrounded by 4 pointed cusps.

**Etymology:** From the Latin *oblongus*, -a, -um, meaning elongated, making reference to the distinctive shape of its hydrothecae.

**Description:** Colony bushy, composed of a bunch of stems, up to 2.8 cm high, arising from creeping stolon. Basal part of stems of varied length, provided with a number of twists above origin from stolon; remainder divided into regular internodes by means of oblique nodes sloping in alternate directions. Internodes relatively short, decidedly geniculate, with smooth, rather thin perisarc, each bearing distally a hydrotheca. Branching subdichotomous, starting among the proximal most internodes, thus making the main stems indistinct; side branches originate from below the bases of stem hydrothecae, either laterally or decidedly shifted to one side of the stem; 1-6 hydrothecae between successive side branches; occasionally, aberrant side branches are given off from within some basal stem hydrothecae; up to 5th or 6th order branching observed; tips of branchlets from various planes often form tendrils, creating anastomoses with neighboring branches; structure of branches identical to that of stem, except for the first internode that may be longer than the subsequent ones. Hydrothecae biseriata, alternately directed left and right, coplanar or nearly so; adnate for about 2/5th their length to the corresponding internode; flask shaped, slightly swollen basally, more conspicuously on adaxial side; free adcauline wall slightly sigmoid, abcauline wall nearly straight; hydrothecal margin with four unequally developed cusps: abaxial one the longest, adaxial one the shortest and conspicuously flaring, and the two laterals of intermediate length; rim not thickened; two latero-adaxial, internal, submarginal cusps; operculum composed of four triangular flaps with concentric striae. Gonothecae (only female known) arising laterally from below the hydrothecal bases; broadly ovoid, surface provided with 5-7 more or less developed wrinkles;

aperture mounted on short distal collar, and surrounded by six rather short spines; embryo development in acrocysts.

**Dimensions:** Ordinary internodes 515-930 µm long, first internodes of side branches 715-1200 µm long; all 170-210 µm wide at nodes. Hydrothecal free adaxial length 320-345 µm, adnate adaxial length 220-230 µm, abaxial length 545-595 µm, maximum width 275-295 µm, diameter at aperture 230-270 µm. Female gonotheca 1690-1925 µm long and 790-910 µm wide.

**Remarks:** The mode of branching, giving rise to three-dimensional, bushy colonies is distinctive. Its hydrothecae recall those of *S. ellisii* (Deshayes & Milne-Edwards, 1836) and *S. mediterranea* Hartlaub, 1901, but the branching pattern is different in these species with otherwise much larger hydrothecae (Ramil *et al.*, 1992).

**Distribution:** Only known from Chile – Región de Magallanes y de Antártica Chilena [Isla Desolación (present study)].

***Sertularella patagonica* (d'Orbigny, 1842)**

Fig. 15A-E; Table 20

*Sertularia patagonica* d'Orbigny, 1842: pl. 11 figs 3-5; 1847: 25. – Hartlaub, 1905: 643, figs H<sup>1</sup>, J<sup>4</sup>. – Nutting, 1904: 81, pl. 16 fig. 3.

*Sertularella striata* Stechow, 1923b: 10 (**syn. nov.**). – Stechow, 1925: 470, fig. 30. – Millard, 1964: 47, fig. 15. – (?) Blanco, 1974: 44, figs 2-8. – Millard, 1975: 304, fig. 97E-F. – Genzano, 1990: 45, figs 11-12. – Blanco, 1994: 201. – Genzano & Zamponi, 2003: 308.

non *Sertularella striata*. – Gili *et al.*, 1989: 104, fig. 29A.

*Sertularella mogotesensis* El Beshbeeshy, 2011: 20 [new name for both Blanco's (1967, p. 115) record of *Sertularella atlantica* Stechow, 1920 and her 1974 record (p. 44) of *Sertularella striata* Stechow, 1923b; *nomen nudum*].

*Sertularella atlantica*. – Blanco, 1967: 115, pl. 3 figs 8-12, pl. 4 figs 1-4 [non *Sertularella atlantica* Stechow, 1920: 21, fig. 2A].

**Description:** Colonies composed of either stolonial hydrothecae or short (up to 11 mm high), erect shoots arising from sinuous, smooth-walled stolon. Cauli thick, monosiphonic, usually unbranched, occasionally sparingly branched (1-3 short, roughly alternate side branches), smooth or with a reduced number (up to 3-4) of basal wrinkles; divided into internodes of varied length, though generally short, by means of rather indistinct, oblique nodes slanting in alternate directions. Proximal end of internodes provided with a couple of spiral twists, distally a hydrotheca. Side branches, when present, arising laterally from below the base of a stem hydrotheca. The latter close to one another, fusiform, free from the corresponding internodes for more than half their adaxial length; walls with 6-8 transverse ridges encircling their whole surface; aperture provided

with 4 short, triangular cusps separated by shallow embayments; no submarginal, intrathecal cusps; a 4-flapped operculum. Perisarc thick throughout the colonies. Gonothecae arising from below the hydrothecal bases, broadly ovoid, walls provided with ca. 10 transverse ridges on nearly the whole surface, apically 3-4 minute spines surrounding the aperture, female with acrocyts.

**Dimensions:** See Table 20.

**Remarks:** One of the original illustrations by d'Orbigny (1842, pl. 11 fig. 5) can be misleading when attempting to compare this species with contemporary records from the study area, as the hydrothecae are figured with a decidedly scaly appearance. However, a similar illustration was provided by Hincks (1868) for *S. rugosa* (Linnaeus, 1758), while recent and more accurate drawings (e.g. Cornelius, 1995; Schuchert, 2001) show a quite common condition of the hydrothecae, typical of a species with transversely ringed walls.

Type material of *S. patagonica* is likely lost, as no mention of it was made by Van Praët (1979) in his catalogue of the type specimens housed in the *Muséum national d'Histoire naturelle* of Paris, France.

The typically short internodes, twisted basally, and the transversely annulated hydrothecae emphasized by d'Orbigny (1847) are characters also noted in Blanco's (1967, as *S. atlantica* Stechow, 1920) account, and it is therefore assumed that both hydroids are conspecific. The latter nominal species, however, originates from the northern hemisphere, and is probably a synonym of *S. tenella* (Alder, 1857) (Picard, 1956; Cornelius, 1995).

In a subsequent paper, Blanco (1974) considered her earlier record as conspecific with her newly-obtained material assignable to *S. striata* Stechow, 1923b. Finally, Blanco (1994) recognized *S. striata* as a synonym of *S. patagonica* but, curiously, kept the former as the valid binomen.

According to the accounts of both Stechow (1925) and Millard (1964), *S. striata* exhibits the same morphological characters as *S. patagonica*, and their respective measurements are highly concordant (see Table 20 herein). For this reason, both nominal species are considered here as coterminous, with d'Orbigny's hydroid name having priority.

The Namibian and South African records by Gili *et al.* (1989) most probably do not belong here, owing to the large size of the hydrothecae in their material.

The morphological similarity between *S. patagonica* and *S. rugosa* Linnaeus, 1758 invoked by both Kirchenpauer (1884) and Hartlaub (1901) is only superficial, and resides in particular in the ringed condition of the hydrothecal wall. However, the hydrothecal aperture is conspicuously tilted downwards in the latter species (Cornelius, 1995; Schuchert, 2001), thus differing from the illustrations provided by both d'Orbigny (1842) and Blanco (1967). In addition, both species are certainly distinct on the account of their very remote areas of occurrence.

**Distribution:** Argentina – Provincia de Buenos Aires [off Mar del Plata (Blanco, 1967, as *S. atlantica*; Genzano, 1990, as *S. striata*); Provincia de Río Negro [Ensenada de Ros (d'Orbigny, 1847); Barranca final (Blanco, 1974; 1994, both as *S. striata*)]. Elsewhere – South Africa (Stechow, 1923b; 1925; Millard, 1964; 1975).

Table 20. Measurements of *Sertularella patagonica* (d'Orbigny, 1842), in  $\mu\text{m}$ .

	Millard (1964), as <i>S. striata</i> (Stechow's type)	Millard (1964), as <i>S. striata</i> (own material)	Blanco (1967), as <i>S. atlantica</i>	(?) Blanco (1974), as <i>S. striata</i>	Genzano (1990), as <i>S. striata</i>
<b>Internode</b>					
- length	450-770	300-760	240-900	460-720	320-400
- diameter at node	100-150	100-160	-	100-170	86-94
<b>Hydrotheca</b>					
- free adaxial length	250-340	180-310	280-330	280-360	190-220
- adnate adaxial length	210-260	200-260	200-280	230-280	110-140
- abaxial length	410-470	360-480	400-500	500-540	320-380
- maximum width	230-300	230-300	200-290	270-330	205-237
- diameter at aperture	170-230	150-210	180-220	230-250	140-170
<b>Gonotheca</b>					
- total length	-	1350-1790	-	1710-1840	1300-1600
- maximum width	-	860-950	-	720-830	600-720



Fig. 15. (A-E) *Sertularella patagonica* (d'Orbigny, 1842). Portion of fertile colony after Genzano (1990, as *S. striata* Stechow, 1923b) (A), Blanco (1967, as *S. atlantica* Stechow, 1920) (B), Blanco (1974, as *S. striata*) (C, D), and Millard (1964, as *S. striata*) (E). (F, G) *Sertularella pauciramosa* Galea & Schories, 2014. Portion of colony from MHNG-INVE-86235 (F) and hydrotheca from HRG-0717 (G). (H) *Sertularella quadrispinosa* Watson, 2003, redrawn after original. (I-M) *Sertularella recta* Galea & Schories, sp. nov. Portions of colonies from MHNG-INVE-79627 (I) and ZMH C11895 (J). Hydrothecae from the same sources (K and L, respectively). Portion of fertile colony with gonotheca from MHNG-INVE-79627 (M). N-R *Sertularella robusta* Coughtrey, 1876. Colony fragments from HRG-0356 (N), Blanco [1963, as *S. tenella* (Alder, 1857)] (O) and NMSZ 1959.33.499 (P). Hydrothecae from former and latter sources (Q and R, respectively). Scale bars: 200  $\mu$ m (G, H, K, L, Q, R), 500  $\mu$ m (M), 1 mm (A-F, I, J, N-P).

***Sertularella pauciramosa* Galea & Schories, 2014**

Fig. 15F, G

*Sertularella pauciramosa* Galea & Schories, 2014 in Galea *et al.*, 2014: 35, pl. 3B, figs 6F & H, 7D.

**Material examined:** MHNG-INVE-86235; Chile, Región de Antofagasta, Taltal, -25.38333° -70.46667°, 22 m, coll. D. Schories, lot #17; 23.04.2012; a 6 cm high, male colony (holotype). – MHNG-INVE-86234; Chile, Región de Antofagasta, Taltal, Punta Morada, -25.36667° -70.45000°, 15 m, coll. D. Schories, lot #13; 20.04.2015; a 4 cm high, female colony (paratype).

**Description:** Colonies arising from creeping, branching, anastomosing stolon. Stems erect, up to 6 cm high, monosiphonic, slightly geniculate to almost straight; a varied number of annuli immediately above origin from stolon, followed by short, smooth, ahydrothecate part; remainder of caulus divided into short internodes by slightly marked to indistinct, oblique constrictions of the perisarc, slanting in alternate directions. Side branches, when present, arising irregularly from below the bases of stem hydrothecae, generally laterally (giving the colony a coplanar appearance), or occasionally slightly in front or the rear side of the stem; base of branch delimited from stem by a rather distinct node (no apophysis present); 1st internode generally longer than subsequent ones. A hydrotheca confined to the distal end of each internode; biseriate, alternate, flask-shaped, slightly curving outwards; adnate for 2/5th their length; free adaxial wall smooth to wavy (in which case provided with 2-3 weak undulations); abaxial wall varied in shape, from slightly concave to straight, to rarely convex; aperture perpendicular to long axis of the theca, constricted below rim; 4 pointed, triangular cusps separated by shallow embayments; operculum 4-flapped. Gonothecae given off from below the bases of stem hydrothecae; ovoid, walls undulated to occasionally rather smooth; male and female similar in shape, though the former longer and slender; aperture mounted on short neck region provided with 3-4 distal projections of perisarc; female with *ca.* 20 oocytes.

**Dimensions:** Internodes 815-1140 µm long and 195-230 µm wide at nodes. Hydrothecal free adaxial length 390-425 µm, adnate adaxial length 315-380 µm, abaxial length 635-690 µm, maximum width 335-365 µm, diameter at aperture 220-275 µm. Length of the female gonotheca 1490-1710 µm, and of the male 1710-1965 µm; maximum width of the female gonotheca 660-805 µm, and of the male 660-730 µm.

**Remarks:** The typical shape of a colony of this species is illustrated in Galea *et al.* (2014, pl. 3B).

**Distribution:** Chile – Región de Antofagasta [around Taltal (Galea *et al.*, 2014)].

***Sertularella quadrispinosa* (Watson, 2003)**

Fig. 15H

*Calamphora quadrispinosa* Watson, 2003: 168, fig. 18.

**Description:** Colonies comprising both stolonal hydrothecae and short, unbranched or sparingly-branched, erect stems arising from creeping, branching, tubular hydrorhiza. Stolonal hydrothecae pedicellate, barrel-shaped, slightly asymmetrical in lateral view, narrowing a little below aperture, walls smooth to weakly undulated, especially on lower third; base pierced by central, circular hydropore with short, upturned collar; hydrothecal margin quadrate, distinctly everted, provided with 4 broad, sharply-pointed cusps separated by low, semicircular embayments; a 4-flapped operculum; hydranths with *ca.* 16 filiform tentacles. Gonothecae stolonal, arising in the vicinity of a hydrotheca; pedicellate, barrel-shaped, walls provided with 6-9 transverse flanges, deepest in distal third, shallower proximally; aperture apical, surrounded by 4 prominent, equidistant, more or less inwardly-curved spines.

**Dimensions:** Length of the hydrothecal pedicel 64-224 µm. Total length of hydrotheca 1100-1280 µm, maximum width 506-561 µm, diameter at aperture 440-480 µm. Length of the gonothecal pedicel 120-176 µm. Maximum width of gonotheca 520-640 µm.

**Remarks:** The present species is included in the genus *Sertularella* because its colonies, besides the commonest stolonal hydrothecae, comprise short, unbranched or sparingly-branched, erect stems. Indeed, Choong *et al.* (2012) stated that “colony form may be an insufficient criterion for assigning species of pedicellate *Sertularella* with individual hydrothecae rising from their hydrorhizae to a separate genus *Calamphora*”. The gonotheca of *S. quadrispinosa* is illustrated by Watson (2003).

**Distribution:** Only known from Macquarie I., Australia (Watson, 2003).

***Sertularella recta* Galea & Schories, sp. nov.**

Fig. 15I-M; Table 21

*Sertularella ? implexa*. – Galea & Schories, 2012a: 40, pl. 3 fig. 4F-J [non *Sertularella implexa* (Allman, 1888)].

*Sertularella polyzonias*. – Allman, 1888: 55, pl. 26, figs 3, 3A. – El Beshbeeshy, 2011: 141, fig. 45 [non *Sertularella polyzonias* (Linnaeus, 1758)].

**Holotype material:** MHNG-INVE-79627; Chile, Región de Magallanes y de la Antártica Chilena, Punta Arenas, Faro San Isidro, -53.78174° -70.97391°, 40 m, coll. D. Schories, lot #11; 05.01.2011; colony composed of several fertile stems, up to 5.5 cm high.

**Additional material:** ZMH C11895; Argentine Shelf, no additional data; several branched and unbranched

colony fragments, up to 1.5 cm high, one of which bears 3 female gonothecae. – ZMH C11888; FRV *Walther Herwig*, Stn. 327, -51.18333°, -56.95000°, 225 m; 29 Jun. 1966; two small, sterile colony fragments likely not belonging to the present species, although considered as conspecific by El Beshbeeshy (2011).

**Diagnosis:** Irregularly-pinnate colonies, with monosiphonic stems branched several times; internodes moderately long, slightly geniculate; hydrothecae flask-shaped, adnate for 1/3rd their length, swollen adaxially, abaxial cusps slightly produced, rim not thickened, internal cusps absent; gonothecae broadly ovoid, transversely wrinkled, aperture surrounded by 3-4 spines.

**Etymology:** From the Latin *rectus*, -a, -um (*rego*), meaning straight, with reference to the macroscopic appearance of both stems and branches.

**Description:** Hydrorhiza missing, but stems above origin from stolon comprising a monosiphonic, ahydrothecate basal part of varied length, with several proximal wrinkles; remainder of stems divided into moderately-long, slightly geniculate internodes by means of oblique constrictions of the perisarc slanting in alternate directions; nodes brownish in older parts of the colony, becoming transparent in younger ones. Branching pattern irregular, with side branches arising every 1-8 stem hydrothecae, immediately below their bases, through short, lateral apophyses; branching repeated several times, introducing a slight torsion in lower-order branches so as to accommodate the newly-formed ones, giving the colony a somewhat three-dimensional appearance, though it is rather compressed antero-posteriorly. Stems and branches

of similar structure, except for the first internodes of the latter, which are comparatively longer than the subsequent ones, and provided with a couple of basal wrinkles. Hydrothecae placed distally on internodes, biserial, alternate, adnate for about 1/3rd their adaxial length; free adaxial wall conspicuously swollen basally, decidedly convex, becoming concave towards aperture; abaxial wall straight or nearly so basally, becoming convex distally, where it forms a neck region, widening towards aperture; the latter tilted outwards and upwards, provided with 4 pointed, triangular cusps separated by deep, rounded embayments; no submarginal, intrathecal cusps. Gonothecae borne on stems and side branches, arising from below bases of hydrothecae; broadly ovoid, walls transversely wrinkled, wrinkles more obvious distally, becoming obsolete proximally; aperture surrounded by 3-4 pointed perisarc projections.

**Dimensions:** See Table 21.

**Remarks:** The material from the Falkland Is. assigned by Allman (1888) to *S. polyzonias* (Linnaeus, 1758) shows striking resemblances to the present species, and is thought to be conspecific (N.B.: Allman's specimen could not be examined, as it is apparently no longer extant in the collection of NHML; A. Cabrinovic, pers. comm.).

In addition, the reexamination of El Beshbeeshy's (2011) sample ZMH C11895, assigned to the Linnean taxon, revealed that it belongs to the new species described herein. Among the material described by El Beshbeeshy, some colonies are reportedly said to reach as much as 19 cm high, their stems remaining always monosiphonic.

The typical shape of the colonies is illustrated in Galea

Table 21. Measurements of *Sertularella recta* Galea & Schories, sp. nov., in  $\mu\text{m}$ .

	Galea & Schories (2012a), as <i>S. implexa</i> (S03)	Galea & Schories (2012a), as <i>S. implexa</i> (S11)	El Beshbeeshy (2011), as <i>S. polyzonias</i>
<b>Internode</b>			
- length (in general)	710-920	770-1245	603-1044
- length of 1st internode	565-1160	950-1410	-
- diameter at node	170-225	180-305	162-255
<b>Hydrotheca</b>			
- free adaxial length	420-510	430-460	394-452
- adnate adaxial length	240-295	240-300	301-330
- abaxial length	595-690	585-660	626-672
- maximum width	295-345	320-345	280-320
- diameter at aperture	255-280	265-275	228-255
<b>Gonotheca</b>			
- total length	2170-2690	-	-
- maximum width	755-920	-	-

& Schories (2012a, pl. 3F, as *S. ? implexa*), and a gonotheca in fig. 4J of the same paper.

**Distribution:** Chile – Región de Magallanes y de la Antártica Chilena [south of Peninsula Brunswick (Galea & Schories, 2012a, as *S. ? implexa*)]. Argentina – scattered records from the Patagonian Shelf, between 43°-53°S (El Beshbeeshy, 2011, as *S. polyzonias*). Falkland Is. (Allman, 1888; El Beshbeeshy, 2011; both as *S. polyzonias*).

### *Sertularella robusta* Coughtrey, 1876

Figs 12D, 15N-R; Table 22

*Sertularella robusta* Coughtrey, 1876: 27, pl. 3 fig. 6. – Leloup, 1960: 234, fig. 7. – Blanco, 1968: 215, pl. 4 figs 4-7. – *p.p.* Vervoort, 1972: 129, figs 40A, 41A. – Leloup, 1974: 33, fig. 27. – Blanco, 1976: 42, pl. 4 figs 1-3; 1994: 200. – Galea, 2007: 66, fig. 15E-I. – Galea *et al.*, 2009: 2, 4. – *p.p.* El Beshbeeshy, 2011: 144, fig. 46A-D. non *Sertularella robusta*. – *p.p.* Vervoort, 1972: 129, fig. 40B (= *Sertularella microtheca* Leloup, 1974). – *p.p.* El Beshbeeshy, 2011: 144, fig. 46E-H (= *S. microtheca*). – Soto Àngel & Peña Cantero, 2015: 996, fig. 7G [= (?) *Sertularella tenella* (Alder, 1856)].  
*Sertularella tenella*. – Jäderholm, 1905: 31, pl. 12 fig. 8. – Ritchie, 1907: 78. – *p.p.* Rees & Thursfield, 1965: 138. – Blanco, 1963: 173, figs 7-8 [non *Sertularella tenella* (Alder, 1856)].  
*Sertularella stepanyantae* El Beshbeeshy, 2011: 20 [new name for Vervoort's (1972, p. 129) record of *S. robusta* Coughtrey, 1876; *nomen nudum*].

**Material examined:** HRG-0626; Chile, Región de los Lagos, southern Chiloé, west of Punta Inio, -43.39300° -74.11769°, 26 m, coll. HSFS, HF6, lot A565; 22.02.2008; male colony composed of both stolonial and erect stems, up to 5 mm high, epizoic on *Symplectoscyphus milneanus* (d'Orbigny, 1842). – HRG-0356; Chile, Región de Magallanes y de Antártica Chilena, Punta Arenas, Faro San Isidro, -53.78174° -70.97391°, 10 m, coll. D. Schories, lot PTA002; 25.02.2010; colony composed of numerous sterile stems, up to 15 mm high. – HRG-0797; Chile, Región de los Ríos, north of Corral, Chaihuin, -39.95730° -73.60245°, 6-12 m, coll. D. Schories; 06.03.2012; sterile stolonial colony epizoic on *Halecium* sp. – HRG-0788; Chile, Región de Aysén, west of Canal Messier, -47.86020° -74.76023°, 5.3 m, coll. HSFS, HF13, lot C176; 16.03.2012; small colony composed of both stolonial hydrothecae and up to 4 mm high erect stems, bearing single male gonotheca. – HRG-1099; Chile, Región de los Lagos, Roca Gloria, -45.662433° -73.849266°, 20 m, coll. HSFS, HF21, lot #99; 05.04.2014; rich, fully fertile (male) colony composed mainly of stolonial hydrothecae and, occasionally, of short, erect stems (2-4 hydrothecate internodes), epizoic on *Symplectoscyphus filiformis* (Allman, 1888). – HRG-1173; Chile, Región de los Lagos, southern Chiloé, Isla

Yencouma, -43.4193° -74.0818°, 10 m, coll. HSFS, HF22, lot #65; 18.01.2015; a male colony composed of mostly stolonial hydrothecae, and a few, up to 3 mm high, erect stems. – NMSZ 1959.33.499; Burdwood Bank, -54.41667° -57.53333°, ca. 102 m, coll. Scottish National Antarctic (*Scotia*) Expedition 1902-1904; 01.12.1903; microslide (Fig. 12D) comprising 4 sterile stem fragments, 6-8 mm high, one of them branched once [material studied by Ritchie (1907, as *S. tenella*), and listed by Rees & Thursfield (1965, p. 138)].

**Description:** Stolonial hydrothecae or short, erect, unbranched or sparingly-branched stems arising from creeping, branching, filiform hydrorhiza. A varied number of annuli at the stem bases, immediately above origin from stolon. Stems and side branches, when present, exclusively monosiphonic, divided into moderately-long, geniculate internodes by means of oblique nodes slanting in alternate directions. A hydrotheca, or a hydrotheca and a lateral apophysis immediately below its basis, confined to the distal end of each internode; basally, a twist. Branches arise irregularly (every 1-7 stem hydrothecae) and in the same plane as the stem; up to 2nd order branching observed; structure similar to stem, though 1st internode comparatively longer than subsequent ones. Hydrothecae biserial, alternate, coplanar; flask-shaped, swollen basally, adnate for 2/5th their adaxial length; surface provided by 4-6 transverse ridges; rim with 4 small, triangular, equally-developed cusps separated by deep, rounded embayments; 3 distinctive, plate-shaped, internal projections of perisarc below the hydrothecal aperture (2 latero-adaxial, 1 abaxial); operculum composed of 4 triangular flaps forming a pyramidal roof. Gonothecae arising from below the hydrothecal bases; broadly ovoid, surface with 6-7 transverse ribs, aperture apical, surrounded by 4 pointed cusps; external acrocysts in female.

**Dimensions:** See Table 22.

**Remarks:** The typical shape of a stolonial colony is illustrated in Galea (2007, fig. 15E), and of an erect stem in Galea (2007, fig. 15F). The gonothecae are illustrated in Galea (2007, fig. 15G, I).

**Distribution:** Chile – Región de los Ríos [north of Corral (present study)]; Región de los Lagos [around Isla Grande de Chiloé (Leloup, 1974; Galea *et al.*, 2009); Golfo de Ancud (Leloup, 1974); Roca Gloria (present study)]; Región de Aysén [Guaitecas Archipelago (Leloup, 1974; Galea, 2007); Canal Puyuhuapi (Galea *et al.*, 2009); Canal Messier (present study)]; Región de Magallanes y de la Antártica Chilena [Canals Castillo, Copihue, Pasaje, and Pitt Chico, as well as Angostura Inglesa and Isla Camello (Galea, 2007); around Punta Arenas (present study); Magellan Strait (*p.p.* Vervoort, 1972)]. Patagonia – no localities given (Leloup, 1960). Argentina – Provincia de Río

Table 22. Measurements of *Sertularella robusta* Coughtrey, 1876, in  $\mu\text{m}$ .

	Blanco (1963), as <i>S. tenella</i>	Blanco (1968)	Blanco (1976)	Vervoort (1972) (Vema 17-48)	Galea (2007), S144	Galea (2007), S23
<b>Internode</b>						
- length	582-658	360-865	515-773	460-890	309-727	227-554
- diameter at node	-	-	-	95-135	-	-
<b>Hydrotheca</b>						
- total length	451-488	-	-	540-555	-	-
- free adaxial side	-	331-350	347-368	350-365	305-327	282-364
- adnate adaxial side	-	166-202	179-210	ca. 245	136-159	145-168
- abaxial wall	-	405-423	399-430	460-530	414-436	377-427
- maximum width	225-250	239-350	210-263	245-255	241-259	204-250
- diameter at aperture	169-180	166-184	137-189	150-165	164-191	132-159
<b>Gonotheca</b>						
- total length	-	-	-	-	1328-1583	-
- maximum width	-	-	-	-	655-726	-

Negro [Golfo de San Matías (Blanco, 1994)]; Provincia de Santa Cruz [Puerto Deseado, Bahía Uruguay (Blanco, 1963, as *S. tenella*)]; Provincia de Tierra del Fuego, Antártida e Islas del Atlántico Sur [Argentinean waters off the northern coast of Isla Nueva, Tierra del Fuego (Blanco, 1968); off the eastern entrance of the Magellan Strait (Blanco, 1976); south of Sloggett Bay, Beagle Canal (Jäderholm, 1905, as *S. tenella*; *p.p.* Vervoort, 1972); around Península Mitre (*p.p.* Vervoort, 1972)]; numerous scattered records from the Patagonian Shelf, between 40°-54° S (*p.p.* El Beshbeeshy, 2011). Between Tierra del Fuego and the Falkland Is. (*p.p.* Vervoort, 1972). Burdwood Bank (Ritchie, 1907, as *S. tenella*).

***Sertularella robustissima* Galea, Häussermann & Försterra, sp. nov.**

Fig. 16A-D

*Sertularella argentinica*. – Galea, 2007: 59, fig. 14A-C. – Galea *et al.*, 2007c: 312, fig. 31 [non *Sertularella argentinica* El Beshbeeshy, 2011 = *Sertularella clausa* (Allman, 1888)].

**Holotype material:** MHNG-INVE-53268; Chile, Región de Aysén, Guaitecas Archipelago, NW of

Melinka, -43.88333° -73.71667°, 10-15 m, coll. HSFS, HF1; 08.03.2005; a 8 cm high, sterile colony.

**Additional material:** HRG-0611; Chile, Región de Magallanes y de la Antártica Chilena, Canal Copihue, -50.33979° -75.37834°, 16 m, coll. HSFS, HF16, lot #084; 16.04.2013; a 8 cm high, sterile colony.

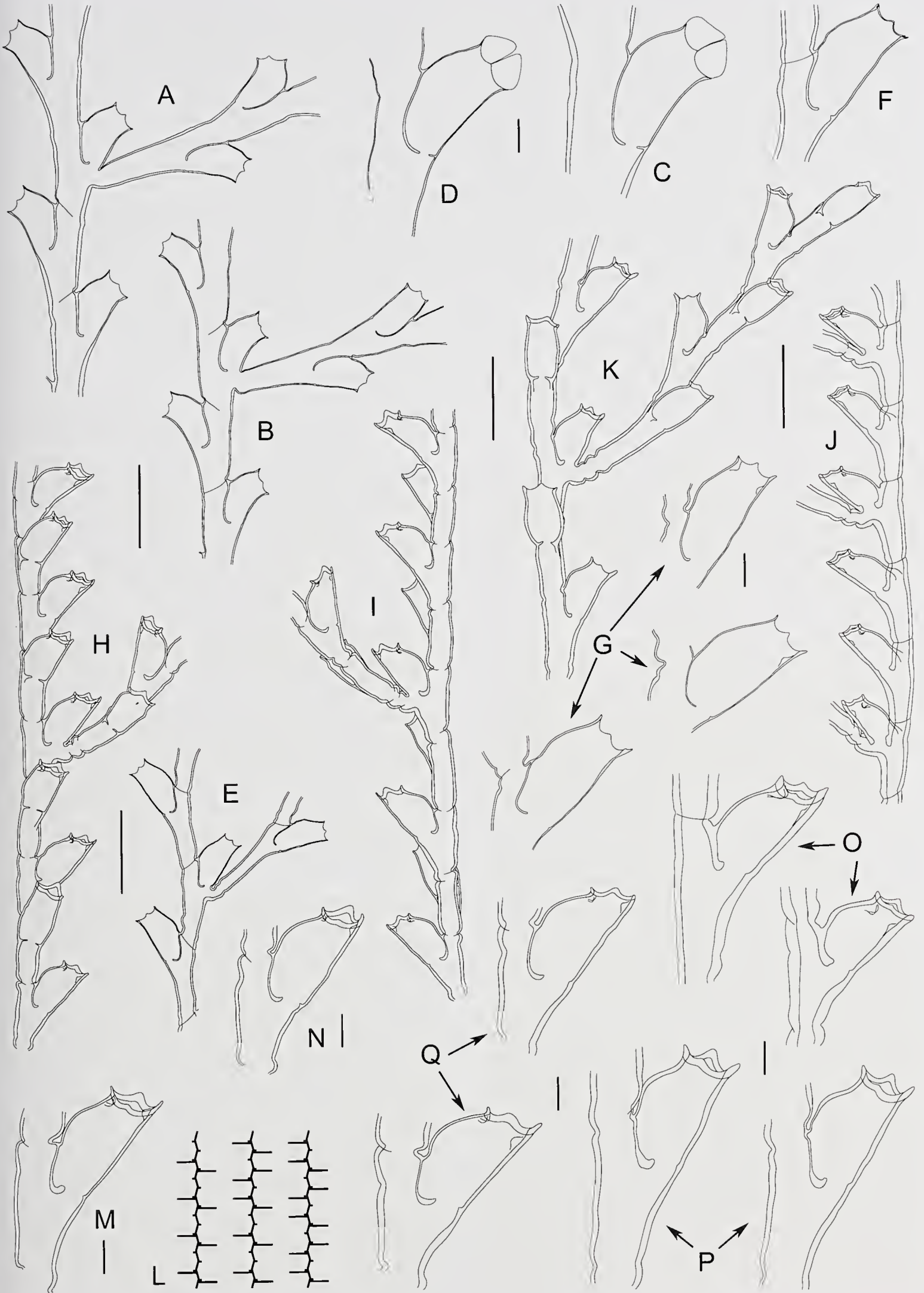
**Diagnosis:** Colonies bonsai-like, with strongly fascicled stems and dark brown perisarc; internodes slightly demarcated, short, almost collinear; hydrothecae short, tubular, curved outwards, marginal cusps separated by large, shallow embayments.

**Etymology:** A superlative of the Latin *rōbustus*, -a, -um, with reference to the sturdiness of the stems of this species.

**Description:** Colonies bonsai-like, up to 8 cm high, arising from well-developed, rhizoid mass of stolonial fibers firmly attached to substrate; composed of single, thick, strongly fascicled stem, unbranched in lower half, and forming numerous, irregularly-directed side branches in upper half; main branches polysiphonic proximally, giving rise to bundles of 2-4 basally parallel, distally diverging, monosiphonic branchlets, up to 3 cm long, each branched again up

Fig. 16. (A-D) *Sertularella robustissima* Galea, Häussermann & Försterra, sp. nov. Colony fragments from MHNG-INVE-53268 (A) and HRG-0006 (B), and hydrothecae from the same sources (C and D, respectively). (E-G) *Sertularella sanmatiasensis* El Beshbeeshy, 2011. Portion of colony from ZMH C11560 (E), and hydrothecae from the same source (F) and Blanco [1984, as *S. polyzonias* (Linnaeus, 1758)] (G). (H-Q) *Sertularella subantarctica* Galea, sp. nov. (part). Portions of stems from ZMH C04206 (H, I, the same seen from both sides), SMNH 123835 (J) and SMNH 123851 (K). Mode of branching (L). Hydrothecae from ZMH C04206 (M, N), SMNH 123835 (O) and SMNH 123851 (P), and ZMH C04384 (Q). Scale bars: 200  $\mu\text{m}$  (C, D, F, G, M-Q), 1 mm (A, B, E, H-K). ▶





to 2 times; branching almost regular, alternate, every 3 consecutive hydrothecae (rarely 2). Both stem and branches delimited into rather short, almost collinear internodes by means of oblique nodes slanting in alternate directions; a hydrotheca, or a hydrotheca and a lateral apophysis below its base, confined to the distal end of each internode. Hydrothecae rather short, tubular, distinctly curved outwards, adnate to the corresponding internode for slightly more than half their length; free adaxial wall smooth to slightly undulated; aperture with 4 small, triangular cusps separated by very shallow embayments; operculum composed of 4 triangular flaps with concentric striae; 1-2 closely-set renovations of the margin. Gonothecae unknown.

**Dimensions:** Internodes 310-493  $\mu\text{m}$  long and 310-352  $\mu\text{m}$  wide at nodes. Hydrothecal free adaxial length 337-393  $\mu\text{m}$ , adnate adaxial length 356-477  $\mu\text{m}$ , abaxial length 477-573  $\mu\text{m}$ , maximum width 399-444  $\mu\text{m}$ , diameter at aperture 337-376  $\mu\text{m}$ .

**Remarks:** The colony structure is illustrated in both Galea (2007, fig. 14A) and Galea *et al.* (2007c, fig. 31).

**Distribution:** Chile – Región de Aysén [Guaitecas Archipelago (Galea, 2007, as *S. argentinica*)]; Región de Magallanes y de la Antártica Chilena [Canal Copihue (present study)].

#### *Sertularella sanmatiasensis* El Beshbeeshy, 2011

Fig. 16E-G; Table 23

*Sertularella sanmatiasensis* El Beshbeeshy, 2011: 148, fig. 47.

– Soto Àngel & Peña Cantero, 2015: 996, fig. 7H-I.

non *Sertularella sanmatiasensis*. – (?) Peña Cantero, 2006: 939, fig. 3L. – (?) Peña Cantero & Gili, 2006: 767. – (?) Peña Cantero, 2008: 459, fig. 2C. – (?) Peña Cantero & Vervoort, 2009: 87, fig. 2B. – Peña Cantero, 2012: 858, fig. 4A; 2013: 130 (possibly all = *Sertularella antarctica* Hartlaub, 1901).

*Sertularella polyzonias*. – Blanco, 1984: 37, pls 31-36; 1994: 200 [non *Sertularella polyzonias* (Linnaeus, 1758)].

**Material examined:** ZMH C11560; FRV *Walther Herwig*, Stn. 283, Argentine Shelf, -42.21667° -58.1000°, 500 m; 21.06.1966; numerous colony fragments up to 2.3 cm high, all sterile, with only the perisarc left (holotype).

**Description:** Colonies composed of upright, monosiphonic, unbranched or sparingly-branched stems, up to 5 cm high; a few basal annuli above origin from stolon; divided by oblique nodes into internodes of varied length, longer basally, gradually decreasing distally; a hydrotheca, or a hydrotheca and a short, lateral apophysis below its base, confined to the distal end of each internode. Branching pattern with a tendency to alternate; first internode with a number of spiral twists proximally, and comparatively longer than subsequent ones. Hydrothecae biserial, alternate, coplanar to occasionally slightly shifted on

to one side of the colony; large, flask-shaped, adnate for about 1/3rd their adaxial length; a characteristic notch at origin of free adaxial wall, then hydrotheca conspicuously swollen on same side, till below the aperture, where it is constricted; perisarc either smooth or with up to 3 undulations; abaxial wall straight to slightly concave; 4 marginal, blunt-ended triangular cusps of equal development separated by shallow, semicircular embayments; 3 intrathecal, submarginal cusps (2 latero-adaxial, 1 abaxial), variably present; rim not thickened, margin occasionally renovated up to 3 times. Gonothecae arising from below the hydrothecae; broadly ovoid, tapering below, walls undulated to nearly smooth; aperture distal, surrounded by 4 pointed cusps in male, less developed or absent in female; acrocysts in the latter.

**Dimensions:** See Table 23.

**Remarks:** The gonothecae of this species, absent in the material studied by El Beshbeeshy (2011), were documented earlier by Blanco (1984, as *S. polyzonias*). The intrathecal, submarginal cusps occur very inconsistently: sometimes only the abaxial one is present, sometimes only the pair of latero-adaxial, and occasionally the complete set of three occurs.

It was stated under *S. antarctica* that it is likely that some records assigned to *S. sanmatiasensis* in various papers (co)authored by Peña Cantero belong in fact to Hartlaub's (1901) species. For instance, it is certain that the materials dealt with in Peña Cantero (2012, 2013) belong to the latter.

**Distribution:** Argentina – between Provincia de Río Negro and Provincia del Chubut [off Golfo San Matías (El Beshbeeshy, 2011)]. Scotia Arc – South Sandwich Is. (Soto Àngel & Peña Cantero, 2015). Antarctica – Isla Baja (Blanco, 1984, as *S. polyzonias*), Palmer Archipelago (Blanco, 1994, as *S. polyzonias*).

#### *Sertularella subantarctica* Galea, sp. nov.

Figs 1G, 12E, F, 16H-Q, 17A-B; Table 24

*Sertularella protecta* p.p. Hartlaub, 1901: 79.

*Sertularia* (*Sertularella*) *polyzonias*. – Pfeffer, 1889: 54 [non *Sertularella polyzonias* (Linnaeus, 1758)].

*Sertularella Almani*. – Jäderholm, 1905: 32, pl. 12 fig. 11; 1910: 5 [non *Sertularella almani* Hartlaub, 1901].

*Sertularella antarctica*. – Jäderholm, 1905: 32, pl. 13 fig. 1 [non *Sertularella antarctica* Hartlaub, 1901].

*Sertularella* sp. – El Beshbeeshy, 2011: 121, fig. 37E.

(?) *Sertularella picta*. – p.p. Millard, 1971: 405, fig. 6B [non *S. picta* (Meyen, 1834)].

non *Sertularella picta*. – Millard, 1971: 405, fig. 6A [= (?) *Sertularella gaudichaudi* (Lamouroux, 1824)].

**Holotype material:** SMNH 123839; South Georgia, Cumberland Bay, coll. Swedish South Polar Expedition 1901-1903; 09.05.1902; microslide (Fig. 12F) comprising three sterile colony fragments, 2.6, 3.0

Table 23. Measurements of *Sertularella sanmatiasensis* El Beshbeeshy, 2011, in  $\mu\text{m}$ .

	El Beshbeeshy (2011)	Blanco (1984), as <i>S. polyzonias</i>
<b>Internode</b>		
- length	690-864	710-1470
- diameter at node	139-208	-
<b>Hydrotheca</b>		
- free adaxial length	365-452	470-600
- adnate adaxial length	249-334	250-330
- abaxial length	527-642	610-780
- maximum width	-	350-390
- diameter at aperture	203-261	250-310
<b>Gonotheca</b>		
- total length		1980-2160 (♂); 2030-2250 (♀)
- maximum width		820-900 (♂); 1190-1260 (♀)

and 3.5 cm high [material incorrectly assigned to *S. antarctica* Hartlaub, 1901 by Jäderholm (1905); illustrated by him in his pl. 13 fig. 1, re-illustrated herein in Fig. 17A; note that the identification written down on the label of the slide is “*Sertularella Allmani* Hartl”].

**Paratype material:** ZMH C04206; South Georgia, German International Polar Year Expedition 1882-1883, coll. K. von den Steinen; (day and month unavailable) 1883; a colony composed of numerous sterile stems, up to 3.2 cm high, on stem of tubulariid hydroid and unidentified substrate, labeled *S. protecta* Hartlaub, 1901, and suspected by El Beshbeeshy (2011) to belong to an undescribed species.

**Additional material:** SMNH 123851; Falkland Is., Port William, coll. Swedish South Polar Expedition 1901-1903, Stn. 39, 40 m; 04.07.1902; microslide (Fig. 1G) containing 2 species: 1) on the right-hand side, two sterile colony fragments, 1.3 and 1.5 cm high, assignable to *S. subantarctica* Galea sp. nov., but identified by Jäderholm (1905) as *S. allmani* Hartlaub, 1901, and illustrated by him in his pl. 12 fig. 11, re-illustrated herein in Fig. 16K, P; 2) on the left-hand side, a ca. 2 cm high, fertile colony of *S. contorta* Kirchenpauer, 1884, illustrated by Jäderholm (1905, pl. 12 figs 9-10), and re-illustrated herein in Fig. 6C, I. – SMNH 123835; Falkland Is., Port William, 12 m, Swedish Magellanic Expedition 1907-1909, coll. C. Skottsberg; 07.11.1907; microslide (Fig. 12E) containing 3 colony fragments, 0.5-1.5 cm, the largest bearing two female gonothecae [material assigned by Jäderholm (1910) to *S. allmani* Hartlaub, 1901]. – ZMH C04384; South Georgia, German International Polar Year Expedition 1882-1883, coll. K. von den Steinen; (day and month unavailable) 1883; two sterile

fragments 1.7 and 3.8 cm high (most probably branches) on seaweed, labeled *S. protecta* Hartlaub, 1901 (it cannot be excluded that this material is part of ZMH C04206). – ZMH C04211; South Georgia, German International Polar Year Expedition 1882-1883, coll. A. Zschau, no additional data; likely 1883; about 3 short (up to 7 mm high), sterile stems (material labeled *S. protecta* Hartlaub, 1901).

**Diagnosis:** Stems monosiphonic, densely and pinnately branched; internodes uniformly short and thick; both hydrothecae and side branches shifted on to one side of the stem at a very acute angle, not exceeding 90°; hydrothecae big, though short (with respect to their width) and swollen adaxially, abaxial cusp produced, rim thickened, 3 internal, submarginal projections of perisarc, not always present.

**Etymology:** Named after its area of distribution.

**Description:** Undamaged colonies most probably exceeding 4 cm high; arising from tortuous, creeping, branching stolon; stems monosiphonic in all material inspected, with 1-5 basal twists; densely and pinnately branched; both stems and branches divided into uniformly short, thick internodes, by means of deep, oblique nodes slanting in alternate directions; a hydrotheca, or a hydrotheca and a short apophysis immediately below its base, confined to the distal end of each internode; a bulge at each end of the internodes; both hydrothecae and apophyses conspicuously shifted on to one side of the colony, giving it an anterior and a posterior side; angle between the two rows of branches acute, not exceeding 90°. Branching pattern (Fig. 16L) distinctive: branches occur in “pairs” composed of two successive internodes bearing lateral apophyses in opposite directions; each pair of branches is separated

from the next one through one (upper part of the stem) or two (lower part of the stem) hydrothecate internodes devoid of apophyses. Branches with similar structure as the stems, except for the 1st internode that is imperceptibly longer than subsequent ones, and provided basally with a couple of distinct twists. Hydrothecae large, flask-shaped, adnate for about 2/5th their adaxial side to the corresponding internode, conspicuously swollen adaxially; abaxial wall slightly concave in middle, to nearly straight throughout; free adaxial wall distinctly sigmoid: convex for most of its length, becoming suddenly concave below aperture; the latter quadrate, surrounded by 4 prominent, triangular cusps; abaxial one conspicuously produced, adaxial one the shortest, lateral ones unequally developed (“anterior” one shorter than “posterior” one); rim thickened, without renovations; 3 internal, submarginal projections of the perisarc (2 latero-adaxial, 1 abaxial), inconstantly present; a 4-flapped operculum. Perisarc thick throughout the colony. Gonothecae borne on side branches, given off from below the base of a hydrotheca; urn-shaped, transversely wrinkled, tapering below, distally provided with a short, neck region, bearing apically the aperture surrounded by 4 short, though strong spines.

**Dimensions:** See Table 24.

**Remarks:** The internal, submarginal cusps are variably present either among the hydrothecae of various stems, or among those of the same stem. For example, in sample SMNH 123839, the abaxial cusp is nearly always present, while the 2 latero-adaxial occur less frequently; conversely, in sample SMNH 123851, the cusps seem to be constantly absent.

**Distribution:** South Georgia – Pfeffer (1889, as *S. polyzonias*); *p.p.* Hartlaub (1901, as *S. protecta*); Jäderholm (1905, as *S. antarctica* in text, and *S. allmani* on the label of slide material); El Beshbeeshy (2011, as *S. sp. nov.*). Falkland Is. – Port William (Jäderholm, 1905, *p.p.* 1910, both as *S. allmani*). (?) South African Subantarctic Islands – Marion I. (Millard, 1971, as *S. picta*).

***Sertularella tenella* (Alder, 1856)**

Fig. 17C-H; Table 25

*Sertularia tenella* Alder, 1856: 357, pl. 13 figs 3-6. – Galea & Schories, 2012a: 45, fig. 5H-J.

non *Sertularella tenella*. – Jäderholm, 1905: 31, pl. 12 fig. 8. – Ritchie, 1907: 78. – *p.p.* Rees & Thursfield, 1965: 138. – Blanco, 1963: 173, figs 7-8 [all = *Sertularella robusta* Coughtrey, 1876].

*Sertularella jorgensis*. – Galea, 2007: 63, fig. 14G, H. – Galea *et al.*, 2007b: 312, fig. 4B [non *Sertularella jorgensis* El Beshbeeshy, 2011 = *Sertularella valdiviae* Stechow, 1923b].

(?) *Sertularella robusta*. – Soto Àngel & Peña Cantero, 2015: 996, fig. 7G [non *Sertularella robusta* Coughtrey, 1876].

**Material examined:** MHNG-INVE-53215; Chile, Región de Magallanes y de la Antártica Chilena, Canal Farquhar, -48.48853° -74.20714°, 32 m, coll. HSFS, HF2, lot #45; 29.03.2005; a colony composed of both stolonal hydrothecae and erect stems up to 1.2 cm high, formerly identified as *S. jorgensis* (see Galea, 2007). – HRG-0361; Chile, Región de los Lagos, Caleta La Arena, Caleta Yervas Buenas, -41.67263° -72.65650°, 20 m, coll. D. Schories, lot DS095; 08.03.2009; two

Table 24. Measurements of *Sertularella subantarctica* Galea, sp. nov., in µm.

	ZMH C04206, as <i>Sertularella</i> sp. nov. in El Beshbeeshy (2011)	SMNH 123851, as <i>S. allmani</i> in Jäderholm (1905)	SMNH 123839, as <i>S. antarctica</i> in Jäderholm (1905)	SMNH 123835, as <i>S. allmani</i> in Jäderholm (1910)
<b>Internode</b>				
- length (in general)	710-845	835-1165	820-1055	515-955
- 1 <sup>st</sup> internode, length	785-1240	1300-1535	1105-1350	980-1140
- diameter at node	230-315	225-315	215-320	190-230
<b>Hydrotheca</b>				
- free adaxial length	490-520	525-575	525-610	455-550
- adnate adaxial length	300-320	290-330	280-290	240-280
- abaxial length	640-755	660-740	750-830	510-730
- maximum width	380-440	390-430	365-410	355-390
- diameter at aperture	325-360	320-365	290-335	260-310
<b>Gonotheca</b>				
- total length	-	-	-	1595-1680 (♀)
- maximum width	-	-	-	995-1080 (♀)

sterile stems, 4 and 7 mm high. – HRG-0359; Chile, Región de los Lagos, Caleta La Arena, Caleta Yervas Buenas,  $-41.67263^{\circ}$   $-72.65650^{\circ}$ , 20 m, coll. D. Schories, lot S15; 26.04.2011; several sterile stems, 4–11 mm high, on worm tube. – HRG-1244; France, Brittany, N of Pointe Penmarc'h, off Gaouac'h rock, 23 m, coll. F-X. Decaris; 14.05.2016; a sterile colony, 2.5 cm high.

**Description:** Short (up to 1.2 cm high), erect, mono-

siphonic, unbranched stems or stolonal hydrothecae arising from creeping hydrorhiza; divided into relatively long, slender, geniculate internodes by means of oblique constrictions of the perisarc slanting in alternate directions; a hydrotheca distally to each internode. Hydrothecae biserial, alternate, coplanar, tronconic, adnate for 1/3rd to their corresponding internodes; abcauline wall straight to slightly concave, with smooth to slightly wrinkled perisarc; free adcauline wall with

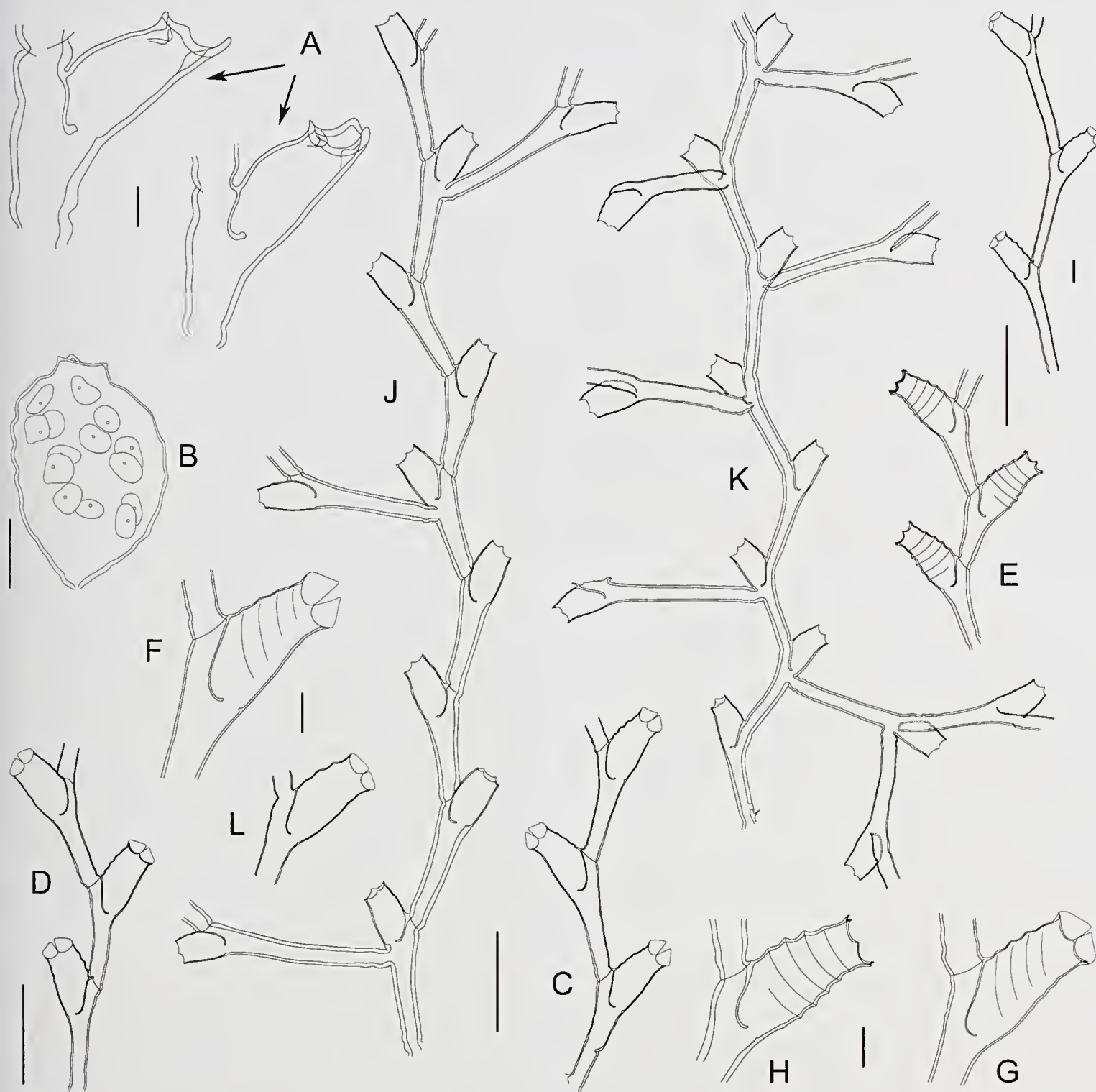


Fig. 17. (A–B) *Sertularella subantarctica* Galea, sp. nov. (continued), hydrothecae from SMNH 123839 (A), and female gonotheca from SMNH 123835 (B). (C–H) *Sertularella tenella* (Alder, 1857). Portions of stems from the Chilean materials HRG-0359 (C) and HRG-0361 (D), and comparison with the European specimen HRG-1244 (E). Hydrothecae from the same sources (F, G and H, respectively). (I–L) *Sertularella valdiviae* Stechow, 1923b (part). Portions of colonies from ZMH C11886 (I), ANT XIX/5 ID.91 (J), and ZSM 20050522 (K). Hydrotheca from ZMH C11886 (L). Scale bars: 200  $\mu$ m (A, F–H, L), 500  $\mu$ m (B), 1 mm (C–E, I–K).

3-4 undulations, not always reaching abcauline side; rim somewhat everted, provided with 4 pointed triangular cusps separated by moderately-deep, semicircular embayments; closing apparatus composed of 4 opercular flaps with concentric striations; no internal, submarginal cusps. Gonothecae absent in all material from the study area.

**Dimensions:** See Table 25.

**Remarks:** The typical silhouette of a stem is shown in Galea (2007, fig. 14G). The hydrothecae in this material are less wrinkled than those of European specimens (compare Fig. 17F, G and H).

The material assigned earlier to *S. jorgensis* El Beshbeeshy, 2011 by Galea (2007) (now recognized as a junior synonym of *S. valdiviae* Stechow, 1923b, see below) differs from that nominal species mainly through the morphology of its hydrothecae (compare Fig. 17F, G and Fig. 18A-C).

The rather thick internodes and the hydrothecae devoid of submarginal, intrathecal cusps in the material identified as *S. robusta* Coughtrey, 1876 by Soto Àngel & Peña Cantero (2015) equally point towards the present species.

**Distribution:** Chile – Región de los Lagos [Seno de Reloncaví (Galea & Schories, 2012a)]; Región de Magallanes y de la Antártica Chilena [Canal Farquhar (Galea, 2007; Galea *et al.*, 2007b; both as *S. jorgensis*)]. Scotia Arc – Burdwood Bank, South Sandwich Is. (Soto Àngel & Peña Cantero, 2015, as *S. robusta*).

### *Sertularella valdiviae* Stechow, 1923b

Figs 12G, H, 17I-L, 18A-D; Table 26

*Sertularella valdiviae* Stechow, 1923b: 11. – Stechow, 1925: 471, fig. 31. – Ruthensteiner *et al.*, 2008: 23.

*Sertularella jorgensis* El Beshbeeshy, 2011: 136, fig. 43 (**syn. nov.**). – Soto Àngel & Peña Cantero, 2015: 994, fig. 7E-F.

non *Sertularella jorgensis*. – Galea, 2007: 63, fig. 14G, H. – Galea *et al.*, 2007c: 312, fig. 4B [= *Sertularella tenella* (Alder, 1856)].

*Sertularella gayi parva*. – Blanco, 1968: 217, pl. 4 figs 8-11; 1994: 199 [non *Sertularella gayi* (Lamouroux, 1821) var. *parva* Billard, 1925].

**Material examined:** ZSM 20050521; French Southern and Antarctic Lands, 7 km west off St. Paul, -38.66667° -77.64333°, 672 m, coll. Deutsche Tiefsee (*Valdivia*) Expedition 1898-1899, Stn. 165; 03.01.1899; microslide (Fig. 12G) comprising five colony fragments of *Sertularella valdiviae* Stechow, 1923, 3-23 mm high, one of which is fertile and bears 8 empty gonothecae. – ZSM 20050522; French Southern and Antarctic Lands, 7 km west off St. Paul, -38.66667° -77.64333°, 672 m; 03.01.1899; coll. Deutsche Tiefsee (*Valdivia*) Expedition 1898-1899, Stn. 165, microslide (Fig.

12H) comprising three colony fragments (one of which bearing a gonotheca) of *S. valdiviae*, 6-14 mm high. – ZMH C11886; FRV *Walther Herwig*, Stn. 257, Argentine Shelf, -53.93333° -63.85000°, depth not recorded; 06.02.1971; several sterile, erect stems of *Sertularella jorgensis* El Beshbeeshy, 2011, up to 5 mm high, showing terminal stolonization, as well as a number of stolonal hydrothecae on the same hydrorhiza, both with remains of coenosarc only. – ANT XIX/5 ID.91; RV *Polarstern*, cruise ANT XIX/5, Stn. 253, Elephant I., -61.40050° -55.41200°, 276-282 m; 25.04.2012; sterile colony composed of several stems up to 3.5 cm high [material studied by Soto Àngel & Peña Cantero (2015), as *S. jorgensis*].

**Description:** Monosiphonic, slender, irregularly and sparingly-branched stems, up to 4 cm high, arising from creeping, filiform hydrorhiza; prisarc smooth or with 2-3 basal twists above origin from stolon. Stems and branches divided into long, geniculate internodes; nodes oblique, not always clearly demarcated; a hydrotheca confined to the distal end of each internode. Branches arising from below a stem hydrotheca, not always strictly laterally, but shifted on to the anterior or posterior sides of the stem, giving the colony a three-dimensional appearance; up to 4th order branching observed; branches with similar structure as that of stem; 1st internode comparatively longer than subsequent ones, and provided with 1-2 basal twists. Hydrothecae biseriate, alternate, distant from one another, occasionally not strictly coplanar; rather long, tronconical to almost tubular, adnate for a varied length, from 1/2 to 2/5th fused with the corresponding internode; abaxial wall slightly concave to straight, free adaxial wall with 2-4 wrinkles extending towards abaxial wall; 4 small, triangular marginal cusps separated by shallow embayments; a 4-flapped operculum; rim occasionally renovated; hydranths with 14-18 tentacles. Gonothecae given off from below the bases of cladial hydrothecae, elongated-ovoid, significantly tapering below, distally rounded, devoid of a neck region and perisarc projections, walls with 4-6 transverse wrinkles.

**Dimensions:** See Table 26.

**Remarks:** By comparing parts of El Beshbeeshy's (2011) and Soto Àngel & Peña Cantero's (2015) materials assigned to *S. jorgensis* to the type of *S. valdiviae* Stechow, 1923b, it appears that there are no morphological differences between them (compare Fig. 17I, J and K, respectively). Both nominal species prove coterminous, with *S. valdiviae* having priority over El Beshbeeshy's species. The gonothecae, not already known in *S. jorgensis*, are only present in the St. Paul material.

**Distribution:** Argentina – Provincia de Tierra del Fuego, Antártida e Islas del Atlántico Sur [off the

Table 25. Measurements of *Sertularella tenella* (Alder, 1856), in  $\mu\text{m}$ .

	Galca (2007), as <i>S. jorgensis</i>	Galea & Schories (2012a)	Naumov (1969)	Calder (1970)	Present study, HRG-1244
<b>Internode</b>					
- length	517-1197	785-2500	-	1000-2100	730-850 (< 1630)
- diameter at node	132-155	130-180	-	116-143	125-170
<b>Hydrotheca</b>					
- free adaxial length	391-460	385-425	420-480	476-608	585-645
- adnate adaxial length	270-345	285-385	140-230	306-348	310-320
- abaxial length	546-632	560-640	500-540	657-791	650-710
- maximum width	316-362	300-360	-		365-390
- diameter at aperture	289-312	260-300	230-270	253-306	280-300
<b>Gonotheca</b>					
- total length	-	-	< 2000	-	-
- maximum width	-	-	< 1000	-	-

Table 26. Measurements of *Sertularella valdiviae* Stechow, 1923b, in  $\mu\text{m}$ .

	Stechow (1925)	Present study, ZSM 20050521 and ZSM 20050522	El Beshbeeshy (2011), as <i>S. jorgensis</i>	Blanco (1968), as <i>S. gayi parva</i>	Soto Àngel & Peña Cantero (2015), as <i>S. jorgensis</i>
<b>Internode</b>					
- length (in general)	ca. 1000	725-1840	696-1189	828-1730	-
- length of 1st internode	-	920-2015	-	1214-2024	-
- diameter (at node)	130-170	110-165	110-133	-	
<b>Hydrotheca</b>					
- free adaxial length	ca. 320	330-360	295-353	331-460	290-340
- adnate adaxial length	250-260	280-300	203-237	257-350	220-260
- abaxial length	380-450	400-450	434-469	441-497	490-550
- maximum width	ca. 255	280-290	-	-	290-300
- diameter at aperture	ca. 185	205-230	203-214	221-239	200-210
<b>Gonotheca</b>					
- total length	ca. 950	800-1105	-	-	-
- maximum width	400-480	470-680	-	-	-

southeastern coast of Isla de los Estados (Blanco, 1968; 1994, both as *S. gayi parva*); scattered records from the Argentine Shelf, ranging between 42°-46° S (El Beshbeeshy, 2011, as *S. jorgensis*). Between Península Mitre and the Falkland Is. (El Beshbeeshy, 2011, as *S. jorgensis*). Scotia Arc – South Sandwich Is., Elephant I. (Soto Àngel & Peña Cantero, 2015, as *S. jorgensis*). French Southern and Antarctic Lands – St. Paul (Stechow, 1923b, 1925).

### *Sertularella vervoorti* El Beshbeeshy, 2011

Fig. 18E; Table 27

*Sertularella vervoorti* El Beshbeeshy, 2011: 151, fig. 48. – Watson & Vervoort, 2001: 167, fig. 9. – Soto Àngel & Peña Cantero, 2015: 996, fig. 7J-K.

*Sertularella cylindritheca*. – Vervoort, 1972: 126, fig. 39A. – Stepanjants, 1979: 90, pl. 14 fig. 5A [non *Sertularella cylindritheca* (Allman, 1888) = *Sertularelloides cylindritheca* (Allman, 1888)].

**Material examined:** ZMH C11552; FRV *Walther Herwig*, Stn. 327, Argentine Shelf, off Provincia de

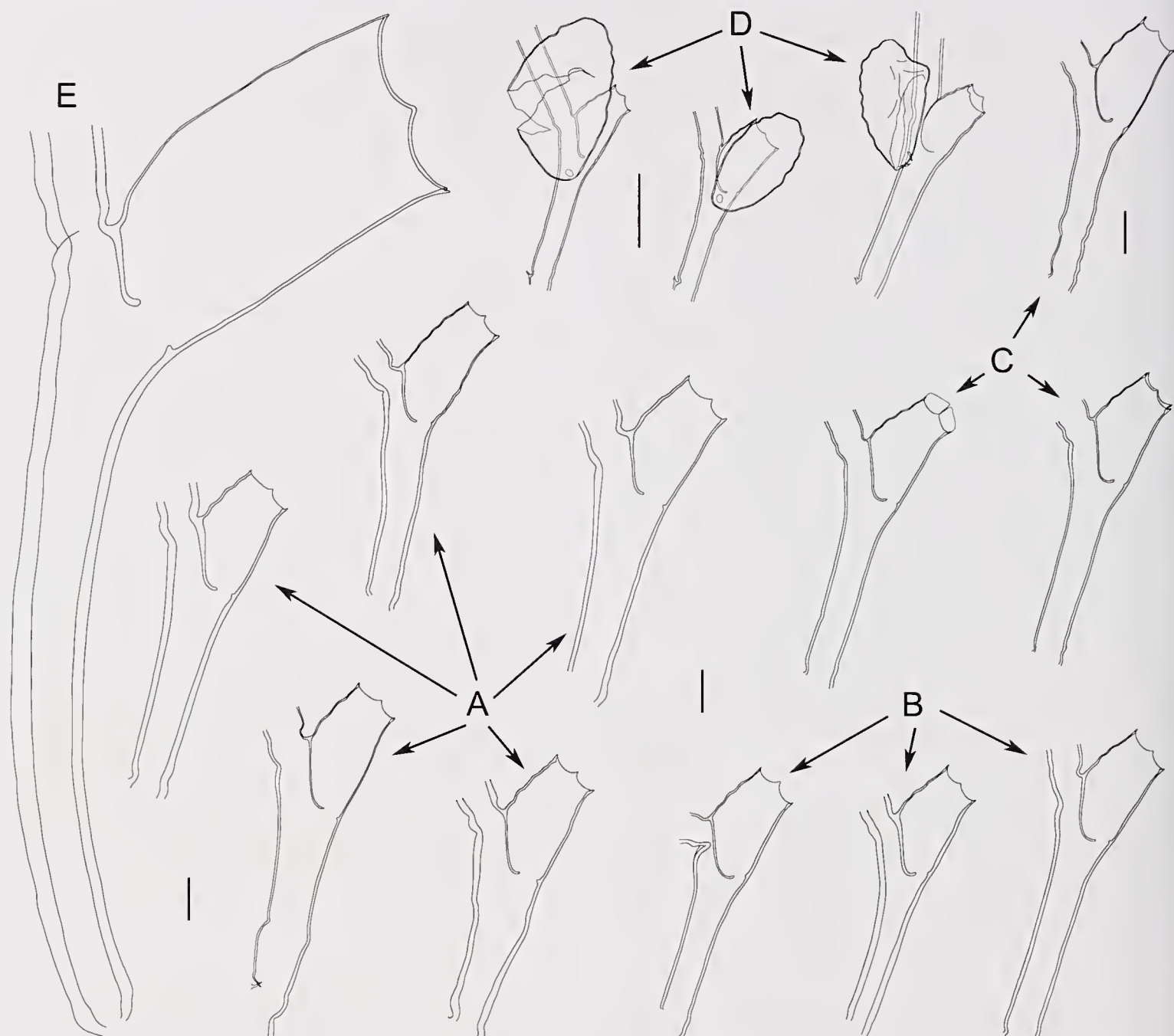


Fig. 18. (A-D) *Sertularella valdiviae* Stechow, 1923b (continued). Hydrothecae from ANT XIX/5 ID.91 (A), ZSM 20050522 (B) and ZSM 20050521 (C). Gonothecae from the latter source (D). (E) *Sertularella vervoorti* El Beshbeeshy, 2011, internode with hydrotheca. Scale bars: 200  $\mu\text{m}$  (A-C, E), 500  $\mu\text{m}$  (D).

Santa Cruz,  $-51.18333^{\circ}$   $-56.95000^{\circ}$ , 225 m; 29.06.1966; sterile, fragmentary colony (fragments 0.5-1.5 cm long) [material studied by El Beshbeeshy (2011)].

**Description:** Erect, though flaccid, up to 3.5 cm high colonies arising from creeping stolon. No definite main stem, the original stem branching several times subdichotomously; whole colony monosiphonic in habit. Both stems and branches divided into long, curved, slender internodes through distinct, oblique nodes; a hydrotheca, or a hydrotheca and one or two lateral, indistinct apophysis(es) immediately below its base; lower order branches arising not laterally, but almost perpendicular (in front or rear side) from their higher order counterparts. Hydrothecae strongly shifted

to one side of the colony; very large, tubular, adnate to the corresponding internode for only a short part of their adaxial length, then curving outwards; abaxial wall almost straight for most of its length, slightly expanded below aperture; free adaxial wall gently curving basally, then straight; perisarc thin and smooth throughout; margin with 4 small, pointed cusps separated by shallow, semicircular embayments; renovations occasional; a 4-flapped operculum; hydranths with 18-20 filiform tentacles. Gonothecae arising from below the hydrothecal bases; elongated-ovoid, tapering basally, walls transversely-wrinkled; aperture distal, large, 4-cusped, and provided with a 4-flapped operculum.

**Dimensions:** See Table 27.



Table 27. Measurements of *Sertularella vervoorti* El Beshbeeshy, 2011, in  $\mu\text{m}$ .

	El Beshbeeshy (2011)	Watson & Vervoort (2001)
<b>Internode</b>		
- length	2425-5145	2925-3500
- diameter at node	278-394	330-350
<b>Hydrotheca</b>		
- free adaxial length	1554-1855	2375-2625
- adnate adaxial length	-	-
- abaxial length	1345-1624	2050-2475
- maximum width	-	-
- diameter at aperture	626-858	800-1000
<b>Gonotheca</b>		
- total length	-	1990-2250
- maximum width	-	800-1100

**Remarks:** The gonothecae of this species were described by Watson & Vervoort (2001), and subsequently found by Soto Àngel & Peña Cantero (2015).

**Distribution:** Argentina – Provincia de Buenos Aires [scattered records from offshore waters (El Beshbeeshy, 2011)]; Provincia de Tierra del Fuego, Antártida e Islas del Atlántico Sur [off the NE coast of Isla de los Estados (Vervoort, 1972, as *S. cylindricheca*)]. Falkland Is. – off the NE coast (El Beshbeeshy, 2011). Scotia Arc – Burdwood Bank, South Georgia (Soto Àngel & Peña Cantero, 2015). Tasmanian seamounts (Watson & Vervoort, 2001).

## CONCLUSIONS

The hydroids assignable to the genus *Sertularella* Gray, 1848 from southern South America and the subantarctic are reviewed. Firstly, a comparison with the taxa originally described by El Beshbeeshy (2011) from the Argentine Shelf was undertaken to verify the accuracy of earlier identifications of Chilean specimens dealt with in a series of recent papers (Galea, 2007; Galea *et al.*, 2007b, 2009, 2014; Galea & Schories, 2012a).

Second, whenever extant, the materials (including the types) mentioned in earlier studies (notably Allman, 1888; Hartlaub, 1901; Jäderholm, 1903, 1905, 1910; Ritchie, 1907; Stechow, 1925; Vanhöffen, 1910) were equally reexamined, in order to: 1) provide modern redescriptions of a few nominal species for which only the original accounts were available to date; 2) reassess the taxonomic status of a number of poorly-known and, hence, “problematic” taxa; 3) verify the accuracy of various literature records, and provide a modern

interpretation of the specific identity of the species involved.

Accordingly, several nominal species described or mentioned in various older accounts were never, or only rarely, dealt with in subsequent papers, *e.g.* *S. kerguelensis* Allman, 1876, *S. lagena* Allman, 1876, *S. unilateralis* Allman, 1876, *S. clausa* (Allman, 1888), *S. implexa* (Allman, 1888), *S. polyzonias* Linnaeus, 1758 [*sensu* Allman (1888)], *S. valdiviae* Stechow, 1923a. Of these, only *S. clausa* and *S. implexa* have been located in the collection of NHML, and *S. valdiviae* in that of ZSM, and all three were reexamined within the present study. A comparison with the species created by El Beshbeeshy (2011) allowed to conclude that his *S. argentinica* and *S. jorgensis* are junior synonyms of *S. clausa* and *S. valdiviae*, respectively. In addition, *S. implexa* is redescribed based on its type material.

One of the most mandatory aspects dealt with relied on the clarification of the taxonomic status of a species group characterized by the unilateral arrangement of their branches along the stems, and of their hydrothecae along both the stems and branches. This group comprises *S. allmani* Hartlaub, 1901, *S. antarctica* Hartlaub, 1901, *S. contorta* Kirchenpauer, 1884, *S. gaudichaudi* (Lamouroux, 1824), *S. paessleri* Hartlaub, 1901, *S. picta* (Meyen, 1834), and *S. protecta* Hartlaub, 1901. Of these, the co-type of *S. contorta* could not be found in ZMB, where Kirchenpauer’s “herbarium” was recently located (C. Lüter, pers. comm.), the schizoholotype slides of *S. gaudichaudi* could not be found in the *Muséum national d’Histoire naturelle*, Paris (A. Andouche, pers. comm.), and *S. paessleri* proved absent from ZMH, where Hartlaub’s material is housed (H. Roggenbuck, pers. comm.).

Based on the data available from the literature, it became

Table 28. Main distinguishing features of *Sertularella* species with “unilateral” hydrothecae and branches.

	<i>Sertularella allinani</i> Hartlaub, 1901	<i>Sertularella antarctica</i> Hartlaub, 1901	<i>Sertularella coutorta</i> Kirchenpauer, 1884	<i>Sertularella gaudichaudi</i> (Lamouroux, 1924)	<i>Sertularella subantarctica</i> Galea, sp. nov.
<b>Habit of stem</b>	Mono- or polysiphonic	Monosiphonic	Mono- or polysiphonic	Mono- or polysiphonic	Monosiphonic
<b>Branching pattern</b>	Colonies feather- to fan-shaped, densely pinnate; two consecutive internodes, each giving rise to an alternate side branch, are separated by 1-2 internodes without apophyses from the following “pair” of branch-bearing internodes	Colonies of irregular shape, sparingly and irregularly branched, with roughly alternate side branches originating every 1-18 internodes	Colonies fan- to bush-shaped, densely branched; two consecutive internodes, each giving rise to an alternate side branch, are separated by generally 2 (though 1-3 possibly present) internodes without apophyses from the following “pair” of branch-bearing internodes	Colonies of straggling appearance, fan-shaped, although densely branched, with almost every single stem internode giving rise to an alternate side branch	Colonies feather-shaped, quite densely pinnate; two consecutive internodes, each giving rise to an alternate side branch, are separated by 1-2 internodes without apophyses from the following “pair” of branch-bearing internodes
<b>Unilateral arrangement</b>	Hydrothecae, stem apophyses and side branches forming an acute angle, giving the colony two distinct sides (anterior and posterior)	Hydrothecae, stem apophyses and side branches forming a wide angle, not giving the colony a pronounced antero-posterior aspect	Hydrothecae, stem apophyses and side branches forming an acute angle, giving the colony two distinct sides (anterior and posterior)	Hydrothecae, stem apophyses and side branches forming a moderately wide angle, giving the colony two distinct sides (anterior and posterior)	Hydrothecae, stem apophyses and side branches forming a very acute angle, giving the colony two distinct sides (anterior and posterior)
<b>Internodes</b>	Of uniform length, 340-640 µm, with a bulge at each end	Of uniform length, 730-1335 µm, with two spiral twists proximally and a distal bulge	Of uniform length, 675-1080 µm, with two spiral twists proximally and a distal bulge	Of highly varied length, 550-3990 µm, with two spiral twists proximally and a distal bulge	Of uniform length, 820-1055 µm, with a bulge at each end
<b>Hydrotheca</b>	“Small”, short, and conspicuously swollen adaxially	“Small”, long, and moderately swollen adaxially to nearly tubular	“Small”, short, and conspicuously swollen adaxially	“Small”, short, and conspicuously swollen adaxially	“Large”, short, and conspicuously swollen adaxially
- free adaxial wall	335-390	470-570	475-535	415-505	525-610
- adnate adaxial wall	135-245	320-375	280-305	235-250	280-290
- abaxial wall	390-540	705-770	535-635	575-620	750-830
- maximum width	275-360	325-350	365-420	290-345	365-410
- diameter at aperture	205-295	255-295	310-355	225-265	290-335
<b>Ratio depth/width</b>	1.45-1.82 (1.67±0.12, n=10)	1.98-2.39 (2.16±0.13, n=10)	1.54-1.77 (1.68±0.08, n=10)	1.51-1.96 (1.83±0.12, n=10)	1.58-2.00 (1.81±0.14, n=10)
<b>Reference(s)</b>	Galea <i>et al.</i> (2009), as <i>S. antarctica</i> Hartlaub, 1901; present study	Galea & Schories (2012b), as <i>S. gaudichaudi</i> (Lamouroux, 1824); present study	Present study	Present study	Present study

possible to establish, with little doubts, that *S. picta* is a junior synonym of *S. gaudichaudi* (see remarks under the latter species, as well as Table 10). In addition, upon the reexamination of the type of *S. protecta*, it is concluded that this, too, should be assigned to the synonymy of Lamouroux's species. Additionally, based on the original description, *S. paessleri* is recognized as a probable synonym of *S. allmani* (see remarks under this species). Consequently, among the species with unilateral arrangement of their hydrothecae and side branches described previously, only four are recognized here as valid, namely *S. allmani*, *S. antarctica*, *S. contorta*, and *S. gaudichaudi*. To these, a fifth species, *S. subantarctica* Galea sp. nov., described herein, should be added. Although of an apparently very similar morphology (notably at microscopic level), these hydroids could be primarily separated specifically through the distinctive appearances of their colonies, followed by the morphology of their internodes and, finally, the size and shape of their hydrothecae. These features are compared thoroughly in Table 28.

Lastly, Table 29 summarizes a list of 37 nominal species created based on material originating from the study area, and equally provides an updated taxonomic status for all of them. Of these, 27 species are considered as valid, 9 are invalid, and one (*S. kerguelensis*) should be regarded as a *nomen dubium*, given its unreliable original description and the loss of its type material.

In addition, all the remaining records of *Sertularella* species (exclusive of the types dealt with in Table 29) are listed, together with their current taxonomic status, in Appendix I. Among the 30 nominal species to which the hydroids were assigned by various authors, it appears that numerous records are based on misidentifications. It is worth underlining that hydroids assignable to *S. conica* Allman, 1877, *S. cylindritheca* Allman, 1888, *S. ellisii* (Milne-Edwards, 1836), *S. gayi* (Lamouroux, 1821), *S. minuscula* (Billard, 1924), *S. peregrina* Bale, 1926, and *S. polyzonias* do not occur in the study area.

Table 29. Nominal species of *Sertularella* described from the study area, and their present taxonomic status.

Basionym and type locality (-ies)	Present taxonomic status and remarks
<b><i>Sertularella allmani</i> Hartlaub, 1901</b>	
1) Chile, Isla Navarino, W of Puerto Pantalón del Weste, -54.9000° -67.9333° (lectotype); 2) Falkland Is., Port Stanley, ca. -51.69° -57.85°	Hartlaub (1901): replacement name for <i>Sertularia (unilateralis) secunda</i> Allman, 1888. Present study: valid species; Hartlaub's and Allman's hydroids proved conspecific upon comparison of their holotypes. Billard (1924): junior synonym of <i>S. gaudichaudi</i> (Lamouroux, 1824).
<b><i>Sertularella antarctica</i> Hartlaub, 1901</b>	
Chilean-Argentinean border, Punta Dúngenness, ca. -52.39° -68.43°	Hartlaub (1901): replacement name for <i>Sertularia unilateralis</i> Allman, 1876. Billard (1924): junior synonym of <i>S. gaudichaudi</i> (Lamouroux, 1824).
<b><i>Sertularella argentinica</i> El Beshbeeshy, 2011</b>	
Argentina, off Chubut, -43.87833° -59.58000°	Present study: <i>S. clausa</i> (Allman, 1888).
<b><i>Sertularella asymmetra</i> Galea &amp; Schories, 2014</b>	
Chile, Corral, -39.95000° -73.61667°	Present study: valid species.
<b><i>Sertularella blanconae</i> El Beshbeeshy, 2011</b>	
Falkland Is., off the E coast, -52.03333° -55.33333°	Present study: valid species.
<b><i>Sertularella clausa</i> (Allman, 1888)</b>	
Uruguay, off Montevideo, ca. -34.95° -56.15°	Present study: valid species.
<b><i>Sertularella contorta</i> Kirchenpauer (1884)</b>	
1) Lemaire Strait, ca. -54.80° -64.92°; 2) Falkland Is., ca. -51.75° -59.35°	Present study: valid species. Cotype reexamined by Hartlaub (1901); could not be located in ZMB. Hartlaub: (?) <i>S. lagena</i> Allman, 1876; (?) <i>S. antarctica</i> Hartlaub, 1901. Billard (1924): <i>S. gaudichaudi</i> (Lamouroux, 1824).
<b><i>Sertularella cruzensis</i> El Beshbeeshy, 2011</b>	
Argentina, off the Province of Buenos Aires, -39.93333° -57.18333°	Present study: valid species.
<b><i>Sertularella curta</i> Galea &amp; Schories, 2014</b>	
Chile, Taltal, -25.38333° -70.51667°	Present study: valid species.

Basionym and type locality (-ies)	Present taxonomic status and remarks
<b><i>Sertularella curvitheca</i> Galea &amp; Schories, 2012</b>	
Chile, Caleta La Arena, -41.67263° -72.65650°	Present study: valid species.
<b><i>Sertularella fuegonensis</i> El Beshbeeshy, 2011</b>	
Argentina, off the eastern coast of Tierra del Fuego, -53.45500° -65.60500°	Present study: valid species.
<b><i>Sertularella hermanosensis</i> El Beshbeeshy, 2011</b>	
Argentina, off the eastern coast of Tierra del Fuego, -53.93333° -63.85000°	Present study: valid species.
<b><i>Sertularella implexa</i> (Allman, 1888)</b>	
Between Cabo Virgenes (Argentina) and the Falkland Is., ca. -53.500° -62.800°	Present study: valid species; “holotype” composed of <i>S. implexa</i> (bulk of the material) + <i>S. hermanosensis</i> El Beshbeeshy, 2011 (3 colony fragments). Hartlaub (1901, 1905), El Beshbeeshy (2011): <i>S. polyzonias</i> (Linnaeus, 1758).
<b><i>Sertularella jorgensis</i> El Beshbeeshy, 2011</b>	
Argentina, off the Province of Chubut, -45.28166° -60.93833°	Present study: <i>S. valdiviae</i> Stechow, 1923b.
<b><i>Sertularella jnanfernandezensis</i> Galea, sp. nov.</b>	
Chile, Juan Fernández archipelago, between ca. -33.64° -78.85° and ca. -33.77° -80.79°	Present study: valid species.
<b><i>Sertularella kerguelensis</i> Allman, 1876</b>	
French Southern and Antarctic Lands, Kerguelen Is., Swains Bay, ca. -49.58° 69.73°	Present study: unidentifiable from original description; not illustrated; type no longer extant in NHM; <i>nomen dubium</i> . Allman (1879): <i>S. polyzonias</i> (Linnaeus, 1758).
<b><i>Sertularella lagena</i> Allman, 1876</b>	
French Southern and Antarctic Lands, Kerguelen Is., Observatory Bay, Royal Sound, ca. -49.41° 69.90°	Present study: most probably a junior synonym of <i>S. contorta</i> Kirchenpauer, 1884. Type no longer extant in NHM. Galea & Schories (2012a): <i>S. ? lagena</i> Allman, 1876. Hartlaub (1901): (?) <i>S. contorta</i> .
<b><i>Sertularella margaritacea</i> Allman, 1885</b>	
Chile, Magellan Strait	Billard (1924): reexamination of a part of the type; likely coterminous with <i>S. gaudichaudi</i> (Lamouroux, 1824).
<b><i>Sertularella microtheca</i> Leloup, 1974</b>	
Chile, Canal Calbuco, -41.813889° -73.16111°	Present study: valid species. El Beshbeeshy (2011), Galea (2007): <i>S. robusta</i> Coughtrey, 1876.
<b><i>Sertularella mixta</i> Galea &amp; Schories, 2012a</b>	
Chile, Punta de Choros, -29.2551° -71.5265°	Present study: valid species.
<b><i>Sertularella novarae</i> Marktanner-Turneretscher, 1890</b>	
French Southern and Antarctic Lands, St. Paul, ca. -38.43° 77.31°	Present study: valid species.
<b><i>Sertularella oblonga</i> Galea, Häussermann &amp; Försterra, sp. nov.</b>	
Chile, Isla Desolación, -52.71578° -74.68245°	Present study: valid species.
<b><i>Sertularella paessleri</i> Hartlaub, 1901</b>	
Falkland Is., Port William, ca. -51.40° -57.46°	Present study: <i>S. allmani</i> Hartlaub, 1901. Type no longer extant in ZMH. Hartlaub (1901): trophosome indistinguishable from that of <i>S. allmani</i> , but “typically” smooth-walled gonothecae (young condition of the material).
<b><i>Sertularella patagonica</i> (d’Orbigny, 1842)</b>	
Argentina, Río Negro, Ensenada de Ros, ca. -41.02° -62.79°	Present study: valid species. Kirchenpauer (1884), Hartlaub (1901): (?) <i>S. rugosa</i> Linnaeus, 1758.
<b><i>Sertularella pauciramosa</i> Galea &amp; Schories, 2014</b>	
Chile, Taltal, -25.38333° -70.46667°	Present study: valid species.

Basionym and type locality (-ies)	Present taxonomic status and remarks
<b><i>Sertularella recta</i> Galea &amp; Schories, sp. nov.</b>	
Chile, Punta Arenas, -53.78184° -70.97391°	Present study: valid species.
<b><i>Sertularella picta</i> (Meyen, 1834)</b>	
1) Eastern coast of Tierra del Fuego; 2) Falkland Is., ca. -51.75° -59.35°	Present study: <i>S. gaudichaudi</i> (Lamouroux, 1824).
<b><i>Sertularella protecta</i> Hartlaub, 1901</b>	
1) Chile, Isla Lennox, ca. -55.28° -66.94° (holotype); 2) Elizabeth I., Magellan Strait; 3) South Georgia, ca. -54.43° -36.58°	Present study: <i>S. gaudichaudi</i> (Lamouroux, 1824) (holotype ZMH C04173 reexamined). Material from Elizabeth Is. possibly no longer extant. Material from South Georgia not confidently related to the specimen ZMH C04384 = <i>S. subantarctica</i> Galea, sp. nov.
<b><i>Sertularella robustissima</i> Galea, Häussermann &amp; Försterra, sp. nov.</b>	
Chile, Guaitecas Archipelago, -43.88333° -73.71667°	Present study: valid species.
<b><i>Sertularella quadrispinosa</i> (Watson, 2003)</b>	
Australia, Macquarie I., ca. -53.93000° 159.09166°	Present study: valid species.
<b><i>Sertularella sanmatiasensis</i> El Beshbeeshy, 2011</b>	
Argentina, off the Province of Río Negro, -42.21666° -58.10000°	Present study: valid species.
<b><i>Sertularella subantarctica</i> Galea, sp. nov.</b>	
South Georgia, Cumberland Bay, ca. -54.22° -36.46°	Present study: valid species.
<b><i>Sertularella unilaterialis</i> Allman, 1876</b>	
French Southern and Antarctic Lands, Kerguelen Is., Swains Bay, ca. -49.63° 69.71°	Hartlaub (1901): secondary homonym of <i>Sertularia unilaterialis</i> Lamouroux, 1824 when this is placed in the genus <i>Sertularella</i> ; renamed <i>S. antarctica</i> Hartlaub, 1901.
<b><i>Sertularella secunda</i> (Allman, 1888) = <i>Sertularella unilaterialis</i> (Allman, 1888)</b>	
French Southern and Antarctic Lands, Kerguelen Is., off Accessible Bay, ca. -49.13° 70.18°	Hartlaub (1901): secondary homonym of both <i>Sertularia unilaterialis</i> Lamouroux, 1824 (when this is placed in <i>Sertularella</i> ) and <i>Sertularella secunda</i> Kirchenpauer, 1884; renamed <i>S. allmani</i> Hartlaub, 1901.
<b><i>Sertularella uruguayensis</i> Mañé Garzón &amp; Milstein, 1973</b>	
Uruguay, Cabo Polonio, ca. -34.40° -53.78°	Present study: <i>S. mediterranea</i> Hartlaub, 1901.
<b><i>Sertularella valdiviae</i> Stechow, 1923b</b>	
French Southern and Antarctic Lands, off St. Paul, ca. -38.66667° -77.64333°	Present study: valid species.
<b><i>Sertularella vervoorti</i> El Beshbeeshy, 2011</b>	
Argentina, off the Province of Río Negro, -41.38333° -57.30000°	Present study: valid species.

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**Appendix I.** Additional species records from the study area, and their present taxonomic status.

Original assignment, geographical origin(s), and reference(s)	Present taxonomic status, with remarks
<b><i>Sertularella allmani</i> Hartlaub, 1901</b>	
Chile: Isla Martha, Magellan Strait (Jäderholm, 1903)	Present study: unidentifiable (no description, no illustration, and species confusion in many of Jäderholm's accounts; material could not be located in SMNH).
Chile: Magellan Strait (Nutting 1904, Albatross Stn. 2776)	Present study: likely <i>S. antarctica</i> Hartlaub, 1901 (moderately-long internodes, hydrothecae elongate).
1) Chile: Isla Navarino; 2) Falkland Is.: Port Stanley (Hartlaub, 1905)	Present study: <i>S. allmani</i> Hartlaub, 1901 (material ZMH C04177, from Isla Navarino, reexamined; specimen from Falkland likely destroyed during WWII).
Falkland Is.: Port William (Jäderholm, 1905)	Present study: <i>S. subantarctica</i> Galea, sp. nov. (material SMNH 123851 reexamined).
Falkland Is.: Port William (Jäderholm, 1910)	Present study: <i>S. subantarctica</i> Galea, sp. nov. (material SMNH 123835 reexamined).
Between Tierra del Fuego and the Falkland Is. (Naumov & Strepanjants, 1962)	Present study, Stepanjants (1979, p. 84, footnote): <i>S. gaudichaudi</i> (Lamouroux, 1824) (long internodes).
<b><i>Sertularella antarctica</i> Hartlaub, 1901</b>	
Chile: 1) Isla Nueva; 2) Isla Lennox; 3) Lennox Cove; 4) Borgin Bay (Jäderholm, 1903)	Present study: <i>p.p. S. gaudichaudi</i> (Lamouroux, 1824) (material SMNH 123837, from Isla Nueva, reexamined; additional material could not be located in SMNH).
Chilean-Argentinean border, Punta Dúngeness (Hartlaub, 1905)	Present study: <i>S. antarctica</i> Hartlaub, 1901 (material ZMH C04161 reexamined).
South Georgia (Jäderholm, 1905)	Present study: <i>S. subantarctica</i> Galea, sp. nov. (material SMNH 123839 reexamined).
Argentina: Punta Peñas, San Julián (Blanco, 1963)	Present study, El Beshbeeshy (2011): <i>S. allmani</i> Hartlaub, 1901 (internodes short and with only a proximal bulge, hydrothecae conspicuously swollen adaxially). Blanco (1994): <i>S. antarctica</i> Hartlaub, 1901.
1) Argentina: off NE coast of Isla de los Estados; 2) Chile: Magellan Strait (Vervoort, 1972)	Present study: likely <i>S. antarctica</i> Hartlaub, 1901 (colonies irregularly branched, long internodes, relatively slender hydrothecae), despite similarities with the type of <i>Sertularia (unilateralis) secunda</i> Allman, 1888 reported by Vervoort (1972).
Chile: S of Chiloé I. (Galea <i>et al.</i> , 2009)	Present study: <i>S. allmani</i> Hartlaub, 1901 (colonies densely pinnate; regularly short internodes with a bulge at each end; short, adaxially swollen hydrothecae).
Argentina: off Punta Dúngeness (El Beshbeeshy, 2011)	Present study: <i>S. antarctica</i> Hartlaub, 1901.
<b><i>Sertularella argentinica</i> El Beshbeeshy, 2011</b>	
Chile: Guaitecas Archipelago (Galea, 2007)	Present study: <i>S. robustissima</i> Galea, Häussermann & Försterra, sp. nov. Soto Ángel & Peña Cantero (2015): doubtful record.
Burdwood Bank (Soto Ángel & Peña Cantero, 2015)	Present study: <i>S. clausa</i> (Allman, 1888).

Original assignment, geographical origin(s), and reference(s)	Present taxonomic status, with remarks
<b><i>Sertularella atlantica</i> Stechow, 1920</b>	
Argentina: Off Mar del Plata (Blanco, 1967)	Present study: <i>S. patagonica</i> (d'Orbigny, 1842) (short, geniculate stems, hydrothecae fusiform and conspicuously ringed throughout). Blanco (1994): <i>S. striata</i> Stechow, 1923b (curiously, this binomen is retained, although it was recognized as coterminous with d'Orbigny's species). El Beshbeeshy (2011): introduced <i>S. mogotesensis</i> = <i>nomen nudum</i> .
<b><i>Sertularella blanconae</i> El Beshbeeshy, 2011</b>	
Chile: Punta Arenas (Galea & Schories, 2012a)	Present study, Galea <i>et al.</i> (2014): <i>S. blanconae</i> El Beshbeeshy, 2011.
Chile: 1) Isla Level; 2) Isla Teresa (Galea <i>et al.</i> , 2014)	Present study: <i>S. blanconae</i> El Beshbeeshy, 2011.
<b><i>Sertularella conica</i> Allman, 1877</b>	
Argentina: off the Province of Santa Cruz, Albatross Stn. 2771 (Nutting, 1904)	Present study: <i>S. cruzensis</i> El Beshbeeshy, 2011. El Beshbeeshy (2011): introduced <i>S. grandensis</i> = <i>nomen nudum</i> . Vervoort (1972): <i>S. conica</i> Allman, 1877.
1) Argentina: from off Bahía Blanca to the S coast of Península Mitre; 2) Chile: Magellan Strait; 3) off NW Falkland Is. (Vervoort, 1972)	Present study, El Beshbeeshy (2011): <i>S. cruzensis</i> El Beshbeeshy, 2011.
1) Argentina: off Península Mitre and off Cabos Bahías; 2) off NE coast of Falkland Is. (Blanco, 1982)	Present study: <i>S. blanconae</i> El Beshbeeshy, 2011 (young, sparingly-branched colonies with monosiphonic stems; both shape and size of the hydrothecae distinctive).
Argentina: Mar del Plata (Genzano & Zamponi, 2003)	Present study: unidentifiable (neither description, nor illustration).
<b><i>Sertularella contorta</i> Kirchenpauer, 1884</b>	
Argentina: Lemaire Strait (Nutting, 1904)	Present study: likely <i>S. contorta</i> Kirchenpauer, 1884.
Chile ( <i>p.p.</i> Hartlaub, 1901)	Present study: <i>S. gaudichaudi</i> (Lamouroux, 1824) [Philippi's material studied by Hartlaub (1901)].
Falkland Is.: Port William (Jäderholm, 1905)	Present study: <i>S. contorta</i> Kirchenpauer, 1884 (material SMNH 123851 reexamined).
Falkland Is.: 1) Port Stanley; 2) Cape Pembroke (Ritchie, 1907; Rees & Thursfield, 1965)	Present study: <i>S. contorta</i> Kirchenpauer, 1884 (materials NMSZ 1921.143.1351C & D, from Cape Pembroke, reexamined; material from Port Stanley not examined here).
<b><i>Sertularella cylindritheca</i> (Allman, 1888)</b>	
Between Tierra del Fuego and the Falkland Is. (Vervoort, 1972)	Present study, El Beshbeeshy (2011): <i>S. vervoorti</i> El Beshbeeshy, 2011.
<b><i>Sertularella ellisii</i> (Milne-Edwards, 1836) f. <i>lagenoides</i> Stechow, 1919</b>	
Chile: 1) Golfo de Arauco, Bahía de Lota; 2) Península de Coquimbo (Leloup, 1974)	Present study: <i>S. mixta</i> Galea & Schories, 2012a (hydrothecal walls smooth, marginal cusps of equal development, 3 internal cusps).
<b><i>Sertularella fuegonensis</i> El Beshbeeshy, 2011</b>	
Chile: Canal Vicuña (Galea, 2007)	Present study: <i>S. fuegonensis</i> El Beshbeeshy, 2011.
<b><i>Sertularella gayi gayi</i> (Lamouroux, 1821)</b>	
Chile: 1) Puerto Harris, Isla Dawson; 2) Punta Arenas (Jäderholm, 1903)	Present study: <i>p.p.</i> <i>S. blanconae</i> El Beshbeeshy, 2011 (material SMNH 123866, from Punta Arenas, reexamined; material from Puerto Harris could not be located in SMNH).
Between Tierra del Fuego and the Falkland Is. (Naumov & Strepanjants, 1962)	Present study: unidentifiable (no description, no illustration).
Argentina: 1) off Península Valdés, Chubut; 2) off Puerto Deseado, Santa Cruz (Vervoort 1972)	Present study: possibly <i>S. blanconae</i> El Beshbeeshy, 2011 (fascicled stems, large hydrothecae, adnate for slightly less 1/2nd their length, free adaxial wall wrinkled).
1) Tierra del Fuego; 2) Falkland Is. (Strepanjants, 1979)	Present study: possibly <i>S. blanconae</i> El Beshbeeshy, 2011.
Argentina: ca. 80 km off the northeastern coast of Isla de los Estados (Blanco, 1982)	Present study: <i>S. clausa</i> (Allman, 1888) (colony structure not thoroughly described, but hydrothecae distinctive in both shape and size).

Original assignment, geographical origin(s), and reference(s)	Present taxonomic status, with remarks
Chile: 1) Fjord Comau; 2) Canal Adalberto; 3) Isla Camello (Galea, 2007)	Galea & Schories (2012a): <i>S. curvitheca</i> Galea & Schories, 2012a.
<b><i>Sertularella gayi parva</i> Billard, 1925</b>	
Argentina: off the SE coast of Isla de los Estados (Blanco 1968)	Present study: <i>S. valdiviae</i> Stechow, 1923b (exceedingly long, slender and geniculate stem internodes, hydrothecae tronconical, free adaxial wall wrinkled). El Beshbeeshy (2011): <i>S. jorgenis</i> El Beshbeeshy, 2011.
<b><i>Sertularella geniculata</i> Hincks, 1874</b>	
Chile: Bahía de Tocopilla (Leloup, 1974)	Galea <i>et al.</i> (2014): <i>S. curta</i> Galea & Schories, 2014.
<b><i>Sertularella geodiae</i> Totton, 1930</b>	
Eastern coast of Tierra del Fuego (Naumov & Stepanjants, 1962)	Present study: likely <i>S. geodiae</i> Totton, 1930 (stems fascicled, branching in one plane, shape of hydrothecae fitting original description).
A perimeter ranging from the Magellan Strait, to the Falkland Is., to Burdwood Bank, Isla de los Estados, and Cape Horn (Vervoort, 1972)	Present study: possibly a mix of <i>S. blanconae</i> El Beshbeeshy, 2011 (polysiphonic stems, very short internodes, hydrothecal shape) and <i>S. hermanosensis</i> El Beshbeeshy, 2011 (hydrothecal shape). El Beshbeeshy (2011): <i>S. hermaoseusis</i> .
Off the eastern entrance of the Magellan Strait (Blanco, 1976)	Present study, El Beshbeeshy (2011): <i>S. blanconae</i> El Beshbeeshy, 2011 (stems fascicled, regularly and alternately ramified, hydrothecae curved outwards, adaxial wall wrinkled).
Crozet Shelf (Millard, 1977)	Present study: likely <i>S. blanconae</i> El Beshbeeshy, 2011 (fascicled cauli, regular branching pattern, hydrothecae adnate for <i>ca.</i> 1/2nd their length, free adaxial wall undulated).
<b><i>Sertularella iuoplexa</i> (Allman, 1888)</b>	
Chile: Punta Arenas (Galea & Schories, 2012a)	Present study: <i>S. recta</i> Galea & Schories, sp. nov.
<b><i>Sertularella jorgeusis</i> El Beshbeeshy, 2011</b>	
Chile: Canal Farquhar (Galea 2007)	Present study: <i>S. tenella</i> (Alder, 1856).
1) South Sandwich Is.; 2) Elephant I. (Soto Angel & Peña Cantero, 2015)	Present study: <i>S. valdiviae</i> Stechow, 1923b.
<b><i>Sertularella lagenia</i> Allman, 1876</b>	
French Southern and Antarctic Lands: Kerguelen Is. (Stechow, 1925)	Present study: <i>S. contorta</i> Kirchenpauer, 1884.
Chile: Punta Arenas (Galea & Schories, 2012a)	Present study: <i>S. antarctica</i> Hartlaub, 1901.
<b><i>Sertularella leiocarpa</i> (Allman, 1888)</b>	
French Southern and Antarctic Lands: St. Paul (Stechow, 1925)	Present study: <i>S. leiocarpa</i> (Allman, 1888).
<b><i>Sertularella mediterranea</i> Hartlaub, 1901</b>	
Argentina: Mar del Plata (Genzano, 1990)	Present study: <i>S. mediterranea</i> Hartlaub, 1901 (habit of colony and microscopic structure as in European material, though of smaller proportions). El Beshbeeshy (2011): <i>S. picta</i> (Meyen, 1834).
<b><i>Sertularella minuscula</i> (Billard, 1924)</b>	
French Southern and Antarctic Lands: Kerguelen Is. (Redier, 1971)	Present study: unidentifiable, though hydrothecae in Redier's so called <i>S. minuscula</i> recall those of <i>S. valdiviae</i> Stechow, 1923b (material could not be located).
<b><i>Sertularella paessleri</i> Hartlaub, 1901</b>	
Falkland Is.: Port Williams	Present study: likely <i>S. allmani</i> Hartlaub, 1901 (material could not be located in collections of ZMH).
<b><i>Sertularella peregrina</i> Bale, 1926</b>	
Chile: Puerto Melinka, Guaitecas Archipelago (Leloup, 1974)	Present study: <i>S. mixta</i> Galea & Schories, 2012a (internodes short, hydrothecae fusiform, smooth, marginal cusps of equal development, 3 internal cusps, gonothecae similar).
<b><i>Sertularella picta</i> (Meyen, 1834)</b>	
Chile: Isla Lennox (Jäderholm, 1903)	Present study: <i>S. gandichaudi</i> (Lamouroux, 1824) (material SMNH 123881 reexamined).
Chile: 1) Isla Navarino; 2) Isla Lennox (Hartlaub 1905)	Present study: <i>S. gandichaudi</i> (Lamouroux, 1824) (material ZMH C04172, from Isla Lennox, reexamined).

Original assignment, geographical origin(s), and reference(s)	Present taxonomic status, with remarks
Chile: Patagonia (Naumov & Stepanjants, 1962)	Present study: likely <i>S. gaudichaudi</i> (Lamouroux, 1824) (profuse branching, long internodes, short hydrothecae, adnate for 1/3rd their length).
Argentina: Puerto Madryn (Blanco, 1963)	Present study: <i>S. gaudichaudi</i> (Lamouroux, 1824) (exceedingly long internodes, hydrothecae short and swollen adaxially).
Argentina: Mar del Plata (Blanco, 1967)	Present study, Blanco (1994): <i>Sertularella mediterranea</i> Hartlaub, 1901 (short, sparingly-ramified stems, hydrothecae with unthickened rim, and no internal, submarginal cusps). El Beshbeeshy (2011): <i>S. picta</i> (Meyen, 1834).
South African Subantarctic Islands: Marion I. (Millard, 1971)	Present study: 1) MAR1014A is likely <i>S. gaudichaudi</i> (Lamouroux, 1824) (internodes moderately long, a proximal "annulation" on each internode, 3-4 twists on proximal end of 1st internodes of the side branches); 2) MAR1113 is possibly <i>S. subantarctica</i> Galea, sp. nov.
1) Argentina: off the N coast of the tip of Peninsula Mitre (Vema 14-14), off Isla de los Estados, off Deseado (Santa Cruz); 2) Chile: off Isla Nueva (Vervoort, 1972)	Present study, El Beshbeeshy (2011): <i>S. fuegonensis</i> El Beshbeeshy, 2011 (Vema 14-14). Present study: <i>S. implexa</i> (Allman, 1888) (remaining samples) (slender cauli, repeatedly branched side-branches, internodes moderately-long, hydrothecae occasionally shifted on to one side of the colony, adnate for 1/3rd, free adaxial wall with 1-3 short, transverse ridges).
French Southern and Antarctic Lands: Kerguelen and Crozet shelves (Millard, 1977)	Present study: <i>S. gaudichaudi</i> (Lamouroux, 1824) (slender and straggling stems, fascicled basally, internodes very variable in length, hydrothecae +/- shifted on one side).
1) Argentina: Patagonian Shelf to east of Peninsula Mitre; 2) eastern coast of the Falkland Is. (El Beshbeeshy, 2011)	Present study: <i>S. gaudichaudi</i> (Lamouroux, 1824).
<b><i>Sertularella polyzonias</i> (Linnaeus, 1758)</b>	
Chile: Canal Trinidad (Ridley, 1881)	Present study: unidentifiable (no real description, no illustration). Hartlaub (1905): <i>S. polyzonias</i> (Linnaeus, 1758).
Falkland Is.: Port William (Allman, 1888)	Present study: likely <i>S. recta</i> Galea & Schories, sp. nov. (material no longer extant in NHM).
South Georgia (Pfeffer, 1889)	Present study: possibly <i>S. subantarctica</i> Galea, sp. nov. Hartlaub (1901): <i>S. protecta</i> Hartlaub, 1901.
1) South Georgia; 2) Falkland Is. (Jäderholm, 1905)	Present study: unidentifiable (neither description, nor illustration, material could not be located in SMNH).
1) Chile: Juan Fernandez Archipelago; 2) Falkland Is.: Port William (Jäderholm, 1910)	Present study: <i>p.p. Sertularella contorta</i> Kirchenpauer, 1884 (material SMNH 123884, from Port William, reexamined); <i>pp. Sertularella juanfernandezensis</i> Galea sp. nov. (material SMNH 123883, from Juan Fernandez, reexamined).
French Southern and Antarctic Lands: 1) St. Paul; 2) Kerguelen Is. (Vanhöffen, 1910)	Present study: <i>S. novarae</i> Marktanner-Turneretscher, 1890 (St. Paul, material ZMB Cni944 reexamined); <i>S. contorta</i> Kirchenpauer, 1884 (material ZMB Cni945 reexamined) and <i>S. gaudichaudi</i> (Lamouroux, 1824) (material ZMB Cni946 reexamined), both from Kerguelen Is.
French Southern and Antarctic Lands: Kerguelen Is. (Naumov & Stepanjants, 1962)	Present study: unidentifiable (neither description, nor illustration).
French Southern and Antarctic Lands: Kerguelen Is. (Redier, 1971)	Present study: unidentifiable (material could not be located).
Chile: Golfo de Ancud (Leloup, 1974)	Galea & Schories (2012a): <i>S. curvitheca</i> Galea & Schories, 2012a. Present study: material from Chiloé (M43) possibly not belonging here (shows affinities with <i>S. hermanosensis</i> El Beshbeeshy, 2011, though not reported from Chile yet).
Antarctica: Low I. (Blanco, 1984)	Present study: <i>S. sammatiasensis</i> El Beshbeeshy, 2011.
Chile: 1) Fjord Comau; 2) Canal Fallos (Galea, 2007)	Galea & Schories (2012a): <i>S. curvitheca</i> Galea & Schories, 2012a.
1) Argentina: Patagonian shelf; 2) off the NE coast of Falkland Is. (El Beshbeeshy, 2011)	Present study: <i>S. recta</i> Galea & Schories, sp. nov.
<b><i>Sertularella protecta</i> Hartlaub, 1901</b>	
Chile: 1) Lennox Cove; 2) Isla Lennox (Jäderholm, 1903)	Present study: <i>p.p. S. gaudichaudi</i> (Lamouroux, 1824) (material SMNH 123894, from Lennox Cove reexamined: exceedingly long –up to 4 mm– internodes, coexisting with short internodes; hydrothecae distinctive; material from Isla Lennox could not be located in SMNH).

Original assignment, geographical origin(s), and reference(s)	Present taxonomic status, with remarks
Patagonia (Rees & Thursfield, 1965)	Present study: <i>S. gaudichaudi</i> (Lamouroux, 1824) (material NMSZ 1959.33.472 reexamined: presence of long stem internodes).
<b><i>Sertularella robusta</i> Coughtrey, 1876</b>	
Patagonia (Leloup, 1960)	Present study: <i>S. robusta</i> Coughtrey, 1876.
Between Península Mitre, Argentina, and Isla Nueva, Chile (Blanco, 1968)	Present study, Blanco (1994): <i>S. robusta</i> Coughtrey, 1876.
1) Argentina: off Deseado, Santa Cruz (Vema 18-18), around Península Mitre, and Slogget Bay (Vema 17-48); 2) Chile: Magellan Strait; 3) between Tierra del Fuego and the Falkland Is. (Vervoort, 1972)	Present study: <i>S. microtheca</i> Leloup, 1974 (Vema 18-18) and <i>S. robusta</i> Coughtrey, 1876 (Vema 17-48). El Beshbeeshy (2011): introduced <i>S. stepanyantae</i> = <i>nomen nudum</i> .
Chile: 1) Golfo de Ancud; 2) around Chiloé I. (Leloup, 1974)	Present study: <i>S. robusta</i> Coughtrey, 1876.
Off the eastern entrance of Magellan Strait (Blanco, 1976)	Present study, Blanco (1994): <i>S. robusta</i> Coughtrey, 1876.
Chile: from the Guaitecas Archipelago to the southern fjords region (Galca, 2007)	Present study: <i>S. robusta</i> Coughtrey, 1876.
Argentine Shelf (El Beshbeeshy, 2011)	Present study: <i>S. microtheca</i> Leloup, 1974 (El Beshbeeshy's fig. 46E-H) and <i>S. robusta</i> Coughtrey, 1876 (El Beshbeeshy's fig. 46A-D).
1) Burdwood Bank; 2) South Sandwich Is. (Soto Ángel & Peña Cantero, 2015)	Present study: (?) <i>S. tenella</i> (Alder, 1856) (thick internodes with respect to the hydrothecal size, lack of intrathecal cusps).
<b><i>Sertularella sanmatiasensis</i> El Beshbeeshy, 2011</b>	
Chile: S of Chiloé I. (Galea <i>et al.</i> , 2009)	Galea & Schories (2012a): <i>S. mixta</i> Galea & Schories, 2012a.
South Sandwich Is. (Soto Ángel & Peña Cantero, 2015)	Present study: <i>S. sanmatiasensis</i> El Beshbeeshy, 2011 (hydrothecal shape distinctive).
<b><i>Sertularella striata</i> Stechow, 1923b</b>	
Argentina: Barranca Final, Gulf of San Matías (Blanco, 1974)	Present study: uncertain identity. Blanco (1994): <i>S. striata</i> Stechow, 1923b. El Beshbeeshy (2011): introduced <i>S. mogotesensis</i> = <i>nomen nudum</i> .
Argentina: Mar del Plata (Genzano, 1990)	Present study: <i>S. patagonica</i> (d'Orbigny, 1842).
<b><i>Sertularella teuella</i> (Alder, 1856)</b>	
Argentina: Slogget Bay, Canal Beagle (Jäderholm, 1905)	Present study: <i>S. robusta</i> Coughtrey, 1876 (long, geniculate internodes, small and transversely-ribbed hydrothecae, submarginal cusps).
Argentina: Puerto Deseado, Bahía Uruguay (Blanco, 1963)	Present study: <i>S. robusta</i> Coughtrey, 1876 (long, geniculate internodes, hydrothecae small and transversely-ribbed, intrathecal cusps).
Off Burdwood Bank (Ritchie 1907, Rees & Thursfield, 1965)	Present study <i>S. robusta</i> Coughtrey, 1876 (material NMSZ1959.33.499 reexamined).
Chile: Caleta La Arena (Galea & Schories, 2012a)	Present study: <i>S. tenella</i> (Alder, 1856).
<b><i>Sertularella uruguayensis</i> Mañé Garzón &amp; Milstein, 1973</b>	
Uruguay: Cape Polonio (Milstein, 1976)	Present study: <i>S. mediterranea</i> Hartlaub, 1901.
<b><i>Sertularella vervoorti</i> El Beshbeeshy, 2011</b>	
1) Burdwood Bank; 2) South Georgia (Soto Ángel & Peña Cantero, 2015)	Present study: <i>S. vervoorti</i> El Beshbeeshy, 2011 (hydrothecal shape and size distinctive).



***Carassius praecipuus*, a dwarf new species of goldfish from the Mekong drainage  
in central Laos (Teleostei: Cyprinidae)**

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**Abstract:** *Carassius praecipuus*, new species, is described from a hill stream in the upper Nam Ngum watershed in Mekong drainage in central Laos. It is distinguished from all congeners by the short dorsal fin, a small number of branched dorsal-fin rays, lateral line scales and gill rakers. It reaches sexual maturity around 70 mm SL. This is the first species of the genus discovered outside East and North Asia and Europe. The upper Nam Ngum watershed includes a part of the Plain of Jars, which had been hypothesised to have allowed the movement of a number of fish lineages between the rivers flowing to the Gulf of Tonkin and the Mekong drainage.

**Keywords:** Nam Ngum River - zoogeography - Oriental Region - Plain of Jars.

## INTRODUCTION

The genus *Carassius* includes about seven species, among them the well known goldfish [*C. auratus* (Linnaeus, 1758)]. They are medium-sized fishes that inhabit mainly swamps, lakes and slow flowing streams. Their natural distribution until now was restricted to northern Palearctic and East Asia. This article describes the first Southeast Asian species of the genus.

## MATERIAL AND METHODS

Measurements and counts follow Kottelat (2001) and Kottelat & Freyhof (2007). Last 2 branched dorsal and anal-fin rays articulating on a single pterygiophore are noted as "1½". Lateral line scale counts are given as (scales on body)+(scales on caudal-fin base). Frequencies of meristic values are indicated in parentheses, if more than one value is observed; asterisks indicate the condition for the holotype. Only the six largest specimens were measured; selected counts were obtained also from the remaining specimens. When possible, toponymy and spelling follow the 1:100'000 topographic map (Service Géographique d'Etat, 1985, sheet E48-14). Abbreviations used: CMK, collection of the author; MHNG, Muséum d'histoire naturelle, Genève; and ZRC, Lee Kong Chian Natural History Museum, National University, Singapore.

## *Carassius praecipuus*, new species

Figs 1-2

**Holotype:** MHNG 2767.087, 55.6 mm SL; Laos, Xiangkhouang Province, Nam Chat upstream of Ban Houay Sod, 19°37'24"N 102°52'17"E, 1142 masl; M. Kottelat *et al.*, 29 February 2012.

**Paratypes:** CMK 22748, 16 (+3 ethanol-fixed); ZRC 56275, 5; 32.7-62.0 mm SL; same data as holotype.

**Comparison material:** *Carassius auratus*: CMK 25714, 3, 68.4-81.5 mm SL; Laos: Houaphan Province: Nam Ma drainage: Nam Long upstream of Ban Kong Koun.

**Diagnosis:** *Carassius praecipuus* is distinguished from all other congeners in having the origin of the anal fin located behind a vertical through the base of last dorsal-fin ray (vs. under dorsal-fin base), fewer branched dorsal-fin rays (9-11½, vs. 11-21½), fewer lateral line scales (25-27 + 1, vs. 27-36 [total]) and fewer gill rakers (total 20-21, vs. 23-128). It reaches sexual maturity around 60-70 mm SL.

**Description:** See Table 1 for morphometric data of holotype and 5 largest paratypes. Largest known specimen 62 mm SL. Body moderately elongate, compressed. Dorsal body profile arched but made of a straight line on top of head, then an angle at nape and a

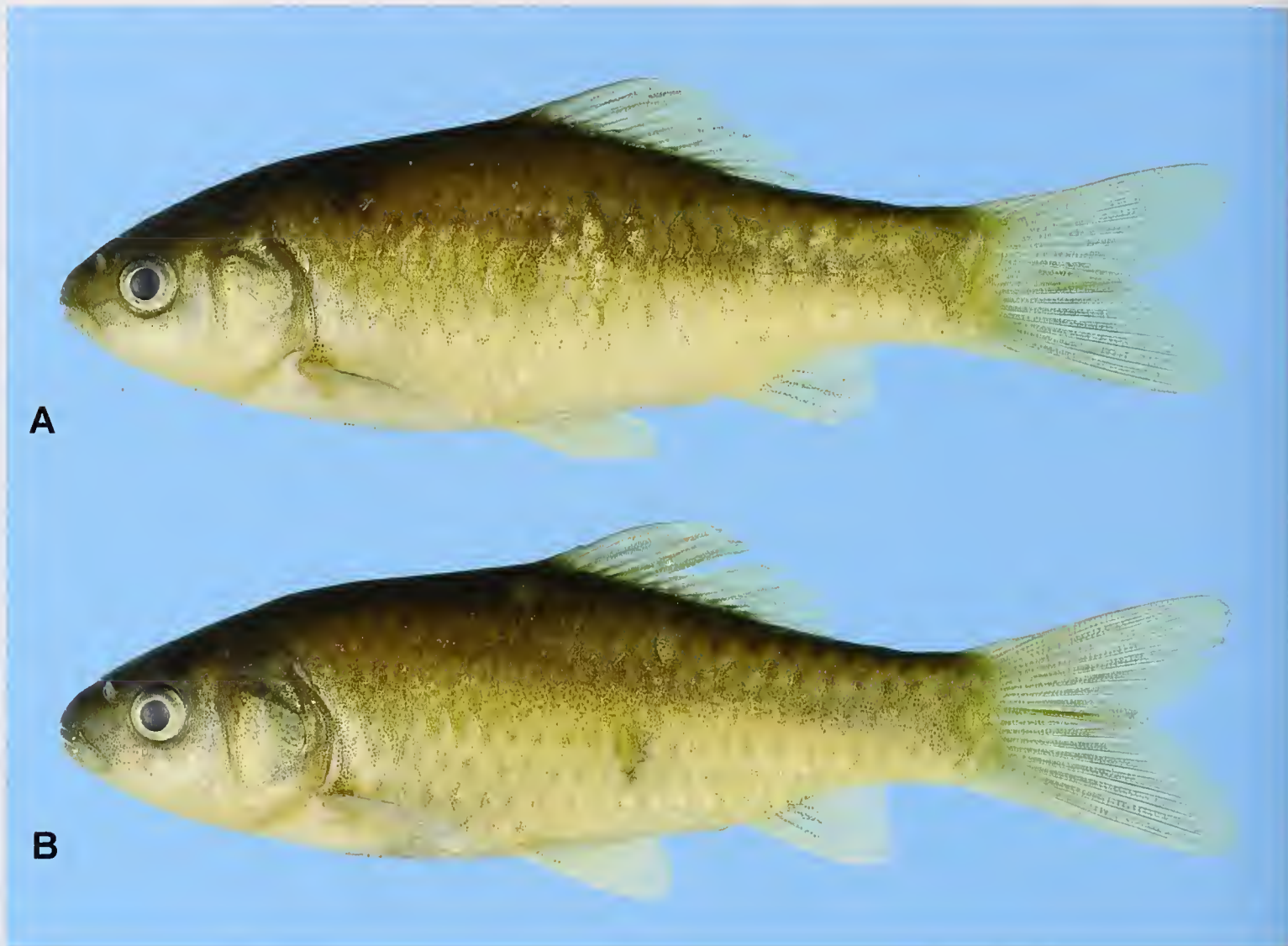


Fig. 1. *Carassius praecipuus*; Laos: Nam Ngum drainage: Nam Chat. (A) MHNG 2767.087, holotype, 55.6 mm SL. (B) CMK 22746, paratype, 62.0 mm SL (reversed).

Fig. 2. *Carassius praecipuus* CMK 22746, paratype, 62.0 mm SL; head (reversed). ►

straight line to dorsal-fin base, then more or less straight to caudal-fin base. Caudal peduncle 1.3-1.4 times longer than deep. Interorbital area convex. Head longer than deep, dorsal profile straight; ventral profile arched from mouth to pelvic-fin base, then straight to anal-fin origin; snout blunt. Mouth terminal to subterminal, anteriormost point of cleft below level of lower margin of eye, upper lip slightly projecting beyond tip of lower jaw. Lower jaw-quadrate junction about at vertical of anterior margin of eye. 10+10 (1), 10+11 (4\*) or 11+10 (1) = 20-21 gill rakers on first gill arch, their length about 1-1.5 times width of arch and about 3-4 times in length of gill filaments at same position.

Dorsal fin with 4 simple and  $9\frac{1}{2}$  (1),  $10\frac{1}{2}$  (6\*) or  $11\frac{1}{2}$  (4) branched rays, second ray longest; last unbranched ray rigid, thick (about 3 times width of branched rays), with 10-16 strong and pointed serrae along posterior edge (number increasing with size); distal margin straight to



slightly convex; origin behind vertical through pelvic-fin origin; dorso-hypural distance reaching between nostril and tip of snout when reported forward from dorsal-fin origin. Pectoral fin rounded, with 15 (4\*) or 16 (2) rays (unbranched and branched); reaching between  $\frac{2}{3}$  to whole distance to pelvic-fin origin. Pelvic fin rounded, with 8 rays (unbranched and branched); reaching slightly



Table 1. Morphometric data of holotype and 5 paratypes of *Carassius praecipuus*. Range and mean include holotype data.

	holotype	range	mean
Standard length (mm)	55.5	46.9-62.0	
Total length (mm)	70.6	62.0-80.8	
<b>In percent of standard length</b>			
Total length	127.1	127.1-132.1	129.6
Head length	29.4	29.4-32.3	30.9
Predorsal length	52.3	52.3-57.8	56.1
Prepelvic length	49.6	49.6-54.3	51.6
Preanal length	74.8	73.5-77.4	75.6
Head depth	23.7	23.3-24.5	23.9
Body depth (anal-fin origin)	34.1	32.5-35.9	33.6
Depth of caudal peduncle	15.3	14.4-15.3	14.9
Length of caudal peduncle	20.8	19.0-21.3	20.1
Head width	17.4	17.4-20.0	18.5
Mouth width	7.1	6.7-7.8	7.2
Eye diameter	6.8	6.6-7.8	7.0
Snout length	8.9	8.7-10.1	9.4
Interorbital distance	11.6	11.6-13.2	12.6
Length of dorsal spine	12.6	12.6-18.1	15.4
Length of dorsal-fin base	23.3	22.7-24.9	23.9
Length of upper caudal-fin lobe	27.1	27.1-29.2	28.3
Length of median caudal-fin rays	17.2	16.3-18.9	17.7
Length of lower caudal-fin lobe	27.4	27.0-29.8	28.4
Length of anal-fin spine	13.2	11.7-14.4	12.9
Length of pelvic fin	17.9	16.6-19.0	18.1
Length of pectoral fin	19.4	18.3-20.3	19.2
<b>In percent of head length</b>			
Head width	59	57-62	60
Mouth width	24	22-25	23
Eye diameter	23	21-24	23
Snout length	30	27-33	30

beyond halfway to anal-fin base; origin in front of vertical through dorsal-fin origin, origin slightly closer to pectoral-fin origin than to anal-fin origin. Anal fin with 3 unbranched and 5½ branched rays, first longest; last unbranched ray stout, rigid, thick (about 4 times thicker than branched rays), with 12-15 strong and pointed serrae along posterior edge (number increasing with size); distal margin straight; origin behind vertical through base of last dorsal-fin ray. Caudal fin with 9+9 (1) or 9+8 (5\*) branched rays; forked, lobes rounded, subequal. Lateral line complete with 25+1 (1\*), 26+1 (3) or 27+1 (2) pored scales. ½5 scale rows between lateral line and dorsal-fin origin; 6½ (1\*) or 7½ (5) between lateral line and ventral midline, counted 2 scales in front of pelvic-fin base; 4 (1\*), 4½ (1) or 5 (4) between lateral line and pelvic-fin origin; 4 (3\*) or 5 (3) between lateral line and anal-fin origin; ½2/1/2½ longitudinal scale rows on caudal peduncle; 12 (1\*), 13 (4) or 14 (1). A single pelvic axillary scale, small, same shape as adjacent scales.

**Coloration:** After 6 weeks in formalin. Head and body yellowish brown, darker on back. Top of head dark brown. Belly yellowish white. Scales on dorsal half of flank, covered by densely set dark pigments (melanophores?); with a thin line of smaller ones along posterior edge; pigments more densely-set on scale pockets, making them appear as poorly contrasted crescentic marks. On lower half of body, scales with only a few large pigments, sparsely set, restricted to anterior half of exposed part of scale; number of pigments decreasing ventrally, no pigments on lowermost 2-4 scale rows. Peritoneum dark grey.

Dorsal fin with pigments on all rays and membranes, denser on rays and on posterior half of membranes. Caudal fin with pigments on rays and on membranes between branches (but not on membranes between rays). Anal fin with pigments larger than on other fins, less densely set, mainly on proximal half of membranes between last unbranched and third branched rays. Pelvic

fin with a few pigments, sparsely set on proximal 1/3 of rays and membranes. Pectoral fin with pigments restricted to edges of all rays.

In life and shortly after fixation: yellowish brown.

**Distribution:** *Carassius praecipuus* has been observed only at the type locality, in the upper Nam Chat in the hills of central Laos (Fig. 3). Security safeguards greatly restricted movement and access to potential additional sampling sites.

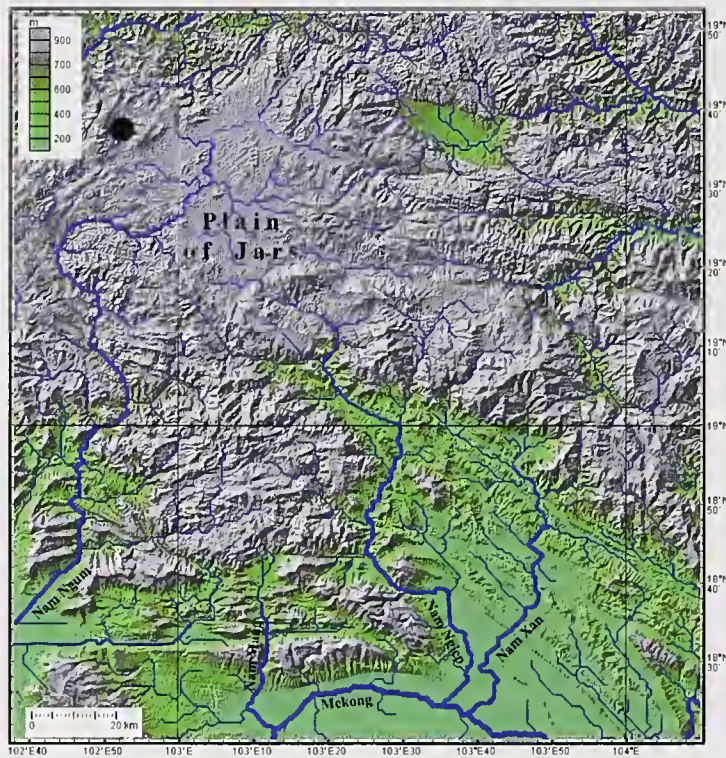


Fig. 3. Laos: the Plain of Jars and the Nam Ngum, Nam Ngiep and Nam Xan drainages, showing the type locality of *Carassius praecipuus*. Shown topography is prior to the construction of the dams.

**Habitat and notes on biology:** The Nam Chat is a tributary of the Nam Ting, itself a tributary of Nam Ngum, entering it at 19°22'15"N 102°43'22"E. It lies at the northern edge of the Plain of Jars, between the Nam Ngum proper and the Nam Khan, another tributary of the Mekong. The sampling site is in the uppermost course of the Nam Chat, about 5 km from its sources, at 1142 masl. The stream was 2-4 m wide, about 30-50 cm deep, up to about 1 m deep in one of the curves (Fig. 4), with moderate current. The bottom was made of gravel and pebble, with some areas covered by a thin layer of sediments, most likely washed from adjacent fields. The stream is at the bottom of a narrow valley, used for agriculture. The shores are mainly covered by bushes and occasional trees.

*Carassius praecipuus* was collected mainly in the deepest areas, under the roots of overhanging trees and bushes. No specimen larger than the types were observed; the sampling was done with electricity and

if larger individuals had been present they would probably have been caught. Other fish species present were: *Opsarius pulchellus* (Smith, 1931) (Cyprinidae), *Schistura coruscans* Kottelat, 2000, *S. defectiva* Kottelat, 2000, *S. personata* Kottelat, 2000, *S. quaesita* Kottelat, 2000 (Nemacheilidae), *Oreoglanis* sp. (Sisoridae) and *Rhinogobius mekongianus* (Pellegrin & Fang, 1940) (Gobiidae).

The largest available specimen (62 mm SL) is a female with mainly white oocytes and a few pale yellow eggs about 1.0 mm diameter, likely unripe. The specimens were collected at the end of February and this suggests that they would have been able to spawn a few weeks later in the coming dry season, or at the beginning of the wet season when the stream would flood the adjacent grassland.

**Etymology:** From the Latin adjective *praecipuus*, *-a, -uu*, meaning 'which is not common', allusion to the unexpected presence of a *Carassius* in the Mekong drainage and the very low dorsal-fin ray, lateral line scale and gill-raker counts.

**Remarks:** The genus *Carassius* occurs naturally from Central Europe to Japan and extends southwards in northern and central Vietnam in the rivers draining to the Gulf of Tonkin. Some species have been cultivated, and especially some of the East Asian species, which have given rise to numerous ornamental varieties, popularly known as goldfishes. Goldfishes and some other species of *Carassius* have been introduced, voluntarily or not, throughout the world and some have proved very damaging pests. *Carassius praecipuus* is the first species of the genus discovered in the Indochinese area (in the zoogeographic meaning; see Kottelat, 1989). A number of characters distinguish *C. praecipuus* from all its congeners and allow to exclude the possibility that it could be a feral population of some cultivated variety accidentally released in the wild (which anyway at the very isolated site would be surprising, although never impossible).

The European and northern Palaearctic species of *Carassius* are described or diagnosed by Berg (1948), Szczerbowski (2002: 7) and Kottelat & Freyhof (2007), the Chinese species by Luo & Chen (2000), the Japanese species by Hosoya (2002) and the Vietnamese species by Nguyen & Ngo (2001). Several meristic characters distinguish *C. praecipuus* from all other species. It has fewer branched dorsal-fin rays (9-11½, vs. 11-21½), fewer lateral line scales (25-27 + 1, vs. 27-36), fewer gill rakers (total 20-21, vs. 23-128). Further, the shorter dorsal fin in *C. praecipuus* is reflected by the more forward end of the base of the fin (in front of a vertical through the origin of the anal fin, vs. behind origin of the anal fin). Based on the literature, some of these meristic values show marginal overlap. The analysis is complicated by the fact that some species of *Carassius* are widely distributed and are of interest for aquaculture and geneticists; the

use of contradictory and sometimes incoherent species concepts, and the non-understanding of the implications of the concepts used, has blurred the taxonomy of the group and makes it difficult to know how many species really exist and how much of the identifications under the same name in different countries are really conspecific. I will focus here only on the populations showing meristic features whose values overlap with the ranges observed in *C. praecipuus*.

A further recurrent problem is that it is not always clear how the different authors obtained some of the counts. Differences exist in the way of counting the last two dorsal-fin rays that articulate on the same pterygiophore. Some authors count them as a single ray, others as two rays; I note them as '1½', a notation that removes ambiguity and also indicates that the author is aware of this issue. Similarly, different authors have reported lateral line scale counts in different ways, including or not the scales on the base of the caudal fin. They are here given separately (e.g. 26+1); again, this notation removes the ambiguity in showing that the author is aware of the issue. In the literature, in many instances, it is not clear if a count indicated as 26 means 24+2, 25+1 or 26+x. There are also instances of authors referring to a method but in fact using another one.

Whichever way they are counted, there are only few literature records of branched dorsal-fin ray counts of 11 or 12. A single species shows overlap with *C. praecipuus*. Hosoya (2002: 254) reports from a small area of Honshu island (Japan) an unnamed "*C. auratus* subsp. 2", which

has 11-14 (= 11-14½ in my notation; explained p. xxxv). This "*C. auratus* subsp. 2" also has some overlap with *C. praecipuus* in lateral line scale count, with 26-30 scales on the body (method explained p. xxxi). However, *C. praecipuus* is distinguished in having 20-21 gill rakers on the first gill arch (vs. 30-38) and the origin of the anal fin is behind a vertical through the base of the last dorsal-fin ray (vs. under dorsal-fin base). It is noteworthy that "*C. auratus* subsp. 2" also has a small size (up to 150 mm SL).

Szczerbowski (2002: 7) compiled a list of counts from the literature for *C. gibelio* (Bloch, 1782). The cumulated variation is 12-19 (apparently =12-19½ in my notation); 12 is reported only in the range 12-18 for a population from Yakutia. Noteworthy is that this Yakutia sample also has the lowest reported lateral line scale count, with 27-35 scales, while others have 28-33. The count supposedly includes the scales on the caudal-fin base (see below) but one cannot be certain since this is a compilation from disparate sources. The reported range of variability of the counts in this Yakutia population is very wide and makes the data suspicious. A variability range of 7 rays for a population with an average 15 rays is something otherwise unknown in cyprinid fishes in which the usual range in species with short dorsal fin would be 2-3 rays (and often no variability); this suggests a serious problem and poor reliability. In any case, *C. praecipuus* is distinguished from *C. gibelio* in having 20-21 gill rakers on the first gill arch (vs. 35-54) and a much smaller size (largest known specimen 62 mm SL, vs. 350 mm



Fig. 4. Nam Chat upstream of Ban Houay Sod, Xiangkhouang Province, Laos, 1142 masl; 29 February 2012. Type locality of *Carasius praecipuus*. Most specimens were obtained in the pool at the rear.

SL). *Carassius gibelio* is a species present from eastern Europe to northeastern China, which possibly includes several species and hybrids and presents a number of taxonomic problems (Kottelat & Freyhof, 2007: 145; Kalous *et al.*, 2012).

Lateral line scale counts of 26 and 27 have been reported for *C. auratus* in the literature as the extreme of a range of 26-31. This is again in a table compiled in Szczerbowski (2002: 7), who supposedly included the pored scales on the caudal-fin base (as most eastern European authors). For the same species, 27-30 scales are reported by Luo & Chen (2000: 430), who supposedly included only the scales on the body (as most Chinese authors). *C. praecipuus* is distinguished in having 9-11½ branched dorsal-fin rays (vs. 13-19½ in *C. auratus*), 20-21 gill rakers on the first gill arch (vs. 37-47), and the origin of the anal fin is behind a vertical through the base of the last dorsal-fin ray (vs. under dorsal-fin base).

A single other species of *Carassius* has been reported from Laos, from the Nam Ma drainage, a river entering Laos from and returning to Vietnam and entering the Gulf of Tonkin near Thanh Hoa. The species has been identified as *C. auratus* (Kottelat, 2001: 42), which may or may not be correct, and may be native or introduced or invasive. In any case, *C. praecipuus* is distinguished from these specimens in having a more slender appearance (compare Figures 1 and 5), a yellowish brown body coloration (vs. golden in life, greyish when preserved), fewer branched dorsal-fin rays (9-11½, vs. 15-18½), the distal margin of the dorsal fin straight to convex (vs. concave to straight), fewer lateral line scales (25-27 + 1, vs. 27-28 + 2), fewer longitudinal scale rows on the caudal peduncle (½2/1/2½, vs. ½3/1/3½), the anal-fin origin behind the base of the last branched dorsal-fin ray (vs. under branched ray 13-14 [or 2-4 when counted from posterior extremity of fin]), strong and pointed serrae

along the posterior edge of the last unbranched dorsal- and anal-fin rays (vs. short and blunt); fewer and shorter gill rakers on the first gill arch (20-21, length about 1-1.5 times width of arch and about 3-4 times in length of gill filaments at same position; vs. about 34 gill rakers in one dissected specimen, about 3-4 times wider than arch and about 2 times in length of gill filaments).

*Carassius* is a genus typical of the East Asian Subregion of the Oriental Region (*sensu* Kottelat, 1989: 34; of Sino-Indian Region *sensu* Bănărescu, 1992) and its presence in the Mekong drainage (Indochinese District, Southeast Asian Subregion, Oriental Region, *sensu* Kottelat, 1989: 34; South Asian Subregion of Banarescu, 1989) is unexpected. Nevertheless, it is not too surprising. The Nam Chat is adjacent to the Plain of Jars and to the Nam Ngum proper at the south. The Nam Ngum, Nam Ngiep and Nam Neun have headwaters on the Plain of Jars where they are separated only by very low divides. The Nam Ngum and Nam Ngiep are tributaries of the Mekong while the Nam Neun flows to the east to Vietnam and the Gulf of Tonkin, which it enters near Vinh. A few species or genera typical of the East Asian fauna are present in the Mekong tributaries on the Plain of Jars [*Opsariichthys hainanensis* Nichols & Pope, 1927, *Vanmanenia* sp., *Rhinogobius milleri* Chen & Kottelat, 2003, *Macropodus opercularis* (Linnaeus, 1758)] (Kottelat, 2017). The species is possibly also present in head waters of the Nam Khan (the next watershed to the north) and of the Nam Neun.

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Fig. 5. *Carassius auratus*, CMK 25714, 68.4 mm SL; Laos: Houaphan Province: Nam Ma drainage.

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**Another new species of *Oedothorax* Bertkau, 1883 from India (Araneae, Linyphiidae)**

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**Abstract:** A new species, *Oedothorax khasi* sp. nov., is described from the Indian state of Meghalaya on the basis of a single male. The species is similar to the Oriental *O. myanmar* Tanasevitch, 2017, different in some details of palpal structure.

**Keywords:** Erigoninae - Oriental Region - Meghalaya - Khasi Hills.

**INTRODUCTION**

At present, the spider fauna of India comprises of 14 species of *Oedothorax* Bertkau in Förster & Bertkau, 1883, which are distributed in equal proportions between the Oriental and the Palaearctic parts of the country (see Tanasevitch, 2015, 2016, 2017). An eighth *Oedothorax* from Oriental India is described below. The single male available of this new species was collected from montane subtropical forests in the Khasi Hills, a territory belonging to the Garo-Khasi range in the Indian state of Meghalaya.

**MATERIAL AND METHODS**

This paper is based on material kept at the Muséum d'histoire naturelle de Genève, Switzerland (MNHG). Specimens preserved in 70% ethanol were studied using a MBS-9 stereomicroscope. The sample number is given in square brackets.

Terminology of copulatory organs mainly follows that of Merrett (1963), Hormiga (2000) and Tanasevitch (2015). Chaetotaxy is given in a formula, e.g., 2.2.1.1, which refers to the number of dorsal spines on tibiae I-IV. The sequence of leg segment measurements is as follows: femur + patella + tibia + metatarsus + tarsus. All measurements are given in mm. Scale lines in the figures correspond to 0.1 mm unless indicated otherwise. Figure numbers are given above the scale lines, the alternative distance below.

**Abbreviations**

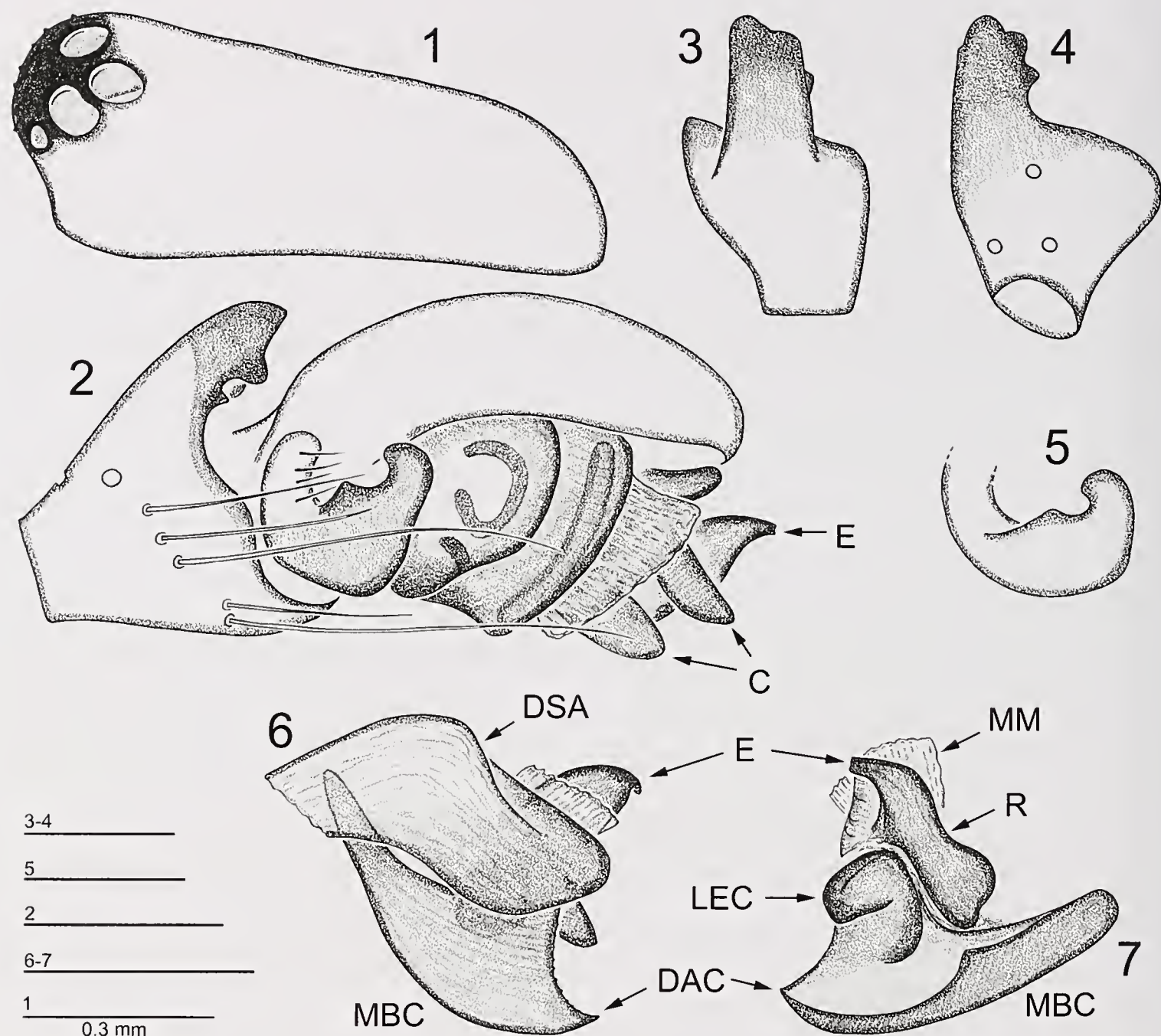
a.s.l.	Above sea level
C	Convector <i>sensu</i> Tanasevitch (1998) = lamella <i>sensu</i> Merrett (1963)
DAC	Distal apophysis of convector <i>sensu</i> Tanasevitch (2015)
DSA	Distal suprategular apophysis <i>sensu</i> Hormiga (2000)
E	Embolus
LEC	Lateral extension of convector <i>sensu</i> Tanasevitch (2015)
MBC	Main body of convector
MM	Median membrane <i>sensu</i> Helsdingen (1965) and Saaristo (1977)
R	Radix
Tml	Position of trichobothrium on metatarsus I

**TAXONOMY*****Oedothorax khasi* sp. nov.**

Figs 1-7

**Holotype:** Male; INDIA, Meghalaya, Khasi Hills, 16 km SW of Mawsynram, between Mawsynram and Balat, 1000 m a.s.l.; sifting in forest, in ravine; 27.X.1978; leg. C. Besuchet & I. Löbl [30b].

**Diagnosis:** The new species is characterized by an essentially unmodified carapace, by the shape of the dorsal apophysis of the palpal tibia, as well as by a relatively large, cylindrical radix and by a very short embolus.



Figs 1-7. *Oedothorax khasi* sp. nov., holotype. (1) Carapace, lateral view. (2) Distal part of right palp, retrolateral view. (3-4) Palpal tibia, dorsal and retradorsal view, respectively. (5) Paracymbium. (6) Distal suprategular apophysis and embolic division, retrolateral view. (7) Embolic division, prolateral view.

**Etymology:** The specific name is a noun in apposition referring to the mountain range in which lies the type locality.

**Description:** *Male (holotype).* Total length 1.80. Carapace 0.85 long, 0.60 wide, pale greyish brown. Cephalic part of carapace somewhat elevated and protruded forward as shown in Fig. 1. Eyes slightly enlarged. Chelicerae 0.33 long, unmodified. Legs pale brown. Leg I 3.46 long (0.93+0.25+0.85+0.78+0.65), IV 3.22 long (0.88+0.23+0.83+0.80+0.48). Chaetotaxy 2.2.1.1, length of spines about 1.5 times diameter of segment. All metatarsi with a trichobothrium. TmI 0.63. Palp (Figs 2-7): Tibia carrying a wide dorsal

apophysis with a small invagination apically and two small tubercles retrolaterally. Paracymbium somewhat L-shaped. Distal surface of tegulum membranous. Distal suprategular apophysis short, wide, rounded distally. Embolus very short, radix relatively large, cylindrical, with a fold on its exterior surface. Convector with a wide lateral extension and a short, pointed distal apophysis. Main body of convector long, tapering posteriorly. Abdomen 1.15 long, 0.63 wide, dorsally pale, with an indistinct grey herring-bone pattern.

*Female.* Unknown.

**Taxonomic remarks:** *Oedothorax khasi* sp. nov. is similar to another Oriental species, *O. myanmar*,



recently described from mountains of the Chin State in Myanmar (Tanasevitch, 2017). The new species is clearly distinguished by the shape of the dorsal apophysis on the palpal tibia, as well as by the relatively large and not curved radix.

**Distribution:** Only known from the type locality in northern India.

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**Reappraisal of *Goezeella* Fuhrmann, 1916 (Cestoda: Proteocephalidae),  
parasites of Neotropical catfishes (Siluriformes),  
with description of a new species from *Pimelodella cristata* (Heptapteridae)**

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**Abstract:** The cestode genus *Goezeella* Fuhrmann, 1916 is reviewed on the basis of taxonomic evaluation of type and newly collected material from pimelodid and heptapterid catfishes (Siluriformes) in the Amazon River basin, South America, and its generic diagnosis is amended. The genus is typified by the exclusively ventral position of the cortical vitelline follicles, the inner longitudinal musculature formed by dense individual muscle fibres, rather than forming bundles as in other proteocephalids, a well-developed metascolex and biloculate suckers. The type species, *G. siluri* Fuhrmann, 1916, is redescribed based on its syntype from *Cetopsis coecutiens* (type-host) (Cetopsidae) and specimens from *Pimelampus pirinampu* (Pimelodidae). The validity of *G. danbrooksi* de Chambrier, Rego & Mariaux, 2004 from *Ageneiosus pardalis* (Auchenipteridae) is confirmed and some erroneous morphological traits are corrected based on examination of its holotype. A new species, *Goezeella mariae* sp. nov., is described from the heptapterid catfish *Pimelodella cristata* (Heptapteridae). The new species differs from congeners by its overall size (much smaller compared to *G. siluri*), morphology of the scolex (strongly wrinkled metascolex and weakly developed interocular septum of suckers) and number of the testes. This is the third proteocephalid cestode described from a heptapterid catfish in South America and the first helminth parasite reported from *P. cristata*. *Goezeella* is unusual among other Neotropical proteocephalids by its occurrence in catfishes of as many as four families; all species of the genus are known only from the Amazon and Orinoco River basins. Molecular data on two of the three valid species and a key to their identification are provided.

**Keywords:** Morphology - taxonomy - tapeworms - Onchoproteocephalidea - systematics - host-associations - Neotropical Region - South America.

## INTRODUCTION

South American catfishes (Siluriformes) are hosts of a vast diversity of tapeworms (Cestoda) of the recently erected order Onchoproteocephalidea Caira, Jensen, Waeschenbach, Olson & Littlewood, 2014 (see Alves *et al.*, 2017a; Scholz & Kuchta, 2017). This order includes the previously recognized order Proteocephalidea Mola, 1928 (all in one family, Proteocephalidae La Rue, 1911) and some members of the polyphyletic order 'Tetraphyllidea' Carus, 1863 (Caira *et al.*, 2014). A total of 87 species of proteocephalids in 36 genera have

been reported from South American catfishes (Alves *et al.*, 2017a; de Chambrier *et al.*, 2017), but new taxa are still being described and new genera erected (e.g. Alves *et al.*, 2015, 2017b; Arredondo *et al.*, 2017). Likewise, evaluation of type-specimens and newly collected material made it possible to elucidate the taxonomic status of some previously insufficiently known genera, such as *Brayela* Rego, 1984, *Megathylacus* Woodland, 1934 and *Chambriella* Rego, Chubb & Pavanelli, 1999 (de Chambrier *et al.*, 2014; Alves *et al.*, 2017b). *Goezeella* Fuhrmann, 1916 was erected to accommodate *Goezeella siluri* Fuhrmann, 1916 from the blue whale

catfish *Cetopsis coecutiens* (Lichtenstein) (Siluriformes: Cetopsidae) in the Amazon River basin (Fuhrmann, 1916). This author distinguished *Goezeella* from *Monticellia* La Rue, 1911, which has also the testes, ovary, vitelline follicles and uterus in the cortex, by its possession of a well-developed metascolex, formed by an enlargement of the neck (proliferation zone) and the posterior part of the scolex (Fuhrmann, 1916).

Woodland (1933a) confused tapeworms found in the pimelodid catfish *Brachyplatystoma vaillantii* (Valenciennes) (Pimelodidae) in the Brazilian Amazonia with *G. silvri*, even though they had eggs with polar projections, whereas *G. silvri* described by Fuhrmann (1916) possessed 'typical' eggs of proteocephalids, i.e. without polar projections. Woodland (1933a) apparently studied a mixture of *G. silvri* from *C. coecutiens* and the species later described as *Amphoteromorphus praeputialis* Rego, Santos & Silva, 1974 [now *Brooksiella praeputialis* (Rego, Santos & Silva, 1974) Rego, Chubb & Pavanelli, 1999]. For cestodes from *B. vaillantii*, which are devoid of polar projections on their eggs, Woodland (1933a) proposed a new species, *Goezeella piramutab* Woodland, 1933; this species was later synonymized with *G. silvri* by de Chambrier *et al.* (2004a).

Brooks & Dcardorff (1980) reported *G. silvri* from the achenipterid catfish *Ageneiosus caucamis* Steindachner (= syn. of *A. pardalis* Lütken) in Colombia, but these cestodes differed from *G. silvri* in several morphological traits, such as the arrangement of the vitelline follicles, number of the testes and relative position of the vaginal sphincter (de Chambrier *et al.*, 2004a). Therefore, the latter authors proposed a new name, *G. danbrooksi* de Chambrier, Rego & Mariaux, 2004, to accommodate the specimens from *A. pardalis*, thus adding the second species to the genus.

As part of long-term studies on the diversity, host associations and interrelations of proteocephalid tapeworms in the Neotropical Region (e.g. de Chambrier & Vaucher, 1999; Alves *et al.*, 2015; de Chambrier *et al.*, 2015a), new material of *Goezeella* spp. from *Pimirampus pirinampu* (Spix & Agassiz) (Pimelodidae) and *Pimelodella cristata* (Müller & Troschel) (Heptapteridae) was collected. Evaluation of this new material, supplemented by examination of type-specimens of *G. silvri* and *G. danbrooksi*, made it possible to revise the genus including emendation of its diagnosis, to redescribe its type-species and to describe a new species from *P. cristata*. In addition, an identification key to the three species of the genus is provided.

## MATERIAL AND METHODS

The present study is based on the evaluation of the syntypes of *Goezeella silvri* and the holotype of *G. danbrooksi* deposited at the Natural History Museum, Geneva and the National Museum of Natural History,

Washington, D.C., respectively, and newly collected specimens from *Pimelodella cristata* and *Pimirampus pirinampu*.

The newly collected tapeworms were removed from the host's intestine and placed in 0.9% NaCl solution. Several posteriormost proglottids were excised and fixed in 96% molecular-grade ethanol for sequencing of the partial large subunit nuclear ribosomal RNA gene (*18S* rDNA gene; D1–D3 domains) (see Brabec *et al.*, 2012 for methodology). The anterior parts (hologenophores *sensu* Pleijel *et al.*, 2008) were placed in a small amount of saline and hot (almost boiling) 4% formaldehyde solution was immediately added to keep the worms straight; after two weeks they were transferred to 70% ethanol before further processing.

Specimens for morphological studies were stained with Mayer's hydrochloric carmine solution, dehydrated in an ethanol series, cleared with eugenol (clove oil) and mounted in Canada balsam. Eggs were drawn in distilled water. For histological sections, pieces of the strobila were embedded in paraffin wax, cross sectioned at 12–15 µm, stained with Weigert's haematoxylin and counterstained with 1% eosin B (acidified with five drops of pure acetic acid for 100 ml solution) following protocol outlined by de Chambrier (2001). For scanning electron microscopy (SEM) observations, scoleces of each species were dehydrated through a graded ethanol series, dried in hexamethyldisilazane, coated with gold and examined in a JEOL JSM-740 1F scanning electron microscope at the Institute of Parasitology, Biology Centre of the Czech Academy of Sciences. Microthrix terminology follows Chervy (2009). All measurements are given in micrometres unless otherwise indicated; abbreviations used in descriptions are: x = mean; n = number of measurements. The fish names follow Froese & Pauly (2017).

## Museum acronym abbreviations:

CHIOC	Helminthological Collection of the Instituto Oswaldo Cruz in Rio de Janeiro, Brazil
IPCAS	Institute of Parasitology, Biology Centre of the Czech Academy of Sciences, České Budějovice, Czech Republic
MHNG-PLAT	Platyhelminthes collection of the Natural History Museum of Geneva, Switzerland
USNM	National Museum of Natural History, Washington, D.C., USA

## TAXONOMIC ACCOUNT

### *Goezeella* Fuhrmann, 1916

**Amended diagnosis:** Onchoproteocephalidea, Proteocephalidae. Testes, ovary, vitelline follicles and uterus cortical. Small to medium-sized, robust worms, strobila acraspedote, with longitudinal and transverse grooves;

proglottids variable in shape and size. Scolex conical, with rounded to quadrangular apical part, without apical organ, wider than proliferative zone (neck); metascolex well-developed, wrinkled, formed by enlargement of neck. Suckers robust, biloculate; loculi variable in shape and size, interocular septum conspicuous or not. Internal longitudinal musculature well-developed, with numerous individual fibres not forming bundles; fibres more abundant on lateral sides of proglottids. Testes in one irregular field, in one or two layers, dorsally overlapping cirrus-sac and vitelline follicles. Cirrus-sac elongated to pear-shaped, internal sperm duct thick-walled, strongly coiled in proximal half of cirrus-sac. Genital pores markedly pre-equatorial, irregularly alternating. Genital atrium present, deep. Ovary with medullary isthmus and 2 follicular (grape-like) lobes penetrating inner longitudinal musculature to dorsal cortex; lobes with numerous dorsal outgrowths. Vagina anterior to cirrus-sac, surrounded by numerous chromophilic cells in distal (terminal) part (*pars copulatrix vaginae*); vaginal sphincter present. Vitelline follicles only on ventral or ventrolateral side of cortex, arranged in two uninterrupted lateral bands, widened towards ovarian level. Uterine development type 2 according to de Chambrier *et al.* (2004b). Parasites of siluriform catfishes in the Neotropical Region.

**Type species:** *Goezeella siluri* Fuhrmann, 1916.

**Additional species:** *Goezeella danbrooksi* de Chambrier, Rego & Mariaux, 2004; *Goezeella mariae* sp. nov.

**Remarks:** The validity of *Goezeella* has been questioned since its establishment, mainly due to different assumptions on the taxonomic usefulness of two morphological traits, i.e. the presence or absence of a metascolex and the distribution of the internal organs in relation to the internal longitudinal musculature. Woodland (1925) synonymized *Goezeella* with *Monticellia* because they share the cortical position of all internal organs, whereas Harwood (1933) synonymized it with *Corallobothrium* Fritsch, 1886 based on the presence of a metascolex in species of both genera (see Scholz *et al.*, 2011 for data on *Corallobothrium*). Based on a cladistic analysis inferred from morphological characters, Brooks (1995) synonymized *Choanoscolex* La Rue, 1911, *Goezeella*, *Jauella* Rego & Pavanelli, 1985 and *Peltidocotyle* Diesing, 1850 with *Spatulifer* Woodland, 1934, questioning validity of *Peltidocotyle*, which should have priority, because of the assumed similarity of the metascolex development shared by these genera (see Brooks & Rasmussen, 1984). However, this synonymy has never been accepted by most of the authors, including Rego *et al.* (1999), de Chambrier & Vaucher (1999) and de Chambrier *et al.* (2004a), who recognized *Goezeella* as a valid genus. Recent molecular data

suggest that the above-mentioned features may not be useful to assess the interrelations among proteocephalids and a more natural classification, reflecting the evolutionary history of the group, should be proposed (de Chambrier *et al.*, 2004b, 2015b; Scholz *et al.*, 2013).

As a result, the subfamilial classification proposed by W. N. F. Woodland and widely used for proteocephalids (Rego, 1994; de Chambrier & Vaucher, 1999; Rego *et al.*, 1999), based on the position of the testes, uterus and vitelline follicles in relation to the internal longitudinal musculature (see de Chambrier *et al.*, 2009 and references therein) is not considered in the present account. Nevertheless, for practical reasons, we compared *Goezeella* with the 11 genera previously placed in the Monticelliinae (Table 1), which are typified by the cortical position of the testes, ovary, vitelline follicles and uterus (Rego, 1994).

*Goezeella* can be readily differentiated from all proteocephalid genera by the vitelline follicles present only in the ventral cortex, i.e. completely absent dorsally, with lateral bands widened at the ovarian level, and by the possession of the inner longitudinal musculature formed by individual muscle fibres rather than forming compact bundles.

#### *Goezeella siluri* Fuhrmann, 1916

Figs 3, 4, 10-19

*Goezeella siluri* Fuhrmann, 1916: 385.

*Monticellia siluri*. – Woodland, 1925: 714.

*Corallobothrium siluri*. – Harwood, 1933: 140.

*Goezeella piramutab* Woodland, 1933a: 488.

*Monticellia piramutab*. – Woodland, 1935: 222.

*Spatulifer piramutab*. – Brooks & Deardorff, 1980: 17.

*Spatulifer siluri*. – Brooks, 1995: 365.

#### Material examined

**Syntype:** MHNG-PLAT-36375, a whole-mounted specimen (2 slides) and 12 slides of serial cross-sections. **Additional specimens:** MHNG-PLAT-19858, a whole-mounted specimen (4 slides) and 6 slides of serial cross-sections, collected on 13.04.1992, host field no. Br 237a. – CHIOC 38858, a whole-mounted specimen (one slide) collected on 30.09.1995, host field no. Br 436. – MHNG-PLAT-21845, 21877, 2 uncomplete whole-mounted specimens (3 slides) and 3 slides of serial cross-sections collected on 02.09.1995, host field no. Br 472. – MHNG-PLAT-21879, CHIOC 38859, a whole-mounted specimen (4 slides) and 6 slides of serial cross-sections collected on 19.10.1995, host field No. Br 811; all specimens from *P. pirinampu* from Itacoatiara, State of Amazonas, Brazil (3°09'S, 58°26'W), collected by A. A. Rego and A. de Chambrier. – MHNG-PLAT-85161, a whole-mounted specimen (3 slides), collected on 07.10.2011, host field no. PI 819a; hologenophore; specimen from *P. pirinampu* from Iquitos, Region of Loreto, Peru (3°47'S, 73°20'W).

Table 1. Selected morphological traits of the genera previously placed in the Monticelliinae (Cestoda: Proteocephalidae), parasites of freshwater fishes in the Neotropical region.

Genus (number of species)	Scolex shape/ metascolex (development)	Suckers appearance/ number of loculi	ILM arrangement/ development	Cirrus-sac shape	Vagina in relation to cirrus-sac	Ovary arrangement	Vitelline follicles arrangement	References
<i>Ageneiella</i> de Chambrier & Vaucher, 1999 (1 sp.)	globose/absent	elongate/ biloculate	bundles of fibres/well developed	elongate	only anterior	isthmus medullary; crossing ILM	two lateral rows	de Chambrier & Vaucher (1999)
<i>Chambriella</i> Rego, Chubb & Pavanelli, 1999 (1 sp.)	conical/absent	large/biloculate	bundles of fibres/ weakly developed	subovate	anterior and/or posterior	only cortical	two lateral rows	Alves <i>et al.</i> (2017b)
<i>Choatoscolex</i> La Rue, 1911 (1 sp.)	conical/present (weakly developed)	large, elongate/ uniloculate	bundles of fibres/ weakly developed	pyriform	anterior or posterior	only cortical	two lateral rows	de Chambrier & Vaucher (1999); Rego <i>et al.</i> (1999)
<i>Goezeella</i> Fuhrmann, 1916 (3 spp.)	conical/present (well developed)	robust, elongate/ biloculate	individual fibres/well developed	elongate to pyriform	only anterior	isthmus medullary; crossing ILM	two ventral rows	present study
<i>Manaosia</i> Woodland, 1935 (1 sp.)	globose/absent	robust, hidden in scolex, horseshoe- shaped muscles/ uniloculate	bundles of fibres/well developed	pyriform	only anterior	isthmus medullary; crossing ILM	two lateral rows	de Chambrier (2003)
<i>Monticelliella</i> La Rue, 1911 (8 spp.)	globose/absent	usually rounded/ uniloculate	bundles of fibres/ variable	usually pyriform	variable in position	usually cortical	two lateral rows	Rego (1994); Arredondo & Gil de Perterra (2010)
<i>Regella</i> Arredondo, de Chambrier & Gil de Perterra, 2013 (1 sp.)	quadrangular/ absent	inverted triangle-shaped/ uniloculate	bundles of fibres/ weakly developed	pyriform	usually posterior	only cortical	two lateral rows	Arredondo <i>et al.</i> (2013)
<i>Riggenbachiella</i> Alves, de Chambrier, Luque & Scholz, 2017 (2 spp.)	quadrilobed/ absent	large/ biloculate	bundles of fibres/ weakly developed	sigmoid, chambered	anterior, exceptionally posterior	only cortical	two lateral rows	Alves <i>et al.</i> (2017b)
<i>Spaskevillina</i> Freze, 1965 (3 spp.)	globose/absent	rounded, covered with conspicuous gladiate spiniriches/ uniloculate	bundles of fibres/ weakly developed	claviform	only posterior	only cortical	two lateral or slightly ventral rows	Pavanelli & Takemoto (1996); de Chambrier <i>et al.</i> (2015b)
<i>Spatulifer</i> Woodland, 1934 (3 spp.)	usually conical/present (well developed)	oval/ uniloculate	bundles of fibres/ weakly to well developed	elongate	only anterior or posterior	only cortical	two lateral or ventral rows	Woodland (1933b, 1935); Arredondo & Gil de Perterra (2008)
<i>Sybranchiella</i> Arredondo, Alves & Gil de Perterra, 2017 (1 sp.)	subspherical to quadrangular/absent	robust, elongate/ biloculate	bundles of fibres/ weakly developed	elongate to pyriform	only anterior	only cortical	two lateral rows	Arredondo <i>et al.</i> (2017)

Abbreviation: ILM, internal longitudinal musculature

**Type locality:** Amazon River basin (specific locality unknown).

**Other localities:** Delta of the Orinoco River, Venezuela; Amazon River, Itacoatiara, State of Amazonas, Brazil; Amazon River, Iquitos, Region of Loreto, Peru.

**Type host:** Blue whale catfish *Cetopsis coecutiens* (Lichtenstein, 1819) (Siluriformes: Cetopsidae).

**Other definitive hosts:** *Cetopsis othonops* (Eigenmann) (Siluriformes: Cetopsidae) and *Brachyplatystoma vaillantii* (Valenciennes) (Siluriformes: Pimelodidae) (doubtful host – see remarks below); *Pirinampus pirinampu* (Spix & Agassiz) (Siluriformes: Pimelodidae).

**Site of infection:** Anterior intestine.

**Prevalence of infection:** Fuhrmann (1916) found 4 tapeworms in one *C. coecutiens*, but did not provide the total number of fish examined; 43 *P. pirinampu* examined/8 fish infected (19%) from Itacoatiara, Brazil.

**Morphological description:** Fuhrmann (1916), de Chambrier *et al.* (2004a), present study.

**Representative DNA sequences:** A fragment of 1491 bp long of the *lsr*-DNA (D1–D3 domains) (GenBank MF370207). The newly generated sequence of an isolate of *G. silvri* from *P. pirinampu* is 483 bp longer than the sequence from the same host and river basin available in the GenBank (AJ388612).

**Redescription** (based on 6 whole worms, serial cross-sections of mature proglottids and 1 scolex studied using SEM from *P. pirinampu*; measurements taken from the syntype in brackets): Proteocephalidae. Testes, ovary, vitelline follicles and uterus cortical; medium-sized worms. Total body length 90–230 mm ( $n = 3$ ), maximum width up to 3 mm ( $n = 3$ ). Strobila acraspedote, anapolytic, with longitudinal and transverse grooves, consisting of about 335–360 proglottids: 195–200 immature (up to appearance of spermatozoa in vas deferens), 45–55 mature (up to appearance of eggs in uterus), 50–55 pregravid (up to appearance of hooks in oncospheres) and 45–50 gravid. Immature and mature proglottids much wider than long (length: width ratio 0.10–0.20), pregravid proglottids wider than long (length: width ratio 0.45–0.55), gravid proglottids wider than long to longer than wide (length: width ratio 0.80–1.93).

Scolex 1.18–1.60 × 1.45–1.94 mm ( $n = 5$ ), much wider than neck (proliferation zone), 1.77–1.80 × 1.40–1.45 mm, bearing 4 robust suckers, biloculate, with loculi variable in size; anterior loculus 210–295 ( $x = 255$ ;  $n = 5$ ) in diameter, posterior loculus 205–255 ( $x = 217$ ;  $n = 5$ ) in diameter; conspicuous septum separating each loculus (Figs 11, 15). Metascolex present, uniformly wrinkled. Apex conical, lacking apical organ, with numerous gland-cells (Figs 3, 4, 11, 15). Apex of scolex and lumen of suckers covered with acicular filitriches, similar in

density (not shown); surface between suckers, base of metascolex and neck covered with capilliform filitriches, similar in density (not shown); pregravid proglottids covered with acicular filitriches (Fig. 10).

Inner longitudinal musculature well-developed, composed by numerous, individual muscle fibres, concentrated on lateral sides of proglottids (Figs 13, 17). Osmoregulatory canals situated at same level, median to lateral-most testes and vitelline follicles, almost straight (Figs 16, 17); ventral osmoregulatory canal wider than dorsal one (Figs 16, 17).

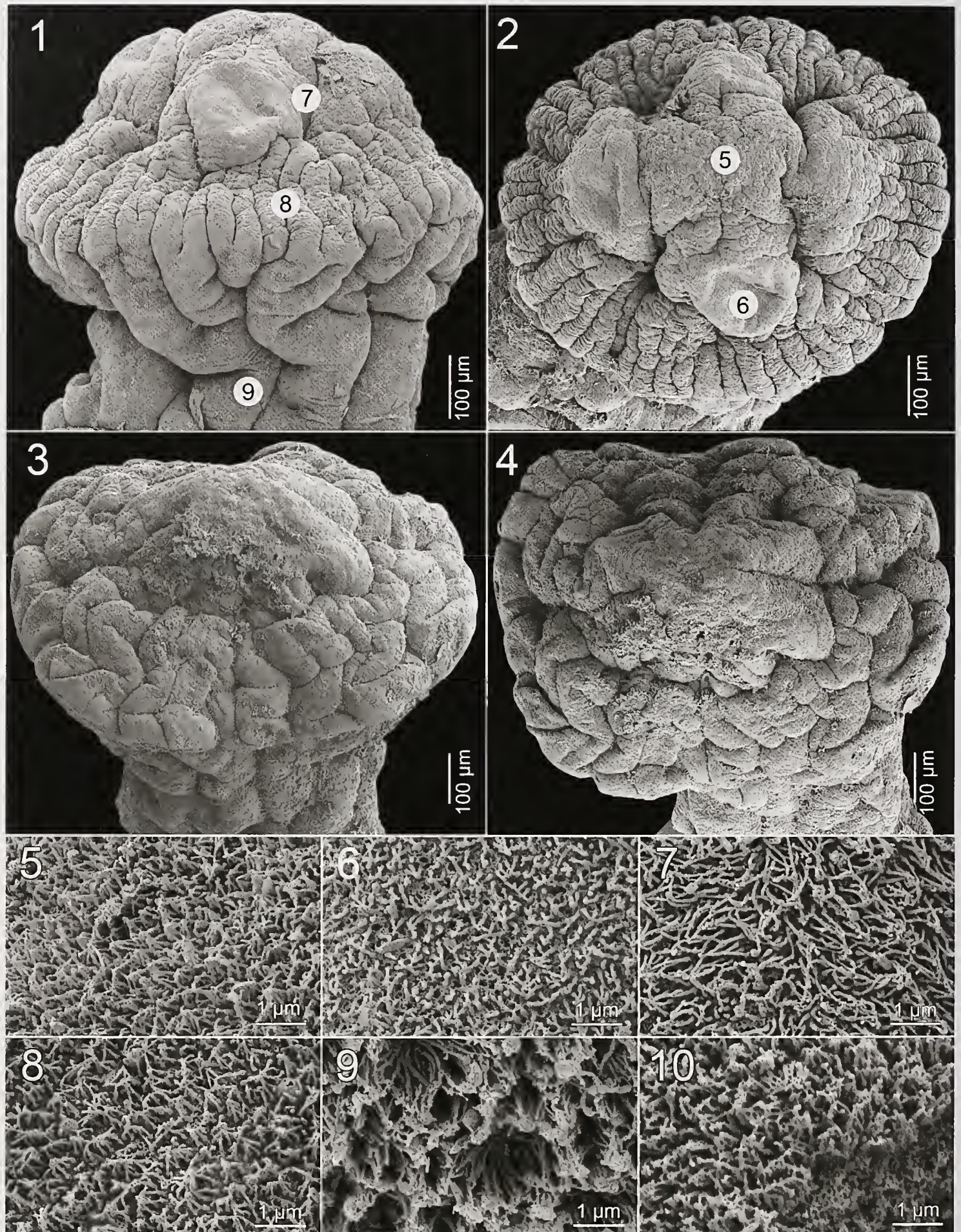
Testes numerous, spherical, small, 55–80 in diameter, in 1 or 2 irregular layers, 282–366 ( $x = 314$ ;  $n = 13$ ) [380–430] per mature proglottids (Figs 12, 16, 18). Testes form 1 irregular field on dorsal side, less numerous in median line of proglottids (uterine stem), usually surpassing osmoregulatory canals, dorsally overlapping cirrus-sac, vitelline follicles and sometimes ovary (Figs 12, 13, 16, 18). Testes present also in gravid proglottids.

Vas deferens coiled, with loops forming elongated field reaching to, but not crossing, median line of proglottid (Figs 12, 16, 18). Cirrus-sac pear-shaped, thin-walled, slightly widened towards distal (terminal) part (Figs 12, 13, 16, 18), 220–340 × 95–145 ( $n = 13$ ) [250–300 × 80–110], its length representing 10–21% ( $x = 15$ ;  $n = 13$ ) [14–25%] of proglottid width. Sperm duct (internal vas deferens) sinuous. Cirrus muscular, reaching up to 82% ( $n = 13$ ) [50%] of cirrus-sac length. Common genital atrium narrow, deep (Figs 12, 13, 16, 18). Genital pores alternating irregularly, markedly pre-equatorial, situated at 3–10% ( $x = 6$ ;  $n = 13$ ) [5–14%] of proglottid length from anterior margin (Figs 12, 16, 18).

Ovary with wide isthmus in medulla and 2 follicular, grape-like lobes penetrating inner longitudinal musculature to dorsal cortex; numerous dorsal outgrowths present (Figs 13, 17). Length of ovary represents 27–37% ( $x = 30$ ;  $n = 13$ ) [33–45%] of proglottid length, its width representing 57–76% ( $x = 68$ ;  $n = 13$ ) [74–86%] of proglottid width (Figs 16, 17). Mehlis' gland about 110–165 in diameter, representing 7–20% of proglottid width ( $n = 13$ ). Relative ovarian size, i.e., percentage of ovary surface to total surface of mature or pregravid proglottids (see de Chambrier *et al.*, 2012), 11–16% ( $x = 13$ ;  $n = 10$ ).

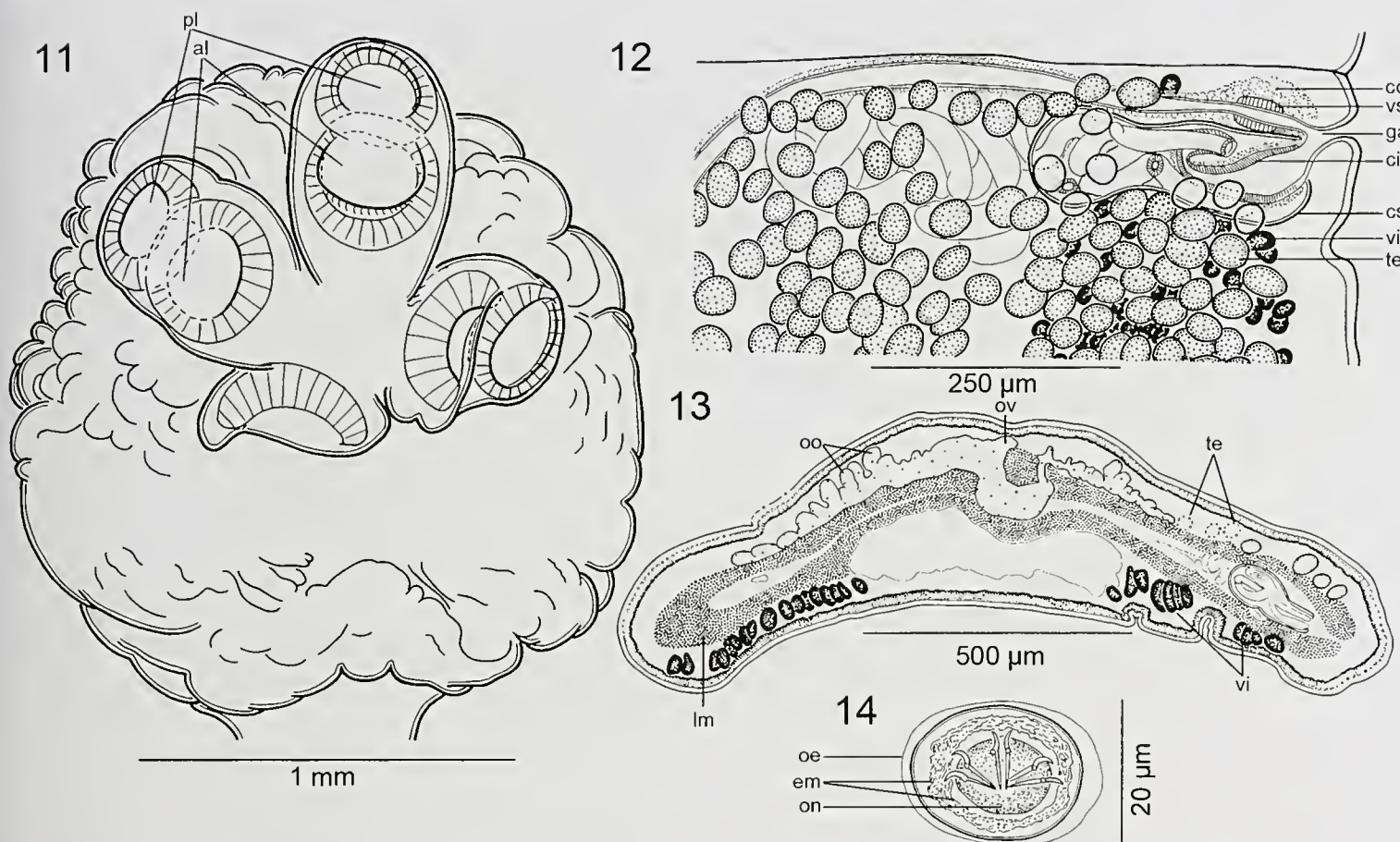
Vaginal canal slightly sinuous, surrounded by chromophilic cells, wider in terminal part (*pars copulatrix vaginae*), possessing a terminal vaginal sphincter (Figs 12, 16, 17). Vagina anterior to cirrus-sac ( $n = 35$ ). Vitelline follicles cortical, ventral, forming 2 long uninterrupted bands, occupying large triangular field, widened and confluent posteriorly at ovary level (Figs 13, 16, 17). Length of bands represents 77–94% ( $x = 86$ ) [94–98%] and 84–98% ( $x = 90$ ;  $n = 13$ ) [91–98%] of length of proglottid on poral and aporal side, respectively (Figs 12, 16).

Uterus cortical, with development of type 2 (see de Chambrier *et al.*, 2004b, 2015b); uterine stem and



Figs 1-10. Scanning electron micrographs of *Goezeella* spp. (1, 2, 5-9) *Goezeella mariae* n. sp. ex *Pimelodella cristata* (IPCAS C-759). (1, 2) Scoleces, dorsoventral and apical views, respectively. (5-9) Microtriches on the apex of scolex, lumen of suckers, surface between suckers and base of metascolex and neck, respectively. (3, 4, 10) *Goezeella siluri* Fuhrmann, 1916 ex *Pinirampus pirinampu* (MHNG-PLAT-21908). (3, 4) Scoleces, dorsoventral and apical views, respectively. (10) Microtriches on the surface of pregravid proglottids. Note: small black numbers correspond to the figures showing higher magnification images of these surfaces.





Figs 11-14. *Goezeella siluri* Fuhrmann, 1916 ex *Cetopsis coecutiens* (syntype MHNG-PLAT-36375). (11) Scolex, apical view. (12) Terminal genitalia, dorsal view. (13) Cross-section at ovary level. (14) Eggs drawn in distilled water. Abbreviations: al – anterior sucker loculus; cc – chromophilic cells; ci – cirrus; cs – cirrus-sac; em – bilayered embryophore; ga – genital atrium; lm – internal longitudinal musculature; oe – outer envelope; on – oncosphere; oo – ovary outgrowths; ov – ovary; pl – posterior sucker loculus; te – testes; vi – vitelline follicles; vs – vaginal sphincter.

diverticula (lateral uterine branches) in mature and pregravid proglottids lined with numerous chromophilic cells, extended much beyond branches (Fig. 16). Uterus with 20-26 [17-22] lateral diverticula on each side (Fig. 16). Eggs oval, outer envelope 22-23 × 19-20, bilayered embryophore 17-18 × 12-14 [21-22 × 14-22], oncosphere 11-12 × 9-10 [10-11 × 7-8], embryonic hooks 6-7 long (Fig. 19).

**Remarks:** The original description of *Goezeella siluri* was detailed and contained basic measurements and illustrations (Fuhrmann, 1916). However, the only complete specimen preserved is slightly decomposed, contracted and twisted on the slide. Moreover, Fuhrmann (1916) overlooked an important feature of the scolex morphology, i.e. the presence of biloculate, rather than uniloculate, suckers (compare the same scolex drawn in his Fig. 2 and Fig. 11 of the present study). This characteristic was first reported by Rego (1975; see his fig. 8), but not by Woodland (1933a) as reported by Brooks & Deardorff (1980). In fact, morphology of the suckers may be difficult to observe, especially if the suckers are hidden within wrinkles of a contracted metascolex (see Fig. 3).

The specimens from *P. pirinampu* are considered conspecific with *G. siluri* even though they differ from

those found in *C. coecutiens* described by Fuhrmann (1916) in the lower number of the testes (282-366 vs. 380-430), a longer cirrus (reaching up to 82% of the cirrus-sac length vs. reaching only up to 50%), and in the anterior extent of the bands of vitelline follicles on the poral side, which represents 77-94% of proglottids length vs. 94-98% in the syntype. These differences are considered to be accounted for by intraspecific variability, but poor quality of the type material of *G. siluri* should also be considered. Therefore, new material of *G. siluri* from its type host, *C. coecutiens*, is needed for confirmation of measurements taken from the type specimen.

Specimens from *Pseudocetopsis othonops* (syn. of *Cetopsis othonops*) in the Orinoco River, Venezuela, reported by Brooks & Rasmussen (1984) as *G. siluri*, possess the vagina anterior or posterior to the cirrus-sac, unlike the exclusively anterior position in all species of *Goezeella* including *G. siluri* and the newly described species (see below). This feature has been broadly used to differentiate species of proteocephalid cestodes (Arredondo & Gil de Pertierra, 2010; Gil de Pertierra & de Chambrier, 2013), but Alves *et al.* (2017b) described conspecific cestodes (genetically identical individuals based on the *lsr*DNA) with both the anterior and posterior vagina in relation to the cirrus-sac. Therefore, this

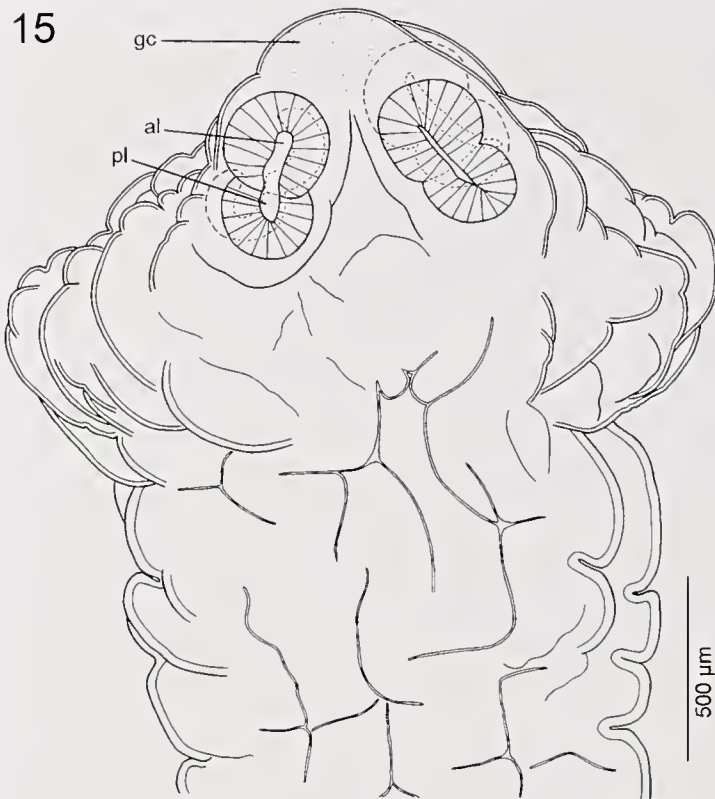


Fig. 15. *Goezeella siluri* Fuhrmann, 1916 ex *Pinirampus pirinampu* (MHNG-PLAT-21845). Scolex, dorso-ventral view. Abbreviations: al – anterior sucker loculus; gc – glandular cells; pl – posterior sucker loculus.

character should be considered with caution. Since all specimens from *P. othonops* were fixed in AFA (alcohol-formalin-acetic acid), they could not be used for DNA sequencing.

Brooks & Rasmussen (1984) also reported immature cestodes identified as *G. siluri* from *B. vaillantii*, but reliable identification of juvenile specimens is almost never possible because they lack key morphological traits that are present only in their mature forms. Two of the present authors (TS and AdC) have not found *G. siluri* in any of the 25 *B. vaillantii* examined (de Chambrier *et al.*, 2015a); therefore, this record of *G. siluri* in a species of *Brachyplatystoma* Bleeker requires verification.

***Goezeella danbrooksi* de Chambrier, Rego & Mariaux, 2004**

Figs 20, 21

*Goezeella siluri*. – Brooks & Deardorff, 1980: 15.

**Holotype:** USNM 1370061 (USNPC 74498), a whole-mounted specimen (2 slides) – USNM 1370107 (USNPC 74544), fragments on 19 slides of serial cross- and frontal sections.

**Type and only known locality:** Magdalena River near San Cristóbal, Province of Bolívar, Colombia.

**Type and only known host:** *Ageuieiosus pardalis*

Lütken (= *A. caucamus* Steindachner) (Siluriformes: Auchenipteridae).

**Site of infection:** Anterior intestine.

**Prevalence of infection:** Unknown.

**Morphological description:** Brooks & Deardorff (1980).

**Remarks:** The description of this species, which was originally identified as *G. siluri* by Brooks & Deardorff (1980), was based on a single specimen, which is partially decomposed. However, de Chambrier *et al.* (2004a) observed several morphological differences between this specimen and *G. siluri*, such as the position of the vitelline follicles, which are ventrolateral in *G. danbrooksi* (vs. only ventral in *G. siluri*), fewer testes (183-310 vs. 380-430), and the position of the vaginal sphincter (at a distance from the genital atrium in *G. danbrooksi* vs. terminal, i.e. close to the genital atrium in *G. siluri*). Based on these differences, de Chambrier *et al.* (2004a) proposed the new name, *G. danbrooksi*, for the tapeworm from *A. pardalis*.

Brooks & Deardorff (1980) reported the vitelline follicles to be present both in the ventral and dorsal cortex. However, the study of the holotype including its histological sections revealed that the follicles are only on the ventral side of the cortex, reaching only to its lateral margin (Figs 20, 21).

The study of the type material of *G. danbrooksi* also showed that some fibres of the inner longitudinal musculature are close together, thus somewhat resembling muscle bundles (Figs 20, 21). However, the tissue of histological sections is partially decomposed and thus a new, well fixed material of the species has to be examined to reveal the actual structure of the inner longitudinal muscles of *G. danbrooksi*.

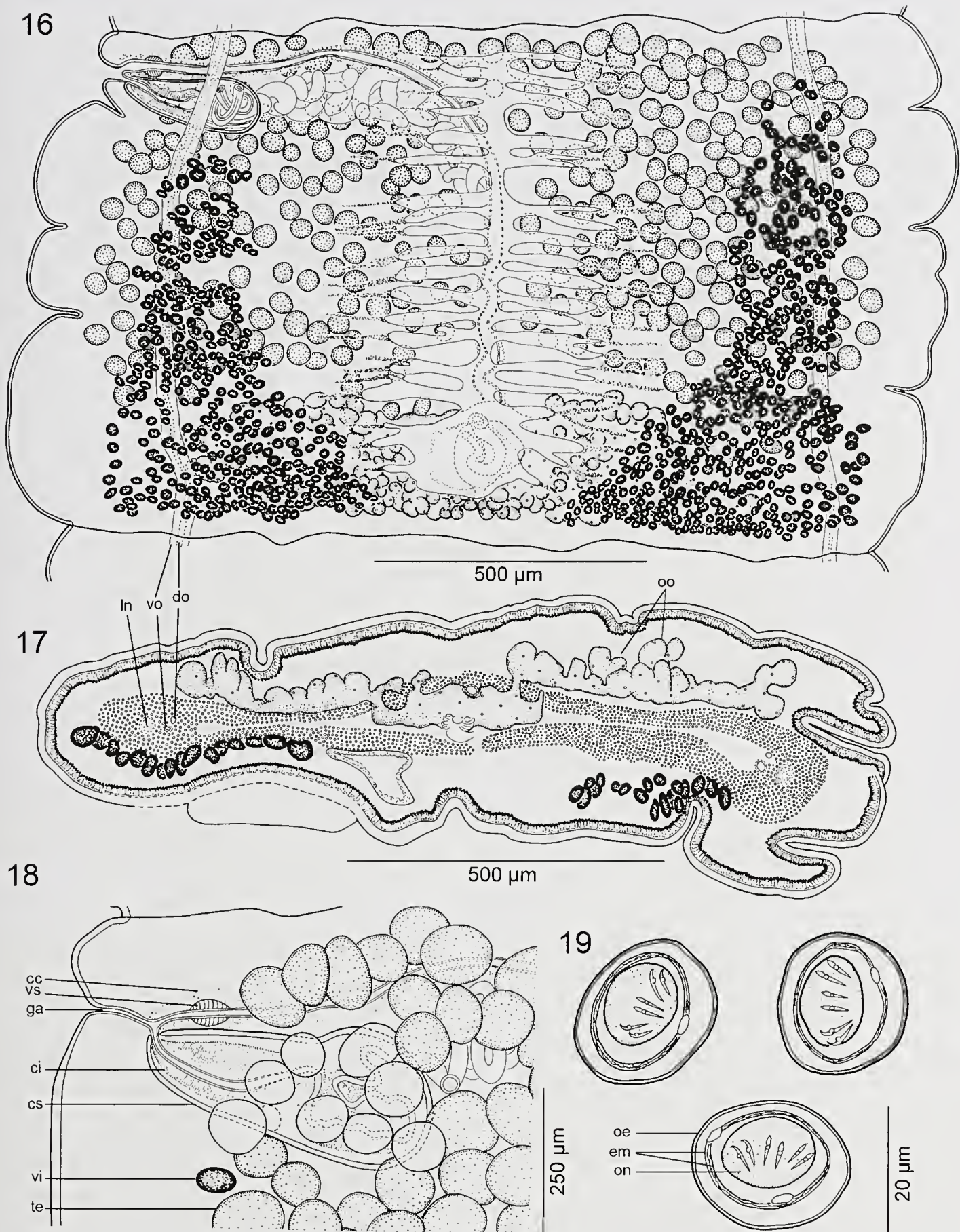
***Goezeella mariae* sp. nov.**

Figs 1, 2, 5-9, 22-30

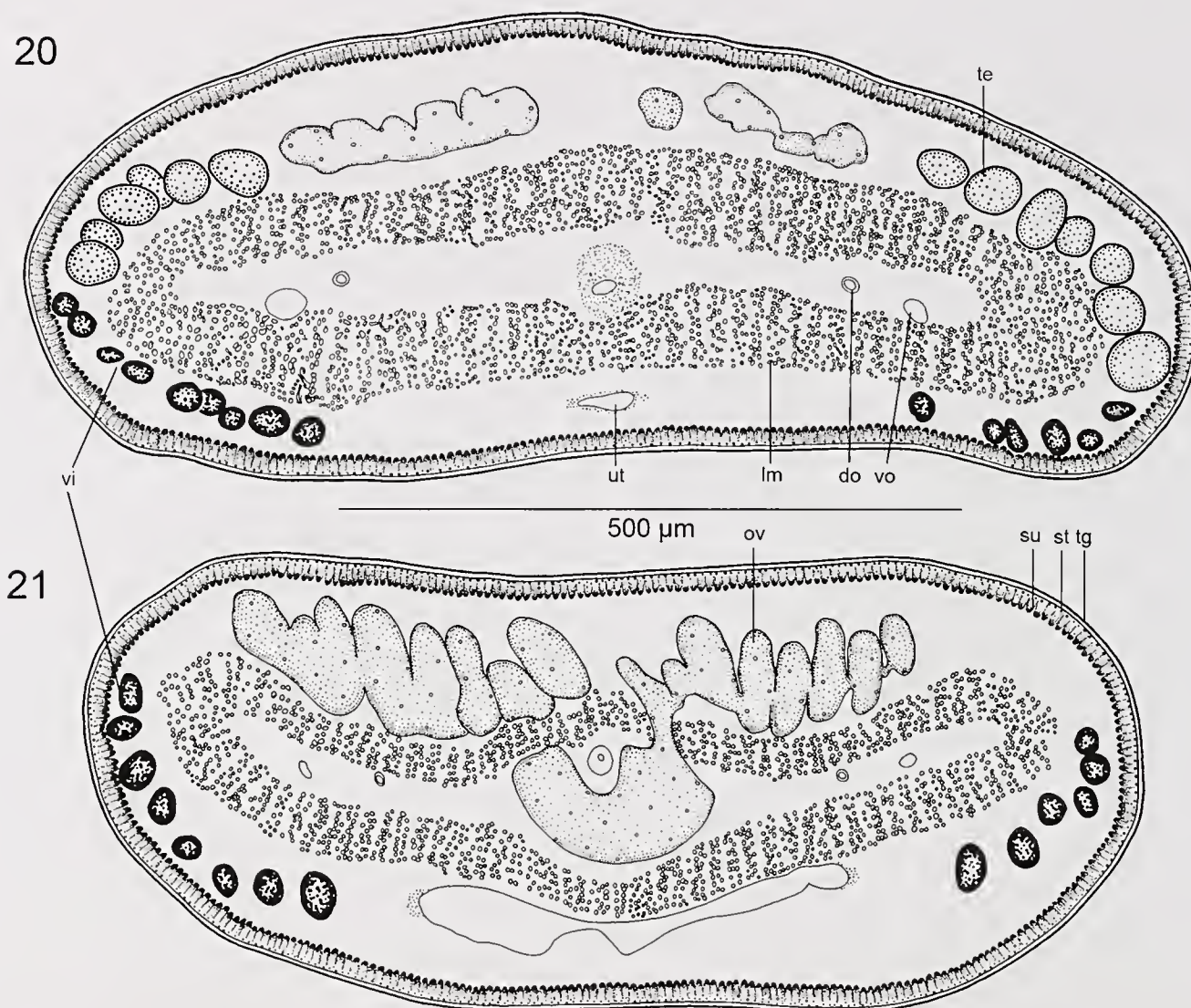
**Holotype:** CHIOC 38860a-f, a whole-mounted specimen (1 slide) and 5 slides of serial cross-sections, collected on 25.05.2013, host field no. BR AMP 46a. – MHNG-PLAT-97017 (2 slides of cross-sections).

**Paratypes:** IPCAS C-759, a whole-mounted specimen (1 slide; hologenophore), host field no. BR AMP 106b. – CHIOC 38861, IPCAS C-759, MHNG-PLAT-86883, a whole-mounted specimen (one slide), 6 slides of serial cross-sections and 2 slides of sagittal sections of scolex, host field No. BR AMP 109a. – MHNG-PLAT-97016, a whole-mounted specimen (one slide; SEM voucher), host field no. BR AMP 111b; all specimens collected on 25.05.2013.

**Type and only known locality:** Lowermost Amazon River near Macapá, State of Amapá, Brazil (00°01'N, 50°59'W).



Figs 16-19. *Goezeella siluri* Fuhrmann, 1916 ex *Pinirampus pirinampu*. (16) Pregravid proglottid, ventral view (MHNG-PLAT-21877). (17) Cross-section at ovary level (MHNG-PLAT-21879). (18) Terminal genitalia, dorsal view (MHNG-PLAT-21879). (19) Eggs drawn in distilled water (MHNG-PLAT-19858). Abbreviations: cc – chromophilic cells; ci – cirrus; cs – cirrus-sac; do – dorsal osmoregulatory canal; em – bilayered embryophore; ga – genital atrium; ln – longitudinal nerve cord; oe – outer envelope; on – oncosphere; oo – ovary outgrowths; te – testes; vi – vitelline follicle; vo – ventral osmoregulatory canal; vs – vaginal sphincter.



Figs 20-21. *Goezeella danbrooksi* de Chambrier, Rego & Mariaux, 2004 ex *Ageneiosus pardalis* (holotype, USNM 1370061). (20) Cross-section at middle part of proglottid. (21) ovary level. Abbreviations: do – dorsal osmoregulatory canal; lm – internal longitudinal musculature; ov – ovary; st – subtegumental muscle fibres; su – subtegumental cells; te – testes; tg – tegument; ut – uterus; vi – vitelline follicles; vo – ventral osmoregulatory canal.

**Type and only known host:** *Pimelodella cristata* (Müller & Troschel) (Siluriformes: Heptapteridae).

**Site of infection:** Anterior intestine.

**Prevalence:** 7 fish examined/4 fish infected (57%).

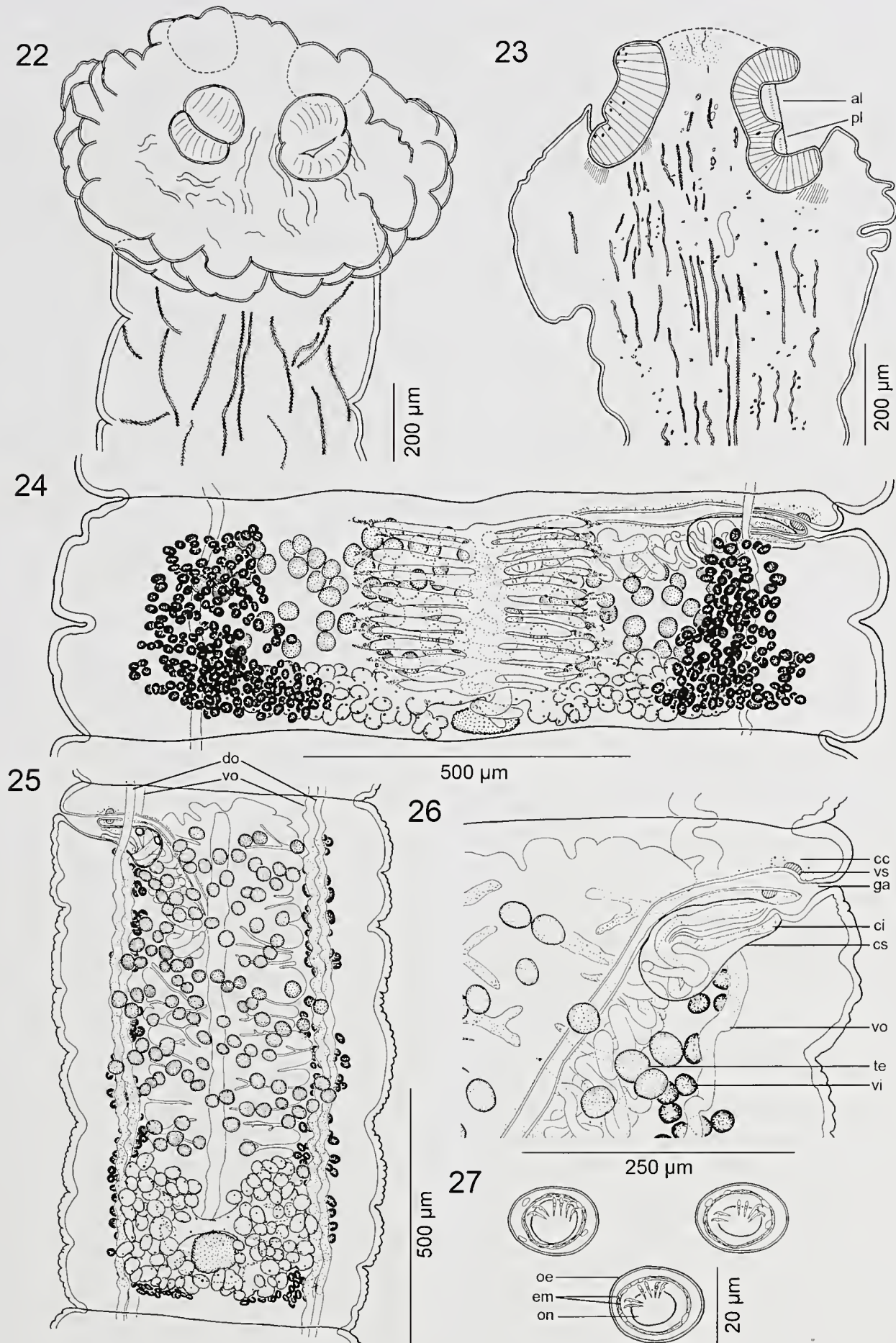
**Representative DNA sequences:** A fragment 1491bp long of the *Isr*-DNA (D1–D3 domains) (GenBank MF370208).

**Etymology:** The species is dedicated to the first author's mother, Maria Thereza Vieira Pinto Alves, for providing continuous support for his studies.

**Description:** (based on 4 whole-mounted worms; 13 slides with serial cross-sections of mature proglottids and 2 slides with sagittal sections of 1 scolex; 1 scolex studied using SEM). Proteocephalidae. Testes, ovary, vitelline follicles and uterus cortical; small-sized worm. Total body length 14–38 mm ( $n = 3$ ), maximum width up to 1.3 mm ( $n = 3$ ). Strobila acraspedote, anapolytic, with longitudinal and transverse grooves, consisting of

about 40–90 proglottids: 27–32 immature, 4–8 mature, 10–15 pregravid and 23–39 gravid. Immature and mature proglottids much wider than long (length: width ratio 0.17–0.35), pregravid proglottids markedly wider than long (length: width ratio 0.40–0.76) and gravid proglottids slightly wider than long to much longer than wide (length: width ratio 0.80–2.60).

Scolex 0.68–0.83 × 0.91–1.15 mm ( $n = 3$ ), much wider than neck (proliferation zone), 0.83–1.20 × 0.75–0.81 mm, bearing 4 biloculate suckers, with loculi unequal in size; anterior loculus 158–161 ( $x = 160$ ;  $n = 3$ ) in diameter, posterior loculus 123–126 ( $x = 125$ ;  $n = 3$ ) in diameter; loculi separated by inconspicuous interocular septum (Figs 1, 2, 22, 23). Metascolex present, more wrinkled than neck (Figs 1, 2, 22). Apex rounded, lacking apical organ, with few gland cells (Figs 1, 2, 22, 23). Apex of scolex, lumen of suckers, surface between suckers and base of metascolex covered with acicular filitriches, less dense on lumen of suckers (Figs 5–8); neck covered with capilliform filitriches (Fig. 9).



Figs 22-27. *Goezeella mariae* sp. nov. ex *Pimelodella cristata*. (22) Scolex, dorsoventral view (holotype, CHIOC 38860a). (23) Scolex, sagittal section (paratype, CHIOC 38861). (24) Pre gravid proglottid, ventral view (paratype MHNG-PLAT-97016). (25) Gravid proglottid, dorsal view (holotype, CHIOC 38860a). (26) Terminal genitalia, dorsal view (holotype, CHIOC 38860a). (27) Eggs drawn in distilled water (paratype IPCAS C-759). Abbreviations: al – anterior sucker loculus; cc – chromophilic cells; ci – cirrus; cs – cirrus-sac; do – dorsal osmoregulatory canal; em – bilayered embryophore; ga – genital atrium; oe – outer envelope; on – oncosphere; pl – posterior sucker loculus; te – testes; vi – vitelline follicles; vo – ventral osmoregulatory canal; vs – vaginal sphincter.

Inner longitudinal musculature well-developed, formed by numerous, individual muscle fibres not forming compact bundles, more concentrated laterally (Figs 28-30). Osmoregulatory canals situated at same level of lateral-most testes, median to vitelline follicles, markedly sinuous (Figs 24-26, 28-30); ventral osmoregulatory canal wider than dorsal one (Fig. 30).

Testes numerous, spherical to oval, small, 34-46 in diameter, in 1 irregular layer, 103-167 ( $x = 134$ ;  $n = 13$ ) per mature proglottid (Figs 24, 25). Testes form 1 irregular field on dorsal side, less numerous alongside median line of proglottids (uterine stem), usually reaching laterally to osmoregulatory canals, dorsally overlapping cirrus-sac, vitelline follicles and sometimes ovary (Figs 24-26, 28-30). Testes present also in gravid proglottids.

Vas deferens coiled, with loops forming elongate field reaching to, but not crossing, median line of proglottid (Figs 24-26). Cirrus-sac elongated to pear-shaped, thin-walled (Figs 24-26, 28),  $130-213 \times 59-85$  ( $n = 13$ ), its length representing 11-24% ( $x = 17$ ;  $n = 13$ ) of proglottid width. Sperm duct (internal vas deferens) sinuous (Figs 24-26, 28). Cirrus muscular, reaching up to 64% ( $n = 13$ ) of cirrus-sac length. Common genital atrium narrow, deep (Figs 24-26, 28). Genital pores alternating irregularly, markedly pre-equatorial, situated at 7-17% ( $x = 11$ ;  $n = 13$ ) of proglottid length from anterior margin (Figs 24-26).

Ovary with wide isthmus in medulla and two follicular, grape-like lobes penetrating to dorsal cortex; numerous dorsal outgrowths present (Figs 24, 25, 30). Length of ovary represents 21-31% ( $x = 26\%$ ;  $n = 13$ ) of proglottid length, its width representing 57-77% ( $x = 66\%$ ;  $n = 13$ ) of proglottid width (Figs 24, 25). Mehlis' gland about 60-138 in diameter, representing 8-11% of proglottid width ( $n = 13$ ). Relative ovarian size, i.e., percentage of ovary surface to total surface of mature or pregravid proglottids (see de Chambrier *et al.*, 2012), 10-15% ( $x = 12\%$ ;  $n = 13$ ).

Vaginal canal slightly sinuous, surrounded by chromophilic cells, wider in terminal part (*pars copulatrix vaginae*); terminal vaginal sphincter present (Figs 24-26). Vagina anterior to cirrus-sac ( $n = 32$ ). Vitelline follicles cortical, ventral, forming 2 long uninterrupted bands, occupying large triangular field, widened and confluent posteriorly at ovary level; lateral to lateral-most testes (Figs 24-26, 29). Length of bands represents 73-91% ( $x = 83\%$ ) and 72-91% ( $x = 83\%$ ) of length of proglottid on poral and aporal side, respectively ( $n = 13$ ) (Figs 24, 25). Uterus cortical, with development of type 2 (see de Chambrier *et al.*, 2004b, 2015b); uterine stem and diverticula (lateral uterine branches) in mature and pregravid proglottids lined with numerous chromophilic cells, extended much beyond branches (Fig. 24). Uterus with 14-25 lateral diverticula on each side (Figs 24, 25). Eggs oval, outer envelope  $21-25 \times 18-19$ , bilayered embryophore  $19-20 \times 13-15$ , oncosphere  $9-10 \times 11-12$ , embryonic hooks 5-6 long (Fig. 27).

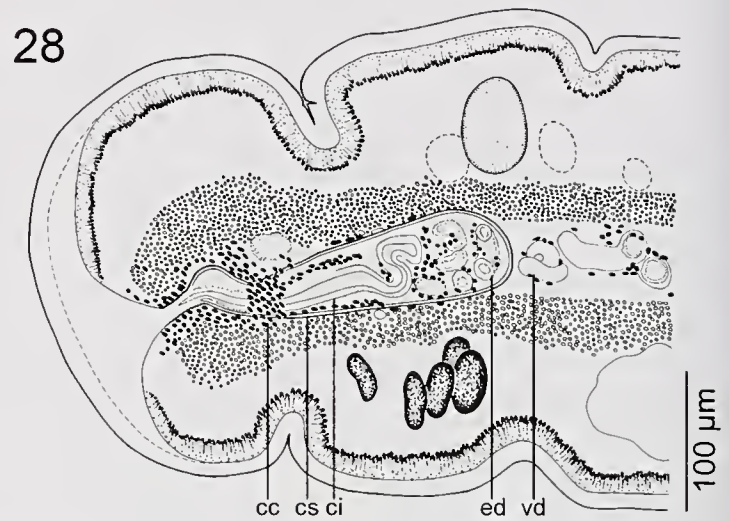
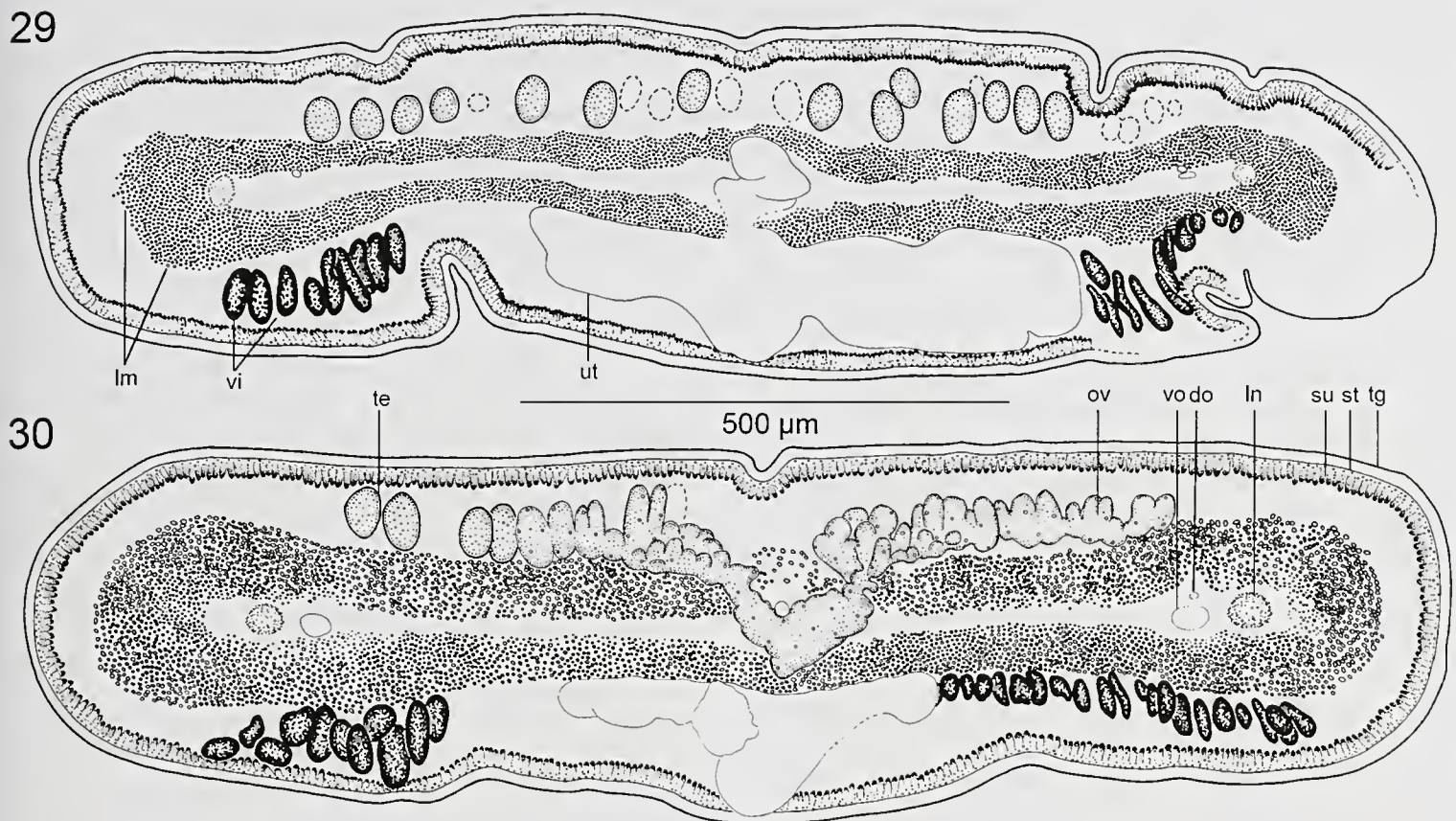


Fig. 28. *Goezeella mariae* sp. nov. ex *Pimelodella cristata*. Cross-section at the cirrus-sac level (holotype, CHIOC 38860d). Abbreviations: cc – chromophilic cells; ci – cirrus; cs – cirrus-sac; ed – ejaculatory duct; va – vas deferens.

**Remarks:** *Goezeella mariae* sp. nov. differs from *G. siluri* and *G. danbrooksi* in having fewer testes (103-167 vs. 183-310 and 282-366 in *G. danbrooksi* and *G. siluri*, respectively) and inconspicuous interocular septum (not obvious in SEM images; see Figs 1, 2), rather than the septum conspicuous as in the two other species. The new taxon can be further distinguished from *G. siluri* by its smaller dimensions, such as the total body length (14-38 mm vs. 90-230 mm), scolex width (0.91-1.15 mm vs. 1.45-1.94 mm) and the length of the cirrus-sac ( $130-213 \mu\text{m}$  vs.  $220-340 \mu\text{m}$ ) as well as the appearance of the metascolex, which is more wrinkled in *G. mariae* sp. nov. compared to that of *G. siluri*; compare Figs 1, 2 with Figs 3, 4. Moreover, *G. mariae* sp. nov. possesses a terminal, rather than markedly subterminal, vaginal sphincter as it is in *G. danbrooksi*.

The new species differs in its sequence of the partial *lsr*-DNA gene (D1–D3 domains) from that of *G. siluri* from *P. piriuauyu* in 14 nucleotides, i.e. genetic divergence 0.9%. A phylogenetic analysis (data not shown) revealed both taxa clustered in a clade comprising also both known species of *Gibsoniela* Rego, 1984, i.e. *G. mandube* (Woodland, 1935) and *G. neursaulti* de Chambrier & Vaucher, 1999, parasites of the auchenipterid catfish *Ageneiosus inermis* (Linnaeus, 1766) in the Neotropical Region, but interrelations within this lineage remain unresolved. Close relationship of species of *Goezeella* with those of the genus *Gibsoniela* is not evident based on their morphology, because they differ in the position of the internal organs in relation to the inner longitudinal musculature (previously used to distinguish individual subfamilies – see Rego, 1994), but also by the morphology of the scolex (no metascolex in the latter genus) and their suckers (biloculate in *Goezeella* vs.



Figs 29-30. *Goezeella mariae* sp. nov. ex *Pimelodella cristata*. (29) Cross-section at middle part of proglottid (holotype, CHIOC 38860d). (30) Cross-sections at ovary level (paratype MHNG-PLAT-86883). Abbreviations: do – dorsal osmoregulatory canal; lm – internal longitudinal musculature; ln – longitudinal nerve cord; ov – ovary; st – subtegumental muscle fibres; su – subtegumental cells; te – testes; tg – tegument; ut – uterus; vi – vitelline follicles; vo – ventral osmoregulatory canal.

triloculate in *Gibsoniella*) (Rego, 1984; de Chambrier & Vaucher, 1999).

To the best of our knowledge, this is the first parasite found in *Pimelodella cristata*. This heptapterid catfish was described from a tributary of the Branco River, Guyana (Bockmann & Guazzelli, 2003) and is distributed throughout the Amazon River basin, inhabiting the sand bottom of creeks and rivers (Reis & Lima, 2009). *Proteocephalus bagri* Holcman-Spector & Mañé-Garzón, 1988 and *P. rhamdiae* Holcman-Spector & Mañé-Garzón, 1988, both from *Rhamdia sapo* (Valenciennes) [syn. of *Rhamdia quelen* (Quoy & Gaimard)] in Uruguay, are the only other proteocephalids known from heptapterids in South America (Holcman-Spector & Mañé-Garzón, 1988). In addition, *Proteocephalus brooksi* García-Prieto, Rodríguez & Pérez-Ponce de León, 1996 was described from *Rhamdia guatemalensis* (Günther) in Mexico by García-Prieto *et al.* (1996).

## DISCUSSION

The present study provides a new insight into the taxonomy, species composition and host associations of *Goezeella*, one of insufficiently known genera of Neotropical proteocephalid cestodes. An important

feature newly added into an amended generic diagnosis is the unique arrangement of the inner longitudinal musculature, which does not form compact bundles as usually in proteocephalids (Rego, 1994). In contrast, the musculature in species of *Goezeella* is formed by numerous individual muscle fibres not forming such bundles. The exclusively ventral or ventrolateral position of the vitelline follicles and the possession of a metascolex with numerous, largely longitudinal wrinkles and biloculate suckers, represent other typical characteristics of this genus.

Species of *Rudolphiella* Fuhrmann, 1916 and *Ephedrocephalus* Diesing, 1850 also have the vitelline follicles restricted to the ventral cortex (not in the dorsal field as given in the key of de Chambrier *et al.*, 2009; see Rego *et al.*, 1999 and Gil de Pertierra & de Chambrier, 2000). However, they differ markedly from *Goezeella* by their topography of the genital organs in relation to the inner longitudinal musculature (see Rego, 1994) and possess the uniloculate, rather than biloculate, suckers (Mola, 1906; Gil de Pertierra & de Chambrier, 2000). *Spatulifer maringaensis* Pavanelli & Rego, 1989, which also shares the same distribution of the internal organs in relation to the inner musculature with *Goezeella* (both were previously placed in the Monticelliinae), and possesses a metascolex and the vitelline follicles limited to the

**Identification key to the species of *Goezeella* Fuhrmann, 1916**

- 1A Vaginal sphincter at a distance from genital atrium; vitelline follicles ventrolateral. In auchenipterids (*Ageneiosus pardalis*) ..... *G. danbrooksi*
- 1B Vaginal sphincter near genital atrium (terminal); vitelline follicles only on ventral side of cortex, missing laterally ..... 2
- 2A Much more than 200 testes per proglottid. In cetopsids (*Cetopsis*) and pimelodids (*Pinirampus*) ..... *G. siluri*
- 2B Much fewer than 200 testes per proglottid. In heptapterids (*Pimelodella cristata*) ..... *G. mariae* sp. nov.

ventral cortex (Arredondo & Gil de Pertierra, 2008), bears only uniloculate suckers, rather than biloculate as in species of *Goezeella*.

Species of *Goezeella* including *G. mariae* sp. nov. have been found in the Amazon and Orinoco River basins, whereas no published record exists from the Paraná River basin. The spectrum of definitive hosts of this genus, i.e. fishes of four siluriform families (Auchenipteridae, Cetopsidae, Heptapteridae and Pimelodidae) is markedly wider than typical for comparably species-rich genera of Neotropical proteocephalids, which are usually specific to only a single fish family (Rego *et al.*, 1999; de Chambrier *et al.*, 2015a).

Several attempts have been made to assess the phylogenetic relationships of the species-rich fauna of Neotropical proteocephalids, but their actual interrelations remain unclear (Zehnder & Mariaux, 1999; de Chambrier *et al.*, 2004b; Hypša *et al.*, 2005; de Chambrier *et al.*, 2015a). Neither the addition of terminal taxa, nor the use of new molecular markers seem to have improved the phylogenetic signal of the large polytomy of the ‘Neotropical superclade’ (de Chambrier *et al.*, 2015a), where *G. siluri* ex *P. pirinaupu* appears together with 37 taxa (including 29 taxa from Neotropical fishes). This lack of phylogenetic resolution was also observed in the recent published studies by Alves *et al.* (2017b) and Arredondo *et al.* (2017). Therefore, no tree is presented in this paper. Addition of a new sequence (a representative of *G. mariae* n. sp.) also did not increase resolution of this clade, but revealed this new taxon within a small clade comprising *G. siluri* and both species of *Gibsoniella*. In contrast, molecular data on *G. danbrooksi* are not available to assess its interrelations to the remaining congeners and thus new material should be collected, similarly as specimens of *G. siluri* from the type host. All attempts of the present authors, who examined seven *C. coecutiens* between 1992 and 1995, to find this cestode in this fish host have failed.

Caira *et al.* (2014) proposed a new order, Oncho-proteocephalidea Caira, Jensen, Waeschenbach, Olson & Littlewood, 2014, to group together phylogenetically closely related, but morphologically and ecologically conspicuously dissimilar hook-bearing parasites of elasmobranchs, placed previously in the ‘tetrphyllidean’ family Onchobothriidae Braun, 1900, with parasites of freshwater bony fishes, amphibians and reptiles of the former order Proteocephalidea Mola, 1926. The

authors speculated that the allegedly synapomorphy of both distinct groups could be the presence of gladiate spinitriches on the strobila. However, these spinitriches were observed neither in *G. siluri* nor *G. mariae* sp. nov., similarly as they are absent in other proteocephalids studied using SEM (e.g. Arredondo *et al.*, 2017). Therefore, identification of morphological synapomorphies for members of this newly erected, conspicuously heterogeneous order is still pending (Arredondo *et al.*, 2014).

To help identify the species of *Goezeella*, a simple morphology-based key is presented above.

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## Systematic notes on some leptomedusa species with a description of *Neotima galeai* n. spec. (Hydrozoa, Cnidaria)

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**Abstract:** This work reports upon observations and identifications of 18 leptomedusae, mostly documenting specimens which have been used for previous molecular phylogenetic studies. All species are illustrated, for some of them links to electronically archived photos are provided. The taxonomy of some genera and species is discussed. The diagnosis of the genus *Neotima* Petersen, 1962 is modified to accommodate the new species *Neotima galeai*, the only member of the genus with subdivided gonads. *Entima sapinhoa* Narchi & Hebling, 1975 is transferred to the genus *Neotima* as *Neotima sapinhoa* (Narchi & Hebling, 1975) n. comb. *Helgicirrha schulzii* Hartlaub, 1909 and *Tima plana* Neppi, 1910 are both regarded as junior synonyms of *Helgicirrha cari* (Haeckel, 1864). *Eirene octonemalis* Guo, Xu & Huang, 2008 is a new junior synonym of *Eirene hexanemalis* (Goette, 1886).

**Keywords:** Marine hydromedusae - Leptothecata - taxonomy - DNA barcoding - new species - digital archive.

### INTRODUCTION

This work reports upon observations and identifications of a number of leptomedusae I have examined during recent years. Many of the animals were used to extract DNA for molecular genetic analyses that have been published elsewhere (e.g. Leclère *et al.*, 2009; Schuchert *et al.*, 2017) or have simply been deposited in GenBank, and for which it was desirable to have more published details on their identification. Comparing DNA sequences (barcodes) has opened many new possibilities in hydrozoan systematics (e.g. Schuchert, 2016; Schuchert *et al.*, 2017, and references therein). However, for many DNA sequences of hydrozoans deposited in GenBank, no information on the species identification is available. This causes sometimes considerable problems when new sequences result in conflicting taxonomic identities and one must assume that a misidentification could be at the origin of the conflict. Ideally, these problems can be resolved relatively easily if voucher specimens are available in public collections and they are cited in the GenBank record. Especially for small hydromedusae, however, it is often not possible to deposit a voucher as the whole specimen is used to extract the DNA for the subsequent sequencing. Photos or drawings of such specimens are thus the only available proof for a correct identification. These illustrations can be deposited e.g. in the BOLD database together with the COI sequences

derived from these samples. This possibility is not readily available for other sequence types deposited in GenBank and it is unfortunate that the identities of many sequences in GenBank remain uncertain and not re-examinable (a parallel problem exists for distributional records, comp. Lindsay *et al.*, 2017). In a taxonomic/systematic context, it is thus essential that the species identifications of published DNA sequences can be verified either by depositing voucher material, publishing descriptions and illustrations of the material, or by submitting photos or drawings to electronic archives. These archives can be institutional libraries, open or commercial archiving services etc. Important in this context is that a DOI number is obtained for the dataset and that a long period of digital preservation is guaranteed. With a DOI number, the documented specimens can be cited and if needed their taxonomy revised in the future.

Hydromedusae collected with plankton nets are rarely obtained in perfect condition. Mostly they are damaged or at least deformed and they do not lend themselves to take publication-quality photos. In such cases, drawings are still one of the best tools to document and publish the identification process. However, also lesser quality photos, which cannot be published in a scientific publication, may still be valuable for other specialists and may serve as proof of a correct identification. This type of data is best submitted as electronic archival material as mentioned above and as it has been done

for several samples of this study and also of previous publications (see Table 1). The DOI numbers can even be cited in the GenBank entries (see e.g. KX355450), thus creating an easy way to verify the identity of a sample. The current repository of any electronic document with a DOI number can easily be accessed by adding the text “<https://doi.org/>” in front of the DOI code and using the whole string as an address in a web browser. More such archived illustrations will be deposited in future and it is hoped that other systematists who generate and publish DNA sequences – or, by the way, also distribution records – might also adopt this approach (*cf.* Whitlock, 2011; Roche *et al.*, 2015 and references therein).

## MATERIAL AND METHODS

For collecting and examining hydromedusae see e.g. Russell (1953), Brinckmann-Voss (1970), Bouillon (1978b), Cornelius (1995), Schuchert (2012), Schuchert *et al.* (2017).

The molecular genetic methods used are described in Schuchert (2005, 2016) and Schuchert *et al.* (2017). DNA isolate numbers refer to DNA extracts in TE buffer kept in the DNA collection of the MHNG. Sequences can be retrieved from GenBank via <https://www.ncbi.nlm.nih.gov/nucleotide/>.

Medusae were either drawn after living or formalin-

preserved material and do not necessarily represent an individual but a composite of several specimens. Inspired by the style of Mayer (1910), schematic illustrations was here preferred over a realistic depiction of the preserved specimen which often obscures the proportions.

Drawings were always made with pencil and then later inked using the image editor software GIMP ([www.gimp.org](http://www.gimp.org)).

Not all family and genus diagnoses and synonyms are given here. These can be found in Schuchert (2017a). Although all known synonyms are given for each species, only the most important citations and references are provided. Usually a source with a more complete list is included.

For the photos and the specimen data (Table 1), pdf files were created using MS Word and then deposited in the ZENODO archive, a free repository of research data (<http://about.zenodo.org/>).

Abbreviations:

NHMD	Natural History Museum of Denmark
MHNG	Muséum d’histoire naturelle de Genève, Switzerland
NIWA	National Institute of Water and Atmospheric Research, Wellington, New Zealand
GenBank	Genetic sequence database of the National Institute of Health, USA <a href="http://www.ncbi.nlm.nih.gov/genbank/">http://www.ncbi.nlm.nih.gov/genbank/</a>

Table 1. Accessory material (photos of specimens) of selected leptomedusae.

Family	species	locality	DNA isolate	DOI (with links)
Campanulariidae	<i>Clytia gregaria</i>	USA, San Juan Islands	920 & 1169	<a href="https://doi.org/10.5281/zenodo.495304">https://doi.org/10.5281/zenodo.495304</a>
Campanulariidae	<i>Clytia islandica</i>	Norway, Raunefjord	1112	<a href="https://doi.org/10.5281/zenodo.495407">https://doi.org/10.5281/zenodo.495407</a>
Campanulariidae	<i>Clytia spec.</i>	Norway, Korsfjord	1183	<a href="https://doi.org/10.5281/zenodo.165754">https://doi.org/10.5281/zenodo.165754</a>
Eirenidae	<i>Eutima gracilis</i>	Sweden, Kristineberg	1063	<a href="https://doi.org/10.5281/zenodo.495383">https://doi.org/10.5281/zenodo.495383</a>
Eirenidae	<i>Eutima gegenbauri</i>	Sweden, Kristineberg	1062	<a href="https://doi.org/10.5281/zenodo.495387">https://doi.org/10.5281/zenodo.495387</a>
Eirenidae	<i>Tima bairdii</i>	Norway, Fanafjord	1116	<a href="https://doi.org/10.5281/zenodo.495392">https://doi.org/10.5281/zenodo.495392</a>
Eireniidae	<i>Eutonina indicans</i>	Norway, Fanafjord	1110	<a href="https://doi.org/10.5281/zenodo.495355">https://doi.org/10.5281/zenodo.495355</a>
Laodiceidae	<i>Laodicea undulata</i>	Sweden, Kristineberg	1137	<a href="https://doi.org/10.5281/zenodo.46237">https://doi.org/10.5281/zenodo.46237</a>
Laodiceidae	<i>Laodicea undulata</i>	France, Villefranche-sur-Mer	1151	<a href="https://doi.org/10.5281/zenodo.165741">https://doi.org/10.5281/zenodo.165741</a>
Laodiceidae	<i>Stauroidiscus gotoi</i>	New Zealand, Hauraki Gulf	126	<a href="https://doi.org/10.5281/zenodo.55257">https://doi.org/10.5281/zenodo.55257</a>
Laodiceidae	<i>Staurostoma mertensii</i>	Norway, Fanafjord	1114	<a href="https://doi.org/10.5281/zenodo.495373">https://doi.org/10.5281/zenodo.495373</a>
Melicertidae	<i>Melicertum octocostatum</i>	Norway, Korsfjord	1161	<a href="https://doi.org/10.5281/zenodo.165766">https://doi.org/10.5281/zenodo.165766</a>
Mitrocomidae	<i>Cosmetira pilosella</i>	Norway, Korsfjord	1165	<a href="https://doi.org/10.5281/zenodo.165761">https://doi.org/10.5281/zenodo.165761</a>
Mitrocomidae	<i>Halopsis ocellata</i>	Norway, Raunefjord	1111	<a href="https://doi.org/10.5281/zenodo.495359">https://doi.org/10.5281/zenodo.495359</a>
Mitrocomidae	<i>Mitrocomella polydiademata</i>	Scotland, Dunstaffnage Bay	1133	<a href="https://doi.org/10.5281/zenodo.495337">https://doi.org/10.5281/zenodo.495337</a>
Mitrocomidae	<i>Mitrocomella polydiademata</i>	Norway, Fanafjord	1115	<a href="https://doi.org/10.5281/zenodo.495350">https://doi.org/10.5281/zenodo.495350</a>
Mitrocomidae	<i>Tiaropsis multicirrata</i>	Norway, Raunefjord	437	<a href="https://doi.org/10.5281/zenodo.495413">https://doi.org/10.5281/zenodo.495413</a>

**BOLD** The Barcode of Life Data System, see Ratnasingham & Hebert (2007).  
**DOI** Digital Object Identifier  
**COI** Cytochrome Oxidase I  
**16S** 16S mitochondrial ribosomal RNA gene sequence

## TAXONOMY

**Family Melicertidae L. Agassiz, 1862**  
**Genus *Melicertum* sensu L. Agassiz, 1862**

***Melicertum octocostatum* (M. Sars, 1835)**

Fig. 1A-B

*Oceania octocostata* M. Sars, 1835: 24, pl. 4 fig. 9a-d.  
*Melicertum campanula*. – Agassiz, 1862: 349. – Mayer, 1910: 207, pl. 23 figs 4-5, pl. 24 fig. 5. – Naumov, 1969: 350, figs 215-216. [not *Medusa campanula* Fabricius, 1780 = ? *Catablema vesicarium*]  
*Melicertum octocostatum*. – Kramp, 1919: 52, pl. 1 fig. 10, pl. 3 fig. 8. – Kramp & Damas, 1925: 294. – Russell, 1953: 245, figs 138-142, pl. 13 figs 2-4. – Kramp, 1959a: 134, fig. 152. – Kramp, 1961: 136. – Kramp, 1968: 63, fig. 164. – Arai & Brinckmann-Voss, 1980: 79, figs 44-45. – Bouillon, 1984: 87. – Cornelius, 1995: 124, fig. 17. – Okuizumi & Kubota, 2003: 39, fig. 1. – Wang *et al.*, 2014: 99, fig. 16.

**Material examined:** MHNG-INVE-48744, 3 specimens 4-5 mm wide and with up to 40 larger tentacles; Norway, Raunefjord, 60.2731°N 5.20728°E, 10 m depth; collection date 14.06.2006; one specimen used for DNA extraction, DNA isolate 433, 16S sequence FJ550510, 18S FJ550595, 28S FJ550451. – MHNG-INVE-94100, one of >4 specimens; Norway, Korsfjord, 60.1846°N 5.196°E; one other specimen used to obtain DNA isolate 1161, 16S KY363951, 18S KY363981, for archived photos see Table 1, remaining medusae used to extract RNA for transcriptome analysis.

**Diagnosis:** Umbrella 5-20 mm wide and high, conical to pyriform with thick, solid apex and thinner sides; per octant 3-7 fine, radial, subumbrellar tissue-thickenings with or without nematocysts (may be absent, or present in fully grown animals only); 40-80 large tentacles alternating with as many small ones, with distinct basal bulb formation; no ocelli, no cirri. Stomach short and broad, octagonal, mouth with 8 small lips when fully grown. 8 sinuous, linear gonads covering almost the full length of the 8 radial canals, getting thicker towards periphery. Colours: stomach and gonads yellow. For polyp stage see Cornelius (1995).

**Remarks:** No subumbrellar nematocysts could be seen in the present animals which were relatively young (small). The tissue thickenings were present though.

**Distribution:** A strictly coastal species occurring in cooler waters of the North-western Atlantic from The

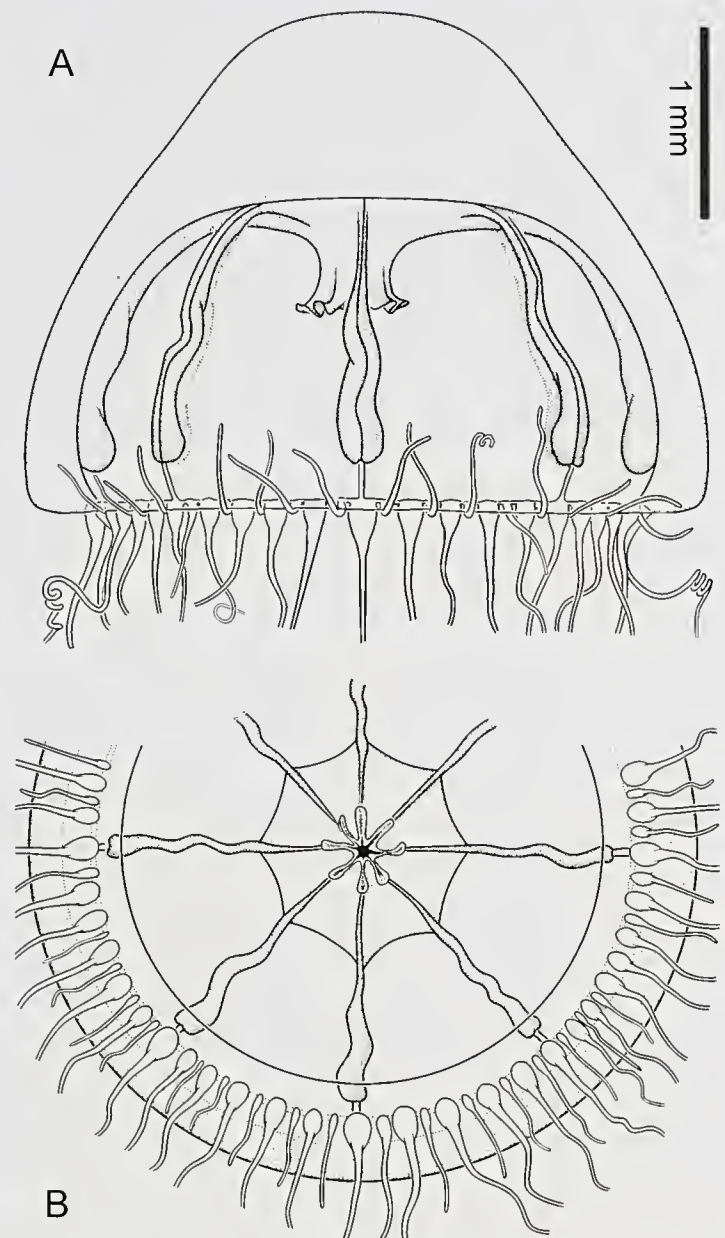


Fig. 1. *Melicertum octocostatum* after photos of living medusae from Norway. (A) Lateral view, tentacles cut. (B) Oral view.

English Channel to the Arctic Ocean; Iceland; North America from Woods Hole to Halifax and western coast of Greenland. Also present in the Pacific from Japan to the Arctic Ocean and British Columbia (Kramp, 1961; Arai & Brinckmann-Voss, 1980; Okuizumi & Kubota, 2003; Wang *et al.*, 2014). An unexpected record is also known from Papua New Guinea (Bouillon, 1984). Type locality: Coastal region of Bergen, Norway.

**Family Laodiceidae L. Agassiz, 1862**  
**Genus *Laodicea* Lesson, 1843**

***Laodicea undulata* (Forbes & Goodsir, 1853)**

Fig. 2A-C

? *Medusa cruciata* Forsskål, 1775: 110, pl. 33 figs A, a1-a2.

? *Medusa crucigera* Gmelin, 1788: 3158, new name for *Medusa cruciata* Forsskål, 1775.

? *Medusa cacuminata* Modeer, 1791: 26, new name for *Medusa cruciata* Forsskål, 1775.

*Laodicea crucigera*. – Lesson, 1843: 294, new genus.

*Thaumantias undulata* Forbes & Goodsir, 1853: 313, pl. 10 figs 7a-d.

*Thaumantias confluens* Forbes & Goodsir, 1853: 314, pl. 10 fig. 8a-d.

*Thaumantias mediterranea* Gegenbaur, 1857: 237, pl. 8 figs 1-3.

*Laodicea calcarata* L. Agassiz, 1862: 350.

*Cosmetira punctata* Haeckel, 1864: 334. – Haeckel, 1879: 132, synonym.

? *Cuspidella costata* Hincks, 1868: 210, pl. 40 fig. 5. – Watson, 2005: 501, fig. 3A-B.

*Laodice ulothrix* Haeckel, 1879: 133, pl. 8 figs 5-7.

? *Ptychogena longigona* Maas, 1893: 64, pl. 6 figs 7-9. – Browne, 1907: 474. – Kramp, 1919: 35, doubtful species.

*Laodicea bigelowi* Neppi & Stiasny, 1911: 396. – Neppi & Stiasny, 1913: 38, pl. 3 figs 30-31. – Kramp, 1961: 142.

*Laodicea cruciata*. – Mayer, 1910: 201, figs 104-105, pl. 21 figs 4-5, pl. 22 figs 2-6, pl. 23 figs 1-3. – Neppi & Stiasny, 1913: 37, pl. 3 figs 27-29.

*Laodicea undulata*. – Russell, 1936: 581, figs 1-7, hydroid stage. – Russell, 1953: 230, figs 123-131, pl. 14 figs 1-3. – Kramp, 1959a: 135, fig. 153. – Kramp, 1961: 141. – Goy, 1979: 272, fig. 12. – Pagès *et al.*, 1992: 28, fig. 29. – Ramil & Vervoort, 1992: 28, fig. 2w-g. – Cornelius, 1995: 99, fig. 22.

**Material examined:** MHNG-INVE-31753, originally 2 specimens in ethanol, one used for DNA extraction; France, Villefranche-sur-Mer, Ligurian Sea, Mediterranean, 43.686°N 7.317°E, depth 2-70 m; collection date 11.05.2001; DNA isolate 125; 16S sequence FJ550471, 18S FJ550390. – 3 specimens; France, Villefranche-sur-Mer, 43.686°N 7.317°E, depth 0-70 m; collection date 04.04.2005. – 2 specimens; France, Villefranche-sur-Mer, 43.686°N 7.317°E, depth 0-70 m; collection date 28.04.2014; used for RNA extraction. – 1 specimen; Sweden, Kristineberg, 58.24385°N 11.43230°E, 0 m depth, collection date 03.10.2014; DNA isolate 1137; 16S sequence KY363963, COI MF000514, 18S KY363985. – 1 specimen; France, Bay of Villefranche-sur-Mer, 43.6963°N 7.3075°E; collection date 25.04.2016; DNA isolate 1151; 16S KY363967.

For archived photos of specimens see Table 1.

**Diagnosis:** Umbrella 10-37 mm wide, usually 10-20 mm; flatter than hemisphere; stomach quadratic, short, with four folded lips; four long, sinuous gonads along radial canals, contiguous with stomach; 100-300 tentacles, basal bulbs faintly developed, with abaxial spur; adaxial ocellus usually on every third to fifth tentacle; spiral cirri, usually one between successive tentacles; cordyli distinctly club-shaped, without nematocysts, usually one between successive tentacles, no statocysts.

For polyp stage see Cornelius (1995).

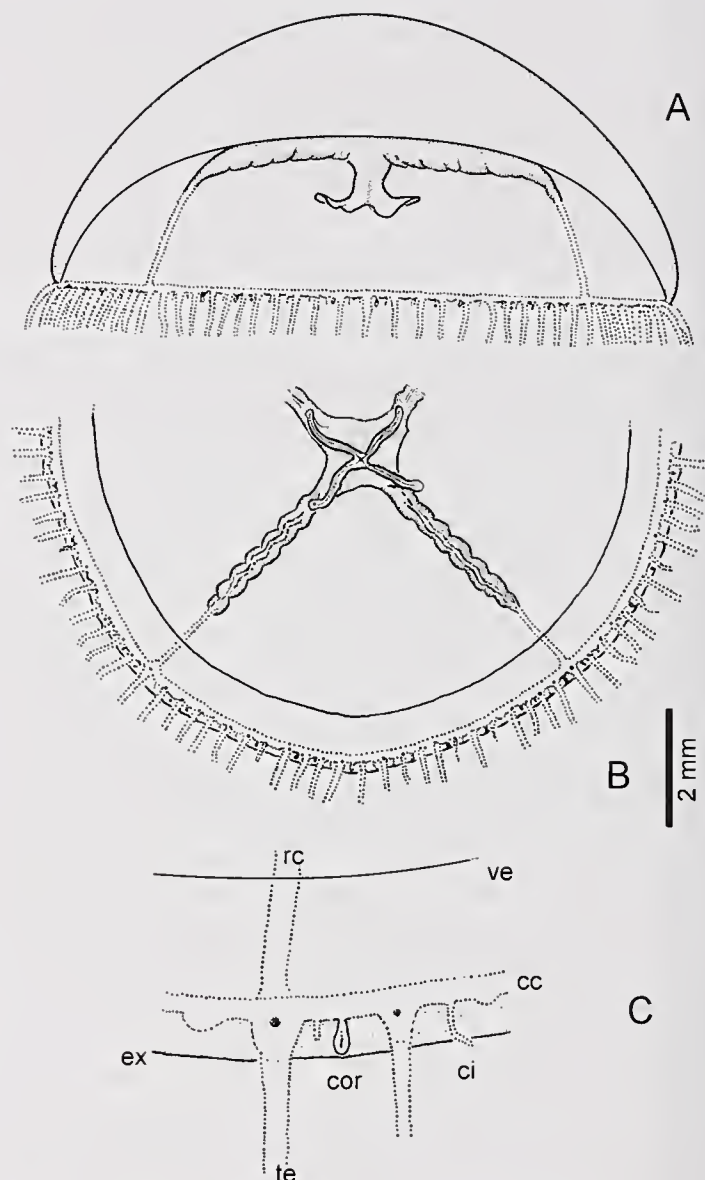


Fig. 2. *Laodicea undulata* after living medusa from the Mediterranean. (A) Lateral view. (B) Oral view. (C) Bell margin seen from oral side. Abbreviations: ci – cirrus, cc – circular canal, cor – cordylus, ex – exumbrella, rc – radial canal, te – tentacle.

**Remarks:** The specimens from the Mediterranean had 60-80 tentacles, the North Sea specimen 280.

**Distribution:** Eastern Atlantic and adjacent waters from Iceland and northern Norway to South Africa; western Atlantic from Nova Scotia to Tierra del Fuego; Mediterranean (Kramp, 1968). Some occasional records from the Indo-Pacific (Pages *et al.*, 1992) require a re-evaluation (Kramp, 1955b: 253; see also below under *L. indica*). Type locality: The Minch, Scotland.

### *Laodicea indica* Browne, 1905

Fig. 3

*Laodicea indica* Browne, 1905b: 136, pl. 1 fig. 5, pl. 4 figs 7-11. *Laodicea indica*. – Mayer, 1910: 202, synonym of *L. cruciata*. – Kramp, 1953: 268, type specimen, synonymy. – Kramp, 1961: 140. – Kramp, 1968: 66, fig. 172. – Bouillon, 1978a: 152, fig. 9. – Bouillon, 1984: 61, revision, life

cycle. – Bouillon, Boero & Fraschetti, 1991: 151, figs 1-3, life cycle.

*Laodice fijiana* var. *indica*. – Maas, 1905: 25, pl. 2 figs 14-15, pl. 5 figs 32-35. – Kramp, 1953: 270, is probably *L. indica*. [not *Laodicea fijiana* Agassiz & Mayer, 1899]

*Laodice maasii* Browne, 1907: 466, new name for *Laodice fijiana* var. *indica* in Maas, 1905. – Kramp, 1953: 270, is *L. indica*.

? *Laodice fijiana*. – Maas, 1906: 89. – Kramp, 1953: 270.

**Material examined:** MHNG-INVE-25646; 1 specimen in ethanol, originally fixed in formalin; Seatoun jetty, Miramar Peninsula, Wellington, New Zealand, 41.31855°S 174.8304°E, depth 0-2 m; date collected 22.03.1994. – MHNG-INVE-54671; 5 badly preserved specimens; Bay of Ambon, Moluccas, Indonesia; expedition Bedot & Pictet 1890; material described in Maas (1906).

**Diagnosis:** Like *L. undulata*, but Indo-Pacific occurrence, tentacle number in mature specimens lower with 30-200. For polyp stage see Bouillon (1984), identical to *L. undulata*.

**Remarks:** There is currently no trait known that would reliably distinguish *L. indica* from the Atlantic *L. undulata*. Also the polyps appear identical (Bouillon, 1984; but see Bouillon *et al.*, 1991). Some authors (e.g. Mayer, 1910; Bouillon, 1984) have therefore synonymised the two names, but Kramp (1953, 1961, 1968) continued to regard them as separate. I also refrained from synonymising the two because some preliminary molecular data indicate that the Pacific *Laodicea* could be rather distinct from the Atlantic ones (10% difference of 16S sequence, unpublished, comp. FJ550471, JQ715946, JQ715947, KY363963).

The medusa from New Zealand had a relatively high number of tentacles (about 200), but which is only slightly higher than the maximal number of 180 given in Kramp (1968).

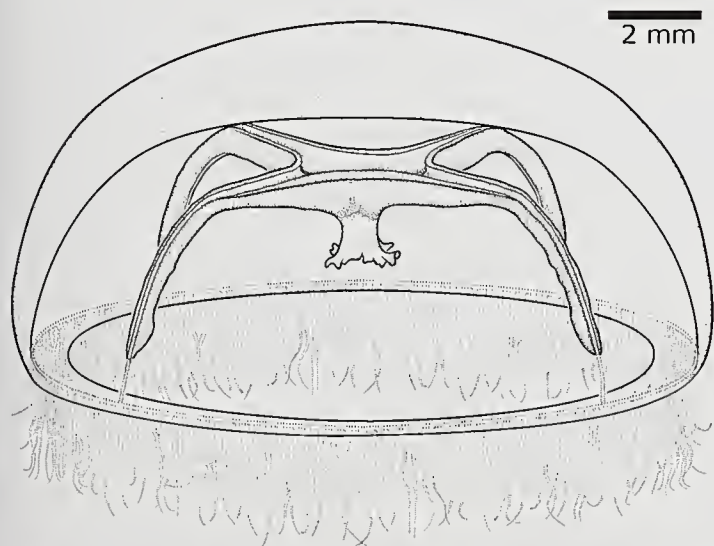


Fig. 3. *Laodicea indica*, schematic drawing after a preserved specimen from New Zealand.

The material identified by Maas (1906) as *L. fijiana* was re-examined for this study. It is not well preserved, but evidently the radial canals lack the diagnostic outgrowths which are characteristic for *Laodicea fijiana* (see Agassiz & Mayer, 1899). The tentacle number is about 60 and it is likely *L. indica* as already suspected by Kramp (1953).

**Distribution:** Tropical to temperate regions of the Indian Ocean and the western Pacific Ocean (Kramp, 1968). Type locality: Mutwal Island, West Coast of Ceylon.

### Genus *Ptychogena* A. Agassiz, 1865

**Diagnosis:** Laodiceidae medusae with large, prismatic manubrium, 4 radial canals connected to stomach via large, funnel-shaped, mesentery-like basal extensions of the manubrium. Along radial canals lateral, transverse, fold-like diverticula on which the gonads are located; bell margin with club-shaped cordyli, no cirri, no ocelli. Hydroids where known like *Stegonomma plicatile* (M. Sars, 1863). Colony erect, branching, polysiphonic, with tendency to ramification in one plane. Hydrothecae on stem and branches, all pedicellate. Hydrothecae tubular, curved outwards gradually narrowing downwards, ending in a gable-shaped operculum. Gonothecae larger than hydrothecae, elongated, almost completely adnate with branches and axis, with or without operculum.

**Remarks:** The diagnosis given in Kramp (1959a) and subsequent authors (e.g. Bouillon *et al.*, 2006) had to be slightly modified. Based on observations on *Ptychogena lactea* A. Agassiz, 1865, influential authors like Haeckel (1879), Mayer (1910), and Kramp (1919, 1933) interpreted the perradial funnel-shaped structures bearing the gonadal folds as widened proximal parts of the radial canals. However, especially in the case of *P. crocea*, these structures are intuitively better interpreted as pockets of the manubrium as seen in many other hydromedusae [see also Russell (1953: 224) who expressed the same opinion for the similar *Chromatonema rubrum* Fewkes, 1882]. These pouches have the same characteristic colour and tissue density as the manubrium, while the radial canals connecting the end of the funnel to the circular canal are thin and transparent like the latter. Whatsoever, they are gastrodermal structures and as such homologous. Interpreting the funnels as radial canals was perhaps influenced by the general diagnosis of the leptomedusae which should have gonads on the radial canals.

The only *Ptychogena* species for which the polyp stage is known is *Ptychogena crocea* (Schuchert *et al.*, 2017), but the other species of the genus could have a similar or identical hydroid.

The medusae of this genus are rather similar or hardly distinguishable from the genera *Modeeria* Forbes, 1848 and *Chromatonema* Fewkes, 1882, although the latter genus has been placed in a separate family, Tiarannidae

Russell, 1940. Currently, the only feasible trait to distinguish *Chromatonema* from *Ptychogena* is the shape of the cordyli: they are club-shaped in *Ptychogena* and spindle-shaped in the *Chromatonema*. It is possible that there are significant differences in the polyp-stage, but the polyps of *Chromatonema* remain unknown. Molecular phylogenies have to re-address the problem. Preliminary data (figs 1-2 in Schuchert *et al.*, 2017) suggest that they are closely related.

### *Ptychogena crocea* Kramp & Dumas, 1925

Fig. 4A-C

*Ptychogena crocea* Kramp & Dumas, 1925: 290, pl. 1 figs 1-7. – Kramp, 1933: 558, fig. 21. – Russell, 1940: 519, figs 18-19. – Rees, 1952: 5. – Kramp, 1959a: 137, fig. 158. – Kramp, 1961: 146. – Schuchert *et al.*, 2017: 168, figs 3-4.

? *Ptychogena crocea*. – Léon *et al.*, 2007: 57, photo 1.

in part *Lafoea plicatilis* M. Sars, 1863: 31.

in part *Stegopoma plicatile*. – Kramp, 1913: 15, figs 1-2. – Broch, 1918: 26, fig. 8. – Edwards, 1973a: 590. – Cornelius, 1995: 114, fig. 25. – Schuchert, 2001: 51, fig. 37A-E. – Schuchert *et al.*, 2017: 168, fig. 4.

**Material examined:** MHNG-INVE-94101, 1 fully grown, formalin preserved specimen of a catch of about 10 specimens; Norway, Korsfjord, 60.1846°N 5.196°E, 0-600 m depth; collection date 14.06.2016; other, younger specimens were used to extract DNA and RNA; sample DNA sample 1163 giving 16S sequence KY363953, 18S KY363983; DNA sample 1195 resulting in 16S sequence KY363958; DNA sample 1196 giving 16S sequence KY363959 (16S all identical, see Schuchert *et al.*, 2017).

**Diagnosis:** Umbrella up to 25 mm wide, height 15 to 25 mm but often flatter than a hemisphere (depending on state of contraction and health). Jelly thick, apical jelly about one third of bell height. Stomach relatively large, prismatic, attached to subumbrella via cross-shaped base, mouth wide, irregular. Four radial canals, transparent but relatively thick in distal half or third of radius, connected to stomach via a funnel-shaped, laterally compressed, mesentery-like basal outgrowth of the manubrium, this structure bears on both sides up to 7 thick, large transverse folds, their upper end not connected to subumbrella and covered by the gonads in a thick layer. Bell margin with up to 80 bulbs of different sizes, about 30 developed into tentacles, others mere marginal warts or rudimentary tentacles and all intermediate stages to fully developed tentacles. Between pairs of tentacles 2-4 cordyli, some attached to bell margin, many also on small marginal warts/rudimentary bulbs. Cordyli club-shaped, with few (<10) nematocysts (about 16 µm long spindle-shaped microbasic mastigophores). Colour: stomach, basal extensions, and gonads all with a characteristic,

intense yellow-orange colouration; bulbs whitish; canals slightly opaque.

The hydroid stage of this species is *Stegomoma plicatile* (M. Sars, 1863) (Schuchert *et al.*, 2017).

**Remarks:** The nematocysts have been described in Russell (1940). The yellow colour is lost in preserved animals. For the difference to *Chromatonema rubrum* and other similar medusae see Schuchert *et al.* (2017).

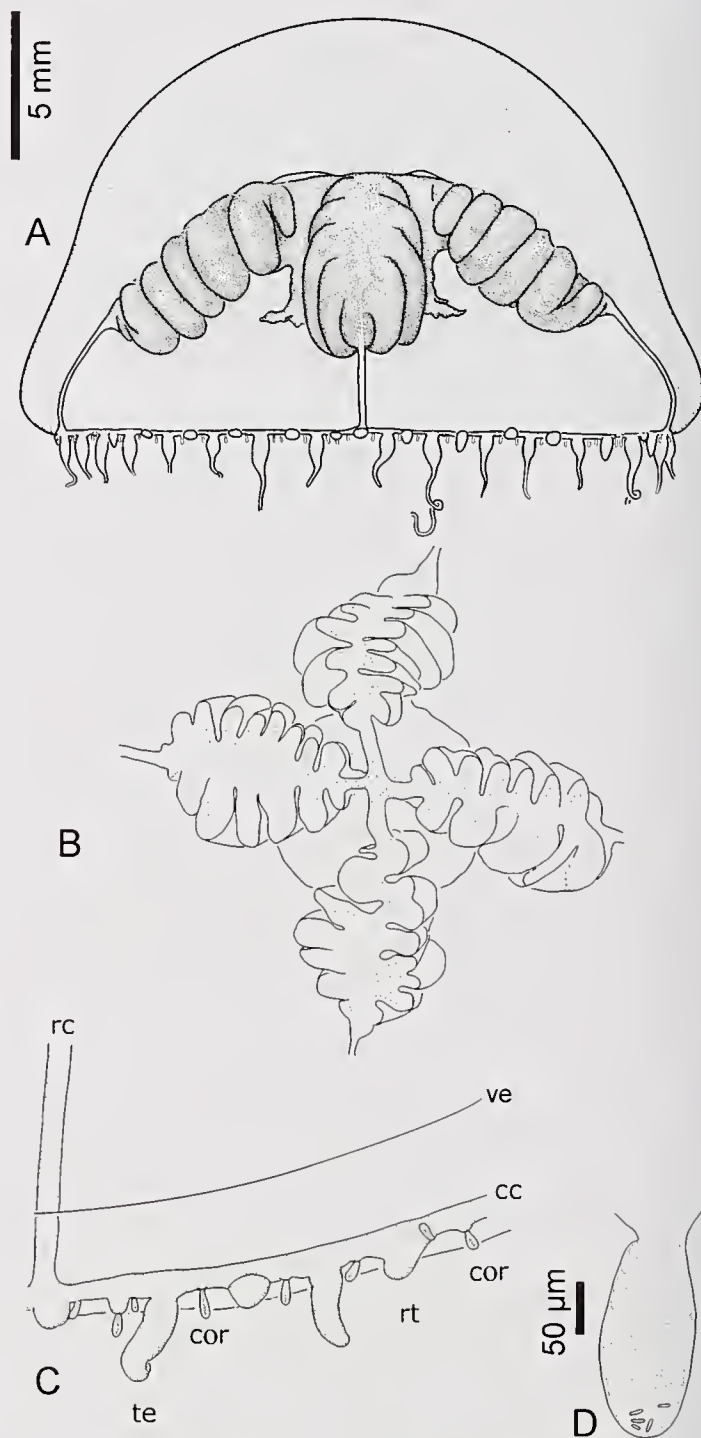


Fig. 4. *Ptychogena crocea*, after living and preserved specimens from Norway. (A) Lateral view. The slight concave lateral walls are a typical sign of beginning deterioration. (B) Stomach and gonads in aboral view. (C) Bell margin seen from oral side (not to scale with A). Abbreviations: cc – circular canal, cor – cordylus, ex – exumbrella, rc – radial canal, rt – rudimentary tentacle or marginal wart, te – tentacle, ve – velum. (D) Cordylus.



**Distribution:** Deep waters (0-1000 m) of Norway. (Kramp & Damas, 1925; Kramp, 1961) and off the south-west coast of Scotland (Fraser, 1974). A single, much damaged specimen has also been recorded from deep waters of the Cape Verde Islands and three specimens from the Gulf of Maine (Léon *et al.*, 2007). Type locality: Norway, Romsdal, deep waters of Moldefjord.

***Ptychogena lactea* A. Agassiz, 1865**

Fig. 5

*Ptychogena lactea* A. Agassiz, 1865: 137, figs 220-224. – Mayer, 1910: 215, fig. 109. – Kramp, 1919: 31, pl. 3. – Kramp, 1959a: 137, fig. 157. – Kramp, 1961: 146. – Kramp, 1968: 67, fig. 175. – in part Naumov, 1969: 321, figs 90, not hydroid. – Arai & Brinckmann-Voss, 1980: 83, fig. 46. – Miyake *et al.*, 2004: 40, fig. 5.

*Ptychogena pinnulata* Haeckel, 1879: 148. – Haeckel, 1882: 7, pl. 2. – Mayer, 1910: 215, synonym. – Kramp, 1955a: 157.

*Ptychogena pinnulata* var. *intermedia* Linko, 1905: 217.

not *Ptychogena lactea*. – Calder, 1970: 1512, pl. 3 fig. 1, hydroid.

**Material examined:** MHNG-INVE-82311; 1 subadult specimen, 20 mm diameter, formalin preserved; Canada, British Columbia, Vancouver Island, 49.36667°N 124.08517°W, depth 0-238 m; date collected 15.06.2012; leg. Moria Galbraith.

**Diagnosis:** Umbrella in mature animals 15-70 mm in diameter, but exceptionally up to 90 mm wide and 30 mm high, bell hemispherical to flatter than a hemisphere (depending on size, state of contraction and health). Jelly thick, apical jelly about one third of bell height. Stomach relatively large, prismatic, attached to subumbrella via cross-shaped base, mouth wide, irregular, rim in folds. Four radial canals, relatively thick, in proximal half connected to stomach via a funnel-shaped, laterally compressed, mesentery-like basal outgrowth of the manubrium. On both sides of each radial canal up to 30 relatively thin, transverse lamellar folds, their upper end connected to subumbrella. The lamellar folds also present distal to the perradial basal outgrowths of the manubrium. Gonads covering lamellar folds. Large animals with papillae along edges of lamellar folds and some folds branched. Bell margin with 70-300 (max. 500) tentacles, no marginal warts or rudimentary tentacles. Between pairs of tentacles 1-3 club-shaped cordyli attached to bell margin.

Colour: gonads, radial canals, and tentacles characteristic milk-white (but also with a peachy or greenish tint, Schuchert *et al.*, 2017).

Hydroid unknown (Schuchert *et al.*, 2017).

**Distribution:** A predominantly Arctic species that penetrates into Boreal zones of the Atlantic and Pacific Oceans. Its southern limits in the Atlantic Ocean are

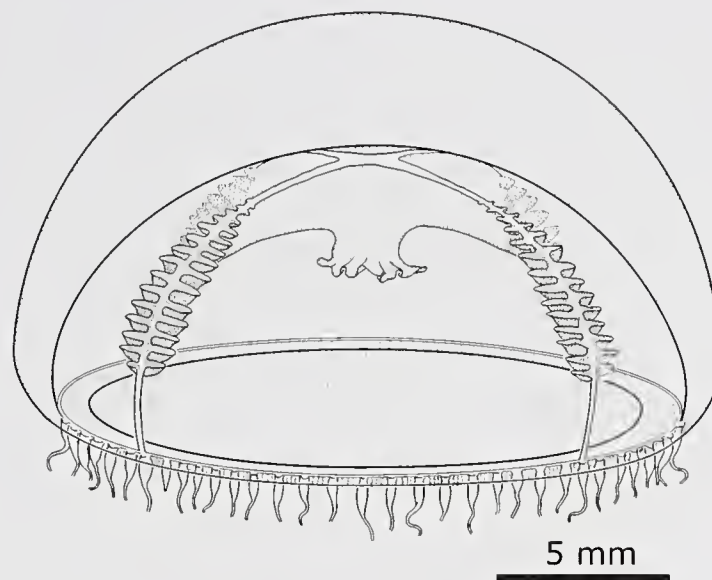


Fig. 5. *Ptychogena lactea*, subadult, schematic after MHNG-INVE-82311.

Cape Cod and the Faroe-Shetland Channel, in the Pacific Ocean northern Japan and British Columbia. Often collected at depths of over 250 m but may be found near the surface where the water is very cold (Arai & Brinckmann-Voss, 1980; Fraser, 1974). Type locality: Nahant, Massachusetts Bay, USA, Atlantic Ocean.

**Family Hebellidae Fraser, 1912**

**Genus *Staurodiscus* Haeckel, 1879**

***Staurodiscus gotoi* (Uchida, 1927)**

Fig. 6A-C

*Staurodiscoides gotoi* Uchida, 1927: 165, figs 1-2.

*Staurodiscus gotoi*. – Kramp, 1961: 147. – Kramp, 1965: 56. – Kramp, 1968: 70, fig. 183. – Xu & Zhang, 1974: 20, fig. 9. – Bouillon, 1984: 65. – Bouillon & Barnett, 1999: 87, fig. 85. – Xu *et al.*, 2014: 577, fig. 455.

**Material examined:** MHNG-INVE-33467, >30 specimens of various developmental stages; New Zealand, Hauraki Gulf, Devonport, Narrow Neck Beach, 36.8123°S 174.8025°E, 0 m; collection date 26.07.2002; DNA isolate 126, 16S sequence FJ550472, COI MF000510, 18S sequence FJ550535, 28S sequence FJ550391; for photos of living specimens see Table 1.

**Diagnosis (NZ material):** Umbrella somewhat higher than hemisphere, diameter 5-8 mm, jelly thick, at apex about half the bell height. Manubrium moderately long, cruciform in section, four simple lips. Four radial canals and circular canal rather broad. Radial canals in proximal half thick and on both sides with 2-4 lateral outgrowths, outgrowths thick, not strictly opposite, covered by gonad tissue, longer ones curved towards bell margin but not connected to circular canal. Bell margin with four large perradial bulbs tapering into

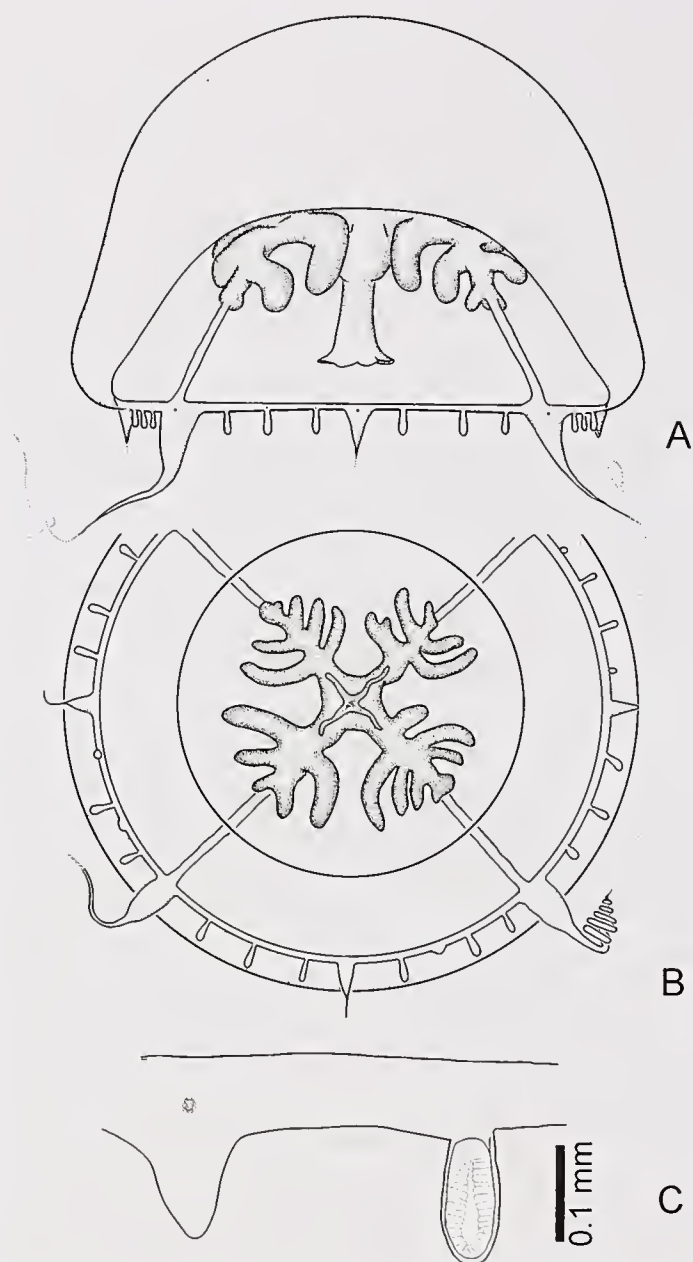


Fig. 6. *Staurodiscus gotoi* subadult, schematic composite drawing made after photographs of living specimens and preserved specimens. Diameter of bell approximately 6 mm (A) Lateral view. (B) Oral view. (C) Circular canal with tentacle-less bulb and a cordylus shown in optical section.

long tentacles. Interradial tentacle bulbs present, in fully mature animals tapering into tentacles but these shorter than the perradial ones. All tentacle bulbs with a black abaxial ocellus. Occasionally some additional, very small adradial bulbs. Between perradial- and interradian bulbs usually three cordyli. Cordyli relatively large, hollow, cylindrical gastrodermal cells, with a few nematocysts at the tip. Some of the cordyli also with an ocellus near their origin.

Polyps unknown.

**Variation:** Young medusae have only two tentacles and very small lateral outgrowths of the radial canals. Xu & Zhang (1974) depicted an animal with 16 tentacles.

**Distribution:** Japan, China, Papua New Guinea, Indonesia, North Island of New Zealand (Kramp, 1965;

Bouillon, 1984; Bouillon & Barnett, 1999). Type locality: Japan, Shizuoka Prefecture, Shimizu Bay.

**Remarks:** The identification of this material as *St. gotoi* was largely influenced by Bouillon & Barnett (1999) who used also material provided by the author. There are nevertheless some differences of the New Zealand medusae to those of Japan and China: there are fewer cordyli (24-26 versus up to 88), the bell diameters are smaller (4-8 versus up to 15), the interradian tentacles are often small or absent, the mesogloea is much thicker, and the lateral outgrowths are limited to the proximal half of the tentacles. It is assumed that these are population differences. Additionally, it was noted that the mesogloea shrinks in formalin-preserved animals. A later transfer into 70% ethanol makes the mesogloea disappear completely, resulting in a condition where the lateral outgrowths of the radial canals reach the bell margin. It is possible that some published illustrations of *Staurodiscus* species are actually based on such material with a shrunken bell.

**Family Eirenidae Haeckel, 1879**  
**Genus *Eirene* Eschscholtz, 1829**

**Diagnosis:** Eirenidae medusa with distinct, broad gastric peduncle; cirri absent; with or without excretory pores; 4-6 simple radial canals; gonads on subumbrellar part of radial canals, not extending to gastric peduncle; numerous statocysts (>8).

The hydroids of '*Campanulina*', '*Campanopsis*' or '*Eugymnanthea*' type (see Bouillon *et al.*, 2006).

**Remark:** *Clytia* species with a short gastric peduncle like *Clytia gregaria* (see below) are formally not distinguishable from *Eirene* species. Thus, some nominal *Eirene* species (Schuchert, 2017a; see Du *et al.*, 2010 for a key to the species) with a shallow peduncle and no excretory papillae could therefore also be *Clytia* species. Life-cycle studies or DNA barcodes (Schuchert *et al.*, 2017) have to confirm the identity of *Eirene pentanemalis* Lin, Xu & Huang, 2013, *Eirene brevistylus* Huang & Xu, 1994, and other similar species.

***Eirene viridula* (Péron & Lesueur, 1810)**

Fig. 7A-C

*Oceania viridula* Péron & Lesueur, 1810: 346, English Channel.

*Geryonia pellucida* Will, 1844: 70, pl. 2 figs 8-12.

*Geryonopsis delicatula* Forbes, 1848: 39.

*Geryonopsis forbesii* Van Beneden, 1867: 87, pl. 3 figs 1-7. – Haeckel, 1879: 202, synonym.

*Tima willi* Neppi, 1909: 368, figs 3, 4, 7, 8, 12, 13, 15, 16, 18-25, 28-45, 47.

*Phortis pellucida*. – Neppi & Stiasny, 1913: 49.

*Perigonimus nudus* Stechow, 1919: 16, fig. D. – Schuchert, 2007: 273, synonym.

*Eirene viridula*. – Russell, 1953: 321, text. figs. 201-205, pl. 20 figs 3-4. – Kramp, 1959a: 158, fig. 215. – Kramp, 1961: 191. – Kramp, 1968: 90, fig. 243. – Cornelius, 1995: 223, fig. 51.

**Material examined:** Several mature specimens; France, Villefranche-sur-Mer, Mediterranean, 43.686°N 7.317°E, 0 m depth; collection date 04.05.2001; DNA isolate 010; 16S sequence KY363937. – 1 specimen; France, Normandy, Luc-sur-Mer, English Channel, 49.31985°N 00.34965°W, 0 m depth; collection date 17.08.2005; DNA isolate 388; 16S sequence FJ550502, 18S FJ550588, 28S FJ550445.

**Diagnosis:** Umbrella up to 30 mm wide, nearly hemispherical, middle portion fairly thick; peduncle

broad, projecting beyond bell margin, shape variable. Velum narrow. 4 radial canals. Stomach fairly small, with four pointed lips and crenulated margin; gonads linear, extending from bell margin to base of peduncle. Up to 70 tentacles of different sizes, large and small frequently alternating, tentacles fine, bulbs conical with distinct adaxial excretory papilla projecting into subumbrella; 50 or more statocysts, each with 1-4 concretions. No cirri. Colourless except for green tinge of manubrium.

Polyp stage see Cornelius (1995).

**Distribution:** North-western Europe; Mediterranean; west coast of Africa; east coast of Africa; Ceylon, Papua New Guinea. Type locality: English Channel.

**References:** Russell (1953), Cornelius (1995).

### *Eirene hexanemalis* (Goette, 1886)

Fig. 8A-C

*Irenopsis hexanemalis* Goette, 1886: 832. – Browne, 1905b: 142, pl. 1 fig. 4, pl. 3 figs 5-8. – Maas, 1905: 37, pl. 6 figs 38-40. – Mayer, 1910: 310, figs 171, 171a. – Vanhöffen, 1911: 229, fig. 19.

*Phortis pellucida* forma *hexanemalis*. – Vanhöffen, 1913: 17.

*Phortis pellucida* forma *pentanemalis* Vanhöffen, 1913: 18.

*Eirene hexanemalis*. – Kramp, 1936: 248, bibliography, synonymy. – Kramp, 1953: 281, fig. 5, variation, seasonality. – Kramp, 1961: 188. – Kramp, 1965: 77, fig. 5, variation. – Kramp, 1968: 91, fig. 245. – Bouillon, 1983: 421, figs 1-3, life cycle, ecology. – Bouillon, 1984: 39, fig. 6, hydroid, nematocysts.

*Eirene octonemalis* Guo, Xu, & Huang, 2008: 61, fig. 1. **new synonym**

? *Eirene pentanemalis* Lin, Xu & Huang, 2013 in: Lin *et al.*, 2013: 756, figs 1-3.

**Material examined:** MHNG-INVE-53565; 22 formalin-preserved medusae, fertile males and females; Abu Dhabi, 24.4666°N 54.3272°E, depth 0 m; collection date 20-26.08.2006; one individual with 12 radial canals; leg. H. Galea.

**Diagnosis:** Mature medusa 10-18 mm in diameter, bell hemispherical, thick apical jelly, gastric peduncle broad, length variable but usually not reaching beyond velum level. Velum narrow. Manubrium six-rayed in cross-section, perradial corners of the mouth drawn out as lips, mouth margin with many folds. Majority of individuals with six radial canals, in a minority with other numbers varying from 4 to 12. Gonads thin, more or less straight, along radial canal from base of peduncle to circular canal. 40-60 short tentacles on small bulbs, bulbs with adaxial, conical excretory papilla. In-between 2 tentacle bulbs 1-2 rudimentary bulbs (marginal warts) and 2-4 round statocysts with one concretion (occasionally 2-4, Browne, 1905b). Polyp planktonic, solitary, see Bouillon (1983).

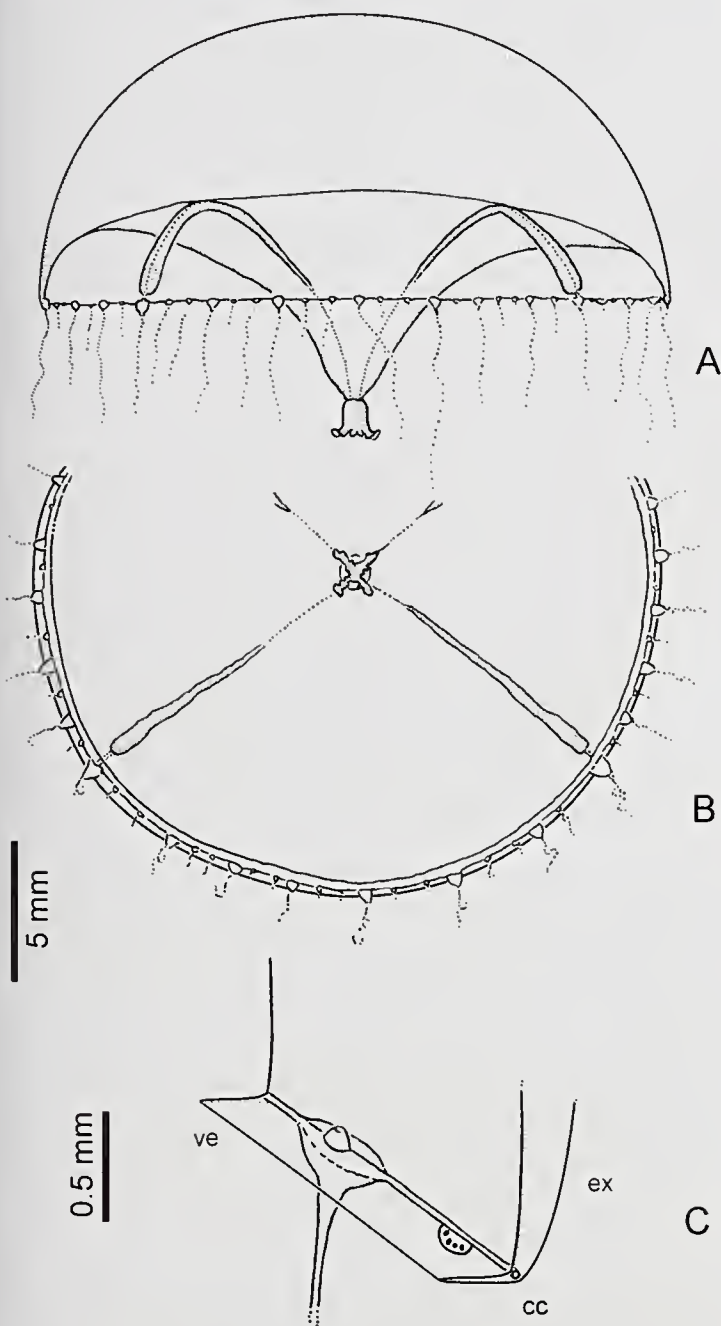


Fig. 7. *Eirene viridula*, after living Mediterranean specimens. (A) Lateral view. (B) Oral view. (C) Marginal bulb in adaxial view, note conical excretory papilla on subumbrellar side of tentacle bulb. Abbreviations: cc – circular canal, ex – exumbrella, ve – velum.

**Distribution:** Coastal waters from South- and East Africa to Australia, Indonesia, China, and Japan (Kramp, 1965). Type locality: Zanzibar, East Africa.

**Remarks:** This is a well-known species, the only new information is the existence of a specimen with 12 radial canals which was mixed with the 22 specimens with 6 radial canals. Until now, the maximal number of canals was 11. The variation in the number of radial canals has been summarized by Kramp (1965) and Bouillon (1983). A minority of individuals of a particular population can have from 4 to 12 tentacles.

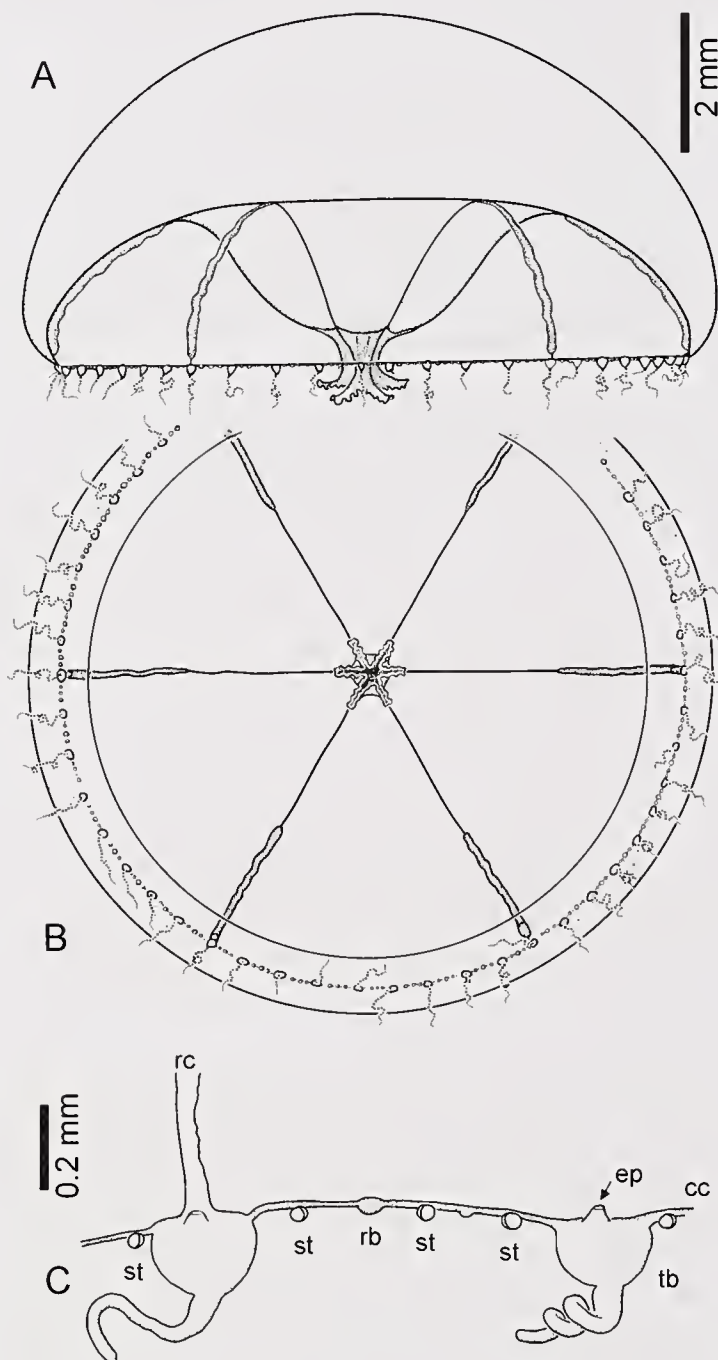


Fig. 8. *Eirene hexanemalis*, after preserved material. (A) Lateral view. (B) Oral view. (C) Schematic view on circular canal from adaxial side. Note presence of conical excretory (arrow). Abbreviations: cc – circular canal, ep – excretory papilla, ex exumbrella, rb – rudimentary bulb, rc – radial canal, st – statocysts (shown without concretion).

It is thus evident that *Eirene octonemalis* Guo, Xu, & Huang, 2008 must be regarded as not separable from *E. hexanemalis*. The former species differs from the latter in having 8 radial canals. The only peculiarity of *E. octonemalis* is that all four known specimens had 8 radial canals. This could, however, be a population specific trait.

Likewise, *Eirene pentanemalis* Lin, Xu & Huang, 2013, which is characterised by five radial canals and the purported absence of excretory papillae, could also be a young *E. hexanemalis*. The species is based on badly mutilated material for which a reliable observation of the excretory papillae appears doubtful.

**References:** Browne (1905b), Kramp (1936, 1953), Bouillon (1983).

### Genus *Helgicirra* Hartlaub, 1909

#### *Helgicirra cari* (Haeckel, 1864)

Fig. 9A-D

*Tima cari* Haeckel, 1864: 332.

*Tima pellucida*. – Schulze, 1874: 138, pl. 2 figs 6a-b. [not *Geryonia pellucida* Will, 1844 = *Eirene viridula* (Péron & Lesueur, 1810)]

*Geryonia pellucida*. – Haeckel, 1879: 201, pl. 12 figs 1-2. [not *Geryonia pellucida* Will, 1844 = *Eirene viridula* (Péron & Lesueur, 1810)]

*Helgicirra schulzii* Hartlaub, 1909: 86. **new synonym**

*Eirene viridula*. – Mayer, 1910: 311, fig. 172. [not *Eirene viridula* (Péron & Lesueur, 1810)]

*Tima plana* Neppi, 1910: 165, figs 2, 2a-b. **new synonym**

*Helgicirra schulzei*. – Kramp, 1936: 254 [subsequent incorrect spelling]. – Russell, 1953: 328, figs 206-212, pl. 20 figs 1-2. – Kramp, 1959a: 159, fig. 218. – Kramp, 1961: 192. – Bouillon, 1971: 362, pl. 7-8, fig. 12. – Brinckmann-Voss, 1973: 68, figs 4-5. – Pagès *et al.*, 1992: 27, fig. 28. – Cornelius, 1995: 238, fig. 55.

*Helgicirra cari*. – Kramp, 1936: 253. – Kramp, 1959a: 160, fig. 219. – Kramp, 1961: 191.

**Material examined:** 1 specimen; France, Bay of Villefranche-sur-Mer, 43.6856°N 7.3178°E, 0 m depth; collection date 29.04.2016; DNA isolate 1153; 16S sequence KY363968, COI MF000519, 18S KY363989.

**Diagnosis:** Umbrella diameter 20-50 mm when mature, distinctly flatter than a hemisphere, apical jelly about 1/3 of total height, gastric peduncle broad, conical, length about bell-height (Fig. 9A). Stomach small, with cruciform mouth opening, drawn out into periradial lips to variable length, mouth margin folded to a variable degree. Velum narrow. 4 radial canals. Gonads thin, extending from stomach to close to bell margin. 40-50 larger bulbs each with a short and fine tentacle, between these bulbs 2-3 small bulbs that occasionally bear tentacle stumps. Most marginal bulbs with a pair of lateral cirri and a conical excretory papilla pointing into the subumbrella (Fig. 9D). 50-100 statocysts, each with 2-3 concretions.

Hydroid stage an athecate polyp with lateral medusa budding, for more details see Brinckmann-Voss (1973) and Bouillon (1971).

**Distribution:** North-western Europe south of Norway, Mediterranean, coast of West Africa, Benguela Current (Pages *et al.*, 1992). Type locality: Nice, Mediterranean.

**Remarks:** Kramp (1936) revised the genera *Eirene* and *Helgicirrha* and kept *H. cari* distinct from the better known *H. schulzii* based on the presence of

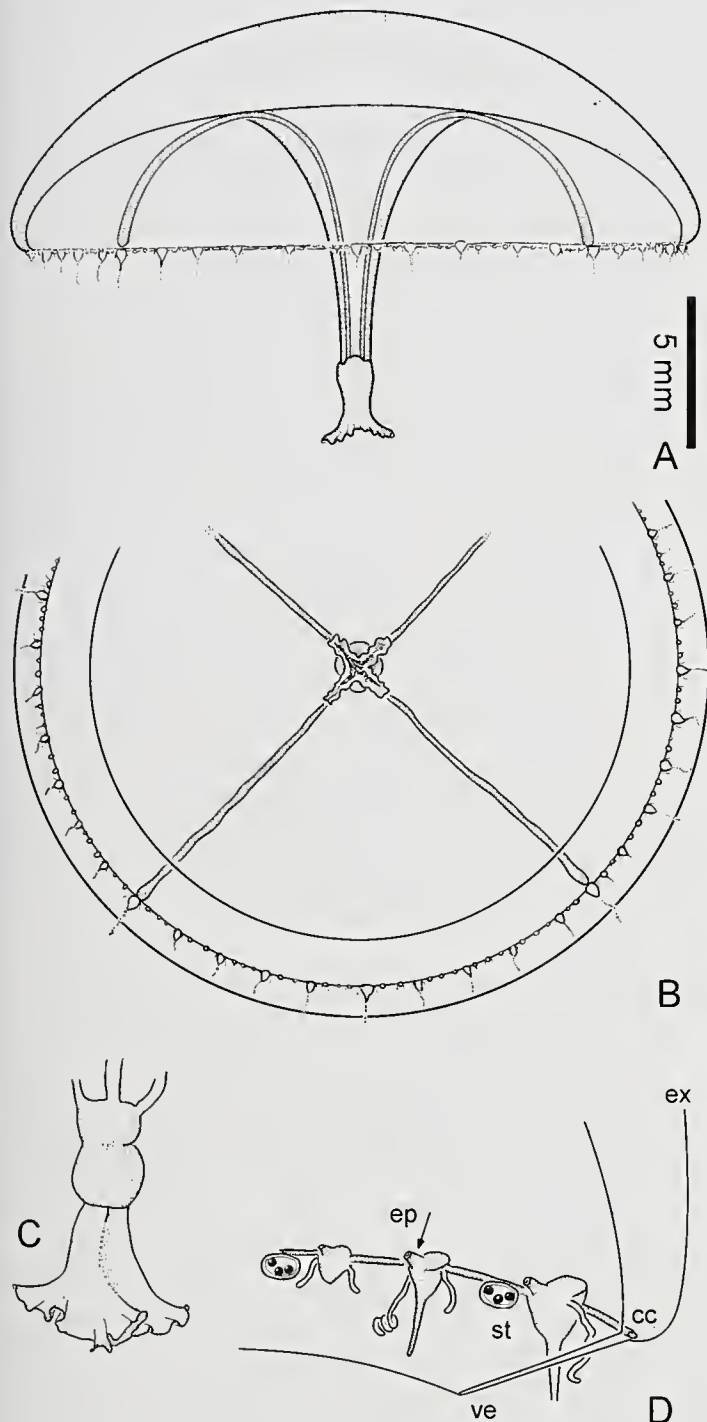


Fig. 9. *Helgicirrha cari*, after living Mediterranean specimen. (A) Lateral view. (B) Oral view. (C) Manubrium. (D) Schematic view on bell margin from adaxial side. Note the presence of conical excretory papillae that project into subumbrella (arrow). Abbreviations: cc – circular canal, ep – excretory papilla, ex exumbrella, ve – velum.

longer mouth lips in *H. cari*. As this is usually a rather variable character and not used to distinguish species of leptomedusae, it is rather doubtful that the two species are really distinguishable. Moreover, in Schulze's (1874) illustration of the species, on which Hartlaub (1909) based the new name *H. schulzii*, the mouth lips are not significantly smaller than the ones observed here (Fig. 9C). These facts indicate that both nominal species are indistinguishable. Additionally, Laakmann & Holst (2013) published COI sequences of *H. schulzii* collected in the North Sea (GenBank numbers KC440021 and KC440025). The two haplotypes differed in one base pair. The COI sequence of the Mediterranean specimen in the present study also had only one nucleotide difference with the sequences from the North Sea. A difference of one base pair represents therefore evidently only an intraspecific variation (comp. also Laakmann & Holst, 2013; Schuchert, 2014, 2016; Zheng *et al.*, 2014; Schuchert *et al.*, 2017 for intraspecific COI variation in Hydrozoa).

To conclude, *H. schulzii* Hartlaub, 1909 must be regarded as a synonym of *H. cari* (Haeckel, 1864), with the latter having precedence.

The specific epithet of *H. schulzii* (original spelling) was modified to *H. schulzei* by Kramp (1936), arguing that the name refers to Schulze. However, this is incorrect as the epithet was likely meant to represent the Latinised form Schulze, which is Schulzi. The second i comes from the genitive declension. Although many subsequent authors used Kramp's spelling, the correct spelling remains *H. schulzii*.

#### Genus *Eutima* McCrady, 1859

**Remarks:** See Vannucci (1957) and Bouillon (1984) for a discussion and comparison of species.

According to Migotto *et al.* (2004), *Eutima sapinhoa* Narchi & Hebling, 1975 lacks cirri and in the adult medusa the gonads stretch from the manubrium to close to the bell margin. Using the classification of Bouillon *et al.* (2006), the species must therefore be transferred to the genus *Neotima* as *Neotima sapinhoa* (Narchi & Hebling, 1975) **n. comb.**

#### *Eutima gegenbauri* (Haeckel, 1864)

Fig. 10A-B

*Octorchis gegenbauri* Haeckel, 1864: 331. – Russell, 1953: 367, fig. 233-23, pl. 22 fig. 4.

*Eutima gegenbauri*. – Neppi & Stiasny, 1913: 48. – Kramp, 1959a: 161, fig. 221. – Kramp, 1961: 195. – Cornelius, 1995: 228, fig. 52.

*Eutima (Octorchis) gegenbauri*. – Kramp, 1933: 588, fig. 58. – Russell, 1970: 260, figs 23s-24s.

*Liriopsis campanulatus* Claus, 1877: 11.

*Octochandra canariensis* Haeckel, 1879: 198, pl. 13 fig. 1.

*Octochandra germanica* Haeckel, 1879: 198, pl. 13 figs 3-8.

**Material examined:** MHNG-INVE-31748; 2 specimens; France, Villefranche-sur-Mer, Ligurian Sea, Mediterranean, 43.686°N 07.317°E, 0 m depth; collection date 04.05.2001; DNA isolate 009; 16S sequence FJ550515, COI MF000489, 18S FJ550600, 28S FJ550456. – MHNG-INVE-89881; >10 specimens; Sweden, Kristineberg, 58.243849°N 11.432305°E, 0 m depth, collection date 03.10.2014; DNA isolate 1062; 16S sequence KY363964, COI MF000515; for archived photos see Table 1.

**Diagnosis:** Umbrella 10-20 mm wide when mature, almost hemispherical. Apical jelly thick (up to 1/2 of bell height), gastric peduncle very long, 2-3 times the bell height, conical, with very broad base. Velum narrow. 4 radial canals. Stomach tubular, with four lips, rim with a few folds. Elongate gonads along radial canals subdivided, 4 on peduncle beginning

near stomach, 4 gonads on subumbrellar parts of radial canals reaching to bell margin, thus a total of 8 gonads. 8-16 tentacles without distinct bulbs, relatively thick and stiff, not coiling; between tentacles marginal warts, about 60-80 in total, with nematocysts, each wart with an adaxial, conical papilla, usually 1-2 lateral cirri, but these often rudimentary or lost, with a few nematocysts. Papillae with nematocysts. 6-8 statocysts, irregularly placed, with 6-12 concretions.

No distinct colours or denser tissues greenish.

Polyp stage: see Cornelius (1995).

**Distribution:** North-western Europe up to mid-Norway; Mediterranean; Canary Islands; Morocco, North Carolina. Type locality: Nice, Mediterranean.

**Remarks:** The marginal warts have an easily visible adaxial, conical papilla. They have reportedly no excretory pore, but this could not be verified in the present material and needs further examination by histological sections (comp. Russell, 1953: 372).

Vannucci (1957) thought that *Eutima curva* could be conspecific with *E. gegenbauri*, a proposal which was not followed by subsequent authors. DNA sequences of material of *E. curva* from New Zealand were clearly distinct from *E. gegenbauri* (Leclère *et al.*, 2009; Schuchert *et al.*, 2017).

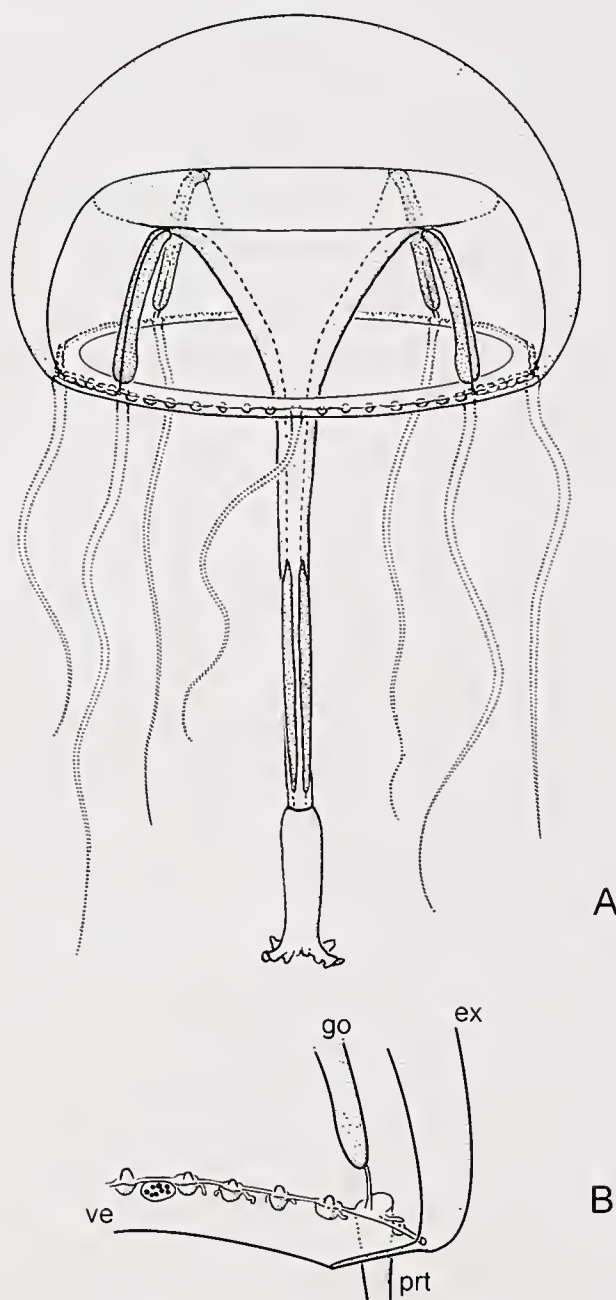


Fig. 10. *Eutima gegenbauri*, after living Mediterranean specimen. (A) Lateral view. (B) Schematic drawing of bell margin seen from adaxial.

#### Genus *Neotima* Petersen, 1962 emended

**Diagnosis:** Eirenidae medusa with large gastric peduncle, four radial canals, 4-8 statocysts, tentacle bulbs or bell margin without cirri, bulbs without excretory papillae, without cordyli, with marginal warts, gonads on entire length of radial canals, either undivided or interrupted in middle part. Hydroid unknown.

**Remarks:** It was necessary to modify slightly the diagnosis of this genus (Bouillon *et al.*, 2006) in order to accommodate the new species described below which has subdivided gonads. The alternative solution, to propose a new genus name, seemed less desirable. Moreover, other genera of the family, like *Eutima*, are also composed of species with entire or subdivided gonads.

The genus *Eutima* McCrady, 1859 differs from the genus *Neotima* by the presence of lateral cirri on the marginal warts (Bouillon *et al.*, 2006). The generic subdivision of the Eirenidae Haeckel, 1879 is likely highly artificial and needs a taxonomic revision.

#### *Neotima galeai* new species

Fig. 11A-B

**Holotype:** MHNG-INVE-93201; 1 mature medusa in ethanol, originally preserved in formalin; Persian Gulf,

Abu Dhabi, 24.4666°N 54.3276°E, 0 m depth, collected 26.08.2006; leg. H. Galea.

**Paratypes:** MHNG-INVE-53566; 4 intact and 1 dissected mature medusae in ethanol; otherwise same data as holotype.

**Type locality:** 24.4666°N 54.3276°E, 0 m depth.

**Diagnosis:** *Neotima* medusa with gonads along radial canals interrupted for some distance, resulting thus in eight gonads in total.

**Etymology:** The species is dedicated to the collector of the type material, Dr Horia Galea, in appreciation of his admirable work on hydrozoan systematics.

**Description:** Medusa nearly hemispherical, diameter 9-11 mm. Aboral jelly thick, 1/3 or more of total height, with a broad gastric peduncle of about the same length as the bell height, basal diameter about half the diameter of the bell, tapering in an even curve to a diameter slightly smaller than stomach diameter. Manubrium small, 1.2 mm high, bell-shaped, mouth opening cruciform as margin drawn out into four perradial lips, entire mouth margin in numerous folds. 26-28 tentacles of which 4 always perradial, contracted 6-7 mm, not coiled, bases laterally compressed, no bulbs, no longitudinal furrows. Between each pair of tentacles 2-7, mostly 4-6, marginal warts, sizes variable but apparently not developing into tentacles, without adaxial papillae. Observed statocyst numbers 6-8, likely normally 8, number of concretions unknown. Cirri absent. Gonads along the four radial canals, reaching from close to junction with circular canal to manubrium, but interrupted for a stretch in middle of the peduncle, gonads thus subdivided into a total of eight gonads, diameter of gonads relatively small compared to other leptomedusae, not much thicker than tentacle base.

Nematocysts: small haplonemes, abundant on tentacles, (6-7)x(2)  $\mu\text{m}$ ; larger haplonemes, relatively rare, along circular canal and in marginal warts, (11-14)x(3)  $\mu\text{m}$ .

Colours: Transparent, gonads whitish.

Polyp unknown.

**Distribution:** Known from type locality only (United Arab Emirates).

**Remarks:** The number of concretions in the statocysts could not be determined as these were missing due to the initial preservation in formalin.

The new species matched the diagnosis for the genus *Neotima* Petersen, 1962 (see also Bouillon *et al.*, 2006), except for the subdivided gonad (see remarks above). It resembles *Neotima lucullana* (Delle Chiaje, 1823), but this Mediterranean species is much larger (diameter up to 87 mm), has a thin aboral jelly, about twice as many tentacles, the tentacles have an abaxial groove, and the gonads are undivided (Petersen, 1962). The only other known *Neotima* species, *Neotima peterseni* Bouillon, 1984, has a similar size and tentacle number as the new

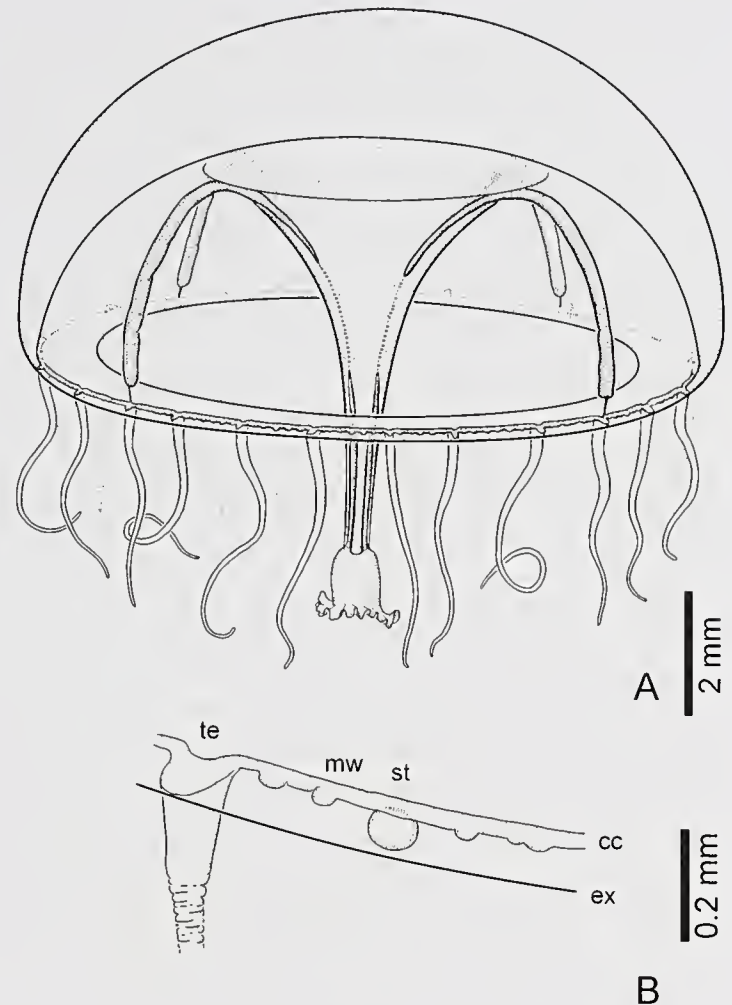


Fig. 11. *Neotima galeai* new spec., schematic drawings after preserved specimens. (A) Lateral view. (B) Bell margin, oblique view from abaxial, concretions of statocyst not shown. Abbreviations: cc – circular canal, ex – exumbrella, mw – marginal wart or rudimentary bulb, st – statocyst, te – tentacle.

species, but the bell shape and thickness of the mesogloea are different, as well as the gonads being undivided (comp. Bouillon, 1984: table 3).

*Neotima galeai* can potentially be confused with *Eutima hartlaubi* Kramp, 1958, a species occurring in the same biogeographic zone. However, the latter species is distinguishable by having marginal warts with lateral cirri, only 12-14 tentacles, and an abaxial spur at the tentacle base (Kramp, 1958; 1968).

The gonads of *Neotima galeai* are relatively thin and one is tempted to regard the observed medusae as subadult. However, the other *Neotima* species also have thin gonads and this seems to be a characteristic trait of the genus and also many other species of the family Eirenidae.

**Family Mitrocomidae Haeckel, 1879**  
**Genus Mitrocomella Haeckel, 1879**

***Mitrocomella browni* (Kramp, 1930)**

Fig. 12A-B

*Trissocoma browni* Kramp, 1930: 23, fig. 9-11.

*Mitrocomella brownei*. – Kramp, 1932: 341, figs 9, 37, revision. – Rees & Russell, 1937: 75, figs 9-10, life cycle. – Russell, 1953: 261, figs 150-155, pl. 15 fig. 4. – Kramp, 1959a: 142, fig. 169. – Kramp, 1961: 155. – Pagès *et al.*, 1992: 32, table. – Bouillon, 1995: 236. – Cornelius, 1995: 140, fig. 31. – Bouillon & Barnett, 1999: 91, fig. 91.

**Material examined:** 3 medusae; France, Roscoff, 48.73°N 04.00°E, 0-20 m depth, collection date April 1998; DNA isolate N119; 16S sequence KX355404, COI MF000485, 18S FJ550521, 28S FJ550374.

**Diagnosis:** Umbrella diameter 4-7 mm, umbrella usually somewhat flatter than a hemisphere, lateral jelly rather thin, apical jelly somewhat thickened, no gastric peduncle. Velum width 1/3 to 1/4 of radius. Manubrium short, cruciform cross-section, base not much larger than oral end, mouth simple, four perradial, slightly recurved lips. Radial canals 4, narrow, straight. Gonads oval, somewhat more elongate in females, situated near the ends of the radial canals, in younger animals more towards middle. Marginal tentacles typically 16, range in adults 11-24, with basal bulbs, 5-7 cirri between adjacent tentacles, coiling spirally. Typically 8 large, adradial statocysts (range 8-11), each with 5-7 concretions in a u-like arrangement. Colours: manubrium greenish, pink, or ochreous yellow.

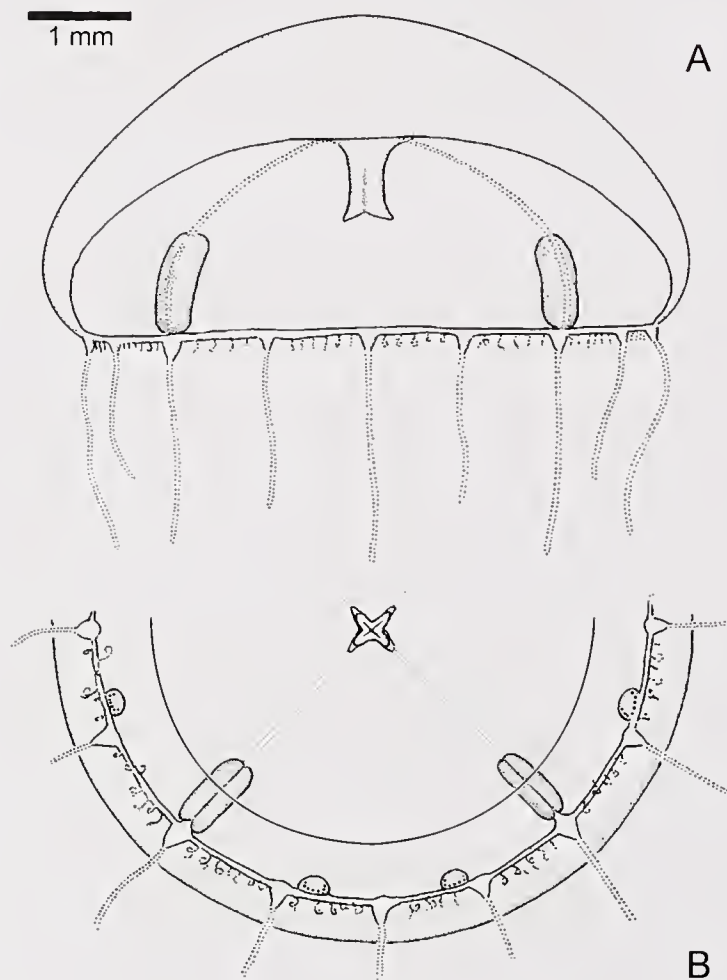


Fig. 12. *Mitrocomella brownei*, male, after life. (A) Lateral view. (B) Oral view.

Polyp stage tiny, of “*Cuspidella*” type, see Cornelius (1995).

**Distribution:** British Isles, Brittany, Mediterranean, New Zealand. Type locality: North Sea.

**References:** Russell (1953), Cornelius (1995), Bouillon & Barnett (1999).

### *Mitrocomella polydiademata* (Romanes, 1876)

Fig. 13A-D

*Tiaropsis polydiademata* Romanes, 1876a: 274, nomen nudum. *Tiaropsis polydiademata* Romanes, 1876b: 526. – Romanes, 1877: 194, pl. 15 fig. 3.

*Mitrocomella polydiademata*. – Kramp, 1932: 346, text-figs 3, 5, 11, 18, 29, 30, 40, pl. 10 figs 3-4. – Russell, 1953: 257, figs 147-149. – Naumov, 1969: 326, fig. 193. – Edwards, 1973b: 601, figs 1-2, life cycle. – Arai & Brinckmann-Voss, 1980: 93, figs 51-52. – Pagès *et al.*, 1992: 32. – Ramil & Vervoort, 1992: 38, fig. 6a-i. – Cornelius, 1995: 143, fig. 32.

? *Cuspidella grandis* Hincks, 1868: 210, pl. 40, fig. 4.

*Cuspidella polydiademata*. – Naumov, 1969: 327, fig. 194.

*Mitrocomella fulva* Browne, 1904: 17, pl. 1 fig. 3, pl. 3 figs 1-2. – Kramp, 1932: 344. – Kramp, 1961: 156. – Edwards, 1973b: 601, synonym. – Pagès *et al.*, 1992: 32.

**Material examined:** 1 specimen; Scotland, Firth of Lorn, Dunstaffnage Bay, 56.455°N 05.434°E, 0 m depth, temperature 8-10°C; collection date 11.05.2004; DNA 1133; 16S sequence KY363939, COI MF000501; archived document see Table 1. – >2 specimens; Norway, Fanafjord, 60.24079°N 05.22941°W, 0 m depth; collection date 23.04.2015; DNA isolate 1115; 16S sequence KY363949, COI MF000508, 18S KY363979; archived document see Table 1.

**Diagnosis:** Umbrella diameter 9-30 mm, mostly around 10-12 mm, umbrella usually hemispherical or slightly higher, apical jelly thickened, no gastric peduncle. Top of subumbrella sometimes rather flat. Velum width about 1/4 of bell radius. Manubrium short, small, cruciform cross-section, base not much larger than oral end, mouth simple, four perradial, slightly recurved lips. Radial canals 4, relatively thick close to manubrium. Gonads elongate in females, covering 2/3 of radial canals, separated from circular canal and manubrium, when fully developed pendant and usually in zig-zag (Fig. 13D). Marginal tentacles typically 28-36 (reportedly up to 64) when mature, with basal bulbs, some bulbs without tentacles, 5-9 cirri between adjacent tentacles, coiling spirally. 16 large statocysts, each with numerous concretions aligned in two curved rows. When irritated, the medusa emits a greenish light. Polyp stage tiny, of “*Cuspidella*” type, see Cornelius (1995).

**Distribution:** Northern boreal species, known from North Atlantic and NE Pacific. Type locality: Cromarty Frith, Scotland.



**References:** Russell (1953), Arai-Brinckmann-Voss, 1980, Cornelius (1995a).

**Family Lovenellidae Russell, 1953**  
**Genus *Eucheilota* McCrady, 1859**

***Eucheilota maculata* Hartlaub, 1894**

Fig. 14A-C

*Eucheilota maculata* Hartlaub, 1894: 193. – Hartlaub, 1897: 499, pl. 20 figs 4-8. – Russell, 1953: 311, text-figs 193-195. – Kramp, 1959a: 154, fig. 206. – Kramp, 1961: 174. – Werner, 1968: 136, figs 2-20, life cycle. – Russell, 1970: 256, figs 19s-20s. – Cornelius, 1995: 157, fig. 35. – Nagata *et al.*, 2014: 304, figs 17-18, Brazil.

*Campanulina hincksi* Hartlaub, 1897: 496, pl. 21, pl. 22 fig. 11. – Cornelius, 1995: 157, fig. 35.

*Camponma hincksi*. – Stechow, 1921: 255.

? *Eucheilota maculata*. – Goy, 1979: 277, fig. 16.

**Material examined:** About 50 specimens; France, Normandy, Luc-sur-mer, 49.32102°N 00.3443527°W, 0 m depth, collected 18.05.2005; DNA isolate 386, 16S sequence FJ550501, 18S FJ550587, 28S FJ550444; DNA isolate of second specimen DNA1136, 16S KY363942.

**Diagnosis:** *Eucheilota* medusa with a large black dot on each of the four interradial sides of the stomach. Umbrella diameter about 13 mm (range 10-20 mm),

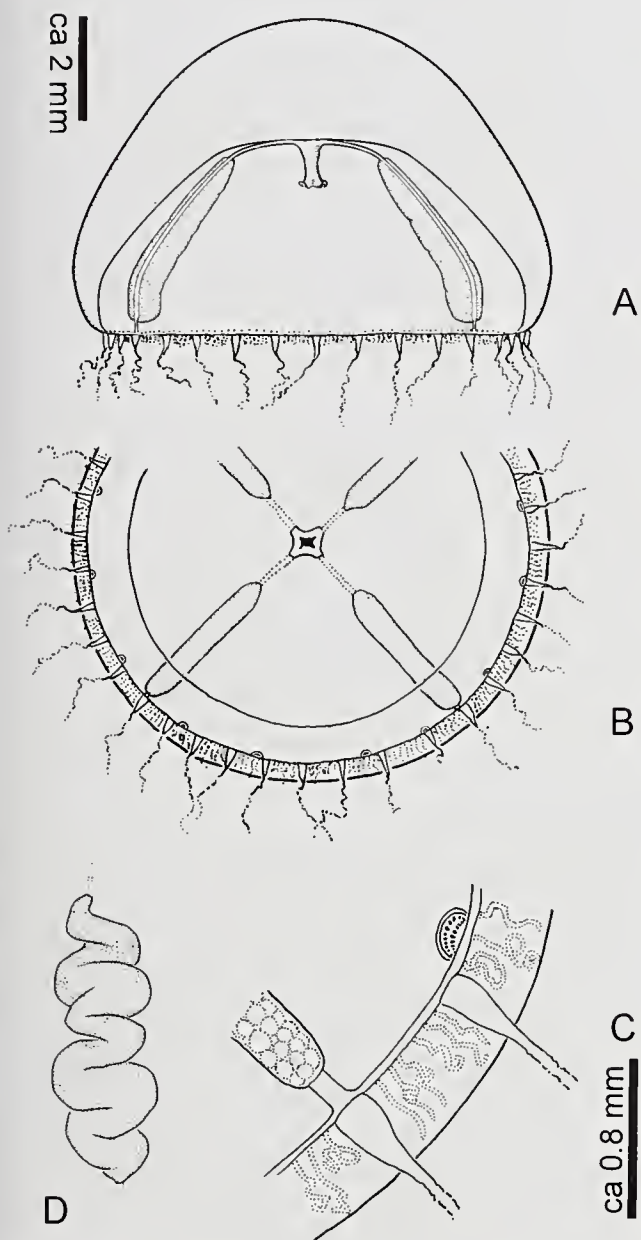


Fig. 13. *Mitrocomella polydiademata*, gonads not fully developed, after life combined from several specimens. (A) Lateral view, diameter about 10 mm. (B) Oral view. (C) Enlarged bell rim showing tentacle bulbs, cirri, and one statocyst. (D) Fully developed gonad, oral view.

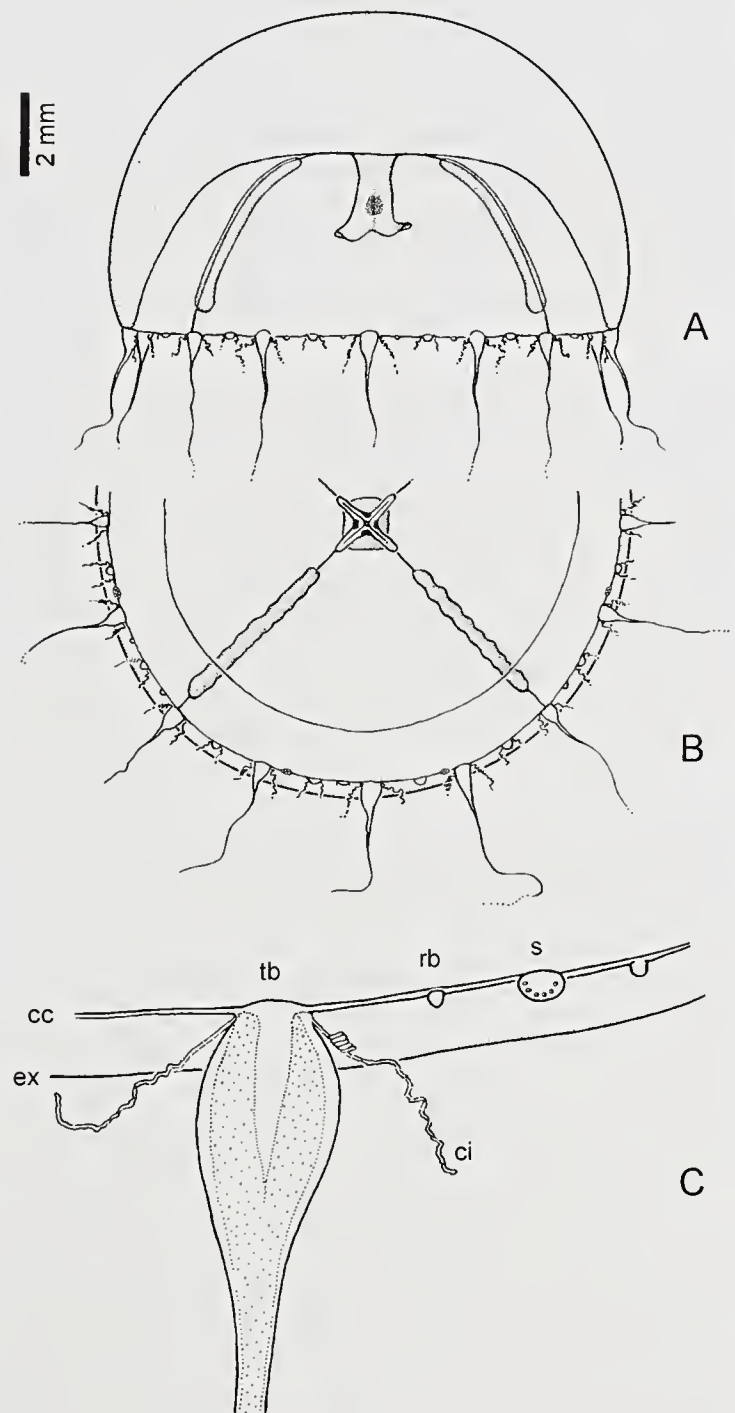


Fig. 14. *Eucheilota maculata*, after life. (A) Lateral view. (B) Oral view. (C) Enlarged bell rim in oral view, showing tentacle bulbs (tb), cirri (ci), and one statocyst (s); cc – circular canal, ex – exumbrella, rb – rudimentary bulb.

usually hemispherical or slightly higher, apical jelly somewhat thickened, no gastric peduncle. Top of subumbrella rather flat. Velum width ca 1/5 of bell radius. Manubrium short, cruciform cross-section, base not much larger than oral end, mouth simple, four perradial, slightly recurved lips. Radial canals four, narrow. Gonads elongate in females, covering 2/3 of radial canals, separated from circular canal and manubrium, when fully developed slightly wavy. Marginal tentacles typically 16 (occasionally 20) when mature, with distinct basal bulbs, between each pair of tentacles 1-3 small, rudimentary bulbs without tentacles. Tentaculate bulbs and sometimes also rudimentary bulbs with a lateral spiral cirrus on each side. Eight closed statocysts with 5-6 concretions each. Polyp stage forming branched colonies of the “*Campanulina*” type, see Werner (1968) or Cornelius (1995).

**Distribution:** Southern North Sea, western Baltic Sea, English Channel, Argentina, Brazil, and southwest of India (Cornelius, 1995; Nagata *et al.*, 2014). Type locality: North Sea, Helgoland.

**References:** Russell (1953), Cornelius (1995).

***Eucheilota menoni* Kramp, 1959**

Fig. 15A-D

*Eucheilota menoni* Kramp, 1959b: 248, fig. 14a-b. – Kramp, 1961: 175. – Kramp, 1968: 82, fig. 221. – Bouillon, 1984: 57. – Bouillon *et al.*, 1988: 217, fig. 12, nematocysts. – Bouillon & Barnett, 1999: 89, fig. 80.

? *Mitrocomium assimile* Browne, 1905b: 137, pl. 1 fig. 3.

? *Lovenella assimilis*. – Kramp, 1961: 177. – Kramp, 1968: 80, fig. 216. – Bouillon, 1984: 76, nematocysts. – Bouillon *et al.*, 1988: 220, nematocysts. – Brylinski *et al.*, 2016: 21, fig. 2.

*Lovenella assimilis*. – Bouillon & Barnett, 1999: 89, Fig. 87.

**Material examined:** Holotype of *Eucheilota menoni*, 1 female medusa, NHMD-98221; Nancowry Harbour, Nicobar Islands, Galathea station 319; 06.05.1951; det. P. L. Kramp. – MHNG-INVE-29469, about 60 mature medusae; collected at several stations between Auckland and Leigh, New Zealand; February 1997; originally in formaldehyde, pigment almost entirely lost. – MHNG-INVE-33457, 8 specimens; Narrow Neck Beach, Hauraki Gulf, New Zealand, 36.8123°S 174.8025°E, 0 m depth; 03.07.2002; 7 specimens originally in formaldehyde, pigments now faint, one specimen preserved for DNA extraction giving sample DNA072; 16S KY363960. – 10 mature medusae, not in permanent collection; same locality as before but collected 26.07.2002; preserved in 95% ethanol; pigments and statocysts preserved; DNA of one individual sample 1131; 16S sequence KY363961. – Several specimens, not in permanent collection; Motutapu Island, Hauraki Gulf, New Zealand, 36.7443°S 174.9044°E, depth 0-3 m, 30.06.2002; specimens used for examination

of life medusae and to extract DNA sample 247; 16S FJ550493, COI KT981899, 18S FJ550570, 28S FJ550427.

**Description of New Zealand material:** Small medusa (diameter up to 3 mm), bell nearly hemispherical, jelly somewhat thickened at apex, otherwise moderately thin, without apical process. Velum width ca 1/6 of bell radius. Manubrium short, cruciform cross-section, base quadrangular, only slightly larger than oral end, mouth cruciform, simple, four perradial, slightly recurved

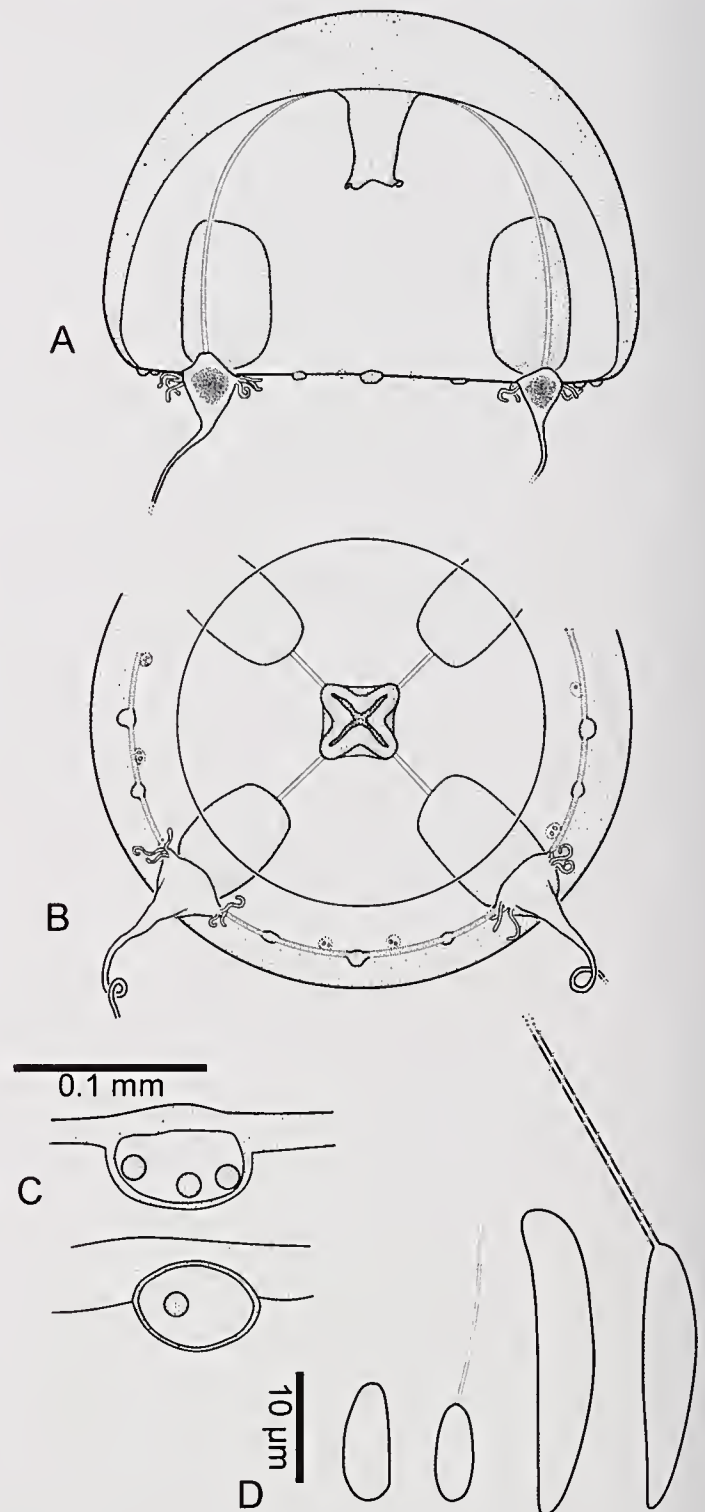


Fig. 15. *Eucheilota menoni* from New Zealand, diameter preserved 1.5 mm. (A) Lateral view. (B) Oral view. (C) Two statocysts, lateral view. (D) Atrichous isorhiza undischarged and discharged, same for large holotrichous isorhizas.

lips. Manubrium without spots of dark pigment. Radial canals four, narrow. Gonads large for the bell-size and already present in small animals (1 mm), covering distal half of radial canals and reaching to level of circular canal; thick, cushion-shaped and projecting deeply into subumbrella, surface smooth, usually without adaxial furrow except in a few animals (and only in 1-2 of the four gonads). Observed egg numbers per gonad about 40. Marginal tentacles 4, between each pair of tentacles 3 small, rudimentary bulbs without tentacles. Tentacles with solid endodermis. Tentaculate bulbs with 3-8 lateral cirri, no cirri on rudimentary bulbs. Tentacular bulbs on abaxial side with a large, conspicuous, black pigment spot. Per quadrant 2-3 statocysts, thus 8-12 in total, each with 1-3 concretions, mostly 2 or 3.

Medusa buds never present.

Nematocysts (preserved material): atrichous isorhizas in tentacles, almond-shaped, size very variable and perhaps 2 size classes, (2.5-3.5)x(7.5-11)  $\mu\text{m}$ ; mainly in tentacle bulbs, large, curved holotrichous isorhizas, end opposite thread opening pointed, spines of thread tiny and hardly visible under light microscopy, capsule size (4-5.5)x(25-26)  $\mu\text{m}$ . Presence of other types cannot be excluded for the examined material (2 medusae).

**Distribution:** Indian Ocean, Red Sea, western Pacific, eastern Pacific (Altuna, 2009), perhaps introduced in the north-eastern Atlantic (Altuna, 2009; Brylinski *et al.*, 2016). Type locality: Nancowry Harbour, Nicobar Islands.

**Discussion:** The material from New Zealand was identified as *E. menoni* because DNA sequences of part of the present material have already been published under this name and also because it mostly matched the diagnosis given in Bouillon & Barnett (1999). However, the identity is not entirely clear and it could as well be attributed to *Lovenella assimilis* (Browne, 1905) as has been argued in detail by Brylinski *et al.* (2016). *Eucheilota menoni* and *Lovenella assimilis* are indeed rather difficult to separate (Bouillon, 1984). Bouillon has reportedly seen both species in Papua New Guinea and he summarised the diagnostic differences of *Lovenella assimilis* and *E. menoni* as follows (in brackets the condition observed in the present material):

- 12 to 20 statocysts versus 8 only (8-12)
- no black pigment on the manubrium versus black dots on manubrium (no dots on manubrium)
- gonads with a longitudinal furrow versus smooth gonads (smooth)
- gonads reaching to bell margin versus gonads reaching close to bell margin (to bell margin).

*Lovenella assimilis* has two concretions per statocyst (Browne, 1905b). Kramp (1959b) could not observe the concretions in his material of *E. menoni*, but in Kramp (1961) he states that there is one concretion only. It could be that he took this from Menon (1932) who described a similar medusa that Kramp thought to be *E. menoni*. The NZ animals had 1-3 concretion, mostly 2-3.

Browne's type material of *Lovenella assimilis* could not be obtained for study, but it is clear from Browne (1905b) that he had a preserved medusa that had lost its pigmentation. This makes *L. assimilis* de facto a "*species inquirenda*", a species that is currently not unambiguously identifiable.

The nematocysts of these two nominal species have been documented by Bouillon (1984), Bouillon *et al.* (1988), Hirano & Yamada (1985), and Altuna (2009). Comparing the results is inconclusive and the interpretation of the capsule types is occasionally subjective.

Bouillon also observed medusa buds in both morphotypes, something never observed by other authors.

To conclude, the present material is not unambiguously attributable to either *E. menoni* or *L. assimilis* and this is also the case for the European material described by Altuna (2009) and Brylinski *et al.* (2016). As already concluded by the latter authors, it is likely that both nominal species as used today are in fact conspecific. Another possibility is that there are more than two species involved and that they all intergrade morphologically. In order to resolve the ambiguity, more specimens of both morphotypes obtained from the western Indian Ocean must be examined morphologically and genetically.

It might seem surprising that two nominal species that are hardly distinguishable have been attributed to two different genera. The medusae of the genus *Lovenella* differ from *Eucheilota* by their number of statocysts, 16-32 versus 4-12 (Kramp, 1968; Bouillon *et al.*, 2006). This seems rather arbitrary, but the separation stems from *Lovenella* Hincks, 1868 being polyp-based, while *Eucheilota* McCrady, 1859 is based on a medusa. A re-assessment of the classification is clearly needed (Cornelius, 1995), and *Lovenella* should be regarded a synonym of *Eucheilota*.

#### Family Malagazziidae Bouillon, 1984

#### Genus *Octophialucium* Kramp, 1955

#### *Octophialucium indicum* Kramp, 1958

Fig. 16A-D

*Octocanna polynema*. – Menon, 1932: 23, pl. 3 fig. 25. [not *Octocanna polynema* Haeckel, 1879 = species inquirenda]

*Octophialucium indicum* Kramp, 1958: 347, figs 2a-b. – Kramp, 1961: 184. – Kramp, 1965: 72. – Kramp, 1968: 87, fig. 235. – Bouillon & Barnett, 1999: 90, fig. 89. – Xu *et al.*, 2014: 623, fig. 510A-B.

*Octophialucium funerarium*. – Wear, 1965: 7, fig. 3E. [not *Octophialucium funerarium* (Quoy & Gaimard, 1827)]

**Material examined:** Numerous mature medusae; Greta Point, Evans Bay, Wellington, New Zealand; 41.3055°S 174.8023°E; surface plankton; 15.11.1993 and 02.02.1994; material used in part for the study of Bouillon & Barnett (1999). – MHNG-INVE-29970, 10 medusae; same locality as previous lot; 26.10.1994;

one medusa used to extract DNA sample N126; 16S AY787897, 18S FJ550522, 28S FJ550375; DNA extract of second medusa (sample DNA 1167) resulted in identical 16S as AY787897.

**Description of NZ material:** *Octophialucium* medusa with bell diameter up to 15 mm, bell flatter than a hemisphere, bell rim somewhat incurved, lateral walls thin and relatively straight, apical jelly thick (1/2 or more of total height). Velum narrow, about 1/10 of radius. Manubrium short, cross-section an eight-pointed star, 8 more or less crenulated lips. Eight radial canals. Gonads short, sausage-shaped, along distal fourth of radial canals but not reaching circular canal. Eight perradial tentacles and 0-8 additional tentacles between perradial tentacles, thus when fully grown usually 16 tentacles in total. Tentacles thin, relatively short. Between each pair of tentacles 3 rudimentary

bulbs, small, without tentacle rudiments. All bulbs with very short, conical excretory papilla projecting into subumbrella, difficult to observe. Bulbs without abaxial spurs. Statocysts closed, oval vesicles along circular canal, 32 or more, small, with 2 (occasionally 1 or 3) concretions. Tissues colourless.

Variation: younger stages have only 4 radial canals, the interradial canals develop by outgrowth from the manubrium. Younger stages may have four developing gonads only.

Hydroid unknown.

**Distribution:** Tropical Indo-West-Pacific from Madagascar to Tahiti and New Zealand (Kramp, 1965). Type locality: Sittwe (formerly Akyab) Harbour, Burma, surface plankton.

**Similar species:** The Atlantic *Octophialucium medium* Kramp, 1955 is very similar, differing only in the more elongated gonads. Another similar species is *Octophialucium sinensis* Huang, Xu, Guo & Qiu, 2010, but this species has only 8 tentacles and smaller bulbs with tentacle rudiments. *Octophialucium funerarium* (Quoy & Gaimard, 1827) from the NE Atlantic has considerably more tentacles, 64-128.

**Remarks:** The identification of the present material was largely based on Bouillon & Barnett (1999), who also had part of this material at their disposal. However, there is one marked difference of the New Zealand material to the original description given in Kramp (1958): the excretory papillae are not long and conspicuous, they are rather small and very inconspicuous (Fig. 16B-C). Additionally, there are fewer tentacles (max. 16 versus 19-28). While the tentacle number difference is likely not significant for a species level distinction, the different excretory papillae could indicate that we have a distinguishable morphotype and perhaps also a different species or a subspecies.

It is possible that not all known nominal *Octophialucium* species are really distinct. Little is known about the inter-population variation in *Octophialucium* species and only molecular genetic studies can reliably assess the status of the different *Octophialucium* species (for species see Schuchert, 2017b; Kramp, 1955b; 1961).

**Family Aequoreidae Eschscholtz, 1829**  
**Genus *Aequorea* Péron & Lesueur, 1810**

***Aequorea macrodactyla* (Brandt, 1835)**

Fig. 17A-D

*Mesonema (Mesonema) macrodactyla* Brandt, 1835: 221. – Brandt, 1838: 359, pl. 4 figs 1-3.

*Polycamma purpurostoma* Agassiz & Mayer, 1899: 169, pl. 8 figs 26-28.

*Aequorea maldivensis* Browne, 1905a: 732, pl. 56, figs 4-12.

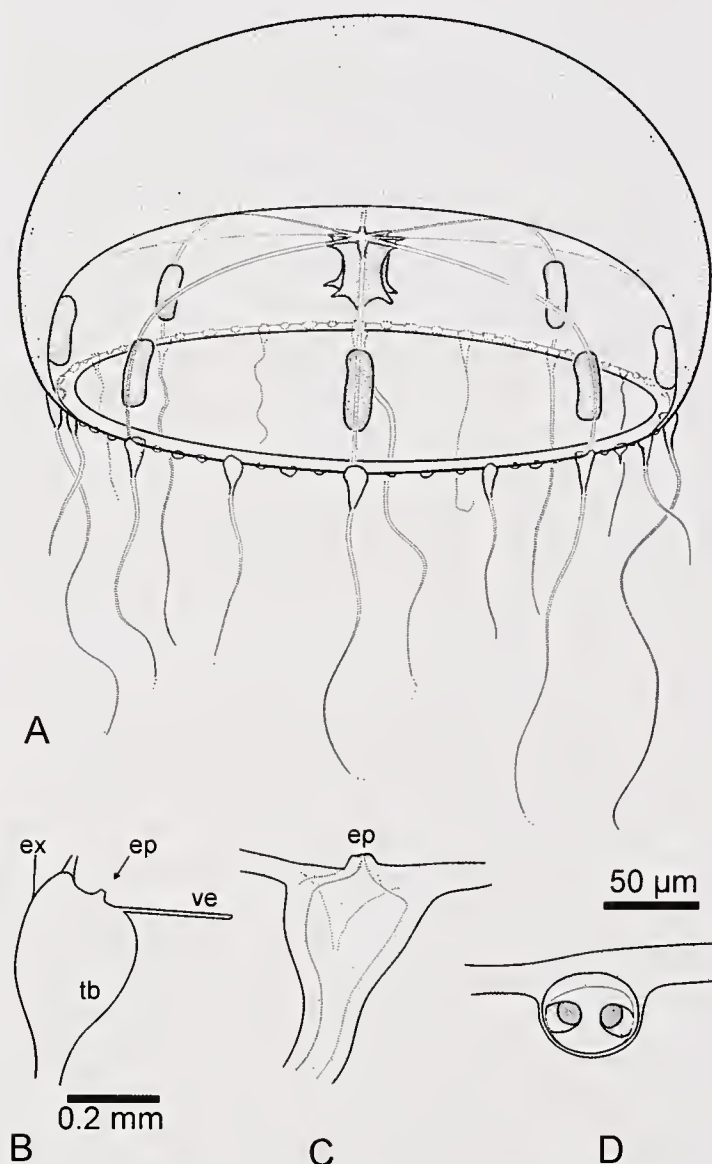


Fig. 16. *Octophialucium indicum*, combined from several preserved specimens. (A) Oblique view, diameter 13-15 mm when alive. (B) Schematic side view of perradial tentacle bulb. (C) Adaxial view of tentaculate bulb in optical section. (D) Statocyst with two concretions. Abbreviations: ep – excretory papilla, ex – exumbrella, tb – tentacle bulb, ve – velum.

*Mesonema macrodactylum*. – Maas, 1905: 40, pl. 8 fig. 52.

*Aequorea macrodactylum*. – Bigelow, 1909: 174, pl. 36. – Bigelow, 1928: 313, pl. 43 fig. 7.

*Aequorea pensilis*. – in part Russell, 1953: 355, fig. 220C-D, 225, pl. 33 figs 1-5 [not *Aequorea pensilis* (Haeckel, 1879)]

*Aequorea macrodactyla*. – Kramp, 1959a: 167, fig. 235. – Kramp, 1961: 207, synonymy. – Kramp, 1965: 87, fig. 8. – Kramp, 1968: 98, fig. 267. – Pagès *et al.*,

1992: 26, fig. 26. – Cornelius, 1995: 208, fig. 48D-E. – Bouillon & Barnett, 1999: 79, fig. 71. – Mizrahi *et al.*, 2015: 59, fig. 1A-D.

? *Aequorea macrodactyla*. – Nogueira *et al.*, 2016: fig. 1.

**Material examined:** NIWA 119801; 8 medusae; from sediment trap in 360 m depth deployed north of Hauraki Gulf, New Zealand, -35.0867°S 174.8833°E, sampling period 28.11.1996 to 05.02.1997; very well-preserved in formalin, 7-30 mm diameter, gonads developed after reaching bell diameters of 20 mm.

**Diagnosis:** Umbrella diameter when mature 20-75 mm, central jelly thick, lens-shaped, margin thin; with conical jelly filling stomach (1/2 subumbrella height); velum spanning about 1/5 of umbrellar opening. Stomach about 2/3 as wide as umbrella, funnel-shaped, mouth region much folded, about as many folds as radial canals. 60-100 (max. 150) radial canals; gonads extending along radial canals from close to circular canal to base of the stomach (and conical jelly). Much fewer tentacles than radial canals, only 10-30 marginal tentacles of variable lengths, all with conspicuous bulbs of variable sizes, also many bulbs without tentacles, but many radial (>50%) canals end in no bulbs. Marginal bulbs characteristically broad and with rounded abaxial keel clasping the bell margin, with excretory papilla on subumbrellar side. Statocysts below circular canal, numerous, 1-3 between two radial canals, 2-5 concretions per statocyst. Colours: stomach wall pink, gonads greyish-blue or violet (after Kramp, 1965, 1968; Pagès *et al.*, 1992; own observations).

Polyp stage unknown. Nematocysts see Russell (1939, as *A. pensilis*).

**Distribution:** Circumglobal, widely distributed in tropical and temperate regions of the Indo-Pacific, less common in the Atlantic Ocean, perhaps introduced in the Mediterranean (Kramp, 1965; Pagès *et al.*, 1992; Mizrahi *et al.*, 2015; Nogueira *et al.*, 2016, the latter with a map and many references of records). Type locality: Equatorial Pacific.

It is rather frequent at depths from the surface to 2000 m, but even sampling with cable lengths of 4000 m yielded specimens (Kramp, 1965).

**Remarks:** The relatively low tentacle number combined with the diagnostic broad marginal bulbs with an abaxial keel (Fig. 17C-D) allows a reliable identification of this species, notably to separate it from *A. pensilis* (Haeckel, 1879) and *A. krampi* Bouillon, 1984. Identifying *Aequorea* species is currently rather difficult (comp. e.g. Arai & Brinckmann-Voss, 1980; Gershwin *et al.*, 2010) and a taxonomic revision based on a worldwide study comparing morphotypes and DNA markers is highly desirable.

*Aequorea macrodactyla* has been recorded from New Zealand before (Kramp, 1965; Bouillon & Barnett, 1999), but the good preservation of the specimens permitted

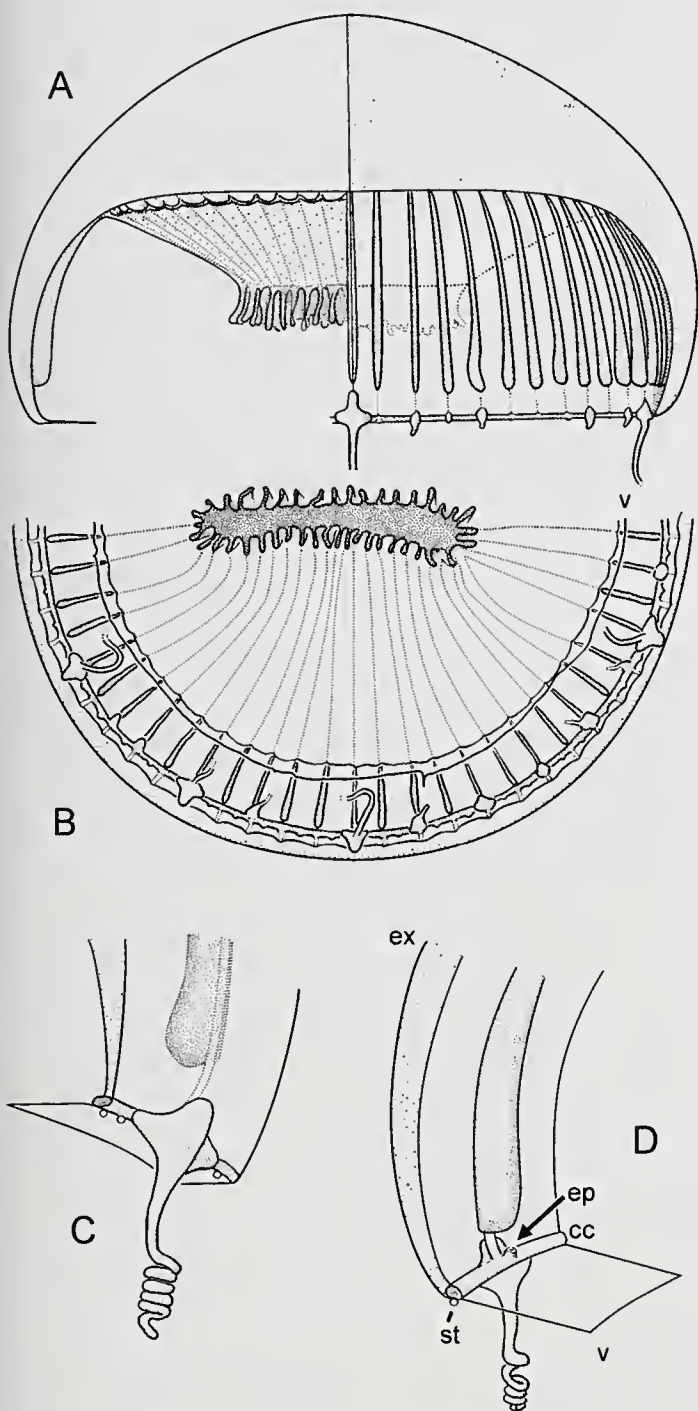


Fig. 17. *Aequorea macrodactyla*, bell diameter about 26 mm, about 70 radial canals, after preserved specimen. (A) Lateral view, left half shown as with umbrella cut away. (B) Oral view. (C) Bell margin seen from outside, note characteristic shape of tentacle bulb. (D) Bell margin seen from inside the bell, note the excretory papilla (arrow, ep). Other abbreviations: cc – circular canal, ex – exumbrella, statocyst, v – velum.

the illustration of some structural details (Fig. 17A-D). As in other *Aequorea* species, the stomach is very wide but relatively shallow and it almost covers the conical jelly that hangs down from the subumbrella like a gastric peduncle.

**Family Campanulariidae Johnston, 1836**

**Genus *Clytia* Lamouroux, 1812**

***Clytia gregaria* (L. Agassiz, 1862)**

Fig. 18A-C

*Oceania gregaria* L. Agassiz, 1862: 353.

*Clytia osterudi* Strong, 1925: 389, pl. 37, hydroid.

*Phialidium gregarium*. – Murbach & Shearer, 1903: 179, pl. 20.

– Kramp, 1961: 167, 444. – Kramp, 1962: 25. – Kramp, 1968: 78, fig. 206. – Roosen-Runge, 1970: 217, figs. 2-25, hydroid. – Arai & Brinckmann-Voss, 1980: 104, figs 59-60.

*Clytia gregaria*. – Bouillon, 1995: 233. – Bouillon & Barnett, 1999: 99, fig. 101.

**Material examined:** Several specimens; USA, Friday Harbor Laboratories, floating docks, 48.545141°N 123.012059°W, 0.5 m depth; collection date 23.05.2011; DNA was isolated from two individuals, DNA 920 giving the sequences 16S MF000539, COI MF000499; DNA isolate 1169 yielding the 16S sequence MF000540. Specimens without black pigment; archived document see Table 1.

**Diagnosis:** Umbrella up to 22 mm wide, hemispherical to lens-shaped. Manubrium small, attached on a short gastric peduncle of variable height, manubrium base cross-shaped and attached to peduncle, mouth with 4 long, folded lips. Gonads linear, undulated, along distal half to two-thirds of radial canals, not touching circular canal; females with >100 eggs per gonad. Marginal tentacles 60-80, marginal bulbs nearly globular, few or no bulbs without tentacles when fully grown; 1 statocyst (or rarely 2 or 3) between successive tentacle bulbs, usually 1, sometimes 2 concretions per statocyst. Without colour or gonads pale yellow to salmon. With or without variable amounts of black or dark brown pigment on margin of lips, gonads, marginal bulbs and ring canal.

**Distribution:** Shallow waters of coastal regions of the NE Pacific Ocean, from British Columbia to Oregon (Arai & Brinckmann-Voss, 1980). Bouillon (1995) and Bouillon & Barnett (1999) recorded it also from New Zealand, mostly in deeper waters. Type locality: Strait of Georgia, British Columbia, Canada, Pacific Ocean.

**Similar species:** Preserved and damaged material of this medusa can easily be confounded with *Eirene mollis* Torrey, 1909 (see Arai & Brinckmann-Voss, 1980 for description). *Eirene mollis* has up to 180 tentacles and a somewhat more pronounced gastric peduncle. It is not known if it has excretory papillae.

**Remarks:** A summary on the identity, taxonomy, biology, and distribution of this species is given in Arai & Brinckmann-Voss (1980). This is a locally very common medusa. It has served for a large number of experimental studies (mostly using the superseded name *Phialidium gregarium*, e.g. Dabiri *et al.*, 2010; Freeman, 2005; Colin & Costello, 2002; Colin *et al.*, 2003; Costello & Colin, 2002; Ridgway & Freeman, 1999; Mills, 1981; and many more references given in these works).

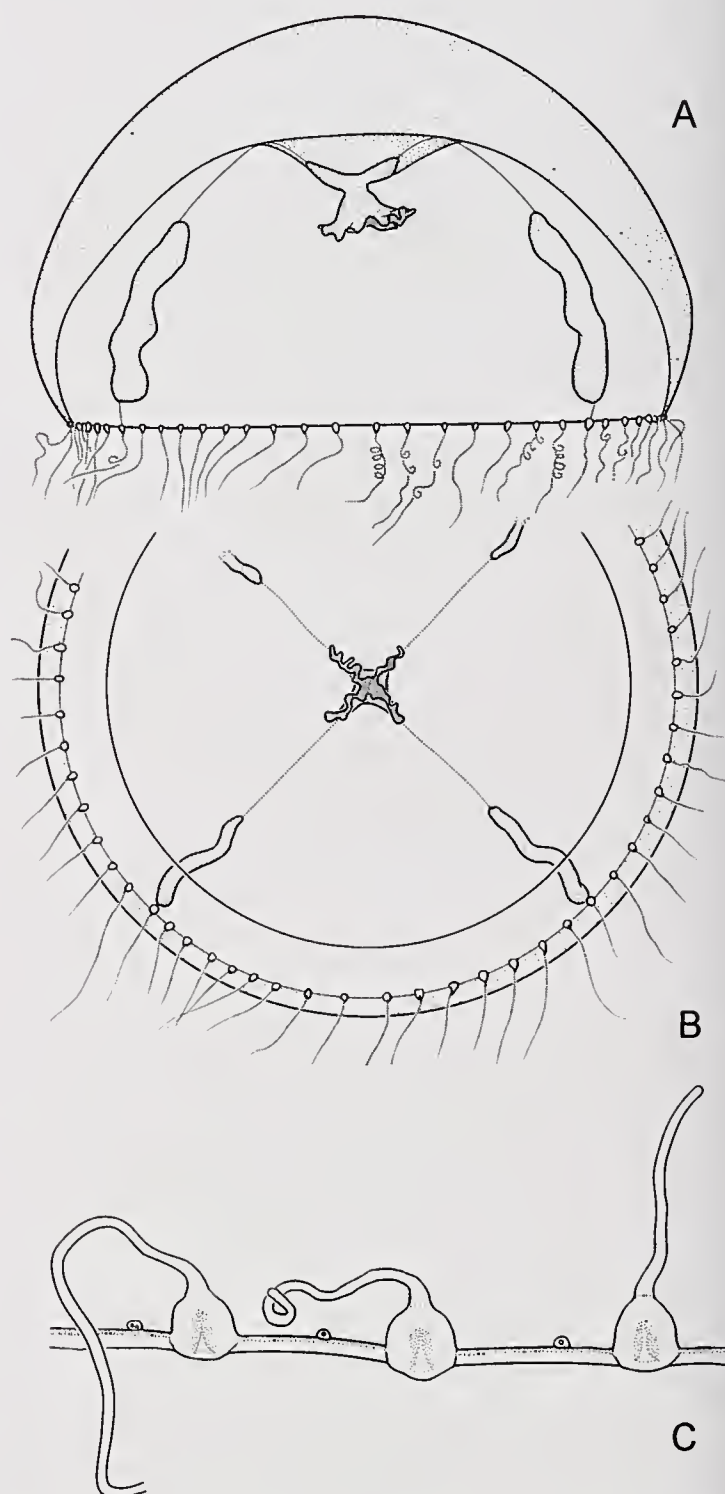


Fig. 18. *Clytia gregaria*, bell diameter about 20 mm, after photographs of living specimens. (A) Lateral view. (B) Oral view. (C) Bell margin in oral view with three tentacles and 3 statocysts.

The hydroid of *Clytia gregaria* has been raised from the medusae several times but it was not possible to relate it to colonies sampled in nature (Arai & Brinckmann-Voss, 1980). The 16S and COI barcode sequence of the present material will hopefully help to identify its polyp stage in nature (cf. Schuchert *et al.*, 2017).

Although rather shallow and sometimes absent, the gastric peduncle of *Clytia gregaria* is rather unusual for the genus *Clytia* and makes the medusa very prone to be mistaken for an *Eirene* species, e.g. the sympatric *Eirene mollis* Torrey, 1909. Some *Eirene* species (cf. Schuchert, 2017) with a shallow peduncle and no excretory papillae could thus turn out to be *Clytia* species.

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## Expanded morphological definition and molecular phylogenetic position of the Tam Dao mountain stream keelback *Opisthotropis tamdaoensis* (Squamata: Natricidae) from Vietnam

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**Abstract:** The description of *Opisthotropis tamdaoensis* Ziegler, David & Vu, 2008, which was based on the male holotype only, is expanded herein on the basis of four newly collected specimens from the type locality of the species, including three adult females. Based on the enlarged sample size and thus extended range of morphological characters in *O. tamdaoensis*, not all characters mentioned in the original description as being distinctive between the latter species and *O. lateralis* Boulenger, 1903, a morphologically similar species, could withstand, such as number and arrangement of preocular, temporal and subocular scales, as well as total size. Presently, the number and arrangement of supralabials in concert with the dorsal colour pattern and the course of the dark lateral stripe still serve as good diagnostic characters to morphologically distinguish *O. tamdaoensis* from *O. lateralis*. Thus, on the basis of the new morphological and for the first time also molecular data, the validity of *O. tamdaoensis* as a distinct species is confirmed. The molecular analyses based on the mitochondrial cytochrome *b* gene revealed *O. tamdaoensis* to be distinct by about 6% genetic divergence from *O. lateralis*, with which it forms a sister relationship.

**Keywords:** Redescription - morphology - molecular phylogeny - *Opisthotropis lateralis*

### INTRODUCTION

Water snakes of the genus *Opisthotropis*, often referred to as Mountain stream keelbacks, are highly aquatic snakes which inhabit flowing streams of hills and mountains of tropical and subtropical Asia. Mountain stream keelbacks are distributed across the mainland of Southeast Asia to

Sumatra (Indonesia), the Philippines and the Ryukyu Archipelago of Japan. This genus, which currently comprises 21 species, is still imperfectly known (Teynié *et al.*, 2013). No less than five *Opisthotropis* species have been discovered in the past decade only: *O. lami* from China, *O. maculosa* from Thailand and China, *O. dnrandi* from Laos, and *O. cucae* as well as *O. tamdaoensis* from

Vietnam (Stuart & Chuaynkern, 2007; Ziegler *et al.*, 2008; David *et al.*, 2011; Teynié *et al.*, 2013; Yang *et al.*, 2013).

From Vietnam, eight species of mountain stream keelbacks have been recorded so far (David *et al.*, 2011; Nguyen *et al.*, 2017), most of which are rare or at least rarely collected and thus poorly known. One of these uncommon mountain stream keelbacks from Vietnam is *Opisthotropis tamdaoensis*, a species recently described from the Tam Dao mountain ridge in northern Vietnam. The original description was based on a single male individual only, which, however, showed peculiar morphological characters compared with its congeners which were the crucial factor for scientific description (Ziegler *et al.*, 2008). Recently, Ziegler *et al.* (2015) reported about another sighting of *O. tamdaoensis* in a forest stream in the surroundings of the Melinh Station for Biodiversity in Vinh Phuc Province, which borders Tam Dao National Park in the West.

During recent herpetological field work in Tam Dao, further *Opisthotropis* individuals were collected in the Bac (Silver) stream, the type locality of *O. tamdaoensis*. Based on this new collection from the type locality, which morphologically was clearly assignable to *O. tamdaoensis*, we herein expand the morphological definition of the species, for the first time including adult female individuals. Based on this new collection we also conducted molecular analyses based on the mitochondrial cytochrome *b* gene to test the distinct taxonomic status and to define for the first time the phylogenetic position within the genus *Opisthotropis*.

The Tonkin mountain stream keelback, *O. lateralis* Boulenger, 1903, is morphologically similar to *O. tamdaoensis*. This species was originally described from northern Vietnam (Manson Mt., nowadays Mao Son Mt., Lang Son Province), and currently is known from central and northern Vietnam as well as from southern China (Guangxi, Guizhou, Hong Kong) (Ziegler *et al.*, 2008; Nguyen *et al.*, 2009; Hecht *et al.*, 2013; Gawor *et al.*, 2016). Based on new collections of the Tonkin mountain stream keelback from northern Vietnam's Bac Giang, Cao Bang and Quang Ninh provinces we additionally provide new information on its morphometry and scalation and morphologically and for the first time also genetically compare *O. lateralis* with *O. tamdaoensis*.

## MATERIAL AND METHODS

This study is based on four newly collected *Opisthotropis tamdaoensis* and nine newly collected *O. lateralis*.

Tissue samples were preserved separately in 95% ethanol and voucher specimens were anaesthetized with ethyl acetate, fixed in approximately 85% ethanol, and then transferred to 70% ethanol for permanent storage.

Individuals were subsequently deposited in the following collections:

IEBR	Institute of Ecology and Biological Resources, Vietnamese Academy of Science and Technology, Hanoi, Vietnam
MHNG	Muséum d'histoire naturelle, Geneva, Switzerland
VNMN	Vietnam National Museum of Nature, Hanoi, Vietnam
ZFMK	Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany.

The holotype of *O. tamdaoensis* is deposited in the Zoological Museum, Vietnam National University, Hanoi, Vietnam (VNUH).

*Opisthotropis tamdaoensis*: IEBR A.2016.32, Suoi Bac (Silver stream), Tam Dao, northern Vietnam, coll. Thanh Ngoc Vu, 29 June 2008. – IEBR A.2016.33, Suoi Bac (Silver stream), Tam Dao, northern Vietnam, coll. Cuong The Pham, 31 May 2014. – MHNG 2767.60, Suoi Bac (Silver stream), Tam Dao, northern Vietnam, coll. Thanh Ngoc Vu, July 2007. – ZFMK 100000, Suoi Bac (Silver stream), Tam Dao, northern Vietnam, coll. Thanh Ngoc Vu.

*Opisthotropis lateralis*: IEBR 3629, Son Dong, Tay Yen Tu, Bac Giang Province, coll. Truong Quang Nguyen, Tung Thanh Tran & Cuong The Pham, 07 April 2008. – IEBR 3644, Son Dong, Tay Yen Tu, Bac Giang Province, coll. Truong Quang Nguyen, Tung Thanh Tran & Cuong The Pham, 09 April 2008. – IEBR 3645, Son Dong, Tay Yen Tu, Bac Giang Province, coll. Truong Quang Nguyen, Tung Thanh Tran & Cuong The Pham, 09 April 2008. – IEBR A.2016.35, Dong Son Ky Thuong, Bac Giang / Quang Ninh provinces, coll. Ha Thuy Duong, June 2013. – IEBR A.2016.36, Tay Yen Tu, Bac Giang Province, coll. Cuong The Pham & Mona van Schingen, 15 May 2015. – VNMN A.2016.14, Bai Tu Long, Quang Ninh Province, coll. Tao Thien Nguyen & Cuong The Pham, 19 September 2009. – VNMN A.2016.15, Cao Bang Province, coll. Tao Thien Nguyen, 08 June 2009. – ZFMK 100805, Tay Yen Tu, Bac Giang Province, coll. Truong Quang Nguyen & Thomas Ziegler, May 2009. – ZFMK 100806, Tay Yen Tu, Bac Giang Province, coll. Truong Quang Nguyen & Thomas Ziegler, 16 May 2014.

In addition, *O. lateralis* specimens recorded in Ziegler *et al.* (2008), Hecht *et al.* (2013) and Gawor *et al.* (2016) were reexamined.

**Morphological examination:** Identification of sex was performed by dissection (inspection of gonads and inspection of presence of hemipenes). Measurements were taken after preservation with a measuring tape. The number of ventral scales was counted according to Dowling (1951). The numbers of dorsal scale rows are given at one head length behind head, at midbody, and at one head length before vent, respectively. Maxillary teeth were counted by dissecting the right maxilla for

teeth / alveoles. Scallation and maxillary teeth number were studied by using a binocular. We herein use the term precloacal instead of anal.

Abbreviations of morphological characters used in the text are as follows.

**Measures and ratios:** SVL: snout-vent length. – TaL: tail length. – TL: total length (SVL + TaL). – TaL/TL: ratio tail length/total length.

**Meristic characters:** ATem: anterior temporal scales (in contact with postocular scale / scales). – DSR: formula of dorsal scale rows. – IL: infralabial scales. – Lor: loreal scales. – PreOc: preocular scales. – PreVen: preventral scales. – PostOc: postocular scales. – PTem: posterior temporal scales (in contact with anterior temporal scale / scales). – SL: supralabial scales. – SL/orbit: supralabial scale / scales touching the orbit. – Subc: subcaudal scales (without tail tip). – SubOc: subocular scales. – Ven: ventral scales.

**Molecular analyses:** The mitochondrial cytochrome *b* gene was employed in this study, because it has been successfully used in previous molecular analyses of *Lycodon* (e.g. Guo *et al.*, 2012). We included three new sequences from samples collected in Vietnam, IEBR A.2016.33 (*Opisthotropis taudaoensis*) from Tam Dao National Park, VNMN A.2016.14 (*O. lateralis*) from Bai Tu Long, and ZFMK 100806 (*O. lateralis*) from Tay Yen Tu (GenBank MF477899 through MF477901). Another sequence of *O. lateralis* (GenBank accession number CG281782) originated from Guangxi Province, China. Other sequences of related species were obtained from GenBank. Three species, *Simonatrix aequifasciata*, *S. annularis*, and *S. percarinata* were used as outgroups based on their phylogenetic relationships to the genus *Lycodon* (Guo *et al.*, 2012) (Fig. 5).

We used the protocols of Le *et al.* (2006) for DNA extraction, amplification, and sequencing. A fragment of the mitochondrial cytochrome *b* was amplified using the primer pair L14910/H16064 (Burbrink *et al.*, 2000). After sequences were aligned by Clustal X v2 (Thompson *et al.*, 1997), data were analyzed using maximum parsimony (MP) and combined (single model of molecular evolution) maximum likelihood (ML) as implemented in PAUP\*4.0b10 (Swofford, 2001), partitioned ML (mixed models of molecular evolution based on codon positions) in IQTree v1.5.5 (Nguyen *et al.*, 2015), and Bayesian combined and partitioned analysis (BA) as implemented in MrBayes v3.2 (Ronquist *et al.*, 2012). Settings for MP, combined ML, and Bayesian analyses followed Le *et al.* (2006), except that the number of generations in the Bayesian analysis was increased to  $1 \times 10^7$  and the number of bootstrap replicates in ML to 1000. Bootstrap support in IQTree was calculated using the ultrafast option (Bui *et al.*, 2013). For MP analysis, heuristic analysis was conducted with 100 random taxon addition replicates using tree-bisection and reconnection (TBR) branch

swapping algorithm, with no upper limit set for the maximum number of trees saved. Bootstrap support was calculated using 1000 pseudo-replicates and 100 random taxon addition replicates. All characters were equally weighted and unordered. The optimal model for nucleotide evolution was set to GTR+I+G for combined ML and Bayesian analyses as selected by ModelTest v3.7 (Posada & Crandall, 1998). In the partitioned Bayesian analysis, models of molecular evolution identified by ModelTest for codon position one, two, and three were GTR+I, TrN+I+G, and TVM+G, respectively. In the partitioned ML analysis, they were determined by IQTree as TN+I, TN+G, and TPM+G, respectively. The cutoff point for the burn-in function was set to 13 and 16 in combined and partitioned Bayesian analyses, respectively, as  $-\ln L$  scores reached stationarity after 13 000 and 16 000 generations in both runs. Nodal support was evaluated using Bootstrap replication (BP) as estimated in PAUP and posterior probability (PP) in MrBayes v3.2.  $BP \geq 70\%$  and  $PP \geq 95\%$  are regarded as strong support for a clade. Uncorrected pairwise divergences (p-distance) were calculated in PAUP\*4.0b10.

## RESULTS

The new *Opisthotropis* series from Silver Stream in Tam Dao was collected in secondary monsoon tropical evergreen forest on granitic soil. Individuals were discovered in between 09:00 to 12:00 am at elevations in between 1200 to 1500 m above sea level. The snakes were in the shallow water in stream sections with open forest.

Subsequent dissections revealed the specimens to represent one adult male and three adult females. The females, which all were collected during the summer, contained large eggs besides small oocytes: IEBR A.2016.33 with eggs up to 24 mm in size (in May), IEBR A.2016.32 with eggs up to 19 mm in size (in June), and MHNG 2767.60 with eggs up to 23 mm in size (in July). Morphometrical data, scalation and dentition of the new *Opisthotropis* series from the type locality of *O. taudaoensis* are summarized in Table 1. Morphologically, the new individuals (Figs 1-3) could be clearly identified as *O. taudaoensis*. However, based on the meanwhile extended sample size, compared with the original description, which was based on a single male individual only, the morphological description of the species must be expanded as follows (based on two adult males, including the holotype, and three adult females): Maximum known total length 555 mm (maximum known snout vent length 475 mm, maximum known tail length 82 mm); tail / total length ratio 0.143-0.157; body stout, cylindrical; head not distinct from neck, dorsally covered with large shields; eye small, with round pupil. Maxillary teeth 25-29. Rostral broader than high; internasals in contact with rostral, nasals, and single prefrontal;

Table 1. Sex, morphometry and scalation of the holotype of *Opisthotropis tamdaoensis* (after Ziegler *et al.*, 2008) and the new series from Tam Dao; values given in brackets indicate infrequent condition.

	VNUH 010606 (holotype)	ZFMK 100000	Range (males)	MHNG 2767.60	IEBR A.2016.32	IEBR A.2016.33	Range (females)	Range (total)
Sex	male	male	female	female	female	female		
TL	555	537	max. 555	459+	522	456	max. 522	max. 555
SVL	475	460	max. 475	420	440	384	max. 440	max. 475
TaL	80	77	max. 80	39+	82	72	max. 82	max. 82
TaL/TL	0.144	0.143	0.143-0.144	-	0.157	0.157	0.157	0.143-0.157
Teeth max	25-26	28	25-28	-	29	-	29	25-29
SL	8/9	9/9	9(8)	9/9	9/9	9/9	9	9(8)
SL/orbit	0/5	5-6/5	5(0, 5-6)	5-6/5	5-6/5-6	5/5	5-6(5)	5, 5-6(0)
IL	10/9	9/10	9-10	10/11	9/10	10/9	10(9,11)	10(9, 11)
PreOc	1/1	1/2	1(2)	1/1	1/2	2/2	1-2	1-2
SubOc	1/1	0/1	1(0)	0/1	0/0	1/1	0-1	1(0)
PostOc	2/2	2/2	2	2/2	2/2	2/2	2	2
Lor	1/2	1/1	1(2)	1/1	1/1	1/1	1	1(2)
Atem	2/2	1/1	1-2	1/1	1/1	1/1	1	1(2)
PTem	4/3	4/3	3-4	2/2	2/3	2/3	2(3)	2-3(4)
DSR	19-17-17	19-17-17	19-17-17	19-17-17	19-17-17	19-17-17	19-17-17	19-17-17
PreVen	4	0	0-4	3	2	3	2-3	0-4
Ven	171	176	171-176	165	163	162	162-165	162-176
Prec	divided	divided	divided	divided	divided	divided	divided	divided
Subc	49+	51	49+-51	-	48	50	48-50	48-51



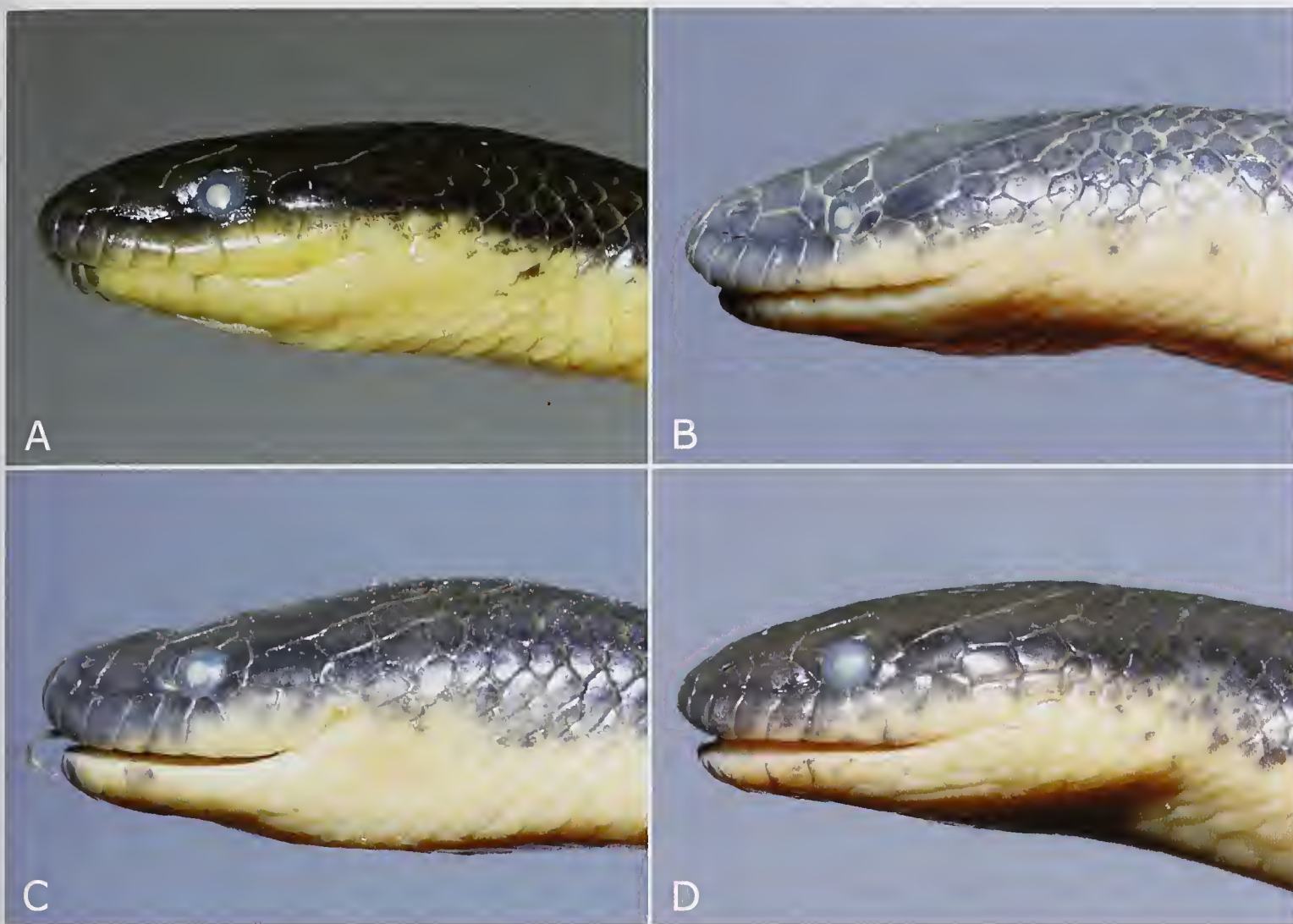


Fig. 1. Head portraits of the new series of *Opisthotropis tamdaoensis* in preserved state, showing the head scalation and the insertion of the black lateral stripe in the midst of the dark dorsal colouration. (A) Female IEBR A.2016.33. (B) Male ZFMK 100000. (C) Female IEBR A.2016.32. (D) Female MHNG 2767.60. Photos: T. Ziegler

frontal pentagonal, widest anteriorly; nasal not divided below nostril; one (rarely two) elongated loreals; loreals not in contact with internasals; one or two preoculars (one preocular in the holotype), two postoculars, one supraocular; one (rarely none) subocular; postoculars followed by one (rarely two) anterior temporals, in the rare latter case the upper one being larger and elongate; anterior temporal(s) followed by (i.e., in contact with) two or three (rarely four) posterior temporals (holotype with 2 anterior and 3-4 posterior temporals); only the holotype shows an additional “postsubocular” scale that is surrounded by the lower anterior temporal, the lower postocular, subocular, and two supralabials; nine (rarely eight) supralabials, the fifth or fifth and sixth (rarely none) in contact with eye; first supralabial not vertical, but directed backward, anterior supralabials distinctly higher than long; mental triangular-shaped, wider than high; ten (rarely nine or eleven) infralabials; first pair of chin shields in contact with first four to five infralabials, and being larger and longer than the second pair of chin shields; posterior chin shields separated by two to three smaller scales.

Dorsal scales in 19 rows at anterior body, in 17 rows at midbody and at posterior body, dorsals finely tuberculate, smooth anteriorly, keeled posteriorly; tail surface distinctly keeled; 0-4 pre- and 162-176 ventrals; preloacal divided; 48-51 divided subcaudals.

Dorsum in preservative nearly uniform olive grey or grey above and paler below, without sharp transition (ca. at the second to third dorsal scale row); dorsum sometimes with rudiments of thin black longitudinal stripes; a more or less distinct dark longitudinal lateral stripe of about 1-2 mm width extends from the eye along the lowermost 3-5 dorsal body scale rows towards the tail tip; supralabials except the completely dark anteriormost ones dark above and pale below; centre of mental and anteriormost infralabials dark; tip of subcaudal region usually with dark mottling. There exists sexual dimorphism related to the number of ventrals, which is higher in males than in females (171-176 versus 162-165) and the relative length of the tail (ratio  $Tal / TL$  0.143-0.144 in males versus 0.157 in females); in addition, males appear to be more slender than the females.



Fig. 2. Characteristic feature of *Opisthotropis tamdaoensis*: the black lateral stripe in the midst of the dark dorsal colouration. (A) Male ZFMK 100000 (left), and female IEBR A.1016.32 (right) in preserved state. (B) Detail of the body side of the female IEBR A.1016.33 in preserved state. Photos: T. Ziegler

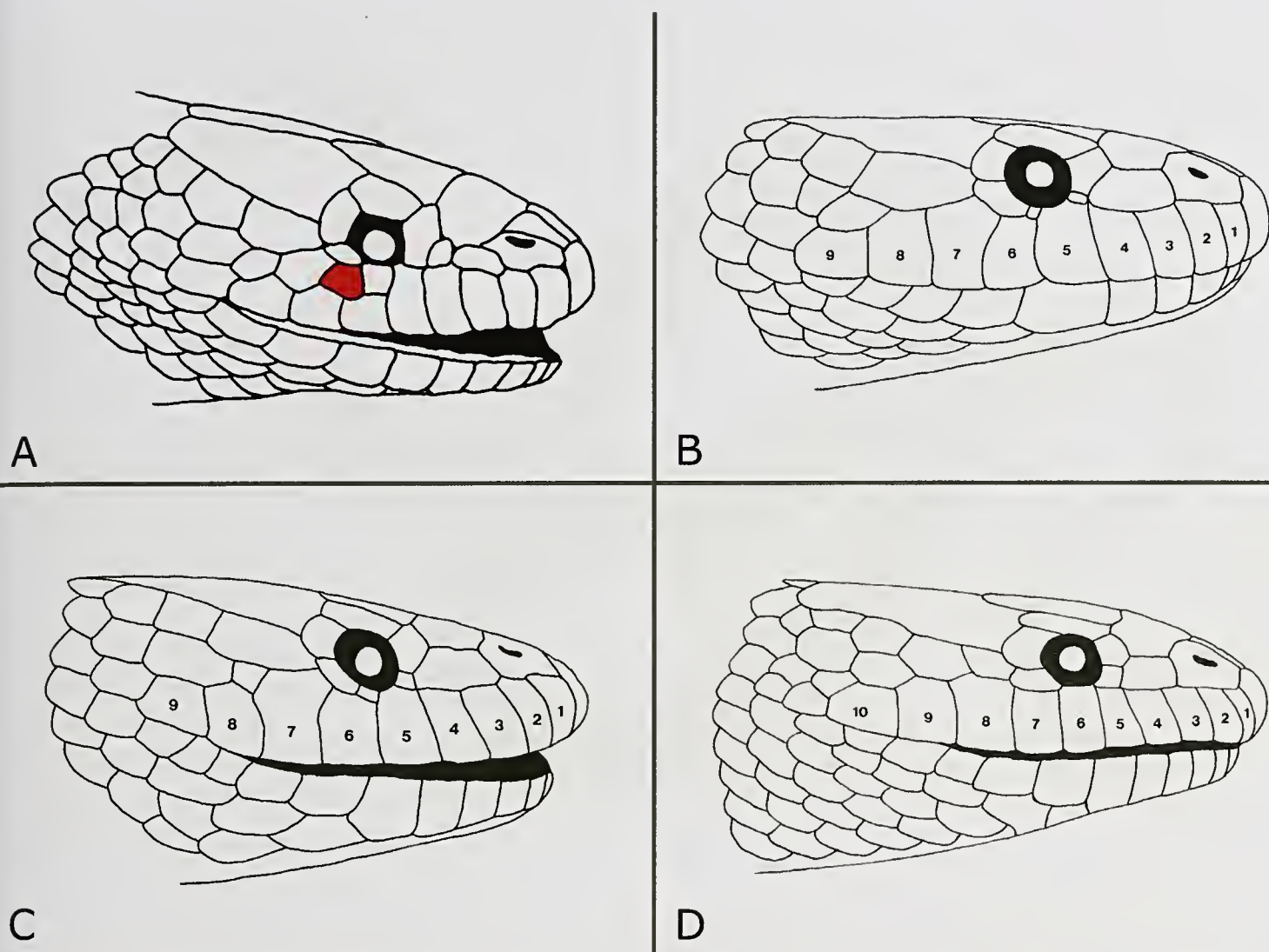


Fig. 3. Drawings showing the head scalation in *Opisthotropis tamdaoensis*. (A) Male holotype after Ziegler *et al.* (2008), with the additional scale below the eye earmarked. (B) Female IEBR A.1016.33. (C) Male ZFMK 100000) compared to *O. lateralis* (D: Male IEBR 3645). Supralabials are numbered to show the differences between the new series of *O. tamdaoensis* (B, C) and *O. lateralis* (D). Drawings: T. Ziegler

Based on the enlarged sample size for *O. tamdaoensis*, the combination of diagnostic characters must be expanded as follows:

- (1) nasal not divided below nostril;
- (2) 1-2 loreals, not in contact with internasals;
- (3) 1-2 preoculars; 2 postoculars; usually 1 subocular;
- (4) 1-2 anterior and 2-4 posterior temporals;
- (5) 9 (rarely 8) supralabials, only the fifth or fifth to sixth supralabial (rarely none) in contact with the eye;
- (6) 9-10 (rarely 11) infralabials;
- (7) first pair of chin shields longer than the second pair;
- (8) dorsal scales smooth anteriorly, keeled posteriorly; in 19-17-17 rows;
- (9) 0-4 pre- and 162-176 ventrals; precloacal divided; 48-51 divided subcaudals;
- (10) uniform olive grey dorsum, with a dark longitudinal lateral stripe within the dark flank coloration; ventral side pale, without sharp transition towards the dark dorsal coloration, tip of the subcaudal region may bear dark mottling.

In the molecular analyses, the final matrix consisted of 1100 aligned characters, of which 268 were parsimony informative. The alignment did not contain gaps. Maximum parsimony analysis of the dataset recovered a single most parsimonious tree with 654 steps (CI = 0.73; RI = 0.71). In the ML analysis, the score of the single best tree found was 4252.62 after 287 arrangements were tried. All ingroup nodes received strong support values from all analyses, except for the placement of *Opisthotropis cheni* + *O. latouchii*, which was only strongly corroborated by the MP analysis. *O. tamdaoensis* was recovered as a sister taxon of *O. lateralis* with high statistical values from all analyses (Fig. 5). Two taxa showed about 6% genetic divergence. The *O. lateralis* from Guangxi in southern China was estimated to be about 2% divergence towards Vietnamese *O. lateralis*.

Based on the meanwhile enlarged sample size and thus extended range of morphological characters in *O. tamdaoensis*, not all characters mentioned in Ziegler *et al.* (2008) as being distinctive between the latter species and *O. lateralis* could withstand, such as number



Fig. 4. Lateral views of two of the newly collected *Opisthotropis lateralis* in life. (A) Male ZFMK 100805. (B) Juvenile ZFMK 100806; the characteristic black lateral stripe that sharply separates the dark dorsal colouration from the light venter is well discernible. Photos: T. Ziegler

and arrangement of preoculars (only one preocular present in the holotype), temporals (2 anterior and 3–4 posterior temporals in the holotype) and subocular scales (existence of an additional “postsubocular” scale that is surrounded by the lower anterior temporal, the lower postocular, subocular, and two supralabials in the holotype), as well as total size.

However, there remain still clear morphological differences between the sister taxa [after Pope (1935), Bourret (1936), Smith (1943), and our own data presented herein, see Tables 2-3, Figs 3-4]:

- 1) *O. tamdaoensis* has 9 (rarely 8) supralabials versus 10 [very rarely 9 or 11] in *O. lateralis*;
- 2) *O. tamdaoensis* has only the fifth or fifth and sixth supralabials (very rarely none) in contact with the eye, whereas in *O. lateralis* very rarely the fifth or even none supralabial, but usually supralabials 5-6, 6, 6-7, or 5-7 are entering the orbit, and
- 3) *O. tamdaoensis* has a black lateral stripe that does not sharply separate the dark dorsum from the pale ventral pattern (sharply separated in the case of *O. lateralis*) and rather takes course within the dark flank coloration; dark dorsum in *O. tamdaoensis* without sharp transition towards the light venter.

## DISCUSSION

Based on a new *Opisthotropis* collection from the type locality of *O. tamdaoensis* the morphological definition of the species could be expanded, for the first time also including complete subcaudal counts and female individuals. The existence of an additional “postsubocular” scale that is surrounded by the lower anterior temporal, the lower postocular, subocular, and two supralabials, considered as a diagnostic character by Ziegler *et al.* (2008), revealed to be an abnormality of the holotype. The molecular analyses revealed *O. tamdaoensis* to be the sister species of *O. lateralis*, which is morphologically similar. Based on the herein expanded morphological definition of *O. tamdaoensis*, not all characters given as distinctive between the latter species and *O. lateralis* in Ziegler *et al.* (2008) could withstand. However, the number and arrangement of supralabials in concert with the dorsal colour pattern and the course of the dark lateral stripe still serve as good diagnostic characters to morphologically distinguish *O. tamdaoensis* from *O. lateralis*. The distinct specific status of the latter taxa is also corroborated by the molecular differentiation of about 6% between both species.

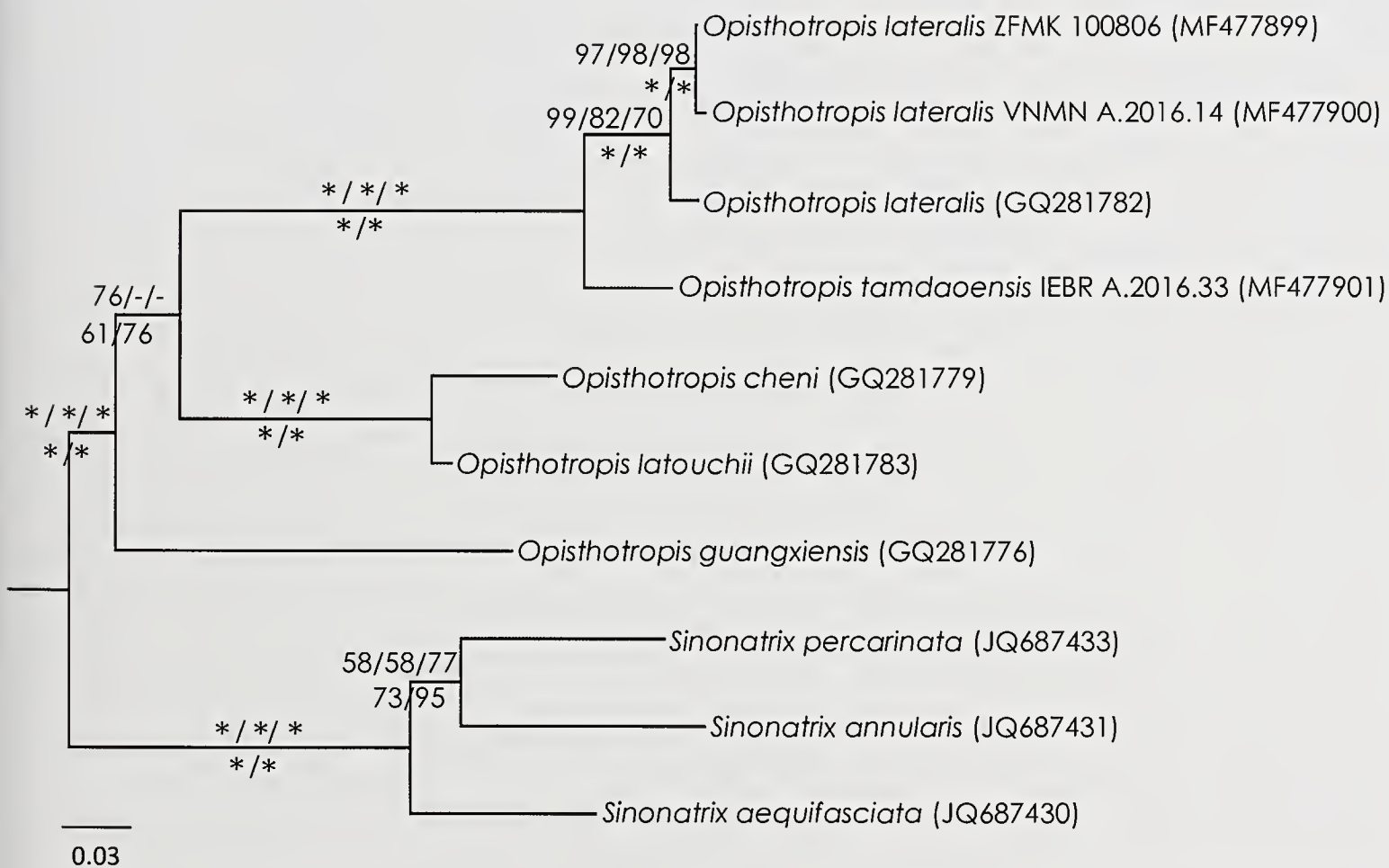


Fig. 5. Combined Bayesian phylogram based on a partial cytochrome *b* fragment. Numbers above and under branches are MP/combined ML/partitioned ML bootstrap values and combined/partitioned Bayesian posterior probabilities (>50%), respectively. Hyphen and asterisk denote <50% and 100% values, respectively.

Table 2. Sex, morphometry and scalation of the new series of *Opisthotropis lateralis* from northern Vietnam's Bac Giang, Cao Bang and Quang Ninh provinces; values given in brackets indicate infrequent condition.

	IEBR 3629	IEBR 3644	IEBR 3645	IEBR A.2016.35	ZFMK 100805	Range (males)	IEBR A.2016.36	VNMN A.2016.15	VNMN A.2016.14	Range (females)	ZFMK 100806	Range (total)
Sex	male	male	male	male	male		female	female	female		juv.	
TL	465	456	463	485	460	Max. 485	490	522	361	Max. 522	223	Max. 522
SVL	397	398	396	420	395	Max. 420	417	438	316	Max. 438	193	Max. 438
TaL	68	68	67	65	65	Max. 68	73	84	45	Max. 84	30	Max. 84
TaL/TL	0.148	0.149	0.144	0.134	0.141	0.134-0.149	0.148	0.160	0.124	0.124-0.160	0.134	0.124-0.160
Teeth max		27-28	-	-	-	27-28	-	27-28	27	27-28	-	27-28
SL	10/10	10/10	10/10	10/10	10/10	10	10/10	10/10	10/10	10	11/11	10(11)
SL/orbit	6-7/6-7	6/6	6/6	5/6	6/6	6(5, 7)	6/6	6-7/5-6	5-6/6	5-6(7)	0	5-7(0)
IL	10/10	8/10	10/10	10/10	10/10	10(8)	10/10	10/10	9/10	10(9)	10/10	10(8, 9)
PreOc	1/1	1/1	2/2	2/1	2/2	1-2	2/2	1/1	1/2	1-2	2/2	1-2
SubOc	1/1	1/1	1/1	1/1	0	1(0)	1/1	1/1	1/1	1	1/2	1(0, 2)
PostOc	2/2	2/2	2/2	2/3	2/3	2(3)	2/2	2/2	2/2	2	2/2	2(3)
Lor	1/1	1/1	1/1	1/1	1/1	1	1/1	1/1	1/1	1	2/1	1(2)
Atem	1/1	2/2	1/1	1/1	1/1	1(2)	1/1	2/1	1/1	1(2)	2/2	1(2)
PTem	2/2	2/3	1/1	3/2	2/2	2(1,3)	3/2	4/2	2/2	2(3,4)	2/2	2(1,3,4)
DSR	19-17-17	19-17-17	19-17-17	19-17-17-	19-17-17	19-17-17	19-17-17	19-17-17	19-17-17	19-17-17	19-17-17	19-17-17
PreVen	2	2	2	2	3	2-3	3	0	2	0-3	2	0-3
Ven	186	183	182	186	186	182-186	176	186	167	167-186	186	167-186
Prec	divided	divided	divided	divided	divided	divided	divided	divided	divided	divided	divided	divided
Subc	-	51	50	48	50	48-51	52	45	-	45-52	51	45-52

Table 3. Sex, morphometry and scalation data of *Opisthotropis lateralis* from the literature (data from Hecht *et al.*, 2013, and Gawor *et al.*, 2016 modified) M: in males, F: in females.

Sex	Pope (1935)	Bouret (1936)	Smith (1943)	Ziegler <i>et al.</i> (2008) male (IEBR 83)	Hecht <i>et al.</i> (2014) male (ZFMK 93904)	Gawor <i>et al.</i> (2016) female (IEBR A.2013.54)
TL	437	360	360	417	472	462
SVL	-	-	-	355	407	387
TaL	-	-	-	62	65	75
TaL/TL	-	-	-	0.149	0.138	0.162
Teeth max	-	-	-	26	-	-
SL	10(9, 11)	10	10-11	11/10	10/10	10/10
SL/orbit	5-7	5-6	5-6	6-7/6	6/6	5-6/5-6
IL	-	-	-	10/10	9/9	9/9
PreOc	1	2	2	2/2	2/2	2/2
SubOc	-	-	-	0/1	0	0
PostOc	2	2	2	2/2	2/2	2/2
Loreal	-	-	-	1/1	1/1	1/1
ATem	1	1	1	1/1	1/1	1/1
PTem	2	2	2	3/3	3/2	2/2
DSR	17 at midbody	17 at midbody	17 at midbody	19-17-17	19-17-17	17-17-17
PreVen	-	-	-	4	2	2
Ven	M: 161-173 F: 159-162	172	159-173	183	184	166
Prec	-	-	-	divided	divided	divided
Subc	M: 51-54 F: 49-56	45	49-56	51	49	45

Concerning the morphological examination of a new series of *O. lateralis* from Vietnam, the dorsal scale row count at the neck in the *O. lateralis* specimen IEBR A.2013.54 from Bai Tu Long was divergent (17 instead 19). However, this seems to represent an abnormality, as another individual from Bai Tu Long (VNMNA.2016.14) showed the species specific dorsal scale row count at the neck (19) and furthermore showed no divergent position in the phylogenetic tree compared to other *O. lateralis* from Vietnam.

The examination of the new series of *O. lateralis* from Vietnam further revealed different ventral scale counts compared with data sorted by sex provided by Pope (1935) for *O. lateralis* from China: 182-186 ventrals in males studied by us from Vietnam versus 161-173 ventrals in males from China, and 166-186 ventrals in females studied by us from Vietnam versus 159-162 in females from China. The herein exemplarily counted maxillary teeth for Vietnamese *O. lateralis* (26-28, n = 4: 2 males, 2 females) agreed well with the known maxillary teeth count of the holotype from northern Vietnam (27); according to Pope (1935), who referred to Chinese *O. lateralis*, Mell (1930) and Fan (1931) only mentioned 18 and 18-20 maxillary teeth respectively, and Pope (1935) furthermore stated how difficult and uncertain this character is. The *O. lateralis* from Guangxi in southern China (Guo *et al.*, 2012) included in the molecular tree (Fig. 5) also showed some genetic divergence towards Vietnamese *O. lateralis*. As recent taxonomic research in a semiaquatic squamate reptiles living in the Vietnam – China border region revealed distinct taxa to be involved (van Schingen *et al.*, 2016), further taxonomic research of *O. lateralis* thus could be interesting and reveal the presence of an undescribed species.

## ACKNOWLEDGEMENTS

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## A revision of the trapdoor spider genus *Liphistius* (Mesothelae: Liphistiidae) in peninsular Malaysia; part 1

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**Abstract:** The currently known *Liphistius* species of peninsular Malaysia are assigned to five species-groups: the *trang*-group, the *malayanus*-group, the *batuensis*-group, the *tioman*-group and the *linang*-group. The latter four are defined and treated here. They are composed of eleven species. Four of them, *L. negara* sp. nov., *L. gracilis* sp. nov., *L. priceae* sp. nov. and *L. linang* sp. nov., are new and here described from males and females. *Liphistius indra* sp. nov., very closely related to *L. linang* sp. nov., is additionally described from the deep south of Thailand. The previously unknown males of *L. endau* Sedgwick & Platnick, 1987 and of *L. tempurung* Platnick in Platnick *et al.*, 1997 are presented for the first time. *Liphistius malayanus cameroni* Haupt, 1983 is placed in the synonymy of *L. malayanus* Abraham, 1923b. Information and illustrations of intraspecific variation in most species of these groups (except for *L. johore* Platnick & Sedgwick, 1984, for which no new material is available) is given together with data on biology and distribution. Taxonomic characters and biogeography are discussed.

**Keywords:** Arachnida - morphology - taxonomy - revision - variation - biology.

### INTRODUCTION

The first ever *Liphistius* described and type species of the genus, *L. desultor* Schiödte, 1849, was found on Penang Island, off the western coast of peninsular Malaysia. Subsequently twelve additional *Liphistius* species (*L. batuensis* Abraham, 1923a; *L. malayanus* Abraham, 1923b; *L. johore* Platnick & Sedgwick, 1984; *L. langkawi* Platnick & Sedgwick, 1984; *L. murphyorum* Platnick & Sedgwick, 1984; *L. panching* Platnick & Sedgwick, 1984; *L. tioman* Platnick & Sedgwick, 1984; *L. yangae* Platnick & Sedgwick, 1984; *L. endau* Sedgwick & Platnick, 1987; *L. kanthan* Platnick in Platnick *et al.*, 1997; *L. tempurung* Platnick in Platnick *et al.*, 1997; *L. laruticus* Schwendinger in Platnick *et al.*, 1997) and one subspecies (*Liphistius malayanus cameroni* Haupt, 1983) were described from that country and are so far known only from there. A fifteenth taxon, *L. rufipes* Schwendinger, 1995, is known from both sides of the Thai-Malaysian border (Schwendinger, 1995; World Spider Catalog, 2017). Five of these species (*L. endau*, *L. johore*, *L. kanthan*, *L. tempurung* and *L. yangae*) were previously known only from females (as *L. johore* still is).

A first compilation of the knowledge (though without regard to taxonomy) on *Liphistius* of Malaysia was

given by Yong (1978), a second by Platnick & Sedgwick (1984) in the context of a generic revision. During the last years considerable new *Liphistius* material (most of it deposited in the Natural History Museum of Geneva) has become available, which allows improved diagnoses for most species from Malaysia, documentation of their interspecific variation, descriptions of unknown males and the reporting of new localities. All this will be presented in two papers, starting here with the species which are assigned to four newly established species groups (distribution given in Fig. 1). The Malaysian species of the species-rich and widely distributed *trang*-group (defined in Schwendinger, 1990) will be treated in the second part of this revision.

### MATERIAL AND METHODS

Morphology was studied and drawn mostly with a Zeiss SV11 stereomicroscope and an attached drawing tube, the ventral side of the *L. malayanus cameroni* vulval plate with a Nikon Optiphot compound microscope with an attached drawing tube. Whenever possible, female copulatory organs were drawn and examined from exuviae. Vulvae of alcohol-preserved specimens were cleared of soft tissue with fine forceps, insect pins

and a paint brush with stiff bristles. Clearing in KOH was avoided, because it often leads to more or less pronounced deformation (bulging) of the vulval plate. With the exception of the paratype of *L. malayanus cameroni*, the ventral cuticular wall of the female genital region was cut off with microscissors to allow an unimpeded view of the ventral side of the vulval plate. Terminology of genital structures follows Schwendinger & Ono (2011), which, with regard to some parts of the male palpal organ, differs considerably from the

terminology used in earlier publications on *Liphistius*. The term “embolus proper” refers to the distal portion of the embolus complex (= sclerite III *sensu* Kraus, 1978) which is more or less deeply divided into a sclerotized part and into a membranous (hyaline, hyaloid) part between which lies the opening of the spermophore. The embolus proper is distinguished from the wide base of the embolus complex which carries the more or less distinctly developed para-embolic plate (a homologue of the conductor in Heptathelinae). The term “vulval plate” is here used to describe the sclerotised ventral wall of the vulva (as opposed to the thin membranous dorsal wall). It is composed of an anterior portion (i.e. the poreplate, perforated by pores that lead to ampulliform vesicles and to a receptacular cluster on its ventral side) and a posterior portion (i.e. the unpigmented or lightly pigmented genital atrium within which lies the strongly pigmented posterior stalk). Opisthosomal tergites are numbered from anterior to posterior, with the anteriormost being tergite I. Body measurements are all in mm (for other measurements the units are given) and were taken on the dorsal side, between midpoint of anterior and posterior margin. Total length includes chelicerae and anal tubercle. The carapace length was measured with the carapace in a slightly forward-inclined position so that its anterior and posterior margin were at the same focal plane. Leg and palp measurement are given in the following manner: total length (femur + patella + tibia + metatarsus + tarsus). In the paragraph “Variation” only relevant taxonomic characters are mentioned. In the figure legends references to illustrations that are to the same scale are separated by commas, references to illustrations of different scales by semi-colons.

The type specimens of most taxa treated here were not re-examined because: (a) those of the “old species” (*L. malayanus*, *L. batuensis*) were redescribed and illustrated in Haupt (1983) and Platnick & Sedgwick (1984); (b) the descriptions and illustrations of the other taxa (except for *L. malayanus cameroni*) are considered sufficient and reliable, and thus a re-examination of the types is not necessary; (c) some of the new specimens presented here were collected at (or very close to) the type localities of their respective species (*L. batuensis*, *L. endau*, *L. panching*, *L. tempurung*, *L. tioman*), and no second *Liphistius* species is known to occur at these localities.

**Museum acronyms:** AMNH = American Museum of Natural History, New York, USA; BMNH = Natural History Museum, London, UK (formerly British Museum of Natural History); MHNG = Muséum d’histoire naturelle de la Ville de Genève, Switzerland; SMF = Senckenberg Museum, Frankfurt, Germany; ZMH = Centrum für Naturkunde (formerly Zoologisches Museum) of the University of Hamburg, Germany; ZRC = Zoological Reference Collection of the National University of Singapore (now housed in the

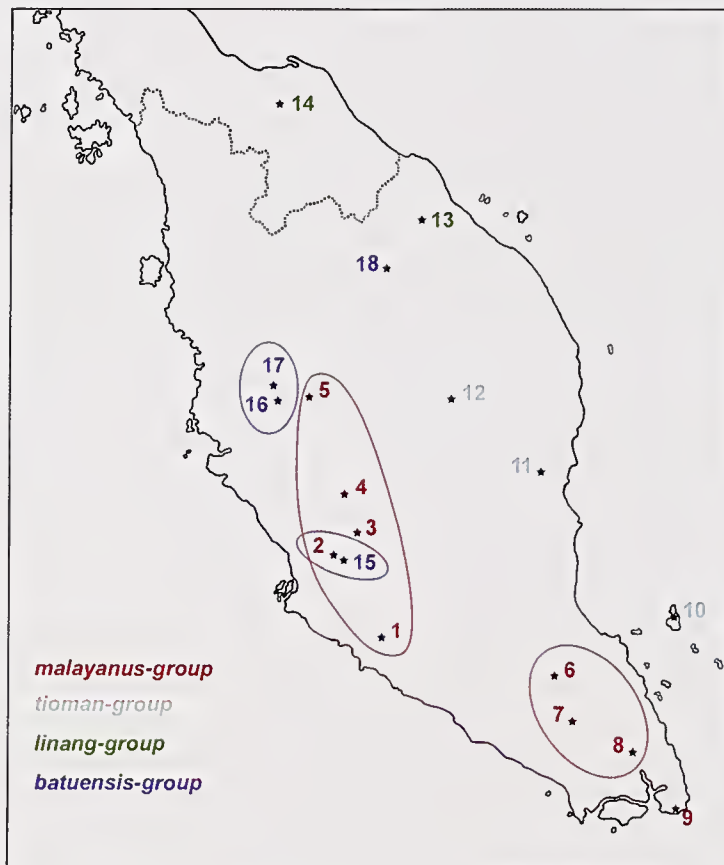


Fig. 1. Localities of *Liphistius* species of the *malayanus*-group, *tioman*-group, *linang*-group and *batuensis*-group in peninsular Malaysia and southern Thailand (coast of Sumatra omitted): 1 - Gunung Angsi (type locality of *L. malayanus*); 2 - Templer Park and Gua Anak Takun (*L. malayanus*, *L. batuensis*); 3 - Genting Highlands (*L. malayanus*); 4 - Fraser’s Hill (*L. malayanus*); 5 - Cameron Highlands (type locality of *L. malayanus cameroni*); 6 - Sungai Jasin in Endau Rompin National Park (type locality of *L. endau*); 7 - Gunung Belumut (*L. endau*); 8 - Gunung Muntahak (*L. endau*; type locality of *L. gracilis* sp. nov.); 9 - Sungai Rengit (type locality of *L. johore*); 10 - Gunung Kajang on Tioman Island (type locality of *L. tioman*); 11 - Gua Charas in Bukit Charas (type locality of *L. panching*); 12 - Nusa Camp in Taman Negara (type locality of *L. negara* sp. nov.); 13 - Jeram Linang Waterfall (type locality of *L. linang* sp. nov.); 14 - Sankalakhierie Mountains (type locality of *L. indra*); 15 - Batu Caves (type locality of *L. batuensis*); 16 - Gua Tempurung (type locality of *L. tempurung*); 17 - Gua Cicak (*L. tempurung*); 18 - Gua Keris (type locality of *L. priceae* sp. nov.). Localities with conspecific populations are encircled. Colours distinguish species groups.

Lee Kong Chian Natural History Museum, Singapore). Other abbreviations used in the text are: AME = anterior median eyes, CDO = dorsal central opening (macropore) of poreplate. Additional abbreviations are explained in the figure legends.

## TAXONOMIC PART

### *Liphistius* Schiödte, 1849

**Type species:** *Liphistius desultor* Schiödte, 1849, described from female holotype deposited in the Natural History Museum of Denmark (= Zoological Museum of the University of Copenhagen).

**Diagnosis and characterisation:** See Platnick & Sedgwick (1984); habitus as in Fig. 2A-B.

### The *malayanus*-group

**Diagnosis:** Distinguished from the *trang*-group by an indistinctly split embolus proper (Fig. 3B, D, F, H) and from all other species groups by distal edge of contrategulum proventrally ending in a V-shaped or U-shaped row of denticles (the clearest synapomorphy of this group; Figs 4C; 6A, C; 8A, D). Vulval plate strongly sclerotised, with a large, undivided CDO and with a large, undivided receptacular cluster (Figs 5, 7, 9).

### Key to the species-groups in peninsular Malaysia:

- 1 Embolus proper deeply split, distal portion of sclerotised and membranous part disconnected from each other on both sides (on retrodorsal side more widely so than on proventral side); ventrolateral wall of sclerotised part and of membranous part basally running into a short but very wide, mostly dorsad-directed fold (called "dorsal lamella" in Schwendinger, 1990: figs 60-62) (Fig. 3A, C, E, G); distal margin of tegulum (corresponding to marginal tegular apophysis of Heptathelinae; see Schwendinger & Ono, 2011) drawn into a more or less distinctly prominent edge; subtegulum with or without apophysis. Poreplate with small CDO and rather small and simple receptacular cluster; mediolateral processes on ventral rim of poreplate present or absent (e.g. Schwendinger, 1990: figs 37-39, 43-45, 47-49, 53-56) ..... *trang*-group
- Embolus proper much less distinctly split, sclerotised and membranous part touching each other on both sides and forming a closed tube; connecting fold mostly long and narrow, indistinct and running prolaterad (Fig. 3B, D, F, H) (in *L. endau* and *L. negara* sp. nov. bent prodorsad instead of running straight proventrad or prolaterad; Figs 6F, H; 8F-G); distal margin of tegulum indistinct, never developed as an edge; subtegular apophysis never present. Poreplate with very large quadrangular, pentangular or trapezium-shaped CDO (see Fig. 5), or (rarely) with small or medium-sized circular CDO (see Fig. 24F), or with indistinct slit-like CDO (see Figs 16A, C-D; 22A, C, E, G); receptacular cluster large or medium-sized, always complex, never simple and digitiform; mediolateral processes on ventral rim of poreplate always absent ..... 2
- 2 Contrategulum with distal edge proventrally ending in a downward-curved, U-shaped or V-shaped row of denticles (Figs 4C; 6A, C; 8A, D); para-embolic plate short or absent. Vulval plate strongly sclerotised; CDO large, of various shapes; receptacular cluster large, always undivided ..... *malayanus*-group
- Distal edge of contrategulum proventrally not ending in a U-shaped or V-shaped row of denticles; para-embolic plate short or long. Vulval plate completely or only partially sclerotised; CDO small to large, rounded, angular or slit-like, entire, medially divided by a longitudinal septum (Fig. 13G), or completely divided into two paramedian openings (Figs 13A, C-D; 14I); receptacular cluster entire or divided into two paramedian halves (Figs 13B, E-F, H; 14J) ..... 3
- 3 Contrategulum with more or less distinct ventral process (Figs 10B, 11F, 14C-D). Vulval plate completely sclerotised; CDO rounded or angular, entire (Fig. 12A, C, F), medially divided by a longitudinal septum (Fig. 13G), or completely divided into two paramedian openings (Figs 13A, C-D; 14I); receptacular cluster always divided into two paramedian halves (Figs 12B, D, G; 13B, E-F, H; 14J) ..... *tioman*-group
- Contrategulum always without ventral process. Posterior portion of vulval plate only partially sclerotised; CDO and receptacular cluster never divided longitudinally ..... 4
- 4 Para-embolic plate long, its distal margin coarsely serrate (Figs 15B-D, 17B-D); dorsal apex of contrategulum narrow and pointed (Figs 15E-F, 17G-H); distal margin of cymbium with two indistinct, subequal lobes (Figs 15B, 17B); tibial apophysis divided into a long part carrying three megaspines and a short part with only one megaspine, all these megaspines short and bent (Figs 15A, G-I; 17A, I-K). Vulval plate with posterior stalk reduced to a small sclerite at posterior margin, far apart from poreplate (Figs 16A-E, 18A-F) ..... *limang*-group
- Para-embolic plate short, its distal margin smooth; dorsal apex of contrategulum wider, tongue-shaped, with rounded or pointed tip (Figs 19D, 21I-L, 23D-G); distal margin of cymbium with prodorsal lobe distinctly longer than proventral one (Figs 19C, 21H, 23J); tibial apophysis undivided, its megaspines long or short, curved but not bent. Posterior stalk wide, close to poreplate, not or only partially connected to poreplate (Figs 20, 22, 24) ..... *batnensis*-group

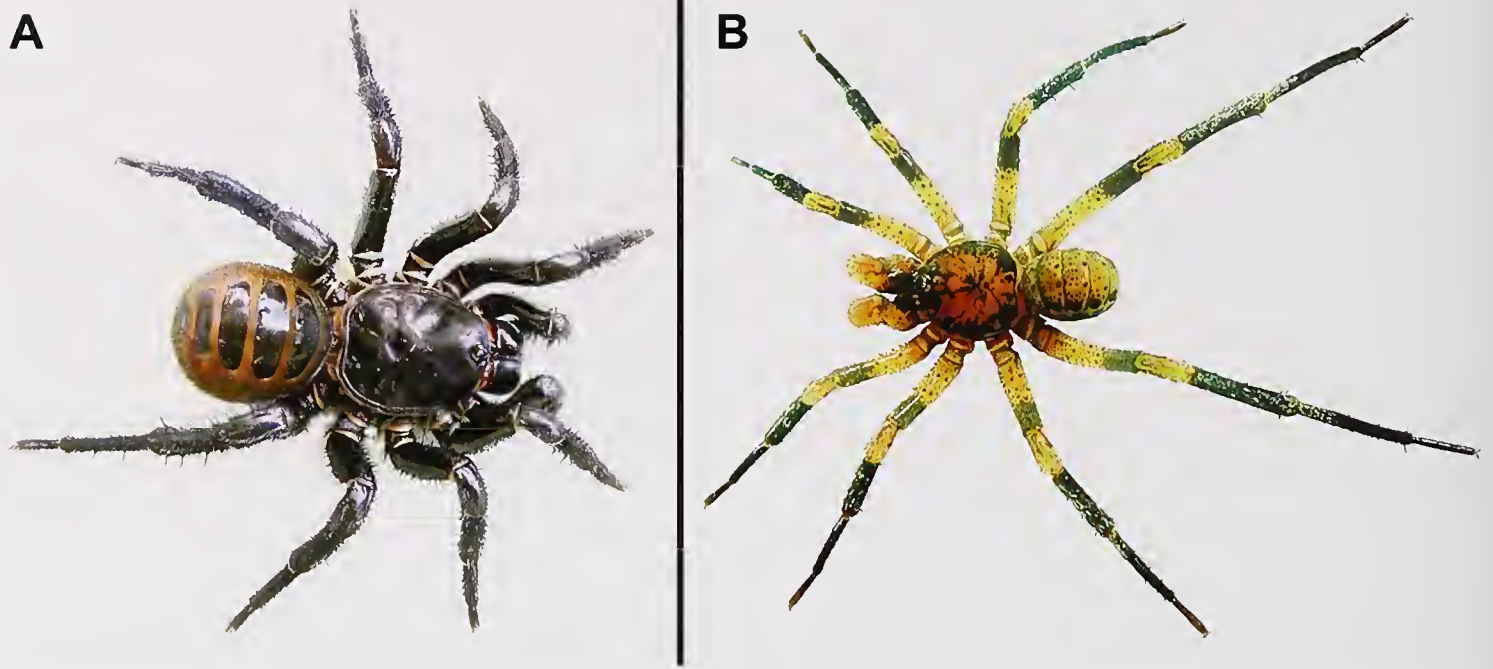


Fig. 2. Habitus of two *Liphistius* species from peninsular Malaysia and southern Thailand. (A) *Liphistius endau*, female from Kota Tinggi (Malaysia), dorsal view. (B) *Liphistius indra* sp. nov., male paratype from the Sankalakhierie Mountains (Thailand), same view.

**Description:** Small to large species (carapace length of males 4.36-12.04, carapace width 3.64-10.99); body colouration uniformly dark (in large species: *L. malayanus* and *L. endau*; Fig. 2A) or brown with annulated legs and palps (in smaller species: *L. johore* and *L. gracilis* sp. nov.). Male palp with membranous and sclerotised part of embolus proper in close contact with each other (both distinctly separated in *trang*-group), together forming a closed tube; dorsal wall of sclerotized part of embolus proper straight and directed proventrad (*L. malayanus*; Fig. 4G-H), curved prodorsad (*L. endau*; Fig. 6F, H) or bent prodorsad (*L. gracilis* sp. nov.; Fig. 8F-G); para-embolic plate short or absent (Figs 4D, 6E); tegulum with coarsely dentate proximal edge (corresponding to dorsal extension of terminal apophysis in Heptathelinae; see Schwendinger & Ono, 2011), distal margin (corresponding to marginal apophysis) indistinct, not drawn into a prominent edge (Figs 4D-F, 6D-E, 8E); contrategulum with indistinct ventral process or without, distal edge carrying several teeth, prolateral ones numerous, tiny and forming a serrate crest (*L. gracilis* sp. nov.; Fig. 8D-G), few and small (*L. malayanus*; Fig. 4G-L), or only represented by a single large triangular tooth (*L. endau*; Fig. 6F, H-O), proventral denticles of distal edge forming a downward-curved V-shaped (Fig. 4C) or U-shaped row (Figs 6A, C; 8D), dorsal apex of contrategulum widely to narrowly tongue-shaped (Figs 4G-L; 6F, H-O; 8F-G); subtegulum always without apophysis; paracymbium quite small and shallow to large and deep (Figs 4A, 6B, 8B); cumulus very low, indistinct, carrying several

long, thick bristles; retrolateral tibial apophysis relatively short and carrying long apical megaspines (*L. malayanus* and *L. endau*; Figs 4A-B, 6A-B) or quite long and carrying distinctly shorter megaspines (*L. gracilis* sp. nov.; Fig. 8A-C, I-J); both apical lobes of cymbium weakly developed (Fig. 8D). Vulva (Figs 5, 7, 9, 10A): poreplate strongly pigmented and sclerotised, wider than long, its anterior margin more or less distinctly recurved, with or without anterolateral lobes or processes, never with mediolateral processes; CDO and ventral receptacular cluster large to very large, both undivided; posterior stalk wide (in *L. endau* even covering entire width of genital atrium; Fig. 7), somewhat trapezium-shaped or almost triangular (Fig. 10A); genital atrium with few to many lateral hairs and with no, few or numerous median hairs.

**Species included:** *Liphistius endau*, *L. malayanus*, *L. gracilis* sp. nov. and presumably also *L. johore* (male still unknown).

**Relationships:** Species of the *malayanus*-group are most similar and probably closely related to species of the *tioman*-group. The two large species, *L. malayanus* and *L. endau*, are closer to each other than to the much smaller *L. gracilis* sp. nov. (distinguished by serrate distal edge of contrategulum and by sharp bend in wide dorsal wall of sclerotised part of embolus proper). Small size, details of the vulval plate and geographical proximity suggest a close relationship between *L. gracilis* sp. nov. and *L. johore*, but this can only be confirmed when the male of the latter species is discovered.

**Key to the species of the *malayanus*-group:**

- 1 Small spiders (carapace length of mature males and females 4.36-5.34, carapace width 3.64-4.22) with brown body colouration and annulated limbs; lateral and posterolateral margins on ventral side of poreplate not bulging (Fig. 9B, D, F; Platnick & Sedgwick, 1984: fig. 80).....2
- Large (carapace lengths in males 7.90-12.04, carapace width 7.0-10.99), uniformly dark-coloured spiders; lateral and posterolateral margins of poreplate on ventral side of vulval plate bulging (Figs 5B, J; 7B, E, G).....3
- 2 Vulval plate with indistinct transition between poreplate and posterior stalk, the latter wide in transition zone; anterior margin of poreplate without or with only indistinct anterolateral invaginations; genital atrium with numerous lateral and median hairs (Fig. 9A, C, E).....*L. gracilis* sp. nov.
- Vulval plate with distinct transition between poreplate and posterior stalk, the latter very narrow in transition zone; anterior margin of poreplate with pronounced anterolateral invaginations; genital atrium without hairs (Fig. 10A) (male unknown).....*L. johore*
- 3 Dorsal and ventral wall of sclerotised part of embolus proper equally wide, both ends facing proventrad (Fig. 4G-H), dorsal wall ending in indistinct rounded lobe (Fig. 4C-F); membranous part of embolus proper distally narrow (Figs 3F, H; 4C); distal edge of contrategulum with one to several small denticles (Fig. 4C, G-L); paracymbium about as deep as wide (Fig. 4A). Dorsal side of vulval plate with anterolateral corners of genital atrium not bulged and elevated above level of poreplate; usually no median hairs in genital atrium (Fig. 5A, C-H, but see Fig. 5I); receptacular cluster not divided into subclusters (Fig. 5B, J).....*L. malayanus*
- Dorsal wall of sclerotised part of embolus proper wider than ventral wall, end of dorsal wall bent prodorsad (Fig. 6F, H) and forming pronounced lobe (Fig. 6C-E); membranous part of embolus proper distally wide (Fig. 6C, F-H); distal edge of contrategulum with a single large triangular tooth (Fig. 6F, H-O); paracymbium much deeper than wide (Fig. 6B). Dorsal side of vulval plate with anterolateral corners of genital atrium bulged and elevated above level of poreplate; median hairs usually present in genital atrium (Fig. 7A, C-D, F); receptacular cluster divided into three more or less distinct subclusters (Fig. 7B, E, G).....*L. endau*

**Distribution:** All described species of this group occur in the western and southern part of peninsular Malaysia (Fig. 1, localities 1-9); an undescribed species appears to be present in the northeastern corner of the country (Fig. 1, locality 13).

***Liphistius malayanus* Abraham, 1923**

Figs 3B, D, F, H; 4-5

*Liphistius malayanus* Abraham, 1923b: 770-774, text-fig. 1a-b (description of female). – Abraham (1929: 674-676, pl. 1, figs 3-4, pl. 2, figs 11-16; first description of male). For synonymy and other taxonomically relevant publications see the World Spider Catalog, 2017.

*Liphistius malayanus cameroni* Haupt, 1983: 282, figs 3e, 4d, 5f, 6f (description of male and female). **New synonym**

**Type material:** BMNH; female holotype of *L. malayanus* (not examined); Negri Sembilan, Gunung Angsi near Seremban; XII.1922; leg. F. de la Mare Norris. – ZMH (A16/84); male holotype and female paratype of *L. malayanus cameroni* (examined); Pahang, Cameron Highlands, Berinchang; 4.III.1981; leg. J. Haupt & T. Dach.

**Remark:** A *L. malayanus* male (not examined) from Fraser's Hill was described by Abraham (1929) and deposited in the BMNH. Haupt (1983: 281, figs 3d, 4c) re-described this specimen and referred to it as the paratype, but it has no type status, having been collected in November 1928, after the publication of the original description of the species.

**Material examined:** ZMH (A16/84); male holotype [left palp detached, macerated and partly collapsed, cymbium and hematodocha cut open to expose tendons inside, all strong spines deformed; right palp without tegulum, contrategulum and embolus complex] (matured VII.1981) and female paratype of *Liphistius malayanus cameroni*; Pahang, Cameron Highlands, Berinchang; 4.III.1981; leg. J. Haupt & T. Dach. – Collection of Joseph Koh, n° JK.14.10.05.0001; 1 male; Pahang, Cameron Highlands, Taman Tringkap NE of Brinchang, 4°28'26"N, 101°22'58"E; 5.X.2014; leg. N. Bay. – MHNG; 1 female, 1 juv. male; Perak, Cameron Highlands, ca 1 km SW of Ringlet, 1060 m; 21.I.1995; leg. P.J. Schwendinger. – MHNG (sample TM-15); 1 juv. male; Pahang, Cameron Highlands, Tanah Rata, trail n° 9, 4°27.620'N, 101°23.400'E, 1210 m; 29.IX.2001; leg. L. Monod. – SMF 7425/2 (ex coll. C. F. Roewer); 2 juv. females (labelled as "1 male and 1 female, det. Roewer, 1935"); Pahang, "Ginting Kial Highlands" [probably a peak in the Cameron Highlands]. – SMF 40602; 1 male; Pahang, Fraser's Hill, roadside at Jalan Girdle; 19.XII.2001; leg. S. Huber. – SMF 56206; 1 female; Pahang, Fraser's Hill, roadside at Jalan Girdle; 19.XII.2001; leg. S. Huber. – MHNG (ex coll. S. Huber, sample O-4, C); 1 male (matured end March 2002), 1 female (moulted 24.VI.2002); Pahang, Fraser's Hill, Jalan Guillemard; 18.XII.2001; leg. S. Huber. – SMF 64093; 1 female; Pahang, Fraser's Hill, 1300 m, 3°43.105'N, 101°45.164'E; 17.VI.2013; leg. P. Jäger. – MHNG

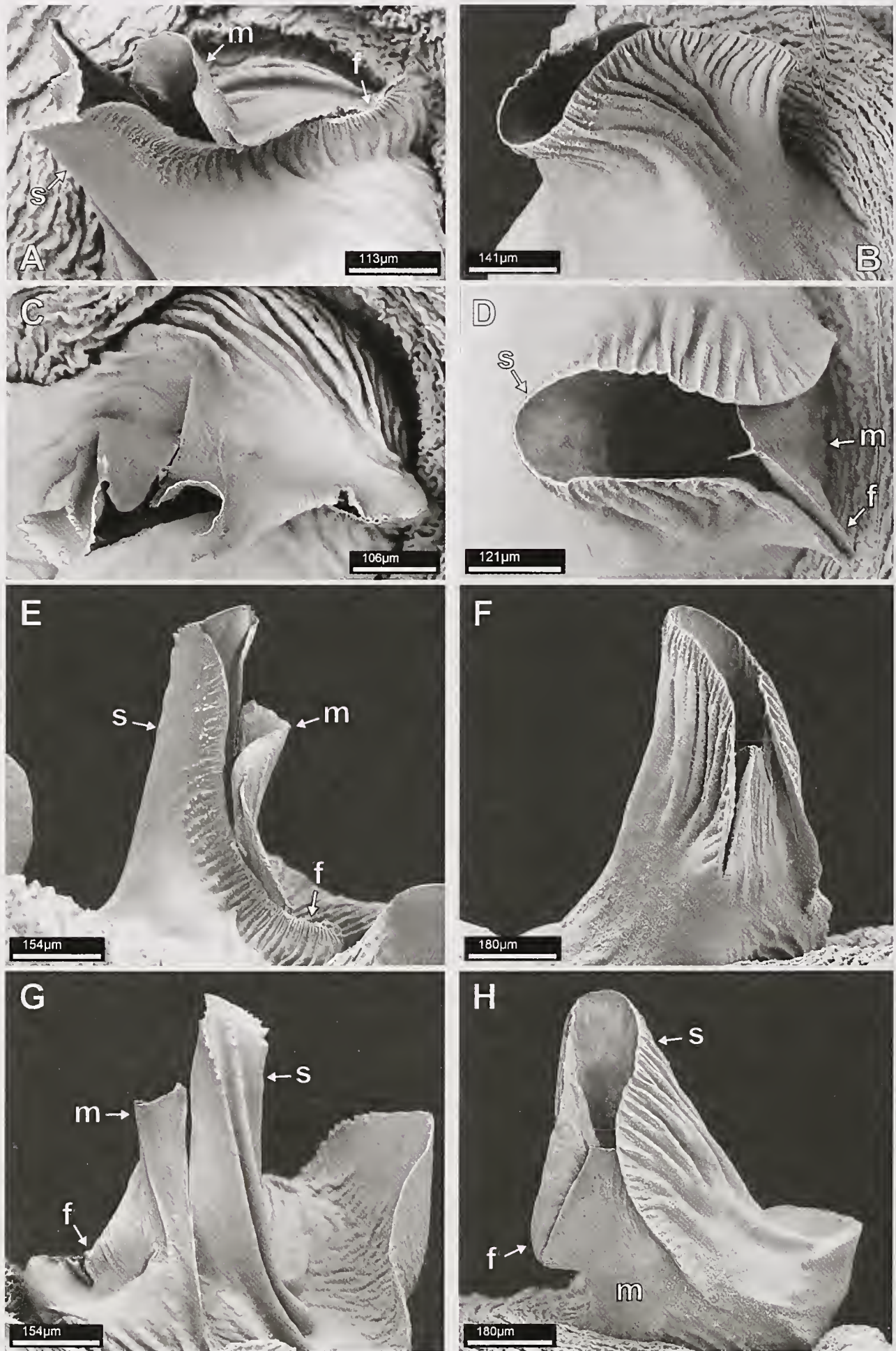


Fig. 3. SEM-micrographs of embolus proper of left palpal organ of two males: *Liphistius desultor* from Penang Hill (A, C, E, G) and *Liphistius malayanus* from Fraser's Hill (B, D, F, H). (A) Retroventral-distal view. (B) Dorsal-distal view. (C) Distal view (dorsal side to the right). (D) Distal view (prolateral side to the right). (E) Retrodorsal view. (F) Prodorsal view. (G) Proventral view. (H) Prolateral view. Abbreviations: f - major embolic fold; m - membranous part of embolus proper; s - sclerotised part of embolus proper.



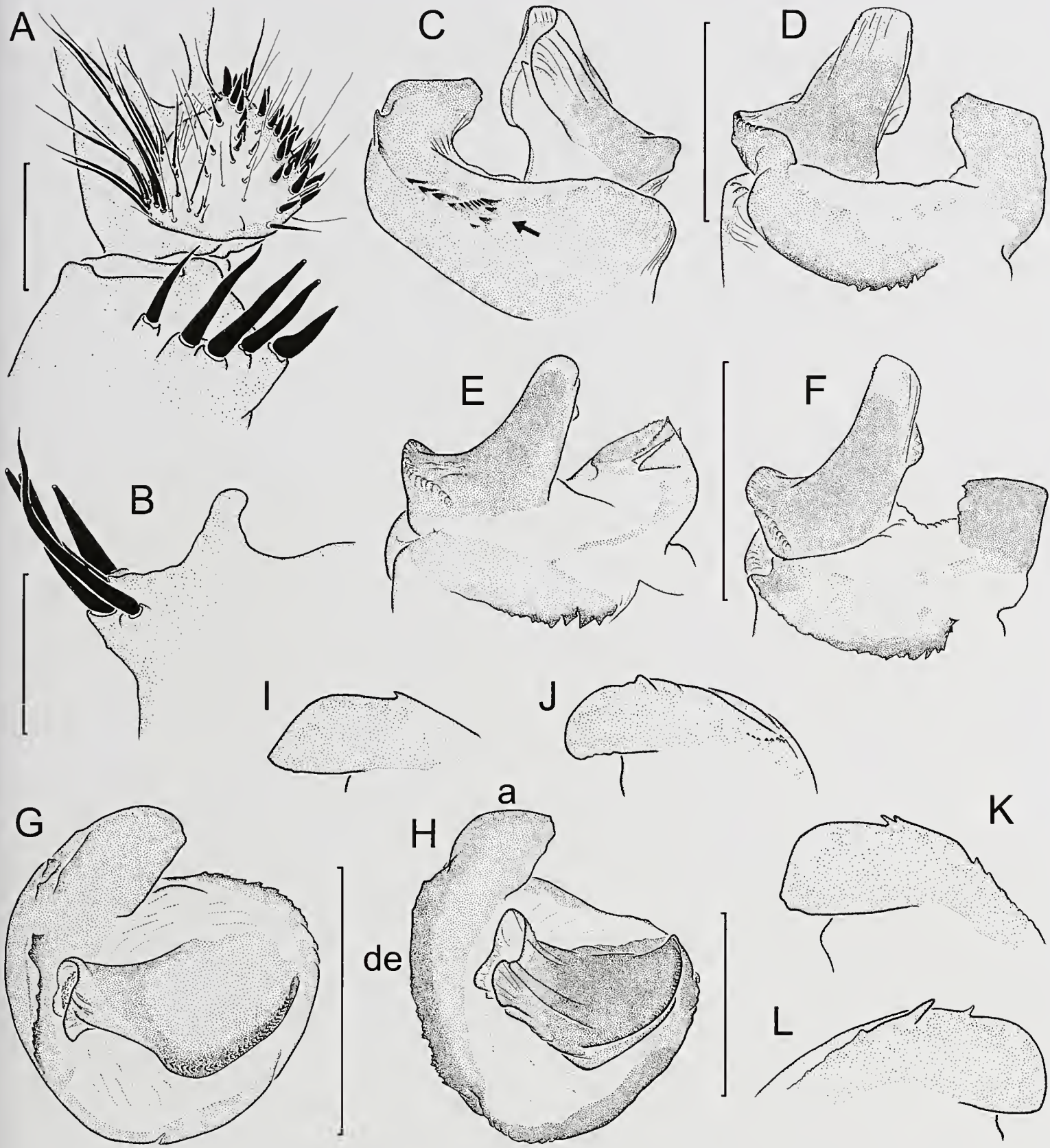


Fig. 4. *Liphistius malayanus*, details of palp of four males: Templer Park (A, C-D, H-I); holotype of *L. malayanus cameroni* (B, E, G); Cameron Highlands, ZRC (F, J), Fraser's Hill, MHNG (K-L). (A) Paracymbium and tibial apophysis of left palp, retroventral view. (B) Tibial apophysis of right palp, ventral view. (C) Distal part of left palpal organ, proventral view (arrow indicating V-shaped row of denticles at proventral end of distal edge of contrategulum). (D, F) Same, retrodorsal and slightly proximal view. (E) Same, retrodorsal view. (G-H) Left palpal organ, distal view (dorsal side up). (I, K) Distal edge of contrategulum of right palp, distal view (dorsal side to the left). (J, L) Same, distal and slightly prolateral view (dorsal side to the right). Abbreviations: a - dorsal apex of contrategulum; de - distal edge of contrategulum. Scale lines: 1.0 mm (A; B; C-D; E, G; F; H-L).

(sample MAL-04/02); 1 male (matured 18.IX.2004), 2 females (moulted 30.VII.2004, 24.I., 28.VIII., 8.XII.2005; 19.X.2004, 30.VII.2005), 4 juveniles; Pahang, Genting Highlands, 3°25'42"N, 101°47'41"E, 1650 m; 18.-19.V.2004; leg. P.J. Schwendinger. – SMF 21946/1; 1 female; without locality data; 10.XI.1933; ex coll. Wiehle, don. W. S. Bristowe. – SMF 60037; 1 female; "Selangor" [should be Pahang], Genting Highlands, 1800 m; 3.II.1989; leg. U. Maschwitz, don. H. Steiner. – SMF 40016; 1 female; Pahang, Genting Highlands, 1200 m; 27.VII.2001; leg. A. Kovac. – MHNG (sample SIM-01/14); 1 male (matured end VIII.2003), 1 female (moulted 31.XII.2001), 1 juvenile; Selangor, Templer Park, 3°17'55"N, 101°37'13"E, 230 m; 13.VII.2001; leg. P.J. Schwendinger.

**Diagnosis:** Large, dark-coloured species in both sexes. Males distinguished from those of other species in the *malayanus*-group by tibial apophysis situated distinctly lower (more proximal) than distal margin of palpal tibia (Fig. 4B); distal edge of contrategulum carrying a series of small denticles (Fig. 4G-L), those at proventral end arranged in a V-shaped row (Fig. 4C), 1-2 at prodorsal end isolated and slightly enlarged; dorsal apex of contrategulum large, wide, tongue-shaped and asymmetrical, its prolateral margin more strongly arched than retrolateral margin (Fig. 4G-L); dorsal wall of embolus proper as wide as ventral wall (Fig. 4G-H); membranous part of embolus proper distally narrower than proximally (Figs 3F, H, 4C). Females distinguished by vulval plate (Fig. 5) with widely trapezium-shaped (posteriorly widest) posterior stalk not connected to pigmented lateral patches in genital atrium; poreplate with distinct anterolateral lobes; CDO large, very variable in shape, mostly longer than wide; receptacular cluster very large, in most cases protruding beyond straight or procurved anterior margin of poreplate.

**Additions to description of male:** *Scopula:* See paragraph "Variation".

*Palp:* Both apical lobes of cymbium equally short, dorsal one usually slightly more pointed than ventral one. Retrolateral apophysis of palpal tibia entire, situated at a clearly more proximal level than distal margin of article (Fig. 4B), carrying four long apical megaspines (Fig. 4A-B). Paracymbium relatively small and shallow, about as deep as cymbium in retroventral view (Fig. 4A; Platnick & Sedgwick, 1984: fig. 64); cumulus low, carrying a compact group of moderately long thick bristles. Subtegulum without apophysis. Tegulum with quite few small teeth only in retrodorsal portion of proximal edge, distal margin not drawn into an edge (Fig. 4D-F). Contrategulum with very indistinct, widely rounded ventral process (Fig. 4G-H); distal edge with a series of small denticles, those at proventral end arranged in a V-shaped row (Fig. 4C), 1-2 enlarged denticles or a sharp keel in prolateral to prodorsal section of distal edge (Fig. 4G-L); dorsal apex of contrategulum developed as a large, linguiform, strongly projecting horizontal plate,

its prolateral margin being more strongly arched than its retrolateral margin (Fig. 4G-L). Embolus complex with para-embolic plate developed as a more or less distinctly elevated, rounded edge (Fig. 4D-F); below it a second small edge present in some cases (Fig. 4D); sclerotised and membranous part of embolus proper in contact for almost their entire length (Fig. 3D, F, H); sclerotized part with numerous longitudinal ribs carrying tiny denticles distally (Fig. 3B, D, F, H), its dorsal and ventral walls equally wide and parallel to each other (Figs 3D; 4G-H), dorsal wall ending in indistinct rounded lobe (Fig. 4C-F); membranous part distally narrower than proximally (Fig. 3D, F, H), its proximal portion essentially unpigmented.

**Additions to description of female:** Vulval plate (Fig. 5) always with few to many hairs laterally in genital atrium, rarely also posteromedially (Fig. 5I). Posterior stalk more or less distinctly trapezium-shaped (posteriorly wider than anteriorly), densely pitted in posterior portion. Poreplate wider than long, with a pair of anterolateral lobes projecting anteriorly and slightly bent ventrad; several of these lobes more or less distinctly constricted at base (Fig. 5A-C, E); anterior margin of poreplate straight to procurved; lateral and posterolateral margins on ventral side of pore plate bulging (Fig. 5B, J). CDO large and of variable shape, mostly longer than wide, rarely wider than long (Fig. 5E). Receptacular cluster large and strongly racemose, in most cases protruding beyond anterior margin of poreplate, rarely not (Fig. 5G).

**Taxonomic remarks:** *Liphistius malayanus cameroni* has been the only subspecies in the genus *Liphistius*. As specimens later collected near the type locality show no relevant differences from specimens of the nominal subspecies, this case became doubtful. Thus a re-examination of the types of *Liphistius malayanus cameroni* was necessary, and it revealed that they differ considerably from the illustrations and explanations given in the original description of this subspecies. The vulva of the female paratype was cleared of tissue, but the ventral wall of the genital region (with bristles still attached) was not removed, thus not allowing a clear view of the ventral side of the poreplate. It therefore appears that Haupt's (1983) illustrations were made with the help of a compound microscope without using a drawing tube, which would explain why the poreplate in the original illustrations is wider than in reality and why the outlines of the posterior stalk are too rounded. The same is probably also the case in the dorsal view of the same poreplate, it being too wide, with a triangular CDO leading to the receptacular cluster and with a peculiar double posterior margin of the posterior stalk (see Haupt, 1983: figs 5f, 6f). In fact the vulva of the paratype of *L. malayanus cameroni* does not differ from the vulvae of the other *L. malayanus* females examined (Fig. 5A-B cf. Fig. 5C-J) in any way that would warrant a distinct taxonomic status.

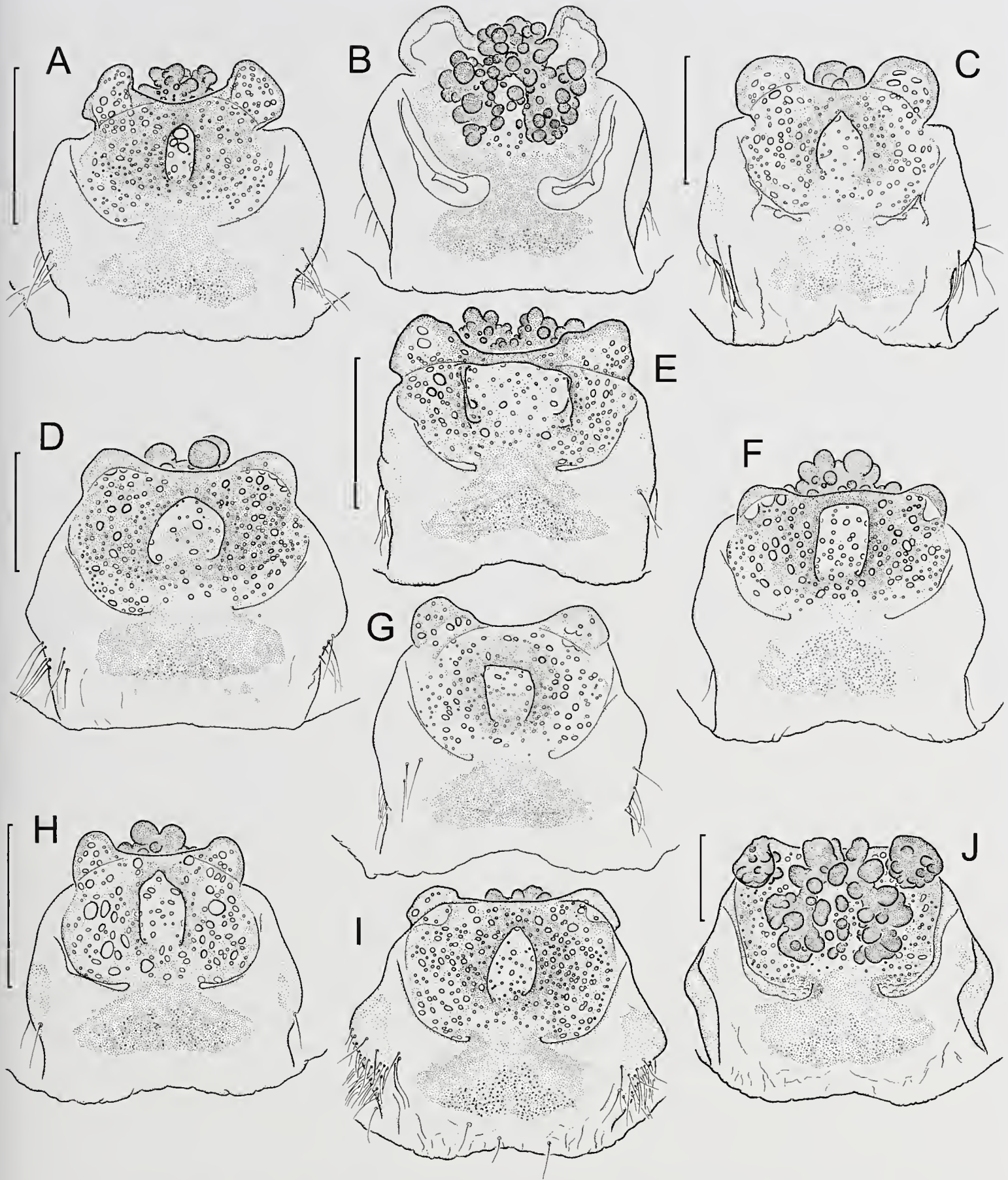


Fig. 5. *Liphistius malayanus*, vulval plate of eight females: paratype of *L. m. cameroni* from Berinchang, Cameron Highlands (A-B); exuvia of female from Ringlet, Cameron Highlands (C); female (SMF 64093) from Fraser's Hill (D); female (moulted 24.VI.2002) from Fraser's Hill; poreplate slightly deformed by brief immersion in cold KOH (E); female (SMF 56206) from Fraser's Hill (F); female (SMF 60037) from Genting Highlands (G); female (moulted 8.XII.2005) from Genting Highlands (H); exuvia of female from Templer Park (I-J). (A, C-I) Dorsal view. (B, J) Ventral view. Scale lines: 1.0 mm (A-B; C, F; D; E, G; H; I-J).

The illustrated differences between the male holotype of *L. malayanus cameroni* and the male that Haupt incorrectly referred to as a paratype of *L. malayanus* (in BMNH, not examined) are mostly due to a slightly different view of the palp and due to the fact that the palpal organ of the BMNH male is expanded (turned clockwise by about 90°) (Haupt, 1983: figs 3D, 4C cf. figs 3E, 4D). None of the *L. malayanus* males examined has the tibial apophysis of the male palp situated as far distally as illustrated by Haupt (1983: figs 3D, 4C), therefore this may also be due to a different view. The embolus proper of the left palp of the *L. m. cameroni* holotype (that of the right palp is missing, together with tegulum and contrategulum) is slightly narrower than that of the second male from the Cameron Highlands and that of other conspecific males examined. This difference is presumably connected to size: the *L. m. cameroni* holotype is the smallest among the *L. malayanus* males examined. The character in which the holotype of *L. m. cameroni* most visibly differs from other conspecific males is a slightly elevated para-embolic plate (Fig. 4E), which is also present in the second male from the Cameron Highlands (Fig. 4F). However, an indistinctly elevated para-embolic plate is present in one of the two males from the Fraser's Hill, whereas all other conspecific males possess only a distinct edge at this place (Fig. 4D). Thus the holotype of *L. m. cameroni* differs from other conspecific males examined in possessing the most extreme states of three quite variable characters, but it is not representative for the population in the Cameron Highlands. I consequently place *Liphistius malayanus cameroni* in the synonymy of *Liphistius malayanus* which makes the species monotypic again.

**Variation:** Carapace lengths in males (n=6; including the holotype of *L. m. cameroni*) 7.90-11.23, carapace widths 7.04-9.69; in the largest female from each locality (n=4; not including the paratype of *L. m. cameroni*) 10.86-16.67 and 10.00-14.07, respectively. The holotype of *L. m. cameroni* is the smallest male examined, with carapace length 7.90, width 7.04; in the second male from the Cameron Highlands it is 9.63 and 8.40, respectively. The largest female is from the Templer Park, measuring 16.67 and 14.07; the second largest female is from the Fraser's Hill, measuring 16.54 and 14.07. The female paratype of *L. m. cameroni* measures 9.26 and 7.53, the second female from the Cameron Highlands 10.86 and 10.12.

The apical megaspines on the tibial apophysis are quite variable in length, but not as thin as illustrated in Murphy & Platnick (1981: figs 8, 11, 14, 17, 20) and in Platnick & Sedgwick (1984: figs 63-67); the ventral-most of them is mostly bent distad and has a thin, long apex (Fig. 4A-B). The ventral megaspine is bent in the male from the Templer Park (Fig. 4A), whereas in the holotype of *L. m. cameroni* (Fig. 4B), in a male from the Genting Highlands, and also in a second male from the Cameron Highlands it is slightly sigmoid.

The distal edge of the contrategulum carries one or two slightly enlarged dorsal denticles at some distance from the projecting dorsal apex (Fig. 4G, I-L); in two males there is a sharp edge at the same place (Fig. 4H), but only on one palp. These larger denticles are followed by a variable number of smaller proventral denticles.

The para-embolic plate is always low, most visibly elevated (but not with a sharp edge) in the holotype of *L. m. cameroni* (Fig. 4E), in a second male from the Cameron Highlands (Fig. 4F) and in a male from the Fraser's Hill. In the second male from the Fraser's Hill it is not elevated; the remaining males examined are intermediate (Fig. 4D). An indistinct second edge, situated below the indistinct para-embolic plate, is found in the only available male from the Genting Highlands and in the only available male from the Templer Park (Fig. 4D), but not in other males examined (Fig. 4E-F).

The size of the embolus proper varies from relatively thick in the male from the Templer Park (Fig. 4D) to distinctly more slender in the holotype of *L. m. cameroni* (Fig. 4E); the other males are intermediate (Fig. 4F). The longitudinal ribs on the sclerotised part of the embolus proper vary from indistinct to distinct (Fig. 3B, D, F, H), so do the denticles on them.

There is considerable variation in the extent of the tarsal scopulae in males. The scopula on tarsus I is always thin and undivided, covering two-thirds of the ventral side in most males, only one half in the male from the Genting Highlands. The scopula on tarsus II is slightly denser than on tarsus I, undivided and covering two-thirds of the ventral side in all males. Tarsal scopula III is like tarsal scopula II in most males, in the non-type male from the Cameron Highlands it is light. Tarsal scopula IV is dense in all males except for the non-type male from the Cameron Highlands (light), undivided in all males except for the same male from the Cameron Highlands (distinctly divided) and for the male from the Genting Highlands (indistinctly divided), covering two-thirds of the ventral surface in most males except for a male from the Cameron Highlands (covering only half of the surface) and the male from the Templer Park (covering three-quarters). The male holotype of *L. malayanus cameroni* had already been returned to its depository when the tarsal scopulae were examined. Even if both males from the Cameron Highlands differed from those of other localities in shape and extent of their tarsal scopulae (especially on tarsus IV), this would not warrant a subspecific distinction. The tarsal scopula in this species is too variable to be of high taxonomic value.

The vulval plates of large females have more lateral hairs in the genital atrium than those of small females (Fig. 5I cf. Fig. 5H). In the largest female (from the Templer Park) hairs are also present posteromedially in the genital atrium (Fig. 5I). The shape of the posterior stalk is quite variable but mostly trapezium-shaped (Fig. 5). Even more variable is the size and shape

of the CDO of the poreplate, ranging from (mostly) longer than wide to (rarely) wider than long, from quadrangular to pentangular and from near-triangular to near-circular (Fig. 5A, C-I). The receptacular cluster is always large, undivided and has a complex structure, covering most of the ventral side of the poreplate (Fig. 5B, J); only in one female examined (from the Genting Highlands) does it not protrude beyond the anterior margin of the poreplate (Fig. 5G). The anterior poreplate margin varies from more or less strongly invaginated (in most cases; Fig. 5A-E, G-J) to slightly arched medially (Fig. 5F).

**Distribution:** *Liphistius malayanus* is known from several lowland and upland localities in the western part of central Malaysia (Perak, Pahang, Selangor and Negeri Sembilan; Fig. 1, localities 1-5). See also Platnick & Sedgwick (1984: 24). *Liphistius* records from other localities near Kuala Lumpur (e.g. Klang Gates; Murphy & Murphy, 2000: plate 2.5) can also be attributed to *L. malayanus*. This species has a relatively wide geographical range (the northernmost locality, in the Cameron Highlands, is about 280 km away from the southernmost locality, Gunung Angsi) and a large vertical distribution (from 230 to 1800 m altitude).

**Biology:** Spiders were collected from quite different habitats: soil on exposed sides of roads and trails inside and outside forests (but never very far from a forest), sides of erosion gullies, sloping forest floor, and in decomposing wood of logs lying on the forest floor. Trapdoors of females were up to 3.8 cm long and 6.5 cm wide. Signal lines (not more than eight) were usually about 10 cm long, in one immature male even 24 cm long. The longest burrow measured was 20 cm long. Two penultimate males had trapdoors with a length of 1.9-2.2 cm and a width of 3.0-3.4 cm, which is probably normal. A juvenile male (moulted again but died before reaching maturity) from near Ringlet in the Cameron Highlands had a surprising 2.9 cm long and 5.0 cm wide trapdoor.

The female paratype of *L. m. cameroni* and two other females (from Fraser's Hill and Templer Park) show bite marks on their carapaces and chelicerae. These were probably caused by specimens of *Ljunghia bristowi*, a species of ectoparasitic laelapid mites originally described from *L. malayanus* (see Halliday & Juvara-Bals, 2016: 837-845).

Mature males were collected in the field in October and December; in captivity males matured between July and March. The mating period in *L. malayanus* appears to be much longer than in other congeneric species. I did not find any egg cases.

### *Liphistius endau* Sedgwick & Platnick, 1987

Figs 2A, 6-7

*Liphistius endau* Sedgwick & Platnick, 1987: 361-363 (description of female). – Foelix & Erb, 2010 (study on venom gland openings on cheliceral fangs). – Foelix *et al.*, 2010 (study on scopula hairs of male).

**Type material:** AMNH; juvenile female holotype (not examined; see paragraph "Variation" below); Malaysia, Johore [sic], Ulu Endau area, from the banks of Sungai Jasin; 10.XI.1985; leg. W.C. Sedgwick.

**Material examined:** MHNG, sample SIM-01/10; 2 males (matured 1.II.2002, 27.II.2003), 2 females (moulted 27.IV.2002, 28.IV.2002), 2 juvenile males, 3 juvenile females; Johor, Endau-Rompin National Park, between Kuala Jasin and Kuala Marong (2°31'44"N, 103°22'02"E), 40 m (rain forest along stream); 3.-5.VII.2001; leg. P.J. Schwendinger. – MHNG; left palp of mature male; Johor, near Gunung Belumut; leg. C. Sainsbury, don. R. Foelix. – MHNG (sample Sum-00/02); 2 females; Johor, Gunung Muntahak, Kota Tinggi Waterfalls (1°49'51"N, 103°49'56"E), 170 m (rainforest near stream); 5.II.2000; leg. P.J. Schwendinger. – MHNG (sample SIM-01/07); 2 penultimate males, 4 females, 1 juvenile; same locality, 170 m; 24.-26.VI.2001; leg. P.J. Schwendinger. – MHNG (sample MAL-04/05); 2 penultimate males, 2 females, 1 juvenile; same locality, 170 m; 26.-27.V.2004; leg. P.J. Schwendinger. – MHNG (sample TM-14/02); 3 males (matured 20.VIII., 22.X., 6.XI.2014), 2 females; same locality, 120 m; 21.-22.VI.2014; leg. P.J. Schwendinger. – MHNG, SMF; 2 males (one killed 30.IX.2010, the other died 22.III.2012), 1 female; Malaysia, locality and collector unknown; don J. Kral.

**Diagnosis:** Large, dark-coloured species. Males distinguished from those of the similar *L. malayanus* by tibial apophysis of male palp situated more distally (Fig. 6A cf. Fig. 4B); paracymbium much deeper (Fig. 6B cf. Fig. 4A); tegulum with more teeth on proximal margin (Fig. 6D-E cf. Fig. 4D-F); distal edge of contrategulum with only one very large, triangular tooth prolaterally; dorsal apex of contrategulum more symmetrical, both lateral margins almost equally arched (Fig. 6F, H-O cf. Fig. 4G-L); dorsal wall of sclerotized part of embolus proper much wider than ventral wall and curved prodorsad (Fig. 6F, H cf. Fig. 4G-H), with a large lobate extension prodorsally (Fig. 6C-E cf. Fig. 4D-F); adpressed membranous part of embolus proper distally much wider than proximally (Fig. 6C cf. Fig. 4C); opening of spermophore a long and narrow slot (Fig. 6F-H cf. Fig. 4G-H). Females distinguished from those of *L. malayanus* by median portion of genital atrium clearly sunk below lateral portions and usually carrying more hairs (mostly no hairs in *L. malayanus*); posterior stalk usually (except in small females) fused

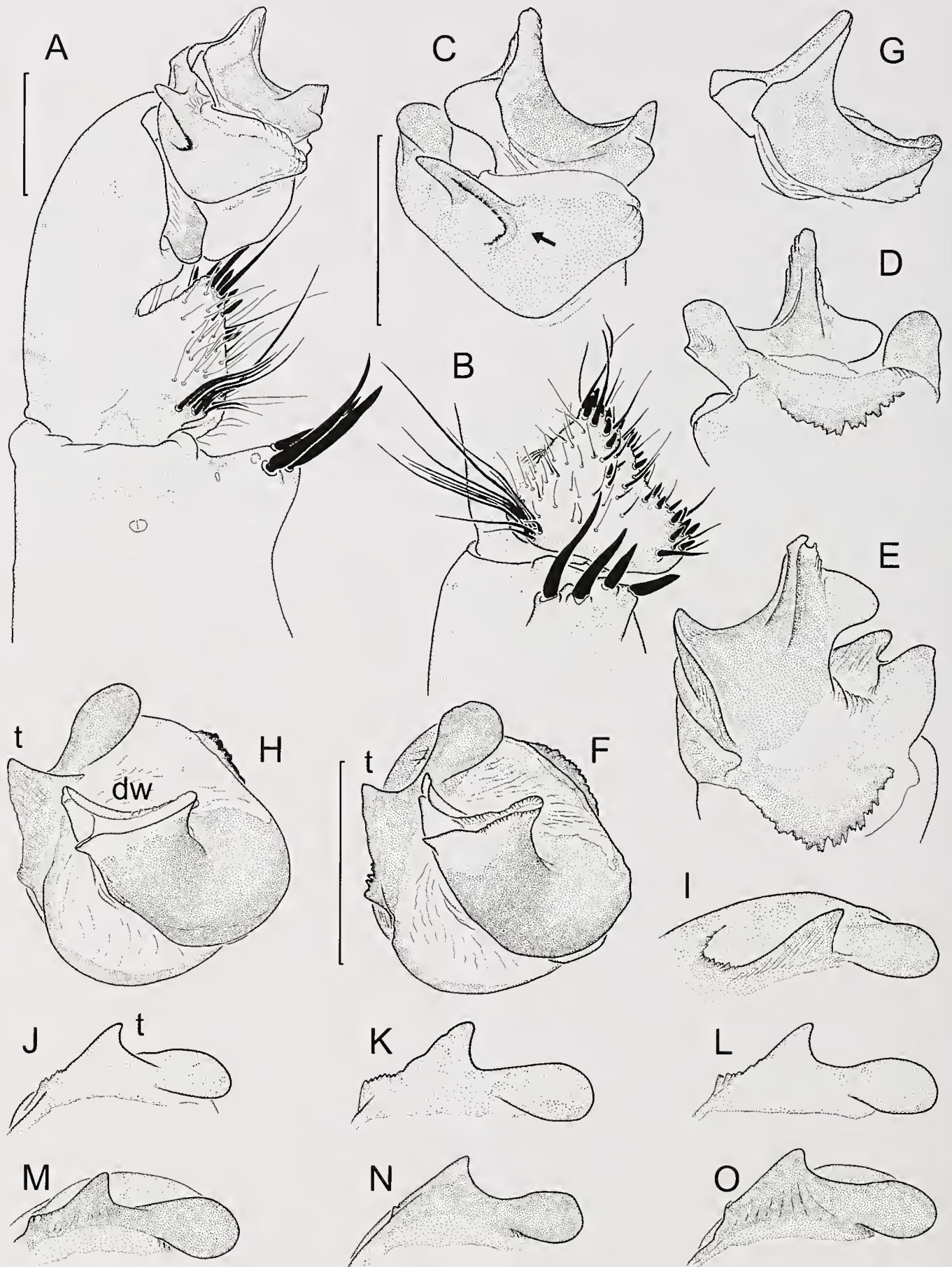


Fig. 6. *Liphistius endau*, details of left palp of eight males: from type locality, matured 27.II.2002 (A-F); from type locality, matured 1.II.2002 (G-I); from unknown locality, died 22.III.2012 (J); from unknown locality, killed 30.IX.2010 (K); from Gunung Belulut (L); from Kota Tinggi, matured 22.X.2014 (M); same place, matured 20.VIII.2014 (N); same place, matured 6.XI.2014 (O). (A) Distal part of palp, ventral view. (B) Paracymbium and tibial apophysis, retroventral view. (C) Palpal organ, proventral view (arrow indicating U-shaped row of denticles at proventral end of distal edge of contrategulum). (D) Same, retrodorsal and slightly proximal view. (E) Same, retrodorsal view. (F, H) Same, distal view (dorsal side up). (G) Embolus complex, proventral and slightly distal view. (I) Distal edge of contrategulum, distal and slightly prolateral view (dorsal side to the right). (J-O) Same, distal view. Abbreviations: dw - dorsal wall of sclerotized part of embolus proper; t - tooth on distal edge of contrategulum. Scale lines: 1.0 mm (A-B; C-E, G-H; F, I-O).

with pigmented lateral patches in genital atrium (Fig. 7A, C-D, F, H-I cf. Fig. 5A, C-I); receptacular cluster not or only slightly protruding beyond anterior margin of poreplate, divided into three more or less distinct subclusters (Fig. 7B, E, G cf. Fig. 5B, J).

**Description of male (matured 27.II.2003):** *Colour in alcohol* (much darker in life; colouration as in female, Fig. 2A): All sclerotised parts uniformly brown, except for cream-coloured proximal portion of chelicerae,

cream-coloured membranes of prosoma and light brown opisthosomal membranes.

*Bristles on carapace:* Short bristles along all margins (strongest on posterior margin, longest behind, on and in front of eye mound); none on coxal elevations; five short bristles anterior to fovea.

*Scopula:* Tarsus I with thin scopula in distal half of ventral side, divided for its entire length by narrow, pale, glabrous longitudinal median stripe and by some

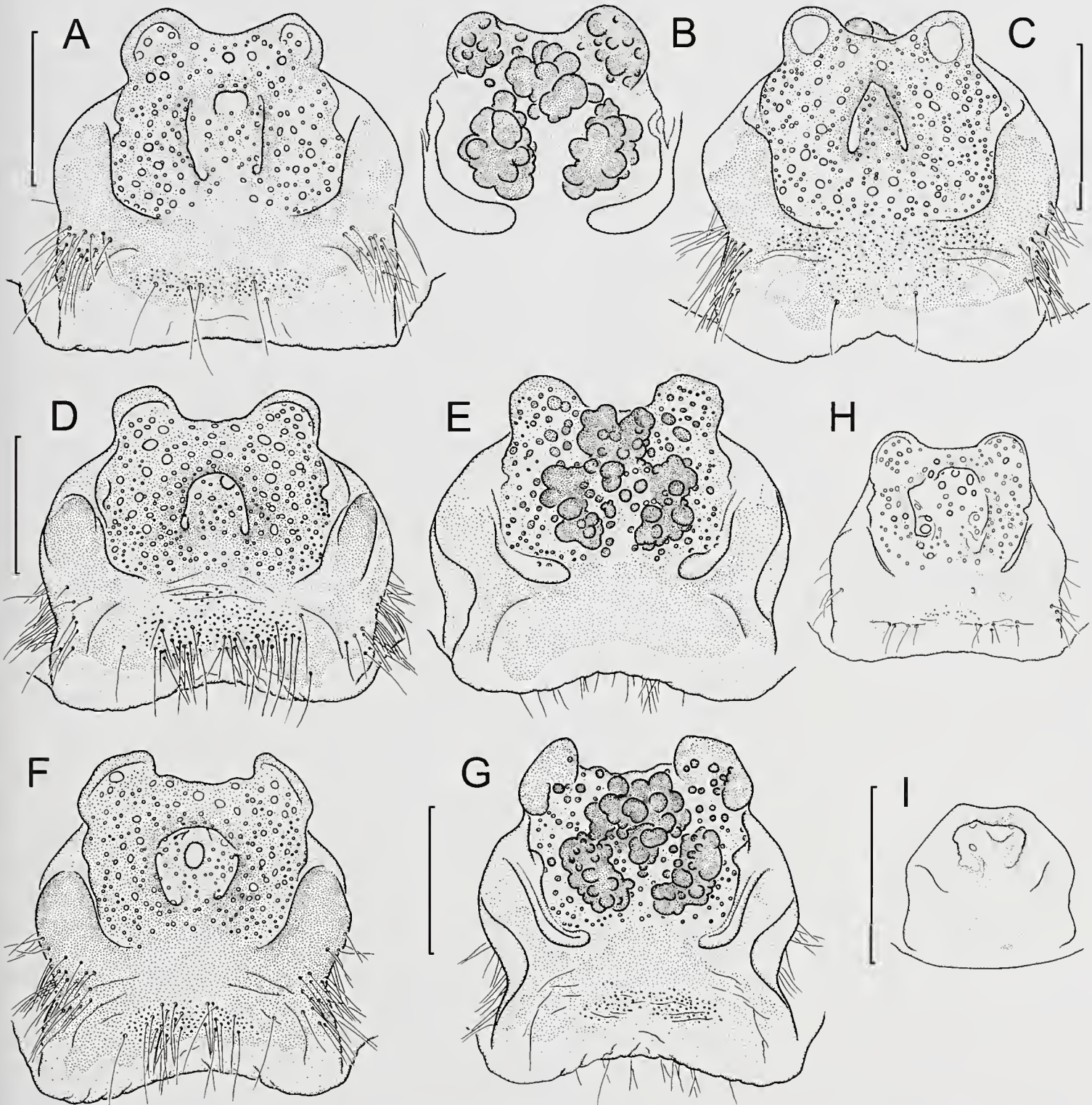


Fig. 7. *Liphistius endau*, vulval plate of six females: adult from unknown locality (A-B); largest female from Kota Tinggi (C); exuvia of reproductive female (moulted 27.IV.2002) from type locality (D-E); exuvia of reproductive female (moulted 28.IV.2002) from type locality (F-G); medium-sized juvenile from type locality (H); small juvenile from type locality (I). (A, C-D, F, H-I) Entire vulval plate, dorsal view. (B) Poreplate, ventral view. (E, G) Entire vulval plate, ventral view. Scale lines: 1.0 mm (A-B; C; D-E; F-G; H-I).

bristles; tarsus II with slightly denser scopula in distal three-quarters, only distally divided by median stripe; tarsi III-IV with dense scopula covering distal four-fifths, only distally divided by median stripe.

*Cheliceral teeth:* Eleven small ones on promargin of cheliceral groove on both sides.

*Palp:* Tibial apophysis situated distally, not clearly set back from distal margin of tibia, carrying four moderately long (dorsal ones shorter than ventral ones) megaspines (Fig. 6A-B). Both apical lobes of cymbium very short and equally rounded. Paracymbium basally very deep (Fig. 6B), its cumulus only slightly elevated, carrying stiff bristles reaching base of contrategulum (looking shorter in Fig. 6A because pointing ventrad rather than distad). Subtegulum without apophysis. Tegulum short and wide, coarsely dentate along entire proximal margin (Fig. 6D-E). Contrategulum with indistinct, widely arched proventral process (Fig. 6F); distal edge with denticles at proventral end distinctly elevated on a U-shaped ridge (Fig. 6A, C), with a single large triangular tooth prolaterally and with spatulate, quite symmetrical dorsal apex (Fig. 6F). Para-embolic plate only little elevated (Fig. 6A, C-E); sclerotised part of embolus proper strongly compressed dorso-ventrally, its dorsal wall distinctly wider than its ventral wall, curved prodorsad (Fig. 6F) and ending in a pronounced, prodorsad-directed, rounded lobe (Fig. 6C-E); membranous part of embolus proper distally much wider than proximally (Fig. 6C), its proximal portion slightly pigmented.

*Measurements:* Total length 22.30; carapace 9.26 long, 8.40 wide; opisthosoma 10.33 long, 7.62 wide; eye mound 1.34 long, 1.50 wide; palpal coxa 2.97 long, 1.98 wide; labium 0.69 long, 1.58 wide; sternum 4.06 long, 2.48 wide (1.29 on ventral surface); palp 15.83 long (4.43 + 2.79 + 5.74 + 2.87); leg I 27.21 long (7.21 + 3.61 + 5.90 + 7.05 + 3.44); leg II 28.11 long (7.21 + 3.61 + 6.15 + 7.62 + 3.52); leg III 30.99 long (7.54 + 3.77 + 6.56 + 9.02 + 4.10); leg IV 38.27 long (9.34 + 3.93 + 7.54 + 12.21 + 5.25).

**Additions to description of female:** Posterior margin of genital sternite more or less distinctly invaginated (Fig. 7A, C-H; 7I is a very small juvenile). Vulval plate (Fig. 7) strongly sclerotised and pigmented, roughly as long as wide, with a more or less distinct lateral constriction in posterior third. Genital atrium with many lateral hairs and in many cases also with additional median hairs; median zone of genital atrium clearly sunken below lateral zones (indistinct in small females). Posterior stalk wide, completely fused with poreplate and with strongly pigmented, bulging lateral parts of genital atrium (Fig. 7A, C-H). Poreplate entirely and strongly pigmented, its anterior margin slightly invaginated, with a pair of pronounced anterolateral lobes. CDO large to very large, its posterior margin not sunken, giving the opening the shape of a horseshoe (Fig. 7C-D, F) or of an open quadrangle (Fig. 7A, H);

enlarged pores inside CDO leading to receptacular cluster (Fig. 7A, C-D, F); the latter large and complex but not or only slightly protruding beyond anterior margin of poreplate, divided into three more or less distinct subclusters (Fig. 7B, E, G).

**Variation:** Carapace lengths in males (n=7) 9.26-12.04, in the largest females (n=4) 13.33-14.94; carapace widths 8.09-10.99 and 10.74-12.84, respectively. The three males from Kota Tinggi have a shorter scopula on their anterior legs (I: very thin, medially divided, covering only distal quarter; II: slightly denser, only apically divided, covering distal half; III: dense, undivided, covering three-quarters; IV: dense, undivided, covering distal four-fifths) than males from the type locality and from an unknown locality (I: thin, divided, distal half; II: slightly denser, apically divided, distal three-quarters; III-IV: dense, undivided, distal four-fifths).

Variation in the shape of the distal edge of the contrategulum is shown in Fig. 6F, H-O, variation in the shape of the vulval plate in Fig. 7. With age (and body size) the number of hairs in the genital atrium of females increases.

All females from Kota Tinggi have fewer hairs in the genital atrium than females from other localities. Among six medium to large-sized females from that locality only one large female has two hairs in a median position (Fig. 7C), all others (including another large female) have none.

The female holotype (in AMNH, not examined) has a carapace length of 7.5 and a width of 6.6, and is thus only about half the size of the three largest females examined. The illustrations of the holotype vulva (Sedgwick & Platnick, 1987: figs 1-2) differ from the vulvae examined by lacking distinct anterolateral lobes on the poreplate (also absent in the smallest juvenile female examined; Fig. 7I). The posterior stalk of the holotype vulva is not yet fused with the pigmented lateral zones of the genital atrium (as it is also the case in the two juvenile females examined; Fig. 7H-I) and it appears to lack lateral hairs (as it is the case in the smallest female examined; Fig. 7I). The holotype is therefore a juvenile female with a not fully developed vulval plate. As (according to the original description) its vulval plate corresponds quite well with vulval plates of juveniles examined from the same area (possibly even from the same locality), and as no other *Liphistius* species is known from that area, there is no doubt that these specimens are conspecific.

**Distribution:** Known from three localities in the northern and western part of Johor State (Fig. 1, localities 6-8).

**Relationships:** Large size, details of the male palp (e.g. shape of distal edge of contrategulum and its dorsal apex; shape of tibial apophysis) and details of the vulval plate (bulging lateral and posterolateral margins on



ventral side of poreplate forming a distinct boundary between poreplate and posterior stalk) indicate that *L. endau* and *L. malayanus* are more closely related to each other than to *L. johore* and *L. gracilis* sp. nov.

**Biology:** The new specimens from the type locality or from very close to it (in the Endau-Rompin N.P.) were found on the banks of a stream in a rain forest; specimens from the Kota Tinggi Waterfall were collected from the sloping forest floor and soil banks on both sides of rain forest stream running over a series of falls. Most burrows were in the soil, but at the Kota Tinggi Waterfall two medium-sized burrows were constructed in the rotten wood of a fallen tree, with the signal lines spread over the wood surface. At the type locality the burrow entrance of a large female had nine signal threads, at the Kota Tinggi Waterfall four burrows (of three large females and one penultimate male) were equipped with nine signal lines; all other burrows had a maximum of eight lines running over rock, soil and tree roots. The longest signal line (of the largest female) was 34 m long, those of other burrows examined were not more than 21 cm long. Trapdoors of four penultimate males were 2.6-3.2 cm long and 4.0-4.7 cm wide; that of the largest female 3.3 and 5.9, respectively. The latter spider lived in a 35 cm long burrow. Males became mature in August, October and November (after 2-5 months in captivity) and in February (after one and a half years in captivity, therefore probably not corresponding to conditions in nature). One male (from the Kota Tinggi Waterfall) ate a half-dead cricket a few days after its last moult but not again later. I also observed this in newly matured males of *L. dangrek* Schwendinger, 1996, and it had been reported for males of *L. desultor* by Murphy & Platnick (1981: 46), but it occurs only rarely and probably only in large species. Usually *Liphistius* males cease feeding when becoming adult.

Egg cases were constructed (all of them in captivity or during transport) in June and July. One egg case built in Geneva by a female from the type locality was 5.0 cm long, 4.7 cm wide, 2.8 cm high and contained 453 eggs. Another female from the same locality built during the transport an egg case of tissue paper, with a 3 cm diameter, containing 331 eggs. A third, old and empty egg case at the Kota Tinggi Waterfall was 4.0 cm long, 54.6 cm wide, 1.8 cm high. A fourth female from the same locality built a tissue paper egg case of 4.2 cm diameter and 2.0 cm height, containing 395 light orange-coloured eggs.

***Liphistius gracilis* sp. nov.**

Figs 8-9

**Types:** MHNG, sample SIM-01/07; male holotype (matured 13.VIII.2001), 5 male paratypes (matured

18.IX., 19.IX.2001, 5.I., 24.III., 3.VI.2002), 5 female paratypes; Malaysia, Johor, Kota Tinggi Waterfalls at foot of Gunung Muntahak, 170 m (evergreen rain forest); 24.-26.VI.2001, leg. P.J. Schwendinger. – SMF, sample TM-14/02; 1 male paratype (matured 5.XI.2016); same locality; 21.-22.VI.2014; leg. P.J. Schwendinger. – MHNG, SMF, sample Sum-00/01; 3 female paratypes [moulted 3.V. (allotype); early VIII.; 26.XII.2000; 16.V., 6.X.2001]; same locality; 4.II.2000; leg. P.J. Schwendinger.

**Etymology:** The species epithet is a Latin adjective meaning “gracile”, “slender”, “slim”, referring to the small body size of this species in comparison with *L. malayanus* and *L. endau*.

**Diagnosis:** Similar to *L. malayanus* and *L. endau* but much smaller in body size, with lighter body colouration and annulated legs and palps. Males distinguished from those of *L. malayanus* (Fig. 4) and *L. endau* (Fig. 6) by tibial apophysis of palp longer and directed more distad (Fig. 8A, C), carrying shorter megaspines, the dorsal one sitting clearly lower than the rest (Fig. 8B, H-J); paracymbium relatively deeper than in *L. malayanus* and shallower than in *L. endau* (Fig. 8A-C cf. Fig. 4A and Fig. 6B, respectively); distal edge of contrategulum serrate (Fig. 8A, D-G), its apex distinctly smaller (Fig. 8F-G cf. Fig. 4G-L and Fig. 6F, H-O); dorsal wall of sclerotised part of embolus proper ending in a sharply prodorsad-bent lobe (Fig. 8D-G) [both walls equally wide in *L. malayanus* (Fig. 4G-H); dorsal wall prodorsal-curved (not sharply bent) in *L. endau* (Fig. 6F, H)]. Vulva of *L. gracilis* sp. nov. (Fig. 9) different from vulvae of *L. malayanus* (Fig. 5) and *L. endau* (Fig. 7) by ventral side of poreplate without bulging lateral and posterolateral margins, thus transition between poreplate and posterior stalk much less marked; anterior margin of poreplate with less distinct anterolateral lobes; receptacular cluster wider than long, more distinctly protruding beyond anterior margin of poreplate. Vulva different from that of *L. johore* (Fig. 10A) by lacking pronounced anterolateral invaginations in the margin of the poreplate, by having a wide and indistinct transition between poreplate and posterior stalk (narrow and distinct in *L. johore*), any by possessing hairs in the genital atrium.

**Description of male (holotype):** *Colour in alcohol* (darker in life): Carapace mostly light brown, with darker patches along margins (medially broken on posterior margin), extending between coxal elevations; dark anterior margin enclosing very dark eye mound; dark W-shaped pattern behind eye mound indistinct; a few small dark spots on pars cephalica; a paramedian pair of dark patches anterior to fovea; chelicerae cream-coloured proximally, grey-brown distally; legs and palps mostly light brown, with darker zone proximally on

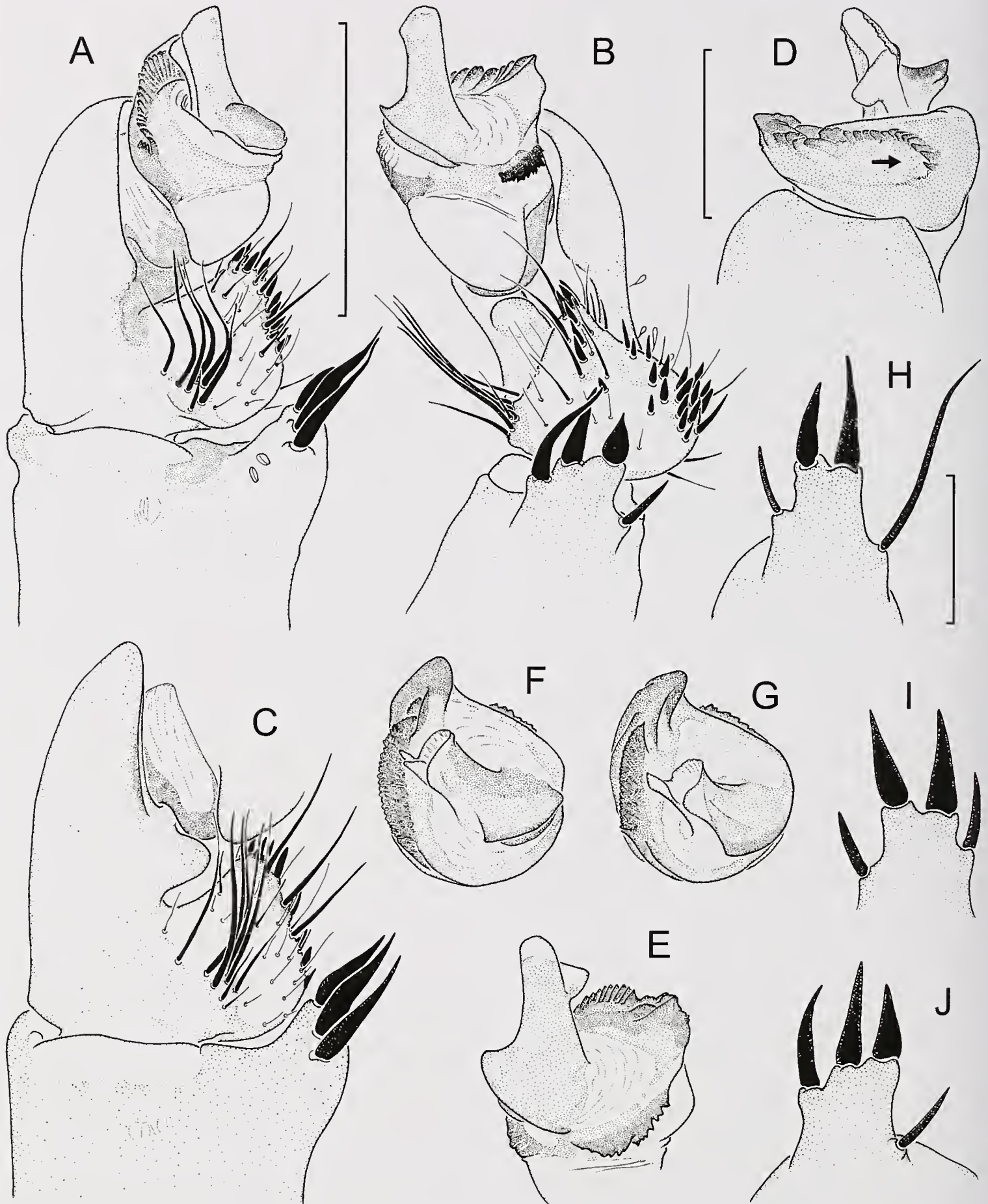


Fig. 8. *Liphistius gracilis* sp. nov., details of palp of three males: paratype, matured 5.I.2002 (A-B, H); holotype (C-F, I-J); paratype, matured 19.IX.2001 (G). (A) Distal part of palp, ventral view. (B) Same, retrolateral view. (C) Subtegulum, cymbium and distal part of palpal tibia, ventral view. (D) Distal part of cymbium and palpal organ, proventral view (arrow indicating U-shaped row of denticles at proventral end of distal edge of contrategulum). (E) Same, retrodorsal view. (F-G) Same, distal view (dorsal side up). (H-I) Right tibial apophysis, retrolateral and slightly proximal view. (J) Left tibial apophysis, same view. Scale lines: 1.0 mm (A-C), 0.5 mm (D-G; H-J).

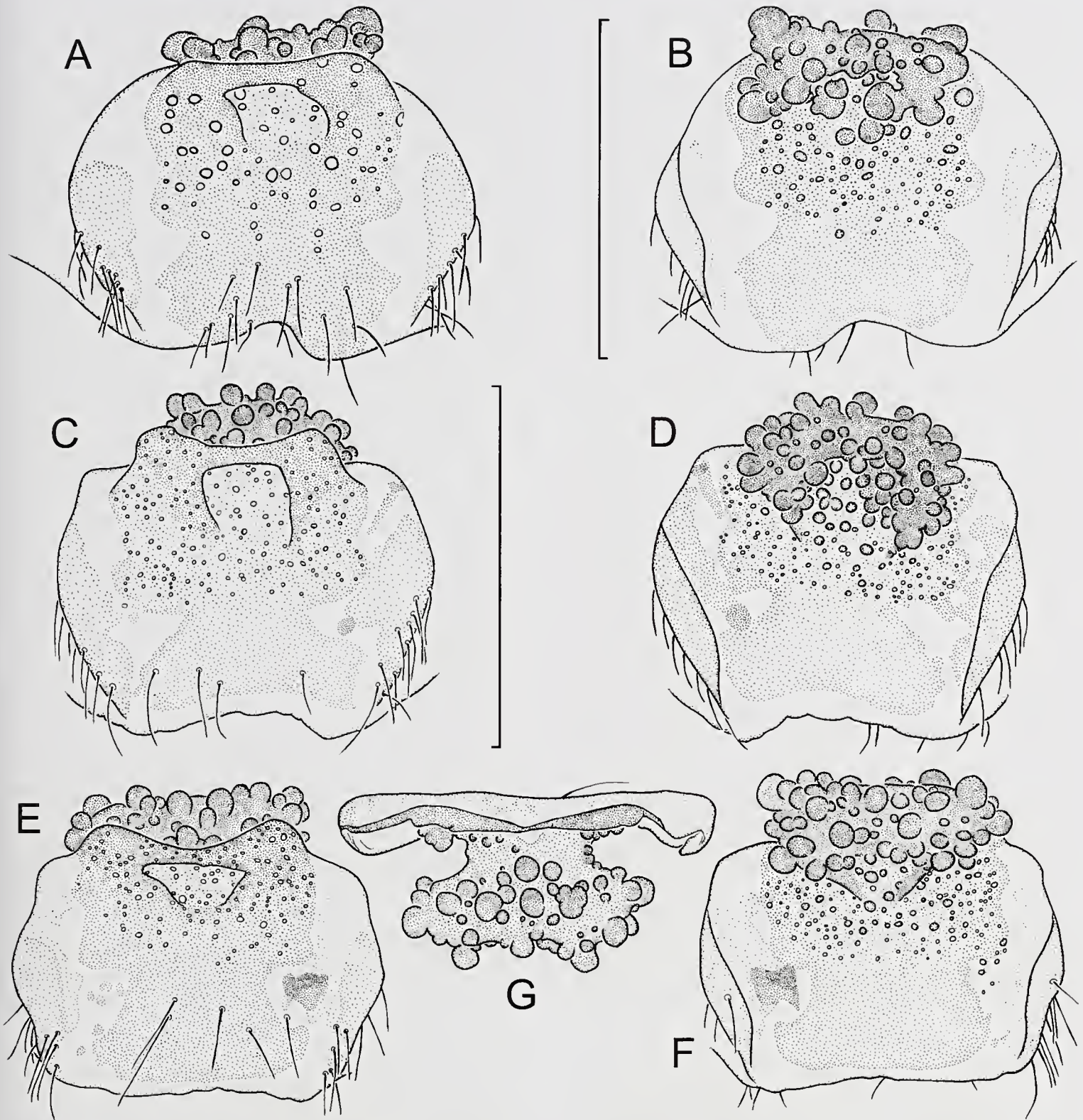


Fig. 9. *Liphistius gracilis* sp. nov., vulval plate of three females (all from exuviae): allotype (A-B); paratype, moult 31.VIII.2001 (C-D); paratype, moult 27.IX.2001 (E-G). (A, C, E) Vulval plate, dorsal view. (B, D, F) Same, ventral view. (G) Same, anterior view. Scale lines: 1.0 mm (A-B; C-G).

patellae and tibiae of legs III-IV, and in proximal half of all metatarsi. Opisthosomal tergites cream-coloured, with dark marginal and central patches on tergite I, other tergites only with lateral and anterolateral patches; membranous part of opisthosoma cream-coloured. Sclerotised parts of ventral side of body light brown.

**Bristles on carapace:** Short bristles along all margins (strongest on posterior margin, longest behind, on and in front of eye mound), on coxal elevations and in area behind fovea, none anterior to fovea.

**Cheliceral teeth:** Ten and eleven small ones on promargin of cheliceral groove of right and left chelicera, respectively.

**Scopula:** Tarsus I with very thin scopula confined to distal fifth of ventral side, divided for its entire length by narrow pale, glabrous longitudinal median stripe and by some bristles; tarsus II with very thin scopula in distal quarter, only distally divided by median stripe; tarsus III with dense scopula covering distal half, only distally divided by median stripe; tarsus IV with dense

scopula covering distal three-fifths, only distally divided by median stripe.

*Claws:* Paired tarsal claws on anterior legs with 4-6 denticles, on posterior legs with 5-6 denticles; unpaired claws in most cases with a single denticle on anterior legs, none on posterior legs.

*Palp:* Tibial apophysis relatively long, situated at distal margin of tibia, inclined distad [Fig. 8A (showing paratype matured 5.I.2002), C], carrying four quite short megaspines, the dorsal one rising from a clearly more proximal position than the others [Fig. 8B, H (showing paratype matured 5.I.2002), I-J]. Both apical lobes of cymbium indistinct, prodorsal one more rounded than retrodorsal one (Fig. 8D). Paracymbium relatively large and basally deep [Fig. 8A-B (showing paratype matured 5.I.2002), C-D], its cumulus indistinctly elevated, carrying moderately long stiff bristles [Fig. 8A-B (showing paratype matured 5.I.2002), C]. Subtegulum without apophysis. Tegulum short and wide, coarsely dentate along entire proximal margin, not or only indistinctly connected to contrategulum on retrodorsal side (Fig. 8E). Contrategulum without ventral process; distal edge finely serrate, proventrally ending in a U-shaped row of denticles (Fig. 8D), dorsally ending in a spatulate asymmetrical apex (Fig. 8F). Para-embolic plate only little elevated (Fig. 8B, showing paratype matured 5.I.2002); sclerotized part of embolus proper without longitudinal keels or ribs and not carrying denticles (Fig. 8A-B, showing paratype matured 5.I.2002), its dorsal wall distinctly wider than its ventral wall, abruptly bent prodorsad approximately at a right angle (Fig. 8F) and ending in a pronounced angular lobe (Fig. 8D-E); membranous part of embolus proper apically widened and lying on lobe of dorsal wall of sclerotised part (Fig. 8D).

*Measurements:* Total length 11.32; carapace 4.67 long, 3.96 wide; opisthosoma 4.83 long, 3.64 wide; eye mound 0.68 long, 0.80 wide, AME well-developed; palpal coxae 1.38 long, 0.95 wide; labium 0.40 long, 0.79 wide; sternum 2.37 long, 1.50 wide (0.83 on ventral surface); palp 7.99 long (2.53 + 1.34 + 2.81 + 1.31); leg I 15.97 long (4.35 + 1.90 + 3.40 + 4.03 + 2.29); leg II 17.01 long (4.43 + 1.90 + 3.56 + 4.63 + 2.49); leg III 18.92 long (4.55 + 1.90 + 4.00 + 5.78 + 2.69); leg IV 23.89 long (5.38 + 2.06 + 5.10 + 8.03 + 3.32).

**Description of female (allotype):** *Colour in alcohol* (darker in life): As in male but with a more pronounced dark pattern on carapace, resulting in a more distinct W-shaped pattern behind eye mound, and with a pronounced, light brown, flower-shaped pattern on pars thoracica; all opisthosomal tergites with larger dark patches, tergites II-V additionally with dark anteromedian patches. Legs light brown, with dark proximal and subapical annulations on femora (also on palpal femur), tibiae, metatarsi (indistinct on posterior legs) and on tarsi (indistinct on posterior legs). Palpal

tibia with dark proximal and apical annulation; tarsus mostly dark, proventral-distal area lighter.

*Bristles on carapace:* Slightly stronger and longer (especially in front of eye mound) than in male.

*Cheliceral teeth:* Eleven strong cheliceral teeth on promargin of cheliceral groove on both sides.

*Claws:* Paired tarsal claws on legs with mostly 4-5 denticles (one claw with only two); unpaired claws with two denticles on legs I-III, 1-2 on leg IV. Tarsi without scopula.

*Vulva:* Vulval plate (Fig. 9A-B) distinctly sclerotised and pigmented, wider than long. Genital atrium uniformly flat, its lateral parts not bulging on dorsal side, with several lateral and median hairs. Posterior stalk wide, indistinctly perforated with tiny micropores; transition to poreplate indistinct, only slightly constricted. Anterior margin of poreplate slightly to distinctly invaginated, with indistinct anterolateral lobes, without anterolateral invaginations; ventral side of poreplate without bulging lateral and posterolateral margins. CDO large, undivided, irregularly quadrangular, close to anterior margin of poreplate. Receptacular cluster clearly wider than long, deep, distinctly projecting beyond anterior margin of poreplate.

*Measurements:* Total length 13.53; carapace 5.34 long, 4.19 wide; opisthosoma 5.70 long, 4.15 wide; eye mound 0.74 long, 0.83 wide; palpal coxae 1.74 long, 1.27 wide; labium 0.63 long, 1.27 wide; sternum 2.53 long, 1.86 wide (0.91 on ventral surface); palp 8.98 long (3.01 + 1.58 + 2.14 + 2.25); leg I 11.82 long (3.56 + 1.94 + 2.73 + 2.25 + 1.34); leg II 12.22 long (3.60 + 1.98 + 2.73 + 2.49 + 1.42); leg III 12.74 long (3.60 + 1.98 + 2.45 + 3.05 + 1.66); leg IV 16.41 long (4.27 + 2.10 + 3.24 + 4.55 + 2.25).

**Variation:** Carapace lengths in males (n=7) 4.36-4.75, in females with a well-developed vulval plate (n=9) 4.29-5.34, in the smallest female with an egg case 4.66. Carapace widths 3.64-4.06, 3.11-4.22 and 3.51, respectively.

In four males (including the holotype) the scopula extends over the distal half of the ventral side of tarsus III and over the distal three-fifths of tarsus IV, in the other three males it extends over the distal three-fifths of tarsus III and over the distal two-thirds of tarsus IV; on legs I-II the extent of the scopula is the same in all males. Variation in the shape of the tibial apophysis of the male palp is shown in Fig. 8A-C, H-J; variation in the shape of the distal edge of the contrategulum in Fig. 8F-G; variation in the shape of vulval plates of the females examined in Fig. 9. Two female paratypes (Fig. 9C, E), but not the allotype (Fig. 9A), have a moderately pronounced anterolateral lobe followed by a slight anterolateral invagination on each side of the poreplate. The largest (oldest) female (Fig. 9A) has more hairs in the genital atrium than smaller (younger) females (Fig. 9E). The posterior margin of the genital sternite of females is almost straight to distinctly invaginated (Fig. 9A-F).

**Distribution:** The types were collected from the surroundings of the Kota Tinggi Waterfall, at the foot of Gunung Muntahak, north of Kota Tinggi, in Johor State (Fig. 1, locality 8). Burrows of probably the same species were seen along the trail to the nearby Pelepah Waterfall. Two juveniles (don J. Kral) from Gunung Belumut, about 32 km further northwest, may also belong to this species.

**Biology:** At the Kota Tinggi Waterfall *L. gracilis* sp. nov. occurs together with the much larger *L. endau* which belongs to the same species-group. Burrows of the two species were seen only a few centimetres from each other. *Liphistius endau* was exclusively found very close to the waterfall and to the stream, *L. gracilis* sp. nov. also further away, but both were absent from high earthbanks (old road sides) in a palm oil plantation adjacent to the rain forest. Most burrows were simple, equipped with a single trapdoor and dug into the soil; a few small ones were sac-like nests with two trapdoors, constructed on the moss-covered surface of rock (as also known from cave species and from juveniles of forest-dwelling species; see Schwendinger, 1987). The trapdoors of seven penultimate males were 1.1-1.3 cm long and 1.6-1.9 cm wide; that of the largest female 1.3 and 2.0, respectively. All burrows had a maximum of eight, relatively long signal lines running over soil, stones and tree roots; the longest signal line (of the largest female) was 21 cm long.

Four males collected in June became adult in August to November of the same year; two males reached maturity in January and February after over 1.5 years in captivity (thus probably not corresponding to conditions in nature). In early July and early August two females built egg cases in captivity, 1.7-2.0 cm in diameter and 1.1-1.4 cm high, containing 30 and 36 eggs suspended on a thin layer of fine silk strands. Adult females moulted twice per year, in May and again in August to November.

lateral and posterolateral margins on ventral side (Platnick & Sedgwick, 1984: fig. 80), with relatively large pores on dorsal side, with a large CDO (at its posterior margin level with the poreplate), and with a large receptacular cluster projecting far beyond anterior margin of poreplate; genital atrium without hairs, including a strongly trapezium-shaped (posteriorly wide, anteriorly very narrow, posterior margin almost straight) posterior stalk (Fig. 10A; Platnick & Sedgwick, 1984: figs 79-80).

**Male:** Unknown.

**Female:** This species was described on the basis of only the female holotype. For an easy comparison with other species treated here, the dorsal aspect of the vulval plate was re-drawn from Platnick & Sedgwick (1984: fig. 79) and is shown in Fig. 10A.

**Relationships:** The vulval plate (with a large CDO, with a huge receptacular cluster projecting far beyond the anterior margin of the well-sclerotised poreplate and with a well-sclerotised posterior stalk fully connected to the poreplate) indicates that *L. johore* is a member of the *malayanus*-group. Relatively small size, the presence of anterolateral invaginations on the poreplate (also present, but less distinct, in some females of *L. gracilis* sp. nov.; Fig. 9C, E) and the apparent absence of bulged lateral and posterolateral margins on the ventral side of the poreplate (not clearly evident from original illustrations of the vulval plate of the holotype, see Platnick & Sedgwick, 1984: fig. 80) indicate that *L. johore* and *L. gracilis* sp. nov. are more closely related to each other than to *L. malayanus* and *L. endau*.

**Distribution and remarks:** The type locality is given as "Sungai Rengit, Pengarang" (Fig. 1, locality 9). Kampung Sungai Rengit and the Pengarang ferry

### *Liphistius johore* Platnick & Sedgwick, 1984

Fig. 10A

*Liphistius johore* Platnick & Sedgwick, 1984: 30, figs 79-80 (description of female).

**Type material:** Bernice Pauahi Bishop Museum, Honolulu, USA; female holotype (not examined); Malaysia, Johore [sic], Sungai Rengit, Pengarang; 19.XII.1961; leg. K.J. Kunchuna.

**Material examined:** None.

**Diagnosis:** Seemingly a fairly small species (carapace length of female holotype 5.15, carapace width 4.00). Female with annulated legs and yellow-coloured to orange-coloured carapace and opisthosomal tergites (Platnick & Sedgwick, 1984: 30); vulva with a wide poreplate with a distinct anterolateral invagination on each side of anterior margin, seemingly without bulging

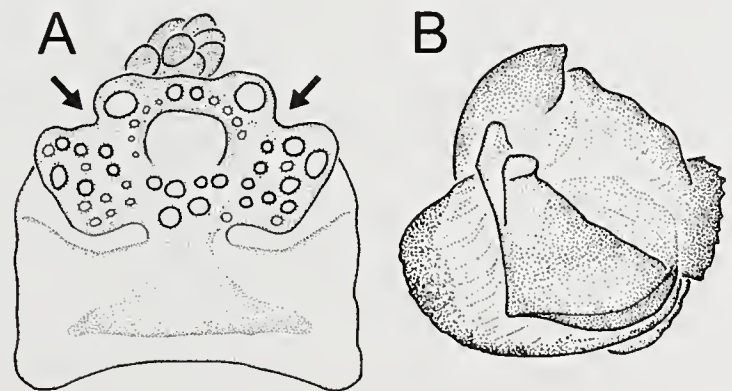


Fig. 10. *Liphistius johore*, female holotype (A); *Liphistius panching*, male from type locality (B). (A) Dorsal view of vulval plate (redrawn from Platnick & Sedgwick, 1984: fig. 79) (arrows indicating anterolateral invaginations in margin of poreplate). (B) Distal view of left palpal organ (dorsal side up) (redrawn from Sedgwick & Platnick, 1986: fig. 5).

terminal and immigration post (with nearby remains of the "Pengarang Battery", a British defence post overrun by the Japanese Army during the fall of Singapore in World War II) are about 15 km apart. I spent a full day searching in both the fairly undisturbed forest on the publicly accessible little hill next to the Pengarang ferry terminal (the nearby, distinctly higher and nicely forested Bukit Pengarang lies on the land of a large Malaysian naval base and is off limits to civilians and foreigners) and in the strongly disturbed forest of Bukit Pelali, about 5 km north of Kampung Sungai Rengit, but found no traces (not even empty burrows) of *Liphistius*.

### *Liphistius* sp.

A single female (in MHNG; leg. P.J. Schwendinger), large (carapace length 12.45, carapace width 11.02) and uniformly dark-coloured, was collected close to the Jeram Linang Waterfall (Fig. 1, locality 13), south of Kota Baharu in the Kelantan State, together with the types of *L. linang* sp. nov. It produced an egg case in late January. Judging from the shape of its vulval plate, this specimen belongs to an undescribed species in the *malayanus*-group,

### The *tioman*-group

**Diagnosis:** Medium-sized to large (carapace length of males 6.23-11.30, carapace length 6.01-10.04), uniformly dark-coloured spiders. Similar to species of the *malayanus*-group, distinguished by distal edge of contrategulum proventrally not ending in a V-shaped or U-shaped row of denticles; ventral process of contrategulum well-developed, basally wide (Figs 10B,

11F, 14C-D); para-embolic plate more elevated (Figs 11B-E, 14E-F); poreplate with CDO medium-sized and undivided (Fig. 12A, C, F) or large and divided by a more or less distinctly developed longitudinal bridge (Figs 13A, C-D, G; 14I); receptacular cluster medium-sized, more or less distinctly divided into two halves by a longitudinal trench (Figs 12B, D-E, G; 13B, E-F, H; 14J).

**Species included:** *Liphistius negara* sp. nov., *L. panching* and *L. tioman*.

**Relationships:** Species of the *tioman*-group are similar and probably closely related to species of the *malayanus*-group. *Liphistius panching* and *L. negara* sp. nov. from the mainland are more similar to each other than they are to the very distinct island-dwelling *L. tioman*.

**Distribution:** Eastern part of peninsular Malaysia and an offlying island (Fig. 1, localities 10-12).

### *Liphistius tioman* Platnick & Sedgwick, 1984

Figs 11-12

*Liphistius tioman* Platnick & Sedgwick, 1984: 28-29, figs 81-87 (description of male and female).

**Type material:** AMHN; male holotype and female paratype (not examined); Malaysia, Pahang, Tioman Island, Gua Sinah and Gua Panah, 2600 ft. altitude; 29.VII.1982; leg. W.C. Sedgwick.

**Material examined:** MHNG, sample SIM-01/09; 1 male (matured 3.I.2002), 7 females (moulted 17.XII.2001; 2.IX.2001, 6.III., 4.X.2002, 7.VI.2003; 8.IX.2001, 16.II., 23.VI.2002), 1 penultimate male;

### Key to the species of the *tioman*-group:

- 1 Tibial apophysis of male palp deeply divided, both parts equally long and carrying very short megaspines (Fig. 11A, H-I); tegulum very narrow, with few denticles on proximal edge (Fig. 11B); para-embolic plate long and distally pointed (Fig. 11C-E). Vulval plate with very wide, indistinctly outlined transition between poreplate and posterior stalk, lateral and posterolateral margins on ventral side of poreplate not bulging; genital atrium without median hairs (Fig. 12)..... *L. tioman*
- Tibial apophysis undivided, carrying long megaspines (Fig. 14G; Sedgwick & Platnick, 1986: figs 1-2, 5); tegulum wide, with numerous denticles on proximal edge (Fig. 14F; Sedgwick & Platnick, 1986: figs 1-2); para-embolic plate short and widely rounded (Fig. 14E-F; Sedgwick & Platnick, 1986: figs 1-2). Vulval plate with narrow, distinctly outlined transition between poreplate and posterior stalk, lateral and posterolateral margins on ventral side of poreplate bulging; genital atrium without median hairs (Figs 13, 14I-J) .....2
- 2 Paracymbium longer than deep (Sedgwick & Platnick, 1986: figs 2-3); ventral process of contrategulum short, its apex widely rounded; distal edge of contrategulum smooth (Sedgwick & Platnick, 1986: fig. 5; Fig. 10B). Vulval plate slightly longer than wide or as long as wide; poreplate anteriorly wider than posteriorly, its anterior margin usually clearly invaginated (Fig. 13) ..... *L. panching*
- Paracymbium deeper than long (Fig. 14A-B); ventral process of contrategulum moderately long, its apex narrowly rounded (Fig. 14C-D); distal edge of contrategulum prodorsally with a single large triangular tooth (Fig. 14C-D). Vulval plate clearly wider than long; poreplate anteriorly narrower than posteriorly, its anterior margin only indistinctly invaginated (Fig. 14I-J) ..... *L. negara* sp. nov.

Pahang, Tioman Island, Gunung Kajang (2°45'45"N, 104°08'43"E), 820-850 m; 30.VI.2001; leg. P.J. Schwendinger.

**Diagnosis:** Males distinguished from those of all other *Liphistius* species by a deeply and widely divided retrolateral apophysis on palpal tibia, both parts being equally long (Fig. 11A, H-I). Males distinguished from those of other species in the *tioman*-group additionally by a long and pointed para-embolic plate (Fig. 11C-E) and by a very narrow tegulum with few denticles on proximal edge, situated very close to dorsal apex of contrategulum (Fig. 11B, F). Females with poreplate widely fused with posterior stalk; receptacular cluster medially more or less distinctly divided; CDO undivided (Fig. 12).

**Additions to description of male:** *Scopula:* In distal two-thirds of ventral side of tarsus I, in distal three-quarters of tarsus II, in distal two-thirds of tarsus III, in distal half of tarsus IV (narrower than on other tarsi). All scopulae thin and only distally (behind the claws) divided by a glabrous longitudinal median stripe.

*Palp:* Tibial apophysis situated apically, not set back from anterior margin of palp (Fig. 11G), deeply divided: retrolateral part deeper, aligned with axis of tibia and carrying three very short pointed megaspines; retrodorsal part much narrower, pointing away from axis of tibia, carrying a single, slightly longer pointed megaspine (Fig. 11A, G-I). Distal margin of cymbium with very indistinct lobes (Fig. 11C). Paracymbium relatively short and moderately deep (Fig. 11A); cumulus indistinct, carrying a fairly compact group of long stiff bristles (Fig. 11A). Subtegulum without apophysis. Tegulum very narrow, its proximal edge carrying few overlapping scale-like denticles, situated close to dorsal apex of contrategulum (Fig. 11B, F). Contrategulum with large, conical ventral process being slightly constricted at base (Fig. 11F); distal edge of contrategulum distinctly elevated and composed of numerous parallel ribs instead of teeth (Fig. 11B-F), dorsal apex relatively small and narrowly rounded, only slightly elevated above underlying surface (Fig. 11B, F). Para-embolic plate long, narrow and asymmetrically triangular (Fig. 11B-E); embolus proper strongly inclined prolaterad (Fig. 11B), distally widened; dorsal wall of sclerotised part distinctly wider than ventral wall, ending in a quadrangular lobe (Fig. 11B-C, F), retrolateral wall not enforced by ridges but only with an indistinct, short distal keel (Fig. 11B, F); membranous part of embolus proper slightly widened distally (Fig. 11C).

**Additions to description of female:** Genital atrium of vulval plate (Fig. 12) without median hairs, few to several lateral hairs present in some females; lateral margin of genital atrium not forming flaps bending ventrad and inwards (as usual in *Liphistius*) but only

indistinct mounds on the dorsal (not the ventral) side (Fig. 12A, C, F). Posterior stalk relatively short and wide, fused with poreplate without recognizable transition, reaching lateral margins of vulval plate in some females. Poreplate of variable shape, in most females examined anteriorly slightly narrower than posteriorly, its anterior margin indistinctly invaginated, without lobes; CDO quite large, undivided, anteriorly deep, posteriorly level with rest of poreplate (Fig. 12A, C, F; but see illustration of paratype in Platnick & Sedgwick, 1984: fig. 86); receptacular cluster quite large and wide, more or less distinctly divided into two paramedian subclusters (Fig. 12B, D-E, G).

**Taxonomic remarks:** The tibial apophysis of the male palp of *L. tioman* is unique and distinctly autapomorphic. A similar divided tibial apophysis is found in males of the *linang*-group, but that is considered to have evolved convergently (see also Discussion). The wide ventral process of the contrategulum, the wide posterior stalk and the divided receptacular cluster indicate a close relationship with *L. panching* and *L. negara* sp. nov.

**Variation:** Carapace lengths in males (n=2; values of the holotype are taken from Platnick & Sedgwick, 1984: 29) 6.23-6.93, carapace widths 6.01-6.34. In females with fully developed copulatory organs (n=7) the carapace length is 5.54-7.92 and the carapace width 5.15-7.38. Variation in the shape of poreplates of the females examined is shown in Fig. 12. The retrolateral tibial apophyses of the left and right palp of the examined male are shown in Fig. 11A and Fig. 11I, respectively.

**Distribution:** Known only from higher altitudes on Tioman Island (Fig. 1, locality 10).

**Biology:** Spiders of this species were found under and between huge granite boulders (some of them touching each other and forming recesses) in a lush rain forest. These recesses probably correspond to the Gua Sinah or Gua Panah which is the exact type locality and which were described as not being real caves (like their Malay names suggest) but just overhung caverns (Platnick & Sedgwick, 1984: 29). Burrows were mostly dug into loamy soil at the base and between the boulders (a few small spiders had silken nests on the surface of boulders just above the ground, as described for juvenile spiders of *L. trang*, see Schwendinger, 1987: fig. 5), and they had up to eight exceptionally long (up to 34 cm) signal lines spread over soil or rock surface. The trapdoor of the adult male (before its final moult) was 1.8 cm long and 3.2 cm wide, that of the largest female was 1.9 cm and 3.2 cm, respectively. When collected at the end of June, four females had egg cases: one was not opened, another was empty, the remaining two were 2.2-2.7 cm long, 2.8-2.9 cm wide and 1.9 cm high; they contained 3rd instar spiderlings (not collected, not counted).

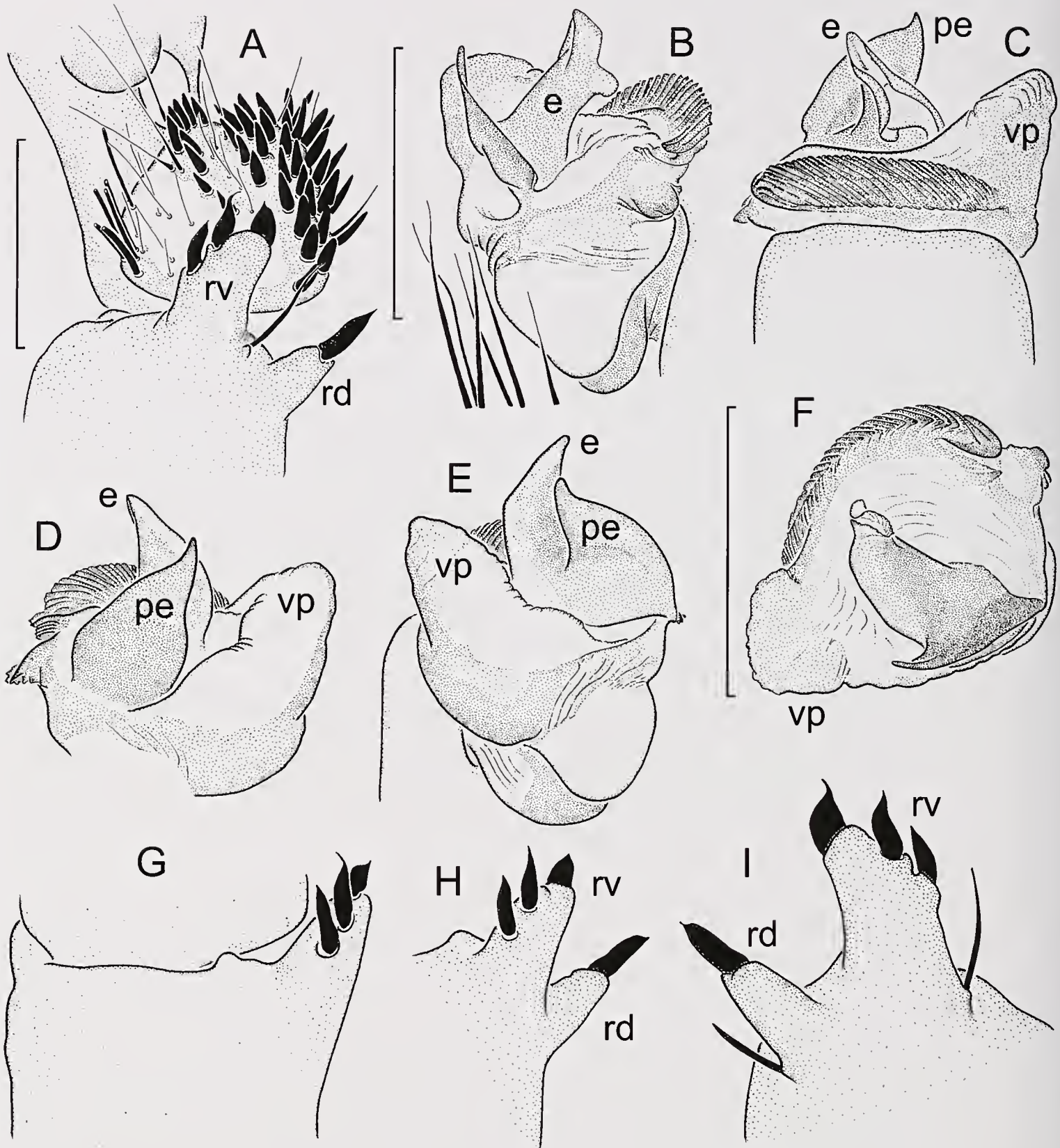


Fig. 11. *Liphistius tioman*, details of left and right palp of a male (matured 3.I.2002) from the type locality; left palp (A-C, E-H) and right palp (D, I). (A) Distal part of tibia and base of tarsus, retroventral view. (B) Palpal organ and tips of bristles on cumulus, retrolateral view. (C) Distal part of cymbium and palpal organ, prolateral view. (D) Palpal organ, retrolateral view. (E) Same, retroventral view. (F) Same, distal view (dorsal side at 1 o'clock). (G) Tibial apophysis, ventral view. (H) Same, retroventral view. (I) Same, retrolateral and slightly proximal view. Abbreviations: e - embolus proper; pe - para-embolic plate; rd - retrodorsal part of tibial apophysis; rv - retroventral part of tibial apophysis; vp - ventral process of contrategulum. Scale lines: 1.0 mm (A, G-H; B-E, I; F).



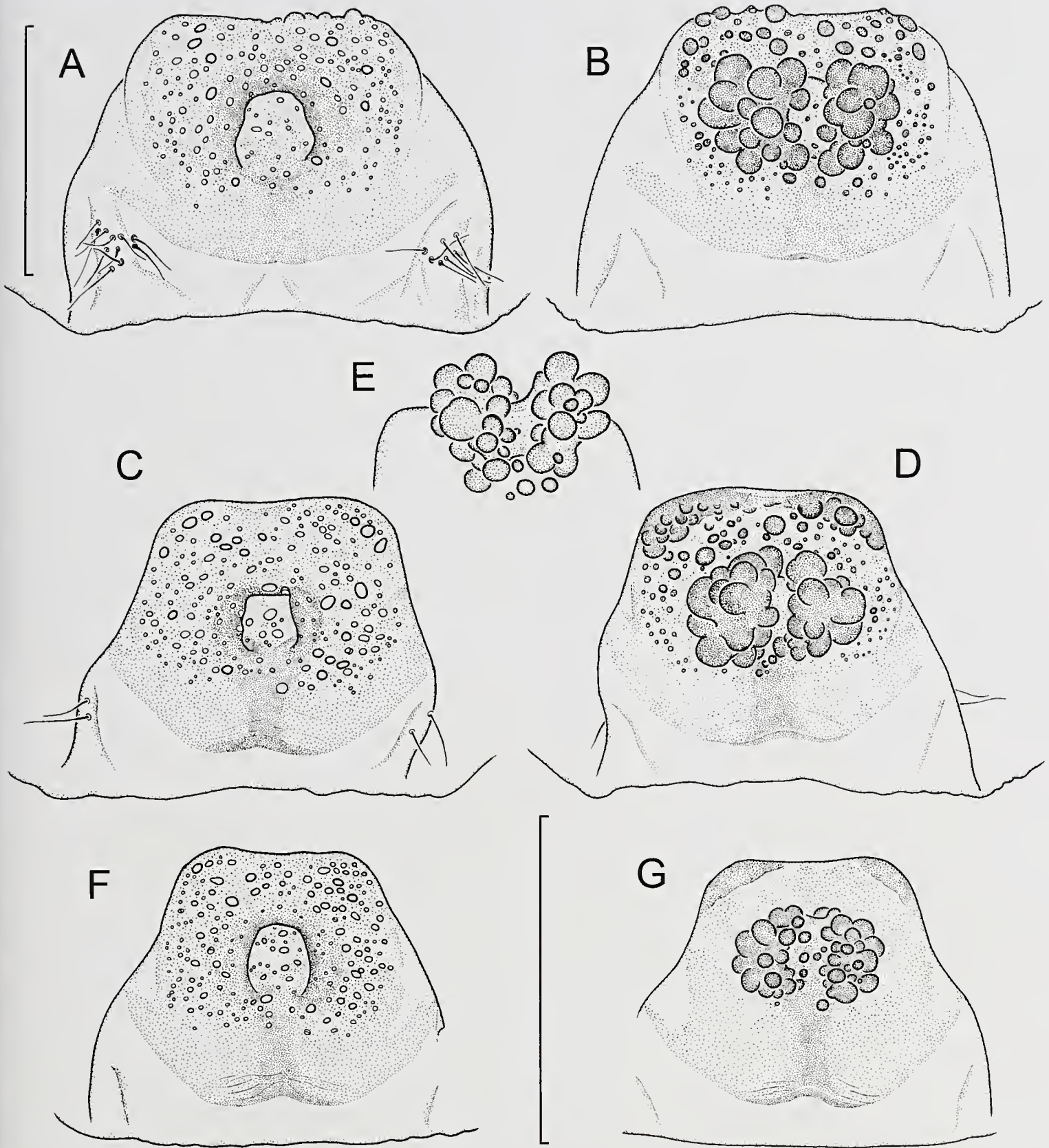


Fig. 12. *Liphistius tioman*, vulval plate of three females from the type locality: specimen moulted 17.XII.2001 (A-B); exuvia, moult 7.VI.2003 (C-E); exuvia, moult 16.II.2002 (F-G). (A, C, F) Entire structure, dorsal view. (B, D, G) Same, ventral view (vesicles in G omitted). (E) Receptacular cluster, ventral and slightly posterior view. Scale lines: 1.0 mm (A-B; C-G).

***Liphistius panching* Platnick & Sedgwick, 1984**

Figs 10B, 13

*Liphistius panching* Platnick & Sedgwick, 1984: 27-28, figs 77-78 (description of female). – Sedgwick & Platnick (1986: 205-206, figs 1-8; description of male).

**Type:** AMHN; female holotype (not examined); Malaysia, Pahang, Gua Panching [= Gua Charas; see paragraph "Distribution"], 24 km N of Kuantan; 31.VII.1982; leg. W.C. Sedgwick.

**Material examined:** MHNG, sample MAL-04/07; 3 females (moulted 30.X.2004, 26.III., 7.IX.2005,

19.II.2006; 8.XII.2004, 30.XII.2005); Pahang, about 1 km north of Kampung Panching, Gua Charas, 3°54'41"N, 103°08'50"E, 120 m; 1.-2.VI.2004; leg. P.J. Schwendinger. – MHNG, sample SIM-01/11; 6 females (moulted 7.VII.2001, XII.2002; 8.VII.2001; 27.II., 16.X.2002), 4 juveniles; same locality; 7./8. VII.2001; leg. P.J. Schwendinger.

**Diagnosis:** Male (see Sedgwick & Platnick, 1986: figs 1-8 and Fig. 10B) distinguished by retrolateral apophysis of palpal tibia in ventral view very wide at base, only little set back from anterior margin of article (Sedgwick & Platnick, 1986: fig. 3); distal margin of

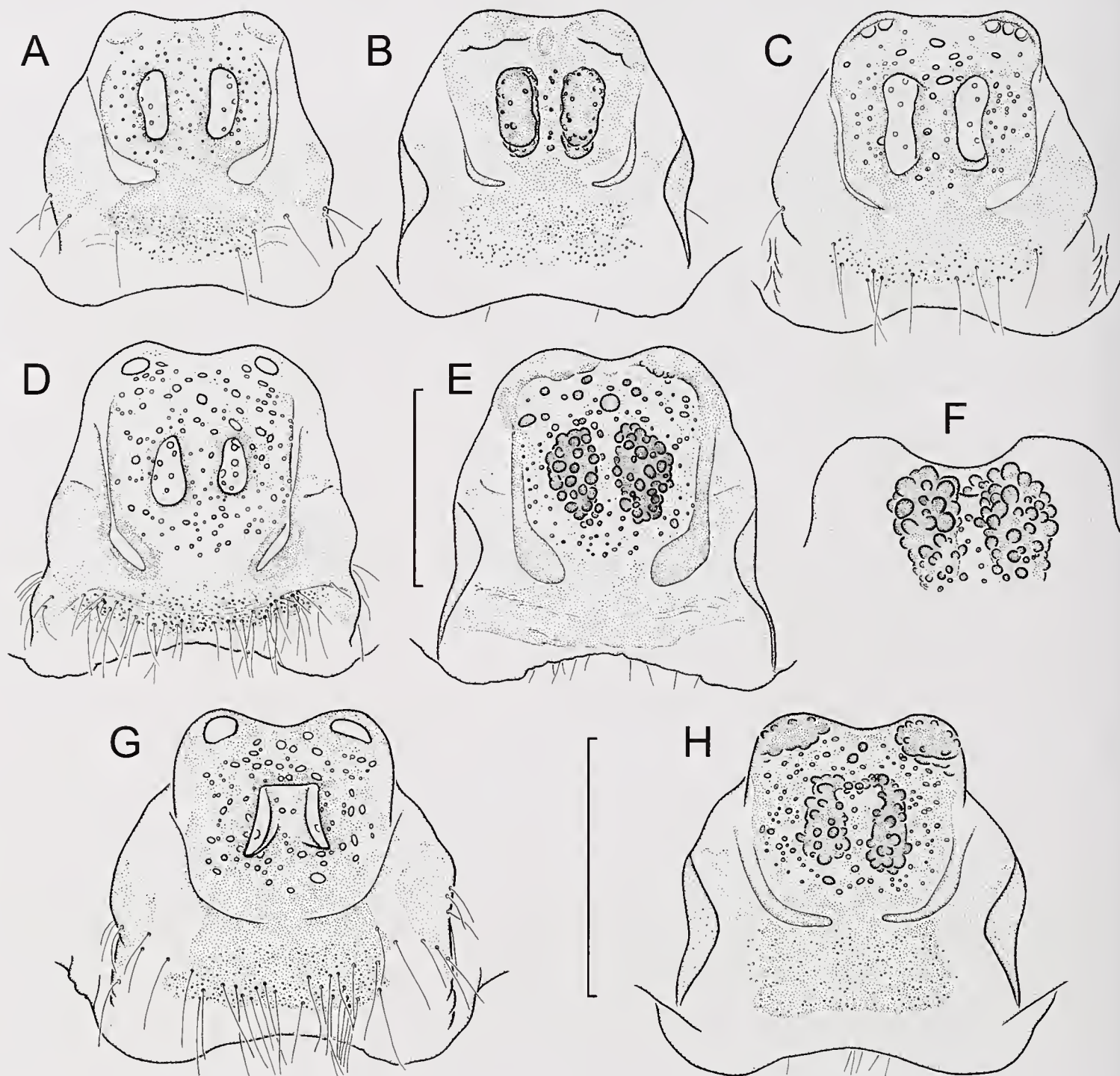


Fig. 13. *Liphistius panching*, vulval plate of four female specimens from the type locality: specimen moulted 16.X.2002 (A-B), moulted VIII.2005 (C), built egg case 16.VII.2001 (D-F), moulted 30.XII.2005 (G-H). (A, C-D, G) Entire structure, dorsal view. (B, E, H) Same, ventral view. (F) Receptacular cluster, ventral and slightly posterior view. Scale lines 1.0 mm: (A-C, F-H; D-E).

cymbium with indistinct lobes (Sedgwick & Platnick, 1986: fig. 4); paracymbium quite shallow, without retrolateral-proximal heel; cumulus indistinct, with moderately long bristles (Sedgwick & Platnick, 1986: figs 1-5); tegulum with many teeth on proximal edge (Sedgwick & Platnick, 1986: figs 1-2); contrategulum with short, very widely arched ventral process pointing proventrad and with pointed dorsal apex (Fig. 10B; Sedgwick & Platnick, 1986: fig. 5); para-embolic plate short (Sedgwick & Platnick, 1986: figs 1-4); embolus proper apically wide (Sedgwick & Platnick, 1986: fig. 3; Fig. 10B), dorsal wall of sclerotized part apparently long and sharply bent prodorsad (Sedgwick & Platnick, 1986: fig. 5). Females (see Platnick & Sedgwick, 1984: figs 77-78 and Fig. 13) distinguished by vulva with few to many lateral and median hairs in genital atrium; posterior stalk wide, quadrangular to trapezium-shaped; poreplate anteriorly wider than posteriorly, with a more or less distinctly invaginated anterior margin and with bulging lateral and posterolateral margins on ventral side; two central dorsal openings (CDO) separated by a wide longitudinal bridge (Fig. 13A, C-D, G); two longitudinal receptacular clusters more or less completely separated from each other by a longitudinal trench (Fig. 13B, E-F, H).

**Remarks:** According to information from Lorenzo Prendini, the current curator of the arachnid collections at the AMNH, the normally developed male of *L. panching* (deposited together with a malformed male) cannot be found at the moment. To my knowledge, this is the only useful male specimen of *L. panching* in any public scientific collection, and a re-examination of details of the palpal organ of this species was therefore not possible. For an easy comparison with other species, the distal aspect of the palpal organ was re-drawn from Sedgwick & Platnick (1986: fig. 5) and is shown in Fig. 10B.

Unlike in any other *Liphistius* species examined, the vulval plates on the exuviae of *L. panching* females (much more than other sclerotised parts of the exuviae) have become partially depigmented; some have almost completely lost their pigmentation. This is probably due to alcohol preservation. In undissected females the vulval plates have retained their original pigmentation.

**Variation:** Sedgwick & Platnick (1986: 205) give the carapace length 9.8 and the carapace width 8.4 for the normally developed male, but no measurements for the teratological male with an incompletely developed palp. Carapace lengths in females with fully developed copulatory organs (n=8) 7.62-8.71, carapace widths 6.63-8.12.

Variation in the shape of the vulval plates examined is shown in Fig. 13. In one female the two receptacular clusters and the two central dorsal openings (CDO) are anteriorly connected with each other (Fig. 13G-H). The larger (older) a female is, the more hair it has in its genital atrium (Fig. 13D cf. Fig. 13A).

**Distribution:** The type locality is given as "Gua Panching [= Panching Cave], a cave 24 km north of Kuantan". This is identical with Gua Charas (Fig. 1, locality 11) in Bukit Charas (= Charas Hill) near Kampung Panching (= Panching Village), which is actually a bit over 20 km northwest of Kuantan. This should not be confused with Bukit Panching, which did not have any caves, was situated about 1.5 km southwest of Bukit Charas and has been completely removed by quarrying in the 1990s. Today only a water-filled depression shows where the hill once stood (Liz Price, personal communication).

**Biology:** All spiders examined were collected from sloping loamy soil in the oligophic zone at the entrance area of the Charas Cave. In captivity one female built an egg case (2.7 cm long, 2.8 m wide and 1.4 cm high) in late July 2001. The eggs (more than 21) were found partially rotten when the egg case was opened.

#### *Liphistius negara* sp. nov.

Fig. 14

**Types:** MHNG, sample MAL-04/14; male holotype (matured 9.VII.2006), 1 male paratype (matured end of July 2005), female allotype, 2 juv. males; Malaysia, Pahang, Taman Negara, trail from Nusa Camp to Abai Waterfall, 4°23'49"N, 102°25'50"E, 110 m; 16.-17. VI.2004; leg. P.J. Schwendinger.

**Etymology:** The species epithet, a name in apposition, is taken from the Malay name of the type locality: taman (= park), negara (= national).

**Diagnosis:** Large, uniformly dark-coloured species in both sexes. Similar to *L. panching*, distinguished by slightly larger size (carapace length of males 10.28-11.30, width 8.70-10.04 versus 9.8 and 8.4, respectively, in male of *L. panching*, see Sedgwick & Platnick (1986: 205). Males with tibial apophysis in ventral view narrower at base, more distinctly set back from anterior margin of tibia (Fig. 14A cf. Sedgwick & Platnick, 1986: fig. 3); paracymbium deeper (Fig. 14B cf. Sedgwick & Platnick, 1986: fig. 2); ventral process of contrategulum narrower and more pointed (Fig. 14C-D cf. Fig. 10B and Sedgwick & Platnick, 1986: fig. 5); distal edge of contrategulum with a large triangular tooth, dorsal apex rounded instead of pointed (Fig. 14C-D cf. Fig. 10B and Sedgwick & Platnick, 1986: fig. 5). Female distinguished from those of *L. panching* by vulval plate wider than long; poreplate anteriorly distinctly narrower than posteriorly instead of anteriorly wider than posteriorly (Fig. 14I-J cf. Fig. 13 and Platnick & Sedgwick, 1984: figs 77-78).

**Description of male (holotype):** Colour in alcohol (much darker in life): Most sclerotised parts uniformly chestnut-brown, on ventral side slightly lighter than on

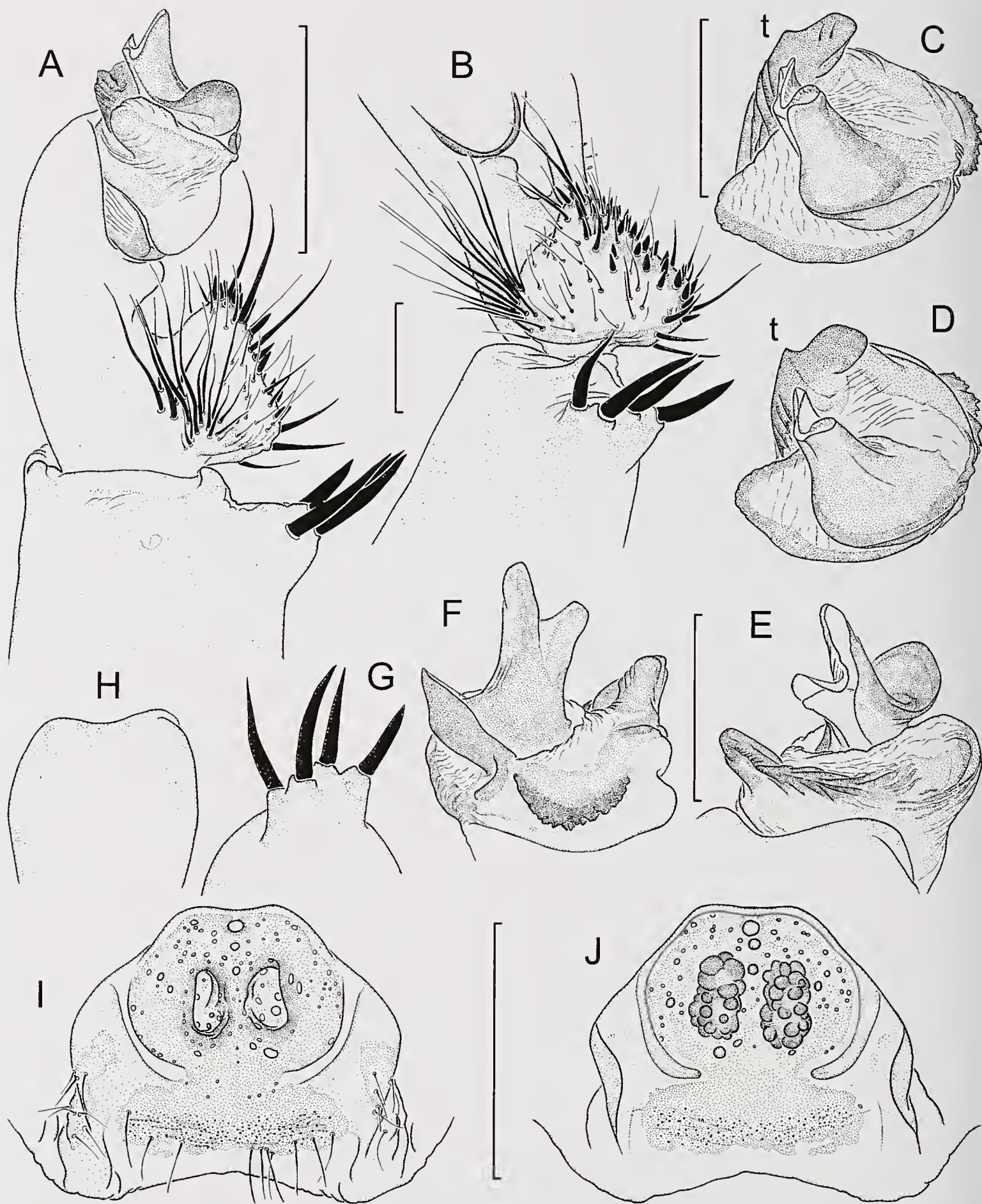


Fig. 14. *Liphistius negara* sp. nov., details of left palp of male holotype (A-C, E-H) and of male paratype (D); vulval plate of female allotype (I-J). (A) Distal part of palp, ventral view. (B) Distal part of tibia and base of tarsus, retroventral view. (C-D) Palpal organ, distal view (dorsal side up). (E) Same, proventral view. (F) Same, retrodorsal view. (G) Tibial apophysis, retrolateral and slightly proximal view. (H) Distal part of cymbium, prolateral view. (I) Vulval plate, dorsal view. (J) Same, ventral view. Abbreviation: t - tooth on distal edge of contrategulum. Scale lines: 1.0 mm (A; B, G-H; C-D; E-F; I-J).

dorsal side; carapace reddish chestnut-brown; proximal portion of chelicerae cream-coloured; membranes of opisthosoma greyish cream, other membranes white.

**Bristles on carapace:** Stiff bristles along all margins (longest anteriorly); many weaker and shorter ones on coxal elevations and behind fovea, fewer of them on both sides of eye mound and in a W-shaped arrangement behind it.

**Cheliceral teeth:** Eleven and twelve small ones on promargin of cheliceral groove on right and left chelicera, respectively.

**Scopula:** Tarsus I with thin scopula confined to distal third of ventral side, divided for its entire length by narrow pale, glabrous longitudinal median stripe and by some bristles; tarsus II with thin scopula in distal half, only distally divided by median stripe; tarsi III-IV with dense scopula covering distal four-fifths, only distally divided by median stripe.

**Claws:** Paired tarsal claws on anterior legs with 4-5 denticles, on posterior legs with 4-6 denticles; unpaired claws in most cases carrying a single denticle.

**Palp:** Tibial apophysis slightly set back from distal margin of tibia (Fig. 14A), carrying four medium-sized pointed megaspines (Fig. 14B, G). Both apical lobes of cymbium indistinct and equally rounded (Fig. 14E, H). Paracymbium basally deep (Fig. 14B), its cumulus indistinctly elevated, carrying moderately long stiff bristles (Fig. 14A-B). Subtegulum without apophysis. Tegulum short and wide, coarsely dentate along entire proximal margin (Fig. 14F). Contrategulum with distinct conical ventral process, its rounded apex directed proventrad (Fig. 14C); distal edge with several oblique ribs and with a large triangular tooth prodorsally, ending in spatulate asymmetrical dorsal apex (Fig. 14C). Parambolic plate short (Fig. 14A, E-F); retrolateral side of sclerotised part of embolus proper without longitudinal keels or ribs and not carrying denticles, dorsal wall much wider than ventral wall and sharply bent prodorsad, thus opening of spermophor forming an L (Fig. 14A, C, E); membranous part of embolus proper distally wider than proximally, with only slightly pigmented proximal portion (Fig. 14E).

**Measurements:** Total length 27.94; carapace 11.30 long, 10.04 wide; opisthosoma 11.55 long, 9.04 wide; eye mound 1.51 long, 1.61 wide, AME well-developed; palpal coxae 3.68 long, 2.26 wide; labium 1.00 long, 2.01 wide; sternum 5.35 long, 3.01 wide (1.34 on ventral surface); palp 18.76 long (5.69 + 3.18 + 6.44 + 3.45); leg I 32.80 long (9.20 + 4.69 + 7.20 + 8.28 + 3.43); leg II 35.06 long (9.45 + 4.69 + 7.70 + 9.54 + 3.68); leg III 38.66 long (9.45 + 4.69 + 8.20 + 12.05 + 4.27); leg IV 47.53 long (11.55 + 4.85 + 9.79 + 15.48 + 5.86).

**Description of female (allotype):** Colour in alcohol (much darker in life) as in male. Carapace with stiff bristles as in male, plus a pair of bristles anterior of fovea. Eleven strong teeth on promargin of cheliceral

groove on both sides. Paired tarsal claws on anterior legs with three denticles, on posterior claws with 3-4 denticles; unpaired claws in most cases with a single denticle (claws worn on all limbs). Tarsi without scopula.

**Vulva** (Fig. 14I-J): Posterior margin of genital sternite slightly and widely invaginated. Vulval plate distinctly sclerotised and pigmented, wider than long. Genital atrium with several lateral and median hairs. Posterior stalk wide, with micropores, fused with poreplate. Poreplate entirely and distinctly pigmented, its anterior margin indistinctly invaginated and clearly narrower than posterior margin. Two central dorsal openings (CDO) separated by a longitudinal bridge; two longitudinal receptacular clusters on ventral side completely separated from each other.

**Measurements:** Total length 22.00; carapace 9.62 long, 8.28 wide; opisthosoma 10.29 long, 8.62 wide; eye mound 1.22 long, 1.42 wide; palpal coxae 3.18 long, 2.01 wide; labium 1.17 long, 2.18 wide; sternum 4.35 long, 2.59 wide (1.59 on ventral surface); palp 16.23 long (5.35 + 3.01 + 4.02 + 3.85); leg I 19.76 long (5.86 + 3.60 + 4.27 + 4.02 + 2.01); leg II 20.57 long (6.02 + 3.68 + 4.35 + 4.43 + 2.09); leg III 22.25 long (6.19 + 3.68 + 4.52 + 5.35 + 2.51); leg IV 30.37 long (8.03 + 3.85 + 6.11 + 8.70 + 3.68).

**Variation:** Carapace lengths in males (n=2) 10.28-11.30, widths 8.70-10.04. The male paratype has the same reduced scopula on anterior legs (especially on tarsus I) as the holotype. Variation in the shape of the palpal organ, see Fig. 14C-D.

**Distribution:** Known only from the type locality in central peninsular Malaysia (Fig. 1, locality 12).

**Biology:** The types were collected from sloping soil and from decaying wood in a rain forest. The largest burrow (of juvenile male, not yet penultimate) had a 2.6 cm long ad 4.1 cm wide trapdoor. The trapdoors of old females thus must be of similar size as those of *L. malayanus* and *L. endau*. The female allotype of *L. negara* sp. nov. appears to be mature (judging from the degree of sclerotisation of its vulval plate), but not yet fully grown. Most burrow entrances had eight signal lines, one had nine. Both males became mature in July, after one and two years of captivity, respectively.

The male paratype has a pronounced pathological outgrowth on the right cheliceral fang, and bite marks of parasitic *Ljungia bristowi* mites on its carapace (many) and opisthosomal tergites (few), but not elsewhere.

### The linang-group

**Diagnosis:** Small to medium-sized spiders (carapace length of males 4.50-6.83, carapace width 3.98-6.21) with a colour pattern on carapace, limbs and opisthosomal tergites (Fig. 2B). Distinguished from the *malayanus*-

**Key to the species of the *linang*-group:**

- 1 Males without scopula on tarsus IV; long bristle retroventrally at base of tibial apophysis thin (Fig. 15A, G-I); paracymbium quite long (Fig. 15A); distal edge of contrategulum with wide gap behind distinctly bent dorsal apex (Fig. 15B). Poreplate with anterior margin distinctly invaginated (Fig. 16A-E); CDO a transverse slit or triangle without enlarged pores lateral to it (Fig. 16A, C-D); receptacular cluster indistinctly divided into lateral halves, its vesicles quite short (Fig. 16B, E) ..... *L. linang* sp. nov. (in Malaysia)
- Males with scopula on tarsus IV; long bristle retroventrally at base of tibial apophysis thick, spine-like (Fig. 17A, I-K); paracymbium short (Fig. 17A); distal edge of contrategulum without gap behind only slightly or not bent dorsal apex (Fig. 17B, G-H). Poreplate with anterior margin only indistinctly invaginated (Fig. 18); CDO a longitudinal slit or semicircular hole with an enlarged pore on each lateral side (Fig. 18A, C, E, G); receptacular cluster not divided into lateral halves, its vesicles quite long (Fig. 18B, D, F, H).... *L. indra* sp. nov. (in Thailand)

group and the *tioman*-group by males possessing a large para-embolic plate with a coarsely serrate distal margin (Figs 15A-D, 17A-D), a narrow and pointed dorsal apex of the contrategulum (Figs 15E-F, 17G-H), and a retrolateral tibial apophysis deeply divided into a long, deep retroventral part and a very short, small retrodorsal part (Figs 15G-I, 17I-K) (tibial apophysis also deeply divided in *L. tioman* but in that species both parts equally long; Fig. 11A, G-I); three megaspines on retroventral part short and bent, single megaspine on retrodorsal part short, curved and weaker than other megaspines (Figs 15A, G-I; 17A, I-K). Females distinguished by a peculiar vulval plate with an only partially sclerotised poreplate widely separated from small remnant of posterior stalk situated at posterior margin of vulva (Figs 16A-E, 18); CDO small, in many cases slit-like (Figs 16A, C-D; 18A, C, E, G).

**Species included:** *Liphistius linang* sp. nov., *L. indra* sp. nov.

**Relationships:** The *linang*-group is morphologically intermediate between the *tioman*-group and the *batuensis*-group. Sharing with *L. tioman* a deeply divided tibial apophysis with the retrodorsal-apical megaspine distinctly separated from the other three megaspines, and sharing with this and other species in the *tioman*-group a distinctly elevated para-embolic plate. Females of the *linang*-group show strong resemblance with those of the *batuensis*-group by possessing an only partially sclerotised poreplate. However, females of *L. linang* sp. nov. have a divided receptacular cluster, as do females of all *tioman*-group species. The relationships of the *linang*-group are therefore not clear.

**Distribution:** Northeastern peninsular Malaysia and southern Thailand (Fig. 1, localities 13-14).

***Liphistius linang* sp. nov.**

Figs 15-16

**Types:** MHNG; male holotype (matured end XII.2001), 4 male paratypes (matured 14.IX., 1.X.1999, early XI.2000, end XII.2001) and 4 female paratypes

(including allotype, moulted 12.II.2002); Malaysia, Kelantan, about 15 km E of Machang, Jeram Linang Waterfall, 5°44'34"N, 102°22'29"E, 50 m; 12.I.1999; leg. P.J. Schwendinger.

**Etymology:** Name in apposition, taken from the Malay name of the type locality: jeram (= rapids), linang (tearful, weeping).

**Diagnosis:** Medium-sized, bicoloured species in both sexes. Similar to *L. tioman*, males distinguished by retroventral part of bipartite tibial apophysis carrying longer and bent megaspines; retrodorsal part of tibial apophysis developed as a small tubercle carrying a weaker megaspine (Fig. 15A, G-I cf. Fig. 11A, G-I); tegulum with wide, distinctly dentate proximal edge (Fig. 15D cf. Fig. 11B); contrategulum without (or with very indistinct) ventral process, its distal edge finely dentate instead of ribbed, prodorsally with a wide gap before reaching hook-shaped dorsal apex (Fig. 15B, E-F cf. Fig. 11C, F); para-embolic plate large, distally wide, with coarsely dentate margins (Fig. 15A-F cf. Fig. 11C-E); dorsal wall of sclerotised part of embolus proper not ending in protruding lobe, as wide as ventral wall (Fig. 15B, E-F cf. Fig. 11B-C, F); scopula on tarsi IV absent.

**Description of male (holotype):** *Colour in alcohol* (much darker in life): Carapace mostly light brown; pars cephalica brown except for indistinct grey-brown W-shaped pattern behind eye mound and light brown medial patch between eye mound and fovea; brown area on pars cephalica connected to brown flower-shaped area around fovea; long brown patches along lateral (wide) and posterior (very narrow) margins of pars thoracica and between coxal elevations. Chelicerae with proximal portion cream-coloured, distal portion dark brown. Palps in proximal half of femur and tibia and in distal half of patella light brown, mottled with dark spots, other parts dark brown; cymbium entirely very dark reddish brown. Legs mostly dark brown except for light brown distal half of all patellae and light brown proximal half of all femora (mottled with dark spots); leg tibiae (in contrast to those of palp) to tarsi entirely dark brown. Opisthosoma mostly light brown, mottled

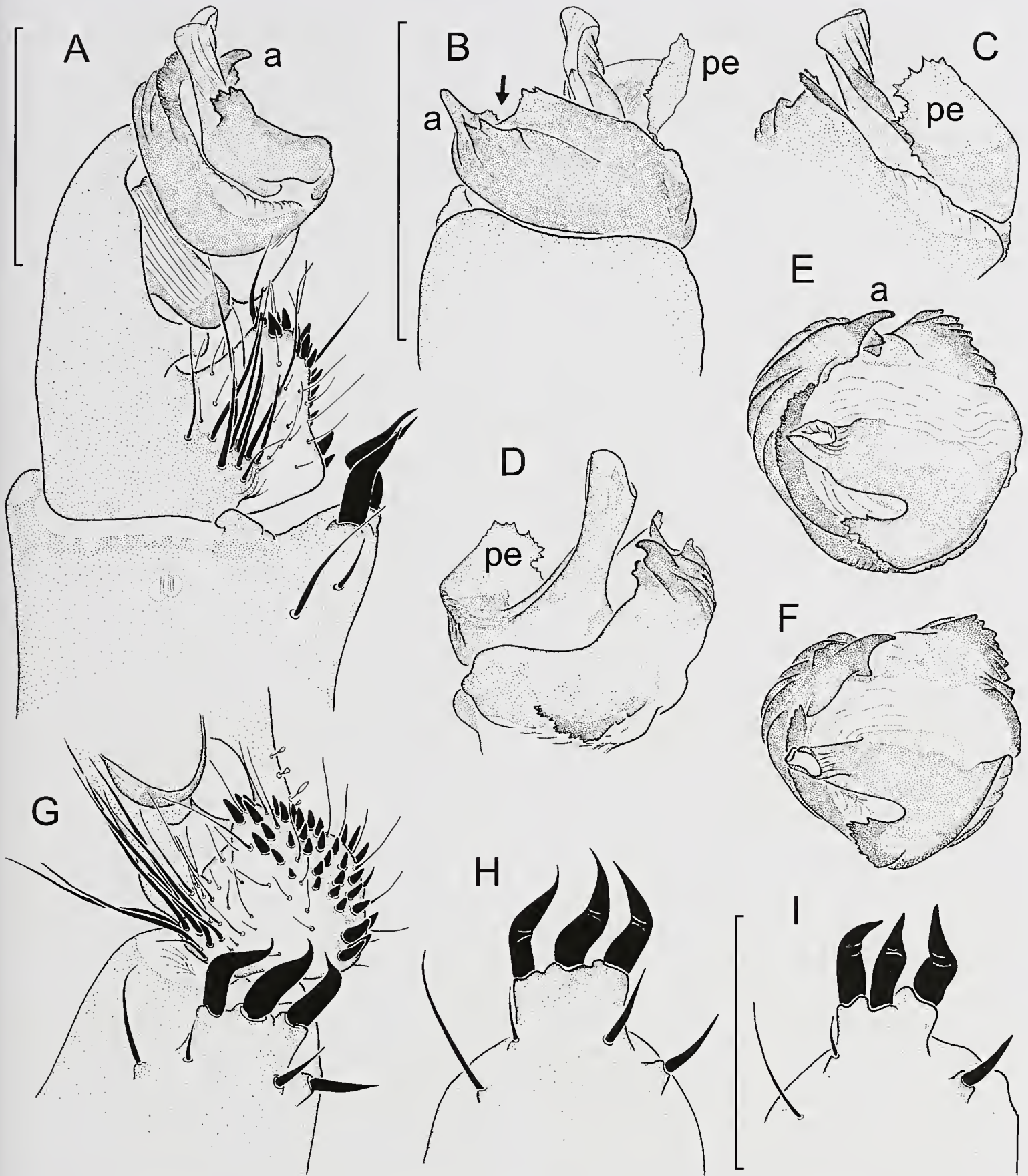


Fig. 15. *Liphistius linang* sp. nov., details of left palp of two males; holotype (A-E, G-H), paratype matured 14.IX.1999 (F, I). (A) Distal part of palp, ventral view. (B) Distal part of cymbium and palpal organ, prolateral view (arrow indicating gap in distal edge of contrategulum). (C) Palpal organ, proventral and slightly proximal view. (D) Same, retrodorsal view. (E-F) Same, distal view (dorsal side up). (G) Paracymbium and tibial apophysis, retrolateral view. (H-I) Tibial apophysis, retrolateral and slightly proximal view. Abbreviations: a - dorsal apex of contrategulum; pe - para-embolic plate. Scale lines: 1.0 mm (A, G; B-F; H-I).

with dark spots laterally; tergites I-II almost entirely dark brown, tergite III light brown with extensive dark lateral and median patches, following tergites with distinct dark lateral spots and increasingly indistinct median spots, last two tergites tiny and entirely dark brown.

*Bristles on carapace:* Few short, weak bristles along all margins except posterior one, on coxal elevations, in front and behind fovea; longer, stronger bristles on, behind and in front of eye mound.

*Cheliceral teeth:* Ten small ones on promargin of cheliceral groove of each chelicera.

*Scopula:* Tarsi I-III with moderately dense scopula in distal two-thirds of ventral side, only distally divided by a short median stripe; tarsus IV entirely without scopula.

*Claws:* Paired tarsal claws on anterior legs with 3-5 denticles, on posterior legs with 4-5 denticles; unpaired claws with one indistinct denticle or without.

*Palp:* Tibial apophysis situated distally, only slightly set back from anterior margin of palp (Fig. 15A), deeply divided: (a) retroventral part long and deep, pointing slightly away from axis of tibia, carrying three medium-sized, bent megaspines; (b) retrodorsal part much smaller and shorter, shaped like a low tubercle, carrying a single bent, relatively weak spine (i.e. a reduced megaspine); long bristle retroventrally below tibial apophysis weak (Fig. 15A, G-H). Distal margin of cymbium with indistinct lobes (Fig. 15B). Paracymbium quite long and moderately deep, with an indistinct retrolateral-proximal heel (Fig. 15A, G); cumulus indistinct, carrying a moderately compact group of long stiff bristles (Fig. 15A, G). Subtegulum without apophysis. Tegulum with wide, distinctly dentate proximal edge (Fig. 15D). Contrategulum without recognizable ventral process; prolateral surface with a few ribs, distal edge sharp in proventral part, finely dentate in prolateral part, with a deep gap in prodorsal part before reaching very narrow, slightly hook-shaped dorsal apex (Fig. 15B, E). Para-embolic plate large, its distal margin wide, strongly dentate and directed proventrad-distad (Fig. 15B-E); embolus proper relatively narrow, inclined prolaterad (Fig. 15A-D), dorsal and ventral walls of sclerotised part equally wide and lying close to each other, retrolateral wall enforced by five weak ridges (Fig. 15E); membranous part of embolus proper narrow, indistinct (Fig. 15B).

*Measurements:* Total length 14.22; carapace 5.83 long, 5.05 wide; opisthosoma 6.86 long, 4.31 wide; eye mound 0.91 long, 1.12 wide; palpal coxae 1.76 long, 1.23 wide; labium 0.49 long, 1.08 wide; sternum 2.55 long, 1.81 wide (1.03 on ventral surface); palp 9.66 long (2.55 + 1.91 + 3.53 + 1.67); leg I 17.64 long (4.80 + 2.30 + 3.82 + 4.61 + 2.11); leg II 18.67 long (4.80 + 2.30 + 4.02 + 5.20 + 2.35); leg III 20.48 long (4.95 + 2.35 + 4.26 + 6.27 + 2.65); leg IV 26.72 long (6.27 + 2.65 + 5.74 + 8.58 + 3.48).

**Description of female (allotype):** *Colour in alcohol* (much darker in life): As in male, except for

carapace with more extensive dark areas, all of them interconnected; W-shaped pattern behind eye mound distinct; metatarsi of legs and palps mostly dark, with a small light zone at base; tibiae with dark proximal and subdistal annulations; light brown femora with indistinct (in comparison to tibiae) dark proximal and subdistal annulations; opisthosomal tergites III-VII with more extensive dark median patches; genital area darker than surrounding parts of genital sternite, with a white, bell-shaped posterior zone (Fig. 16F).

*Bristles on carapace:* Stiff bristles as in male, plus an additional pair just anterior to fovea.

*Cheliceral teeth:* Nine strong teeth on promargin of left cheliceral groove, ten on right side.

*Claws:* Palpal claw with three denticles on right side, none on left side. Paired claws with two denticles on anterior legs, 2-3 denticles on posterior legs; unpaired claws with 1-2 denticles on legs I-III, none on leg IV. All tarsi without scopula.

*Vulva:* Posterior margin of genital sternite invaginated (Fig. 16F). Vulval plate (Fig. 16A-E, illustrations of paratypes) with pigmentation and sclerotisation completely lost in median zone. Posterior stalk reduced to a small isolated, ventrad-bent posterior sclerite at some distance from or on posterior margin of genital sternite; posterior stalk and poreplate widely separated from each other. Genital atrium slightly sunken below level of poreplate, carrying numerous hairs on both sides of remnant of posterior stalk. Poreplate with indistinctly outlined lateral and posterior margins, these not bulging from ventral side of plate; anterior margin distinctly and widely invaginated, forming two more or less pronounced anterolateral lobes. CDO relatively small, wider than long, transversally slit-like or triangular, situated in unpigmented or weakly pigmented area of poreplate (Fig. 16A, C-D, paratypes). Ventral receptacular cluster quite large and racemose, longitudinally divided into two lateral subclusters, its individual vesicles globular, about as long as wide (Fig. 16B, E, paratypes).

*Measurements:* Total length 17.25; carapace 5.93 long, 5.00 wide; opisthosoma 7.89 long, 6.13 wide; eye mound 0.82 long, 1.04 wide; palpal coxae 1.91 long, 1.37 wide; labium 0.64 long, 1.37 wide; sternum 2.65 long, 2.11 wide (1.27 on ventral surface); palp 10.00 long (3.24 + 1.86 + 2.30 + 2.60); leg I 12.40 long (3.77 + 2.16 + 2.50 + 2.50 + 1.47); leg II 12.90 long (3.82 + 2.21 + 2.55 + 2.75 + 1.57); leg III 13.73 long (3.92 + 2.25 + 2.60 + 3.24 + 1.72); leg IV 19.71 long (5.10 + 2.55 + 4.07 + 5.54 + 2.45).

**Remark:** In the female allotype the long spinnerets (anterior and posterior laterals) are bent anteriad, which is an artefact resulting from having been pressed against the wall of the vial in that position for some time.

**Variation:** Carapace lengths in males (n=5) 4.91-6.15, carapace widths 4.19-5.09; in females with well-developed vulval plates (n=4) 5.53-5.90 and 4.29-5.03,



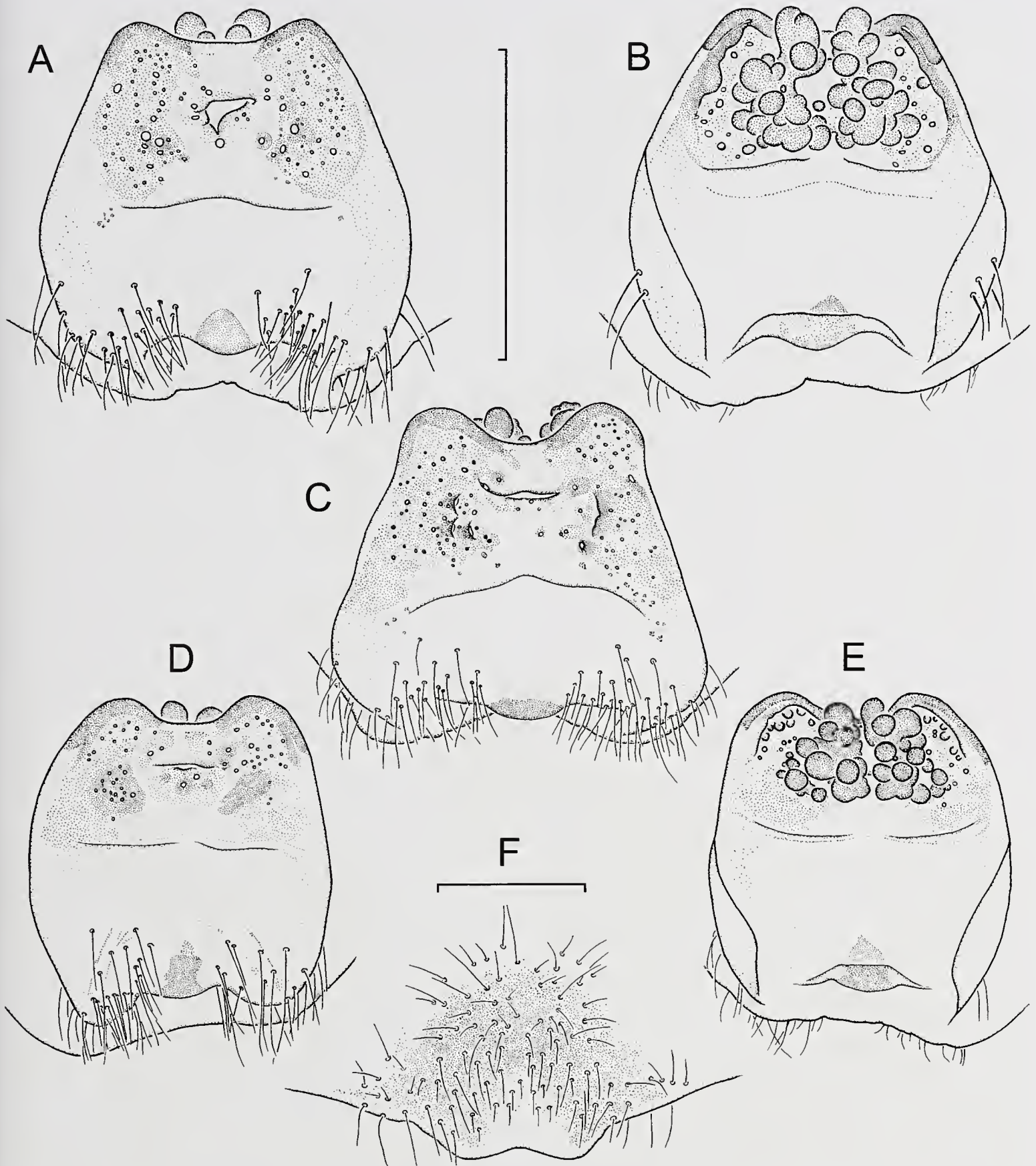


Fig. 16. *Liphistius linang* sp. nov., vulval plate of three female paratypes (A-E): specimen moulted 30.VII.1999 (A-B), moulted 10.III.2000 (C), exuvia, moult 14.IX.1999 (D-E); undissected genital sternite of allotype (F). (A, C-D) Dorsal view. (B, E, F) Ventral view. Scale lines: 1.0 mm (A-E; F).

respectively. All males lack a scopula on tarsus IV. Variation in the shape of the retrolateral tibial apophysis of the male palp is shown in Fig. 15G-I; variation in the shape of the prolateral-distal edge of the contrategulum in Fig. 15E-F; variation in the shape of the vulval plate in Fig. 16A-E.

**Distribution:** Known only from the type locality (Fig. 1, locality 13) in the northeastern corner of peninsular Malaysia. At the same locality, only metres away from burrows of *L. linang* sp. nov., a single female of another, much larger, dark-coloured *Liphistius* species was found. This female (mentioned under

*Liphistius* sp. at the end of the presentation of the *malayanus*-group) appears to be more closely related to *L. endau* than to the geographically closer *L. negara* sp. nov.

**Biology:** Spiders of this species were quite abundant in a lush rain forest along the stream above the Jeram Linang Waterfall. The burrows had a single trapdoor and mostly nine signal lines (up to 4 cm long) spread over soil surface. Trapdoors of penultimate males (n=5) were 1.2-2.0 cm long and 1.8-2.3 cm wide, those of reproductive females (with egg case; n=5) 1.2-1.7 cm and 1.8-2.3 cm, respectively.

Two males matured in mid-September and at the beginning of October of the year when they were collected. The three other males were raised from eggs (hatched in late May); one of them matured in November of the following year, the other two one year later in December. Less than one and a half years from hatching to maturation is exceptionally short for a *Liphistius* male, and this may be due to conditions in captivity in Geneva. Three females built egg cases in captivity between early February and early March, two of them were 1.7-1.9 in diameter, 1.25-1.3 cm high, and contained 40 and 84 light beige-yellow eggs suspended on a thin mesh of fine silk threads. The first generation females in captivity moulted in April, July and September.

***Liphistius indra* sp. nov.**

Figs 2B, 17-18

**Types:** MHNG; male holotype (matured 27.IX.2011), 8 male (matured 24.VIII., 7.IX., 10.IX., 17.IX., 25.IX., 26.X.2011, 30.IX., 4.X.2012) and 13 female paratypes (including allotype which did not moult); Thailand, Pattani Province, about 20 km NW of Yala, Sankalakhierie Mountains, 6°39'09"N, 101°05'55"E, 200 m; 12.VII.2011; leg. P.J. Schwendinger. – MHNG, SMF; 1 male (matured 17.XI.2000) and 5 female paratypes; same locality, 260 m; 22.X.1999; leg. P.J. Schwendinger.

**Etymology:** The species epithet refers to one of the two old names of the type locality: Indragiri (= Indra's mountain) and Bukit Besar (= big mountain) (Skeat, 1953: 21). Indra ("Phra In" in Thai mythology) is the king of the Vedic gods. Name in apposition.

**Diagnosis:** Medium-sized, light brown-coloured species in both sexes. Very similar to *L. linang* sp. nov., distinguished by males with a ventral scopula on tarsus IV; long bristle retroventrally below tibial apophysis much stronger, resembling a megaspine (Fig. 17A, I-K cf. Fig. 15A, G-I); paracymbium distinctly shorter, more globular (Fig. 17A, I cf. Fig. 15A, G); distal edge of contrategulum without dentate gap, ending in a beak-like rather than a hook-like dorsal apex (Fig. 17B, G-H cf. Fig. 15B, E-F). Females distinguished from those of *L. linang* sp. nov. by anterior margin of poreplate

less deeply and less widely invaginated; very weak pigmentation (in contrast to none) in anterior part of genital atrium (corresponding to reduced anterior part of posterior stalk); CDO semicircular or longitudinally slit-like instead of transversally slit-like, flanked by an enlarged pore on each side (Fig. 18A, C, E, G cf. Fig. 16A, C-D); receptacular cluster larger, not divided into two lateral subclusters, its individual vesicles (especially posterior ones) longer (Fig. 18B, D, F, H cf. Fig. 16B, E).

**Description of male (holotype):** *Colour in alcohol* (much darker in life; see Fig. 2B for paratype): Carapace with wide grey-brown margin (broken posteromedially) including most of pars cephalica and connected to flower-shaped patch of same colour around fovea; three very light brown areas between eye mound and fovea (anterior two small, kidney-shaped and in a pair, posterior one larger, inverted lanceolate) and light patches between darker central and marginal areas. Chelicerae with proximal portion cream-coloured, distal portion grey-brown. Palps in proximal half of femur and tibia and in distal half of patella light brown, mottled with dark spots, other parts grey-brown; cymbium entirely reddish brown. Legs mostly grey-brown except for light brown distal half of all patellae and light brown proximal half of all femora (mottled with dark spots); leg tibiae (in contrast to those of palp) to tarsi entirely dark brown. Membranous parts of opisthosoma light brown; tergite I almost entirely grey-brown, tergite II with extensive dark lateral and median patches, following tergites with distinct dark lateral spots and increasingly indistinct median ones, last two tergites tiny and mostly grey-brown.

*Bristles on carapace:* Few short, weak bristles along most of its margins (completely absent posteriorly and largely absent laterally), on coxal elevations and in front of fovea (not behind); longer, stronger bristles on, behind and in front of eye mound.

*Cheliceral teeth:* Eleven small ones on promargin of cheliceral groove of each chelicera.

*Scopula:* Tarsi I-III with moderately dense scopula in distal half of ventral side, only distally divided by a short median stripe; tarsus IV with weak scopula in distal quarter, medially divided for its entire length.

*Claws:* Paired tarsal claws with 3-4 denticles on anterior legs, 2-4 denticles on posterior legs; unpaired claws with 1-2 indistinct denticles on tarsi I-III, none on tarsus IV.

*Palp:* Tibial apophysis situated distally, only slightly set back from anterior margin of tibia (Fig. 17A), deeply divided: (a) long and deep retrolateral part pointing slightly away from axis of tibia, carrying three medium-long and bent megaspines; (b) short and small retrodorsal part carrying a single, slightly curved megaspine (Fig. 17I); long bristle retroventrally below tibial apophysis very strong, almost as thick as megaspines (Fig. 17A, I). Distal margin of cymbium with short lobes (Fig. 17B, showing paratype matured 4.X.2012). Paracymbium



Fig. 17. *Liphistius indra* sp. nov., details of left (A-I) and right (J-K) palp of three males; holotype (A, C-D, G, I), paratype matured 4.X.2012 (B, F, H, K), paratype matured 24.VIII.2011 (E, J). (A) Distal part of palp, ventral view. (B) Distal part of cymbium and palpal organ, prolateral view. (C) Palpal organ, retrodorsal view. (D) Same, proventral and slightly proximal view. (E-F) Tegulum, retrodorsal view. (G-H) Palpal organ, distal view (dorsal side up). (I) Paracymbium and tibial apophysis, retrolateral view. (J-K) Tibial apophysis, retrolateral and slightly proximal view. Scale lines: 1.0 mm (A, I; B-F, H; J-K), 0.5 mm (G).

globular, quite short and shallow, without retrolateral heel (Fig. 17A, D); cumulus indistinct, carrying a group of long stiff bristles (Fig. 17A, D). Subtegulum without apophysis. Tegulum with moderately wide, strongly dentate proximal edge (Fig. 17C). Contrategulum without recognizable ventral process; prolateral surface with a few ribs; distal edge sharp throughout, with an indistinct, very short and wide invagination (not a gap) prodorsally

(Fig. 17B, showing paratype matured 4.X.2012) before reaching very narrow, beak-shaped dorsal apex (Fig. 17G). Para-embolic plate large, its distal margin wide, strongly dentate (Fig. 17A, C, G); embolus proper slightly inclined prolaterad, relatively narrow (Fig. 17A, C-D), dorsal and ventral walls of sclerotised part equally wide and lying close to each other, retrolateral wall with few indistinct longitudinal ridges (Fig. 17G);

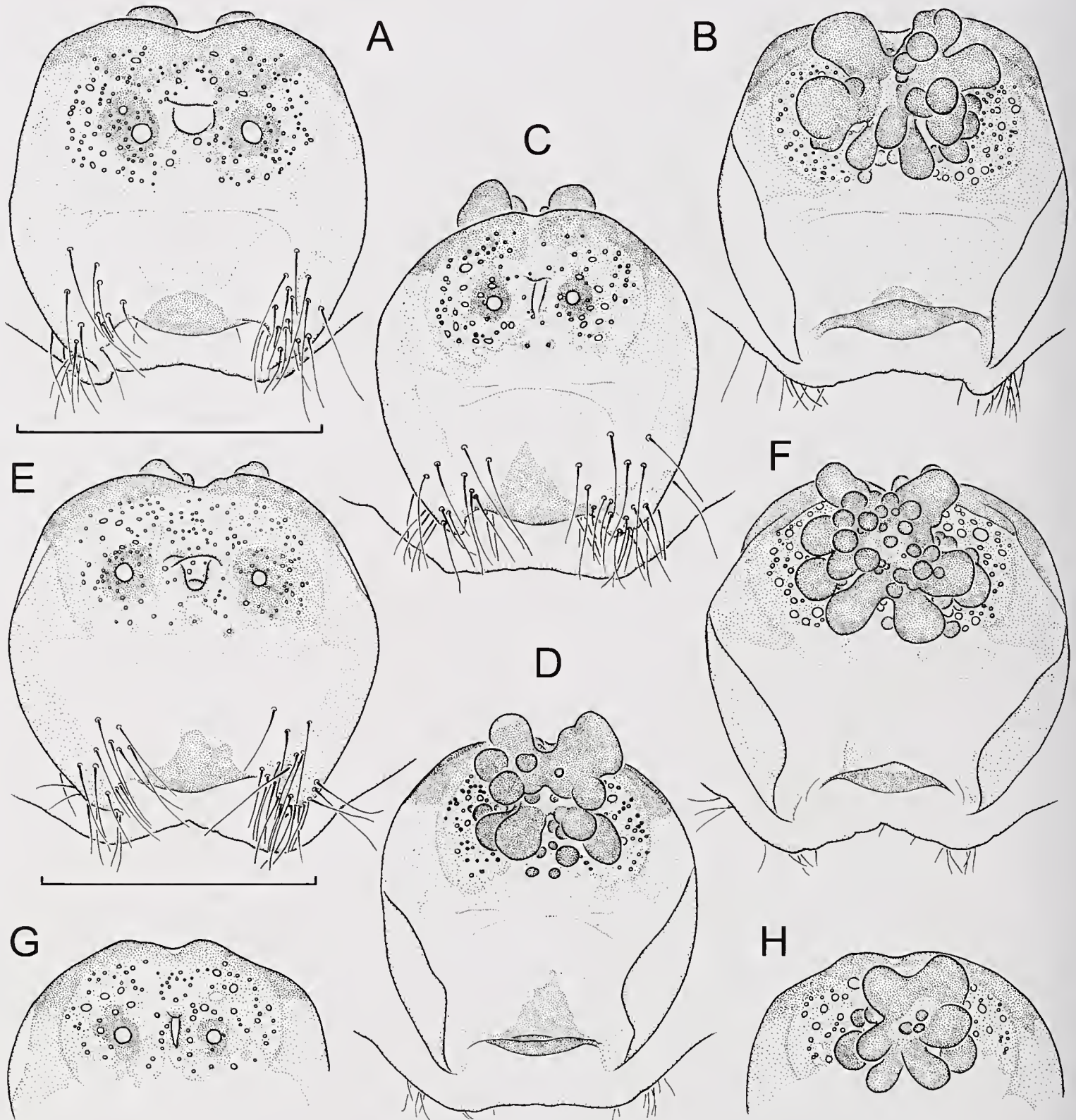


Fig. 18. *Liphistius indra* sp. nov., vulval plate of four female paratypes (all from exuviae): moult 15.III.2012 (A-B), moult 10.II.2001 (C-D), moult 15.VIII.2002 (E-F), moult 3.XI.2001 (G-H). (A, C, E) Entire structure, dorsal view. (B, D, F) Same, ventral view. (G) Anterior part of vulval plate, ventral view. (H) Receptacular cluster, ventral view. Scale lines: 1.0 mm (A-D, G-H; E-F).

membranous part of embolus proper narrow, indistinct (Fig. 17B, showing paratype matured 4.X.2012).

**Measurements:** Total length 11.57; carapace 5.08 long, 4.49 wide; opisthosoma 4.25 long, 2.91 wide; eye mound 0.80 long, 0.97 wide; palpal coxae 1.61 long, 1.10 wide; labium 0.43 long, 0.98 wide; sternum 2.24 long, 1.57 wide (0.87 on ventral surface); palp 9.10 long (2.72 + 1.65 + 3.31 + 1.42); leg I 15.36 long (4.13 + 1.97 + 3.31 + 3.98 + 1.97); leg II 15.83 long (4.17 + 2.01 + 3.31 + 4.33 + 2.01); leg III 17.32 long (4.41 + 2.05 + 3.46 + 5.04 + 2.36); leg IV 22.91 long (5.67 + 2.20 + 4.88 + 7.01 + 3.15).

**Description of female (allotype):** *Colour in alcohol* (much darker in life): Generally darker reddish-brown than male; light areas on carapace mottled with dark brown spots, flower-shaped area around fovea less clearly outlined; tarsi and metatarsi of legs and palps mostly dark, with a small light zone at base of palpal tarsi and leg metatarsi; all tibiae with dark proximal and subdistal annulations; femora with indistinct (in comparison to tibiae) and broken proximal and subdistal annulations; opisthosomal tergites II-V with larger dark median patches; genital area darker than surrounding parts of genital sternite, with a light posterior margin.

**Bristles on carapace:** As in male, plus several tiny bristles behind fovea.

**Cheliceral teeth:** Eleven mostly strong cheliceral teeth on promargin of left cheliceral groove, nine on right.

**Claws:** Palpal claws with two denticles. Paired claws with 2-3 denticles on anterior legs, 2-4 denticles on posterior legs; unpaired claws with two denticles on tarsi I-III, none on tarsus IV. All tarsi without scopula.

**Vulva:** Posterior margin of genital sternite slightly and widely invaginated. Vulval plate (Fig. 18, illustrations of paratypes) with pigmentation much reduced but still discernible in median zone. Posterior stalk reduced to a very weakly pigmented, wide to narrow anterior part and a small, strongly pigmented, ventrad-bent posterior sclerite at some distance from posterior margin of genital sternite. Genital atrium with numerous hairs on both sides of remnant of posterior stalk. Lateral and posterior margins of poreplate indistinctly outlined, not bulging from ventral side; anterior margin only slightly invaginated at midpoint, not forming anterolateral lobes. CDO relatively small, longitudinally slit-like or semicircular, lying in weakly pigmented area of poreplate (Fig. 18A, C, E, G, showing paratypes). Ventral receptacular cluster quite large and racemose, not divided into two lateral subclusters, its individual vesicles mostly digitiform, longer than wide (Fig. 18B, D, F, H, showing paratypes).

**Measurements:** Total length 19.45; carapace 6.61 long, 5.67 wide; opisthosoma 8.27 long, 6.69 wide; eye mound 0.95 long, 1.01 wide; palpal coxae 2.20 long, 1.54 wide; labium 0.75 long, 1.73 wide; sternum 3.15 long, 2.20 wide (1.26 on ventral surface); palp 11.61 long (3.78 + 2.20 + 2.83 + 2.80); leg I 14.25 long (4.49 + 2.48 + 2.95

+ 2.87 + 1.46); leg II 14.68 long (4.49 + 2.56 + 2.95 + 3.11 + 1.57); leg III 15.43 long (4.57 + 2.56 + 2.99 + 3.58 + 1.73); leg IV 22.44 long (6.30 + 2.91 + 4.57 + 6.14 + 2.52).

**Variation:** Carapace lengths in males (n=10) 4.50-6.83, carapace widths 3.98-6.21; in females with well-developed vulval plates (n=18) 5.55-7.24 and 4.80-6.30, respectively. All ten males possess a weak ventral scopula on tarsus IV; it is medially divided in three of them (including the holotype), undivided in the others. Three males have more or less distinct remnants of “tibial spurs” (*sensu* Platnick & Goloboff, 1985) on legs I-III. A male lacks one of its AME; in all other specimens examined both AME are well-developed. Variation in details of the male palp, see Fig. 17G-H, I-K; variation in the morphology of the vulval plate, see Fig. 18. One of the larger females examined has a small knob-like sclerite in the membranous dorsal wall of its vulva which fits into the CDO of the ventral wall (= vulval plate). Such a structure was also observed in some (but only few) vulvae of large females of other species. This is an unlikely (because inefficient) plugging device and more probably a by-product of increased sclerotisation of the vulval plate in old females.

**Distribution:** Known only from the type locality (Fig. 1, locality 14) in the deep south of Thailand. This area lies in the former Sultanate of Pattani which was an independent Malay kingdom until 1785, then became a tributary of the kingdom of Siam, and in 1909 formally a Siamese province. A second species, *Liphistius* cf. *thaleban* Schwendinger, 1990, occurs at the same locality. That species is much larger, has orange-coloured femora in larger juveniles and adult females, and belongs to the *trang*-group.

**Biology:** The spiders examined were collected in an evergreen rain forest, close to a stream. Their burrows had a single trapdoor, usually opening downwards, and 8-10 (mostly nine) relatively short signal lines (up to 4 cm long) spread over soil surface. Trapdoors of penultimate males (n=8) were 1.25-1.8 cm long and 1.65-2.3 cm wide, those of females (n=17) up to 2.1 cm long and 3.0 cm wide.

Males matured in captivity between August and November, most (six out of ten) in September. Adult females in captivity usually moulted twice per year, in January to April and in June to November. As all females were collected in July and October (outside the breeding season), no egg cases were observed.

Upon being provoked, one mature male and one large female displayed “tiptoeing” but without the pumping movements (raising and lowering the body above the surface) usually observed in large *Liphistius* spiders.

Two females carried mites of the genus *Ljunghia* (see Halliday & Juvara-Bals, 2016: 857) which left clearly visible dark bite marks on the carapace and on the light

proximal portion of the chelicerae, but not on other parts of the body. The mites were seen to aggregate in the fovea, around the sternum, under the spinnerets and on the ventral side of the leg femora of the spiders. One mite was seen inserting its gnathosoma into one of the bite marks on the carapace, obviously taking in food.

Two immature males (with swollen palpal tarsi and thus possibly penultimate; not paratypes) had a swollen, light-coloured (like porcelain) opisthosoma when collected and died soon afterwards. This indicates an infection with Rickettsiales (see Haupt, 2003: 66-67, fig. 41D). Haupt (2003: 67, figs 24A, 25A) reported rickettsia-like microorganisms in the spermophore of the mesothelid *Ryuthela nishihirai* (Haupt, 1979) and assumed that infection can occur through copulation. This was certainly not the case in the two immature males of *L. indra* sp. nov.

At the type locality, *L. indra* sp. nov. occurs together with *Liphistius* cf. *thaleban*. Burrows of both species were found side by side.

#### The *batuensis*-group

**Diagnosis:** Small to medium-sized spiders (carapace length of males 4.42-6.46, carapace width 4.02-5.87). Distinguished from species of other groups by males with a strongly reduced proximal edge on the tegulum (Figs 19H, 21B, 23I) and with an elongated prodorsal-apical lobe on the cymbium (Figs 19C, 21H, 23J). Females similar to those of the *linang*-group in possessing a vulval plate with reduced pigmentation and sclerotisation, distinguished by a relatively wider vulval plate with the poreplate only partially connected to the

large and wide posterior stalk or separated by a short distance (Figs 20, 22, 24).

**Species included:** *Liphistius batuensis*, *L. tempurung* and *L. priceae* sp. nov.

**Relationships:** The reduced pigmentation and sclerotisation of the vulval plate and the reduced posterior edge of the tegulum point to a close relationship with the *linang*-group, but a loss or reduction is only a weak indication for common ancestry. At present the relationships of the *batuensis*-group with other groups are unclear, but there is strong morphological evidence for close relationship among the species of the *batuensis*-group. Moreover, all three species have a strong association with caves (much more so than in species of the *tioman*-group).

**Distribution:** Western and central part of peninsular Malaysia (Fig. 1, localities 15-18). All species are known exclusively from limestone caves.

#### *Liphistius batuensis* Abraham, 1923

Figs 19-20

*Liphistius batuensis* Abraham, 1923a: 15-21, pl. 1, figs 1-9 (description of male and female). Synonymy and taxonomic literature, see World Spider Catalog (2017).

**Types:** BMNH; male lectotype (designated by Haupt, 1983: 282) and 11 female plus 4 juvenile paralectotypes (all not examined); Malaysia, Selangor, Batu Caves; XII.1921-I.1922; leg. H.C. Abraham.

**Material examined:** MHNG; 1 male; Selangor, Kuala Lumpur, Batu Caves; 24.VII.1969; leg. R. Pilet. – MHNG; 2 females; Batu Caves, près de Kuala Lumpur;

#### Key to the species of the *batuensis*-group:

- 1 Tibial apophysis of male palp carrying long megaspines (Fig. 19A); distal edge of contrategulum with quite long parallel ridges pointing towards dorsal apex (Fig. 19D-E, I); para-embolic plate medium-long (19E-I); dorsal wall of sclerotised part of embolus proper wider than ventral wall, its end sharply bent proventrad (Fig. 19D-F, I). Poreplate with very wide CDO (Fig. 20A, C-D, F-G) ..... *L. batuensis*
- Tibial apophysis with medium-long or short megaspines (Figs 21E-G; 23B, K-O); para-embolic plate short (Figs 21A-B; 23A, H-I); distal edge of contrategulum with quite short parallel ridges pointing towards embolus (Fig. 21C, I-L; 23D-E, H); dorsal wall of sclerotised part of embolus proper as wide as ventral wall, not bent ventrad (Figs 21I-L, 23D-E). Poreplate with rounded and moderately wide, or slit-like or drop-like CDO (Figs 22A, C, E, G, K, I; 24A, C, E-F) ..... 2
- 2 Scopula covering only one-third of ventral side of male tarsus IV. Tibial apophysis short and basally wide in ventral view (Fig. 21E), carrying medium-long megaspines (Fig. 21E-G); paracymbium quite small (Fig. 21A, D); dorsal apex of contrategulum wide, tongue-shaped (Fig. 21I-L). Poreplate of vulva with distinctly invaginated anterior margin (Fig. 22A-I); CDO slit-like or drop-like, sitting in a posteriorly indistinctly outlined hollow (Fig. 22A, C, E, G, I) ..... *L. tempurung*
- Scopula covering two-thirds of ventral side of male tarsus IV. Tibial apophysis quite long and basally narrow in ventral view (Fig. 23B), carrying short megaspines (Fig. 23B, K-O); paracymbium quite large (Fig. 23A-B); dorsal apex of contrategulum narrow, spatulate (Fig. 23D-G). Poreplate with indistinctly or not invaginated anterior margin (Fig. 24A, C-F); CDO round or angular, distinctly outlined on all sides (Fig. 24A, C, E-F) ..... *L. priceae* sp. nov.

XI.1976; leg. B. Koepchen. – MHNG, sample SIM-01/13; 2 males (matured 18.X.2001, 8.II.2002), 2 females (moulted 13.I.2002; 24.I.2002), exuviae of 3rd female (spider not collected); Selangor, Batu Caves, Dark Cave, Caverns B, C, D (3°14'12.7"N, 101°41'00.0"E), 100 m; 12.VII.2001; leg. P.J. Schwendinger. – SMF-13907, n° 3; 2 females, 1 juv. male; Selangor, Batu Caves; leg. Clark, det. Roewer, 1962 (identified as 3 females). – SMF-13908, n° 4; macerated remains of 2 specimens (one a juvenile male, the other without opisthosoma); Selangor, Batu Caves; leg. Clark, det. Roewer, 1962. – SMF-21945/1; 1 female; no locality data; 19.XI.1933; det. W. S. Bristowe.

**Diagnosis:** Medium-sized, light brown-coloured species in both sexes. Males characterized by cumulus carrying a group of very long, thick bristles (Fig. 19A-B); tegulum with exceptionally small and narrow proximal edge carrying few denticles (Fig. 19H); distal edge of contrategulum with 2-4 quite long parallel ridges pointing towards dorsal apex, without denticles (Fig. 19D-E, I); para-embolic plate distinctly elevated (Fig. 19E-I), with sharp proventral angle at base (Fig. 19D-E, G; see arrows); apex of embolus proper wide in prolateral and retrolateral view (Fig. 19E-F, H), its dorsal wall much wider than its ventral wall, end of dorsal wall sharply bent proventrad (Fig. 19D-F, I). Females characterized by poreplate largely unpigmented in its posterior portion, more or less distinctly separated from short, wide posterior stalk; posterior portion of genital atrium not markedly bent ventrad; no anterolateral lobes on poreplate; CDO very wide, its anterior margin sunken and clearly outlined, its posterior margin at level of poreplate and not clearly outlined; genital atrium in most cases without hairs, its lateral folds weakly developed (Fig. 20).

**Additions to description of male:** *Scopula:* Tarsus I with thin scopula in distal half of ventral side, divided for its entire length by a narrow pale, glabrous longitudinal median stripe and by some bristles; tarsus II likewise, scopula only distally divided; tarsus III with thin scopula in distal three-fifths, only distally divided; tarsus IV with thin scopula (narrower than on other tarsi) in distal half, only distally divided.

*Palp:* Tibial apophysis basally wide in ventral view, moderately long, slightly set back from distal margin of tibia (Fig. 19A), its apical megaspines relatively long and thin (but not as thin as illustrated in Murphy & Platnick, 1981: figs 9, 12, 15, 21 and in Platnick & Sedgwick, 1984: figs 70-72, 74), dorsal ones longer than ventral ones. Prodorsal-apical lobe of cymbium distinctly longer and more pointed than proventral-apical one (Fig. 19C). Paracymbium of average size and depth (Fig. 19A-B), carrying very long (longest ones reaching base of embolus complex), thick bristles in a loose group on non-elevated cumulus (Fig. 19A). Subtegulum without

apophysis. Tegulum with very small proximal edge carrying only few denticles (Fig. 19H). Pigmented bridge between tegulum and contrategulum on retrolateral side of palpal organ disconnected (Fig. 19H). Contrategulum with indistinct, short and wide ventral process; distal edge with 2-4 parallel ridges pointing towards tongue-shaped dorsal apex (Fig. 19D-E, I). Para-embolic plate distinctly elevated (Fig. 19E-I), with sharp proventral angle at its base (Fig. 19D-G, see arrows). Embolus proper with wide apex (Fig. 19E-F, H); dorsal wall of sclerotised part much wider than ventral wall, end of former sharply bent ventrad and partly overlapping membranous part of embolus proper (Fig. 19D-F, I); sclerotised part of embolus proper retrolaterally with a single longitudinal distal keel (Fig. 19D-F, G); membranous part of embolus proper unpigmented throughout.

**Additions to description of female:** Posterior margin of genital sternite straight or indistinctly invaginated (Fig. 20). Vulval plate (Fig. 20) short, wide; posterior portion and lateral margins of poreplate largely unpigmented, more or less distinctly separated from short, wide, well-pigmented posterior stalk; posterior part of genital atrium only slightly and gradually curved ventrad; anterior margin of poreplate slightly and widely invaginated, without anterolateral lobes; CDO very wide, its anterior margin sunken and clearly outlined, its posterior margin level with poreplate and not clearly outlined (Fig. 20A, C-D, F-G); receptacular cluster very large, strongly protruding anteroventrad, reaching beyond anterior margin of poreplate; genital atrium without lateral hairs and in most cases without median hairs, its lateral folds indistinctly developed (Fig. 20B, E, H).

**Remarks:** The apical megaspines on the tibial apophysis of the male palp are not as thin as illustrated by Platnick and Sedgwick, and the one situated most dorsally is not as long as shown by these authors (Platnick & Sedgwick, 1984: figs 70-72, 74).

It is not clear what Platnick & Sedgwick (1984: 25) mean with their diagnostic character “short, erect tegular apophysis”.

**Variation:** Carapace lengths in males (n=3) 5.24-5.99, in females with fully developed vulval plate (n=7) 4.76-6.67; carapace widths 4.60-5.56 and 4.09-5.56, respectively. The scopula on tarsus I is divided for its entire length in two males, only distally so in the third; the scopula on tarsus IV extends over the distal half in two males, over the distal three-fifths in the third. One mature male retains a proventral “tibial spur” (*sensu* Platnick & Goloboff, 1985) on its right leg I. Variation in the shape of the vulval plate of females examined is shown in Fig. 20 (see also Murphy & Platnick, 1981: figs 26-27 and Platnick & Sedgwick, 1984: figs 75-76). One female has a single median hair in its genital atrium (Fig. 20D); in all other females examined the genital

atrium is completely devoid of hairs (Fig. 20A-C, E-H). Most specimens examined have fully developed anterior median eyes; only one small female has a reduced (but cornea present) AME on one side.

**Distribution:** First reported from the Batu Caves by Ridley (1899: 580), this species is only known from the Dark Cave and the Rift Cave which are part of the Batu Cave system (Lim & Yussof, 2009: 127-128; Fig. 1, locality 15) north of Kuala Lumpur, and from the

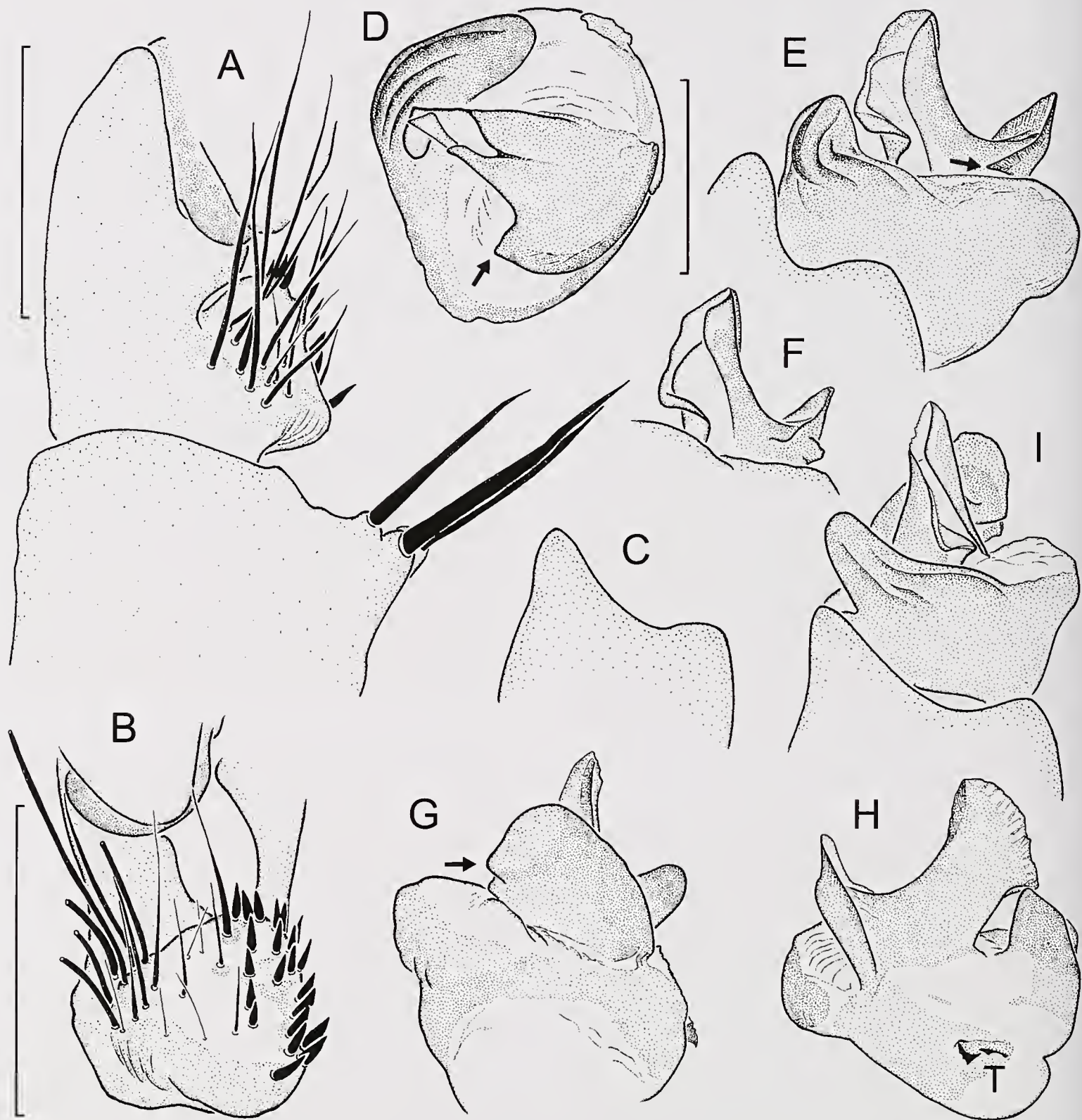


Fig. 19. *Liphistius batuensis*, details of left palp of two males from type locality: specimen collected 24.VII.1969 (A-B, F, I), specimen matured 8.II.2002 (C-E, G-H). (A) Distal part of palp (palpal organ not indicated), ventral view. (B) Paracymbium, retrolateral view. (C) Distal part of cymbium, prolateral view. (D) Palpal organ, distal view (dorsal side up; arrow indicating proventral angle at base of para-embolic plate). (E) Palpal organ, proventral view (arrow indicating same structure as in D). (F) Embolus complex, proventral view. (G) Palpal organ, retroventral and slightly proximal view (arrow indicating same structure as in D-E). (H) Same, retrodorsal view. (I) Same, prolateral view. Abbreviation: T - tegulum. Scale lines: 1.0 mm (A, C; B) and 0.5 mm (D-I).



Anak Takun Cave in the Templer Park which lies about 9 km further north (Fig. 1, locality 2). The latter record is based only on females and juveniles (Platnick & Sedgwick, 1984: 26). The Gua Anak Takun population was reported to contain hundreds of burrows in 1961 (McClure *et al.*, 1967), only one in 1986 (Yusof, 1987), three in 2006 (Lim & Yusof, 2009). Steiner (1998:

148) reported that the Gua Anak Takun population had probably become extinct, which fortunately proved to be incorrect. Nevertheless the future of this population, which no longer receives legal protection, is bleak (Lim & Yusof, 2009: 131). Fortunately the Batu Cave populations are doing much better (Lim & Yusof, 2009: 125-126).

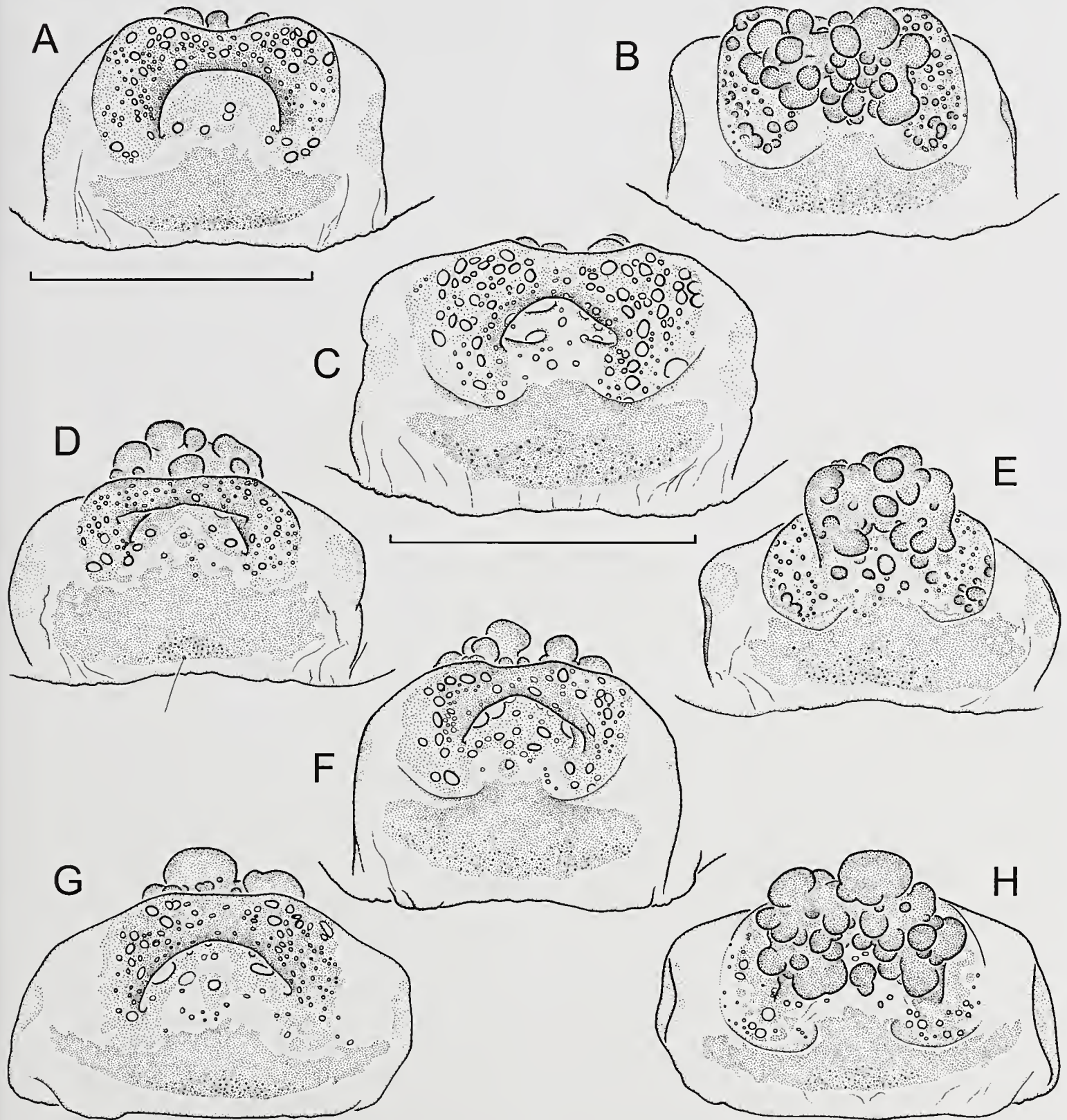


Fig. 20. *Liphistius batuensis*, vulval plate of five females from the type locality: exuvia, moult 24.I.2002 (A-B); specimen SMF 13907 (C); exuvia, moult 12.VII.2001 (D-E); specimen leg. XI.1976 (F); exuvia, moult 13.I.2002 (G-H). (A, C-D, F-G) Dorsal view. (B, E, H) Ventral view. Scale lines: 1.0 mm (A-B, D-E, G-H; C, F).

**Biology:** I collected spiders of this species only from sac-like nests on cave walls in the aphotic zone of the Batu Caves. No burrows were seen in the soil. The largest nest inspected (of a female) was 6 cm long and had a 1.9 cm long and 3.0 cm wide front door, as well as a 1.2 cm long and 1.9 wide back door. Penultimate males in captivity built nests with 1.6-1.8 cm long and 2.4 cm wide trapdoors. An egg sac of 1.8 cm diameter and 0.9 cm depth was found in the cave; it contained no eggs. One mature male was collected (by R. Pilet) in the cave in late July; two males matured in captivity (three and six and a half months after capture) in late October and early February. The mating period of *L. batuensis* appears to be relatively long, as it is the case in other congeneric species in peninsular Malaysia. Despite the fact that all specimens examined were found in the dark portions of caves, no troglobiomorphic adaptations are visible apart from a relatively light body colouration in living spiders.

An excellent and very detailed account of the biology of *L. batuensis* was given by Klingel (1967). Similar but shorter presentations of this species and its habitat appeared in Abraham (1923a), Bristowe (1933, 1952) and McClure *et al.* (1967). Lim & Yussof (2009) gave a detailed account of the state of the three known populations of this species.

### *Liphistius tempurung* Platnick, 1997

Figs 21-22

*Liphistius tempurung* Platnick in Platnick, Schwendinger & Steiner, 1997: 4-6, figs 10-11 (description of female).

**Type:** AMNH; female holotype (not examined); Malaysia, Perak, Gua Tempurung; 18.V.1996; leg. H. Steiner.

**Material examined:** MHNG, sample MAL-04/17; 3 males (matured 25.IX., 26.IX.2004, 13.XI.2005), 6 females (moulted 21.X.2004; 9.XII.2004; 19.XI.2004 and 3.IV.2005; 30.XII.2004 and 17.X.2005 and 24.V.2006 and 22.I.2007; IX.2004 and 13.IX.2005 and 8.II.2006; 8.X.2004 and 1.III.2005); Perak, 25 km south of Ipoh, Gua Tempurung, 4°24'58"N, 101°11'15"E, 90 m (limestone cave, dark zone); 22.VI.2004; leg. P.J. Schwendinger. – MHNG, sample 200/01; 1 juvenile; Perak, Gunung Lanno, Gua Cicak, 80 m; 16.XI.2001; leg. H. Steiner. – MHNG, sample MAL-04/16; 3 males (matured 31.XII.2004, 23.I.2005, 17.VI.2005), 3 females (moulted 8.I.2005; 17.I.2005); Perak, Gunung Lanno, Gua Cicak; 21.VI.2004; leg. P.J. Schwendinger.

**Diagnosis:** Medium-sized, light brown-coloured species in both sexes. Similar to *L. batuensis*, males distinguished by much shorter and stouter megaspines on tibial apophysis of palp (Fig. 21E-G cf. Fig. 19A); proximal edge of tegulum without denticles (Fig. 21B cf. Fig. 19H); retrolateral bridge between tegulum

and contrategulum unbroken (Fig. 21B cf. Fig. 19H); contrategulum with more pronounced, rather conical ventral process; distal edge with several short parallel ridges situated near base of ventral process and directed towards embolus; dorsal apex of contrategulum wider, without ridges (Fig. 21I-L cf. Fig. 19D); embolus proper more slender (Fig. 21A-B cf. Fig. 19E, H), dorsal wall of its sclerotised part without sharply bent end overlapping membranous part (Fig. 21C, I-L cf. Fig. 19D-F, I); base of embolus complex without sharp proventral angle (Fig. 21I-L cf. Fig. 19D-E, G), para-embolic plate less elevated (Fig. 21B cf. Fig. 19H). Females distinguished from those of *L. batuensis* by anterior and posterior margins of vulval plate distinctly invaginated (Fig. 22 cf. Fig. 20); posterior part of genital atrium more strongly curved ventrad, clearly visible on female specimen when viewed from posteroventrally (Fig. 22M-N); poreplate with much smaller CDO (Fig. 22A, C, E, G, I, K cf. Fig. 20A, C-D, F-G).

**Description of male (matured 26.IX.2004):** *Colour in alcohol* (slightly darker in life): Sclerotised parts light brown, except for cream-coloured proximal portion of chelicerae, whitish membranes of prosoma and cream-coloured membranes of opisthosoma.

*Bristles on carapace:* Short bristles along all margins (longest and strongest in front of eye mound); few on coxal elevations; four short bristles anterior to fovea; thick (spinelike) bristles on eye mound.

*Scopula:* Thin (weakest and narrowest on tarsus IV) and only distally divided by median stripe on all leg tarsi; covering distal half of ventral side of tarsi I-III, only distal one-third of tarsus IV.

*Cheliceral teeth:* Eleven small teeth of different sizes on promargin of right cheliceral groove, twelve on left cheliceral groove.

*Palp* (illustrations mostly of male matured 13.XI.2005): Tibial apophysis basally quite wide in ventral view, distinctly set back from distal margin of tibia (Fig. 21E), carrying four medium-long apical megaspines, the second from ventral situated clearly lower (more proximal) than others (Fig. 21E-F). Apical lobes of cymbium distinct, prodorsal one longer and narrower than proventral one (Fig. 21H). Paracymbium of average length but quite shallow (Fig. 21A, D), carrying long thick bristles in a widely spaced group on non-elevated cumulus (Fig. 21A, D). Subtegulum without apophysis. Tegulum with proximal edge indistinct and completely without denticles, distinguished from rest of tegulum only by a stronger pigmentation (Fig. 21B). Pigmented bridge between tegulum and contrategulum on retrolateral side of palpal organ unbroken (Fig. 21B). Contrategulum with distinct, somewhat conical (in distal view) ventral process, with several parallel ridges directed towards embolus and situated near base of ventral process; dorsal apex of contrategulum large and widely tounge-

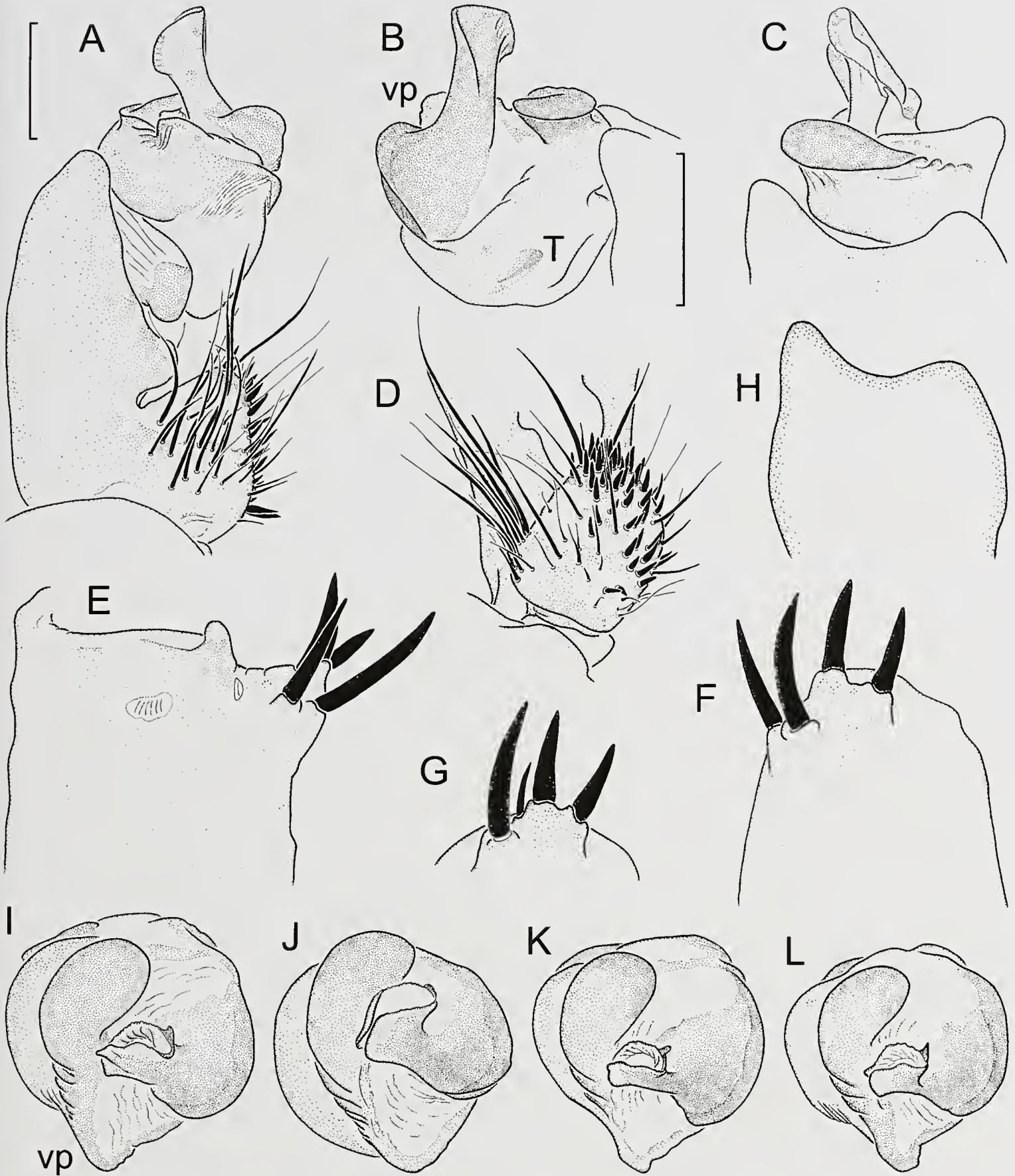


Fig. 21. *Liphistius tempurung*, details of left palp of four males: specimen from type locality, matured 13.XI.2005 (A-F, I); from Gua Cicak, matured 23.I.2005 (G, J); from type locality, matured 26.IX.2004 (H, K); from type locality, matured 25.IX.2004 (L). (A) Cymbium and palpal organ, ventral view. (B) Palpal organ, retrodorsal and slightly distal view. (C) Distal margin of cymbium and palpal organ, prolateral view. (D) Paracymbium, retrolateral view. (E) Distal part of palpal tibia, ventral view. (F) Tibial apophysis, retrodorsal and slightly proximal view. (G) Same, retrolateral and slightly proximal view. (H) Distal part of cymbium, prolateral view. (I-L) Palpal organ, distal view (dorsal side up). Abbreviations: T - tegulum; vp - ventral process of contrategulum. Scale lines: 0.5 mm (A, D-G; B-C, H-L).

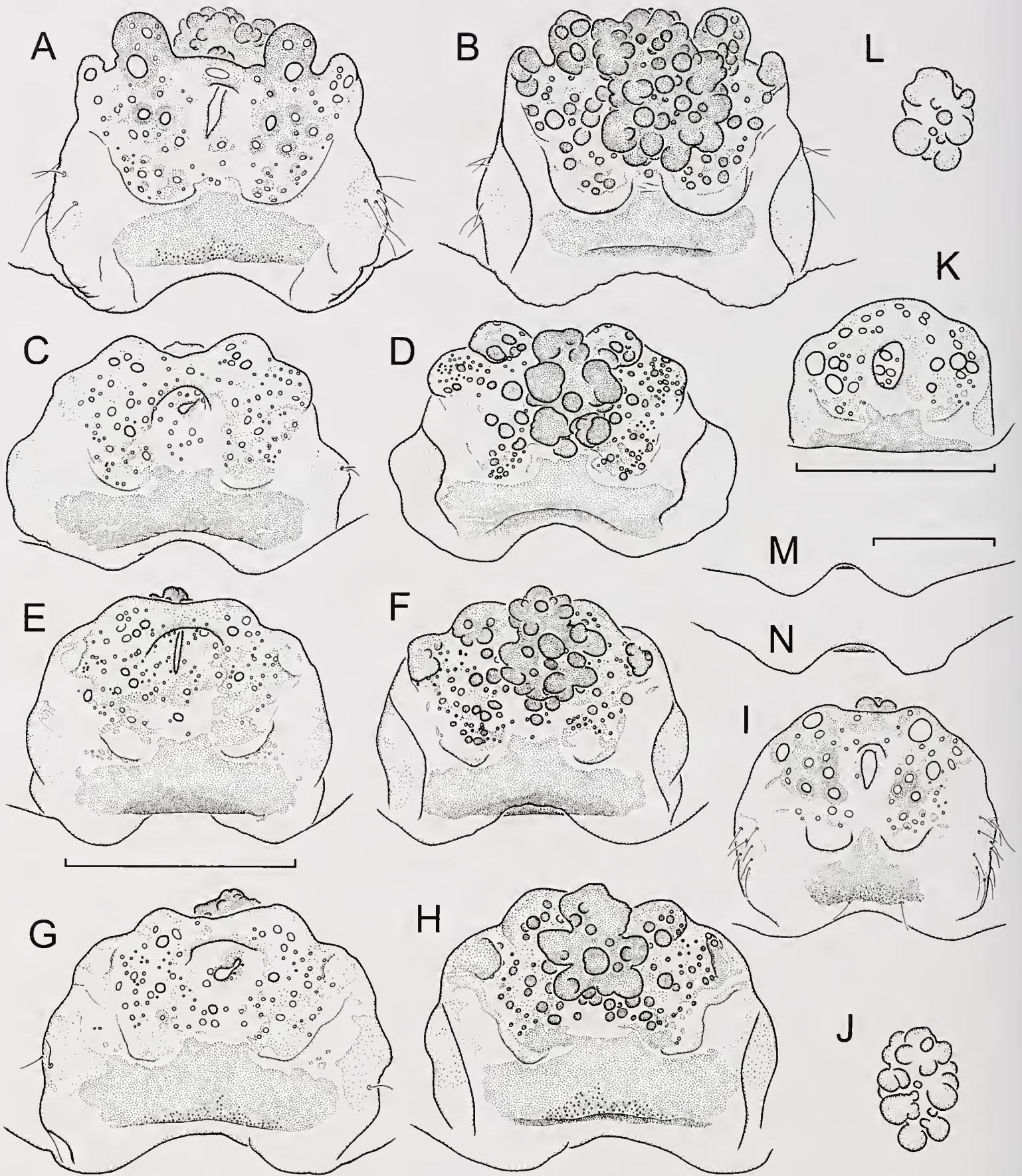


Fig. 22. *Liphistius tempurung*, details of copulatory organ and genital sternite of six females: Gua Cicak, specimen moulted 8.I.2005 (A-B, N); Gua Tempurung, exuvia, moult 22.I.2007 (C-D, M); Gua Tempurung, exuvia, moult 9.XII.2004 (E-F); Gua Tempurung, exuvia, moult 21.X.2004 (G-H); medium-sized female from Gua Cicak (I-J); small female from Gua Tempurung (K-L). (A, C, E, G, I, K) Vulval plate, dorsal view. (B, D, F, H) Same, ventral view. (J, L) Receptacular cluster, ventral view. (M-N) Posterior margin of genital sternite, ventral view. Scale lines: 1.0 mm (A-D, I-L; E-H; M-N).

shaped (Fig. 21I). Para-embolic plate short (Fig. 21B); no sharp proventral angle on and no sharp edge below para-embolic plate. Embolus proper with moderately wide apex (Fig. 21A-B); dorsal and ventral walls of sclerotised part equally wide, without modification (Fig. 21I), retrolateral wall carrying a distinct distal keel (Fig. 21B); membranous part of embolus proper narrow, unpigmented throughout (Fig. 21C).

**Measurements:** Total length 14.55; carapace 5.69 long, 5.25 wide; opisthosoma 6.04 long, 5.15 wide; eye mound 0.67 long, 0.83 wide; palpal coxae 1.68 long, 1.19 wide; labium 0.45 long, 0.99 wide; sternum 2.52 long, 1.68 wide (on ventral surface 0.79); palp 9.80 long (2.97 + 1.73 + 3.47 + 1.63); leg I 16.78 long (4.85 + 2.13 + 3.61 + 4.16 + 2.03); leg II 18.07 long (4.95 + 2.13 + 3.96 + 4.65 + 2.38); leg III 19.65 long (5.00 + 2.13 + 4.21 + 5.64 + 2.67); leg IV 25.45 long (6.04 + 2.38 + 5.25 + 8.12 + 3.66).

**Additions to description of female:** Posterior margin of genital sternite widely W-shaped (Fig. 22A-I), in slightly posteroventral view posterior edge of posterior stalk of vulval plate clearly visible between paramedian lobes (Fig. 22M-N). Vulval plate (Fig. 22A-I, K) moderately wide; large parts of poreplate unpigmented, particularly central area around CDO; CDO indistinct, composed of a small drop-shaped or longitudinally slit-shaped opening lying within a larger hollow with a distinct, sunken anterior margin and an indistinct (level with poreplate) posterior margin (Fig. 22A, C, E, G, I); receptacular cluster large and complex (Fig. 22B, D, F, H), slightly protruding beyond widely invaginated anterior margin of poreplate; posterior stalk strongly pigmented, more or less completely separated from pigmented areas of poreplate, its posterior portion finely pitted and bent ventrad at right angles; genital atrium with few or without lateral hairs, most vulvae without posterior hairs (Fig. 22A, C, E, G, I, K).

**Variation:** Carapace lengths in males (n=6) 5.51-6.46, carapace widths 4.92-5.87; in the largest females with a well-developed vulval plate (n=9) 5.94-7.87 and 4.80-6.69, respectively. In two females from Gua Tempurung both AME are completely absent, in other specimens they are reduced (without cornea), tiny (smaller than the pits from which nearby bristles arise) or normally developed. There is only minor variation in the tarsal scopula of males: covering distal two-thirds of tarsus II in two males (both from Gua Cicak), only distal half in all other males; being very thin (in two males from Gua Cicak) or thin (in remaining males) on tarsus IV, always weaker than on tarsi I-III.

Variation in the shape of the ventral process of the contrategulum is shown in Fig. 21I-L, variation in the shape of vulval plates in Fig. 22A-I, K. One male from the Gua Cicak has one of the four apical megaspines on its tibial apophysis weakly developed on both palps (Fig. 21G). The number of lateral hairs in the genital

atrium of females ranges from a few to none (Fig. 22A-I); one female (from Gua Cicak) has additionally two paramedian hairs in the posterior part of its genital atrium (Fig. 22I). Females from Gua Cicak have more hairs in the genital atrium than females from the type locality. The CDO is relatively large and clearly discernible only in the two smallest females from each locality (Fig. 22I, K); in all larger females examined it is small and lies in a depression (Fig. 22A, C, E, G).

**Biology:** All specimens examined were collected from burrows in sandy or loamy soil on the floor in the aphotic zone of two caves. Unlike in *L. batuensis*, no nests were found on cave walls. Most burrows ran into the depth of the soil and were closed by a single trapdoor. Only one burrow ran under the soil surface and had a second door at the opposite end, about six centimetres away from the first door. From the main entrance up to eight quite long (as usual in cave-dwelling *Liphistius*) signal lines (the longest 20 cm) ran over the soil surface (in a few cases also over nearby rock). The trapdoor of the largest female was 1.8 cm long and 3.0 cm wide, in penultimate males trapdoors were 1.2-1.8 long and 2.0-2.8 wide.

Despite the fact that all spiders examined were found in the dark portions of these two caves, no noteworthy troglobiomorphic adaptations are visible, apart from a relatively light body colouration in all living spiders and a more or less distinct reduction of the AME in some spiders.

An illustrated presentation of *L. tempurung* (together with *L. kanthan*) and its habitat is given in Steiner (1998). An extensive bibliography on *Liphistius* and many other animals in caves of Malaysia can be found on Liz Price's website (Price, 2017).

**Distribution:** Known only from inside two limestone caves (Fig. 1, localities 16-17), about 13 km apart, southeast of Ipoh in the Perak State. A short description of Gua Tempurung and photographs of the cave and some spider nests are given in Platnick *et al.* (1997: 2-3, figs 1-3).

**Remarks:** First reported from a "cave in Gunong Tempurong" by Bullock (1972: 138) under *L. batuensis*, this is a narrowly endemic species restricted to caves. Like the other cave-living *Liphistius* species in Malaysia [*L. batuensis*, *L. kanthan* (currently on the IUCN list of critically endangered species; <http://www.iucnredlist.org/search?page=52>) and *L. priceae* sp. nov.], *L. tempurung* is at great risk of becoming extinct if overcollected, or if their habitats change or are destroyed. Quarrying of limestone hills for cement production is widespread in Malaysia and elsewhere in Southeast Asia, and poses the greatest danger for these species.

*Liphistius priceae* sp. nov.

Figs 23-24

**Types:** MHNG (most types, including the holotype), SMF (1 male and 1 female paratypes), sample MAL-04/10; male holotype (matured late VIII.2004), 8 male paratypes (matured 20.VII., 1.VIII., 18.IX. 2004, mid-VII.; 11.VIII.2005; 3 male paratypes collected mature at the site) and 11 female paratypes (including allotype, moulted 24.XI.2004); Malaysia, Kelantan, about 5 km S of Dabong, Gua Keris (= Kris Cave) and Gua Pagar (locally also called Gua King Kong), 130 m; 8.-9. VI.2004; leg. P.J. Schwendinger. The precise type locality is Gua Keris.

**Etymology:** The new species is named in honour of Liz Price (London, UK), a former long-time resident in Kuala Lumpur, and a very active speleologist who over 30 years explored and published on caves and cave faunas all over Southeast Asia. She was also involved in conservation and trying to save some caves from destruction by quarrying in Malaysia.

**Diagnosis:** Small to medium-sized, light-brown-coloured species, similar and closely related to *L. tempurung*. Both sexes slightly smaller than those of *L. tempurung* (carapace length of males 4.42-5.23 versus 5.51-6.46 in *L. tempurung*). Males distinguished by scopula on tarsus IV more extensive; palpal tibia with a longer retrolateral apophysis carrying much shorter megaspines (Fig. 23B, K-O cf. Fig. 21E-G); paracymbium larger, with a more prominent retrolateral-proximal part (Fig. 23A cf. Fig. 21A); tegulum with more clearly outlined proximal edge (Fig. 23I cf. Fig. 21B); contrategulum with series of oblique ribs on distal edge extending further prolaterally, dorsal apex much smaller and narrower, with a more pointed tip (Fig. 23D-G cf. Fig. 21I-L); para-embolic plate with more prominent, angular distal margin (Fig. 23A, D-E cf. Fig. 21A, I-L); sclerotised part of embolus proper with more pointed apex (Fig. 23A, I cf. Fig. 21A-B). Females distinguished from those of *L. tempurung* by larger and more prominent receptacular cluster (Fig. 24 cf. Fig. 22); CDO much wider and more distinctly outlined, not sitting in a hollow (Fig. 24A, C, E-F cf. Fig. 22A, C, E, G, I); anterior margin of poreplate not or only indistinctly invaginated; posterior stalk anteriorly narrower.

**Description of male (holotype):** *Colour in alcohol* (slightly darker in life): Body mostly light brown, carapace with indistinct cream-coloured and flower-shaped area around fovea. Chelicerae with proximal portion cream-coloured, distal portion light brown. Cheliceral fangs, palpal tarsi and sclerites of palpal organ reddish brown (darker than rest of body). Legs with indistinct annulations (light median rings) on all tibiae and metatarsi; legs and palps with a light distal zone on patellae. Opisthosomal tergite I uniformly

light brown, following tergites with increasingly larger light areas in posterior part (except for bases of paired para-median spines); membranous part of opisthosoma cream-coloured.

**Bristles on carapace:** Stiff bristles on anterior and posterior margins, as well as on and behind eye mound; fewer weaker bristles on lateral margins and on posterior coxal elevations; no bristles anterior to fovea.

**Cheliceral teeth:** Twelve small teeth on promargin of cheliceral groove of each chelicera.

**Scopula:** All tarsi with indistinctly outlined scopula on roughly distal two-thirds of ventral side, only behind claw divided by a short median stripe; scopula on tarsus I very thin and its proximal limit difficult to identify; scopula on other tarsi denser and more clearly delimited.

**Claws:** Paired tarsal claws with 3-4 denticles on anterior legs, 4-5 denticles on posterior legs; unpaired claws with one indistinct denticle or without.

**Palp:** Tibial apophysis well-developed and quite long, slightly set back from anterior margin of tibia, distinctly pointing away from axis of tibia (Fig. 23B), carrying four very short megaspines, the ventral one being longest, a median one set back from distal margin (Fig. 23K). Distal margin of cymbium with elongate prodorsal lobe (Fig. 23J). Paracymbium quite large and moderately deep, with a distinct retrolateral-proximal bulge (Fig. 23A, C); cumulus indistinctly elevated, carrying few long stiff bristles (Fig. 23A, C). Subtegulum without apophysis. Tegulum with wide, sharp, non-dentate proximal edge (Fig. 23I). Contrategulum with somewhat widely conical (its apex narrowly rounded) ventral process; distal edge with long row of oblique parallel ridges pointing towards embolus; dorsal apex asymmetrical, quite small and narrow, with narrowly rounded tip (Fig. 23D). Para-embolic plate low, its distal margin angular (Fig. 23A, D, I); embolus proper with slightly widened and obliquely truncate apex (Fig. 23A, I), dorsal and ventral walls of sclerotised part equally wide and lying close to each other (Fig. 23D), retrolateral side enforced by a long, distinct keel (Fig. 23D, I); membranous part of embolus proper narrow, indistinct (Fig. 23H).

**Measurements:** Total length 9.96; carapace 4.51 long, 4.24 wide; opisthosoma 3.96 long, 2.61 wide; eye mound 0.64 long, 0.76 wide, AME well-developed; palpal coxae 0.99 long, 0.95 wide; labium 0.40 long, 0.87 wide; sternum 2.02 long, 1.47 wide (0.75 on ventral surface); palp 7.77 long (2.46 + 1.39 + 2.69 + 1.23); leg I 14.69 long (3.96 + 1.82 + 3.17 + 3.64 + 2.10); leg II 15.61 long (4.08 + 1.82 + 3.29 + 4.08 + 2.34); leg III 17.18 long (4.16 + 1.86 + 3.56 + 4.91 + 2.69); leg IV 21.62 long (5.07 + 1.90 + 4.51 + 6.69 + 3.45).

**Description of female (allotype):** *Colour in alcohol* (slightly darker in life): Mostly as in male, annulations on tibiae and metatarsi of legs slightly more distinct; palpal tarsus reddish brown only at tip. Opisthosomal tergites generally darker, light patches smaller.

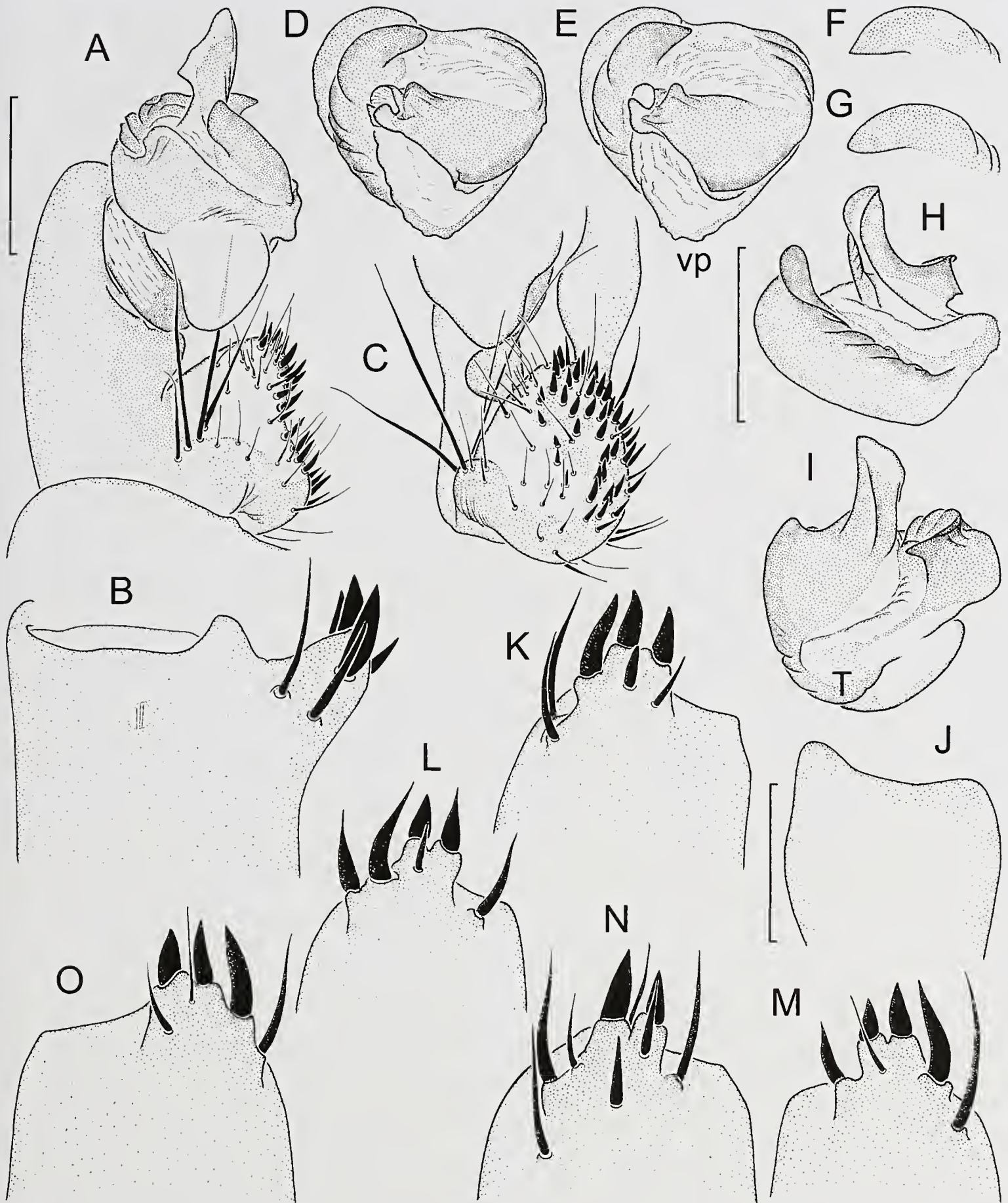


Fig. 23. *Liphistius priceae* sp. nov., details of palp of six males; holotype (A-D, H-K), male paratype collected mature (E), paratype matured 20.VII.2004 (F), paratype matured 1.VIII.2004 (G), paratype matured 18.IX.2004 (L-M) and paratype matured II.VIII.2005 (N-O). (A) Left cymbium and palpal organ, ventral view. (B) Distal part of left tibia, ventral view. (C) Left paracymbium, retrolateral view. (D-E) Left palpal organ, distal view (dorsal side up). (F-G) Dorsal apex of contrategulum of right palpal organ, distal view (dorsal side to the left). (H) Distal part of left palpal organ, prolateral view. (I) Same, retrodorsal and slightly distal view. (J) Distal part of cymbium, prolateral view. (K-L, N) Left tibial apophysis, retrolateral and slightly proximal view. (M, O) Right tibial apophysis, same view. Abbreviations: T - tegulum; vp - ventral process of contrategulum. Scale lines: 1.0 mm (A-C, K-O), 0.5 mm (D-I; J).

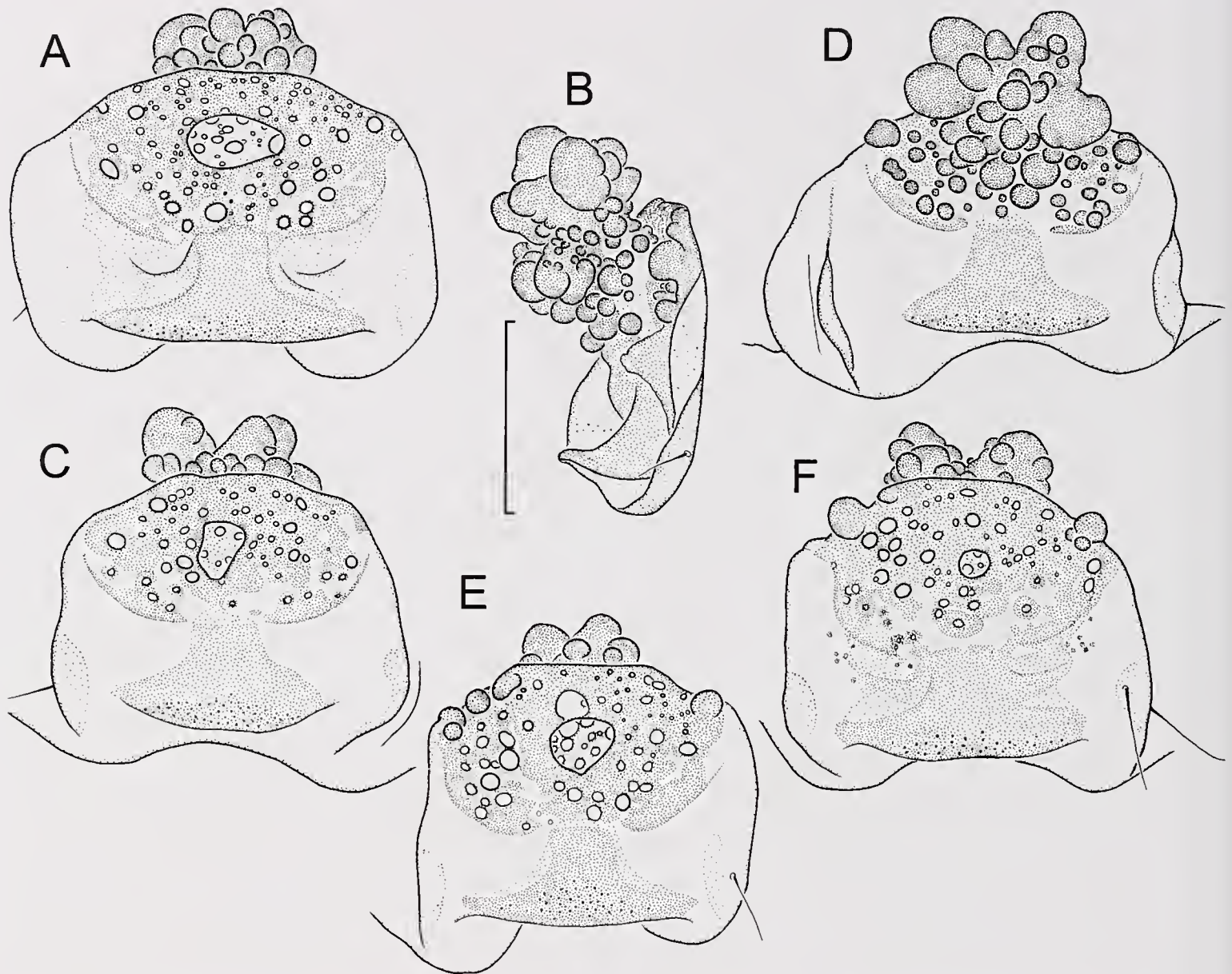


Fig. 24. *Liphistius priceae* sp. nov., vulval plate of four female paratypes (all from exuviae): paratype, moult 1.1.2006 (A-B), allotype, moult 24.11.2004 (C-D), paratype, moult 13.11.2005 (E), paratype, moult 2.4.2005 (F). (A, C, E-F) Dorsal view. (B) Lateral view. (D) Ventral view. Scale lines: 0.5 mm (A-F).

*Bristles on carapace:* Mostly as in male, additionally with very few tiny bristles on anterior coxal elevations.

*Cheliceral teeth:* Eleven strong teeth on promargin of left cheliceral groove, twelve on right side.

*Claws:* Each palpal claw with three worn denticles. Paired leg claws with 2-4 denticles; unpaired claws of legs I-III with 2-3 denticles, leg IV with 0-2. All tarsi without scopula.

*Vulva:* Posterior margin of genital sternite widely W-shaped (Fig. 24C-D), in slightly posteroventral view posterior edge of posterior stalk clearly visible between paramedian lobes. Vulval plate (Fig. 24C-D) wider than long; posterior part of poreplate partly unpigmented; CDO distinctly outlined, somewhat quadrangular, longer than wide (Fig. 24C), leading into large and complex receptacular cluster (Fig. 24D); the latter strongly protruding beyond slightly arched anterior margin of

poreplate (Fig. 24C); posterior stalk strongly pigmented, trapezium-shaped, anteriorly much narrower than posteriorly, indistinctly separated from pigmented areas of poreplate, its posterior portion finely pitted and bent ventrad at right angles (Fig. 24B, showing paratype).

*Measurements:* Total length 15.38; carapace 6.18 long, 4.91 wide; opisthosoma 6.49 long, 4.83 wide; eye mound 0.69 long, 0.82 wide; palpal coxae 1.90 long, 1.43 wide; labium 0.63 long, 1.43 wide; sternum 2.85 long, 1.90 wide (1.11 on ventral surface); palp 10.26 long (3.33 + 1.82 + 2.65 + 2.46); leg I 12.91 long (4.12 + 2.06 + 2.81 + 2.61 + 1.31); leg II 13.42 long (4.12 + 2.10 + 2.85 + 2.81 + 1.54); leg III 14.30 long (4.20 + 2.14 + 2.93 + 3.33 + 1.70); leg IV 19.46 long (5.23 + 2.38 + 4.08 + 5.39 + 2.38).

*Variation:* Carapace lengths in males (n=9) 4.42-5.23, carapace width 4.02-4.76; in females with well-



developed copulatory organs (n=9) 5.54-5.85 and 4.61-5.04, respectively. In a male and in a female one of the two AME is absent, in all other specimens both are distinct. In two males (including the holotype) the W-shaped marking behind the eye mound is indiscernible, in the other males it is more or less well-developed. No noteworthy variation in size and density of the tarsal scopula of males was detected. The arrangement of distal megaspines on the tibial apophysis of the male palp is quite variable (Fig. 23K-O). A male paratype has fewer bristles on the cumulus of both palps than the other males; one of the cumulus bristles of the illustrated holotype palp runs to the dorsal side of the palpal organ (Fig. 23A, C). The dorsal apex of the contrategulum is narrowly rounded to pointed (Fig. 23D-G). Variation in the shape of the vulval plates is shown in Fig. 24. The CDO is small to large, wider than long or longer than wide, circular, elliptical or quadrangular (Fig. 24A, C, E-F). The posterior stalk is more or less distinctly separated from the pigmented area of the poreplate. The lateral walls of the genital atrium are developed as narrow folds (Fig. 24D) or as simple trenches. Three of the females examined have 1-2 lateral hairs on only one side of the genital atrium (Fig. 24A-B, E-F), the allotype has none (Fig. 24C-D).

**Distribution:** Known only from two caves in the same limestone hill (Fig. 1, locality 18) in the north of peninsular Malaysia.

**Biology:** The spiders examined were all collected in different zones (from the euphotic entrance area to the aphotic interior) of both caves. No such spiders were found in the adjacent degraded rain forest. Despite apparently being confined to these caves, *L. priceae* sp. nov. shows no noteworthy cave adaptations in its morphology.

Quite short burrows with a single door and relatively long signal lines (no measurements were taken), as usual for cave-dwelling *Liphistiini*, were built in horizontal or sloping loam at or near the cave entrance, as well as in cracks and holes of the walls at the entrance and in deeper portions of the caves. No sac-like retreats on rock surface, as constructed by some other cave-dwelling *Liphistiini*, were seen. The trapdoor of the largest female was 1.4 cm long and 2.4 cm wide, in penultimate and adult males they were 1.15-1.6 long and 1.55-2.0 wide.

Three males were adult when collected in early June 2004; four others matured not long afterwards, between late July and late September; the remaining two males matured in mid-July and late August of the following year. Adult females usually moulted twice per year: between March and August and again between September and January. No egg cases were found in the field and no eggs were laid in captivity, which means that the females had not yet mated when collected in early June.

## DISCUSSION

**Morphological characters:** The polarity (plesiomorphy versus apomorphy) of genital characters in liphistiid spiders is difficult to assess. No other animals than the Araneae have the palps of males modified as gonopods, and no other living spiders are more primitive than the Liphistiidae. An outgroup comparison for male copulatory characters is therefore not possible. However, we have indications of the possible evolution of female copulatory organs in spiders from ingroup comparison. Schwendinger & Ono (2011: 626-628) discussed five hypotheses given in the literature and concluded that the female copulatory organs of Heptathelinae are much closer to a hypothetical ancestral form than those of the Liphistiinae (which are quite unique within the Araneae). If female copulatory organs of a given group are primitive, then it can be assumed that this also holds true for the corresponding male copulatory organs. Exciting new fossil evidence supports this assumption. Wunderlich (2017a: 97-99, figs 17-18, 20) very recently described and illustrated the male palps of two mid-Cretaceous mesothelid species which suggest (unfortunately not all details are visible) that these are more similar to heptatheline palps than to liphistiinae palps. Micro-CT scans will one day hopefully reveal more details of these fossil palps. They may not belong to species that are ancestors of the Liphistiidae, but we now have proof – for the first time – that male mesothelids already had complex palps (with an incrassate tibia, a large paracymbium carrying spinules, and with a cymbium as typical for extant liphistiids) about 100 million years ago. As these fossil palps lack a retrolateral tibial apophysis, they strongly resemble male palps of extant Heptathelinae. On this basis, genital characters of the *Liphistiini* species treated here – and of the Liphistiidae in general – are interpreted as follows (this interpretation is not based on a phylogenetic analysis):

- The embolus proper of Heptathelinae is undivided and wholly sclerotized, without a membranous part but with some light pigmentation and a small groove-like fold in the dorsal embolic wall of some species; see Haupt, 2003: figs 48-50, 52; Schwendinger & Ono, 2011: fig. 5; also observed in males of *Qiongethela australis* (Ono, 2002), *Q. nui* (Schwendinger & Ono, 2011), *Vinathela abca* (Ono, 1999) (male not yet described but palp illustrated in Logunov & Vahtera, 2017: figs 17-19), *V. tomokunii* (Ono, 1997), *V. tonkinensis* (Bristowe, 1933) and in two undescribed heptatheline species from Vietnam. Therefore the bipartite embolus proper of *Liphistiini* (unique among spiders) is believed to be derived. The deeply split embolus proper of the *trang*-group is consequently more derived than the rather closed embolus proper in other groups of *Liphistiini* species.
- The orientation of the embolus complex on the palpal organ differs by an angle of about 90°. In most *trang*-

group species the major embolic fold (marked “f” in Fig. 3; called “dorsal lamella” in Schwendinger, 1990: 347, figs 58, 61) that connects the retrolateral wall of the sclerotised part with the membranous part is wide (Fig. 3A, C, E, G) and essentially directed dorsad (in males examined ranging from prodorsad to retrodorsad; see e.g. Schwendinger, 1996: figs 6-7). A second, always very short and indistinct minor embolic fold (called “ventral lamella” in Schwendinger, 1990: 347, figs 59, 62) is also present and connects both embolic parts on the opposite side. In all other species groups (including the ones treated here) the major embolic fold is very narrow (Fig. 3B, D, F, H) and always points proventrad or prolaterad (e.g. Fig. 4G-H). The latter is similar to the situation in the Heptathelinae. Heptatheline spiders do not have a membranous part of the embolus proper, but the narrow end of the spermophore opening (seen in distal view), where the membranous part is situated in *Liphistius*, is directed prolaterad. This position is therefore considered as plesiomorphic. Males of *L. tenuis* Schwendinger, 1996 (Schwendinger, 1996: figs 16-17) and of an undescribed, closely related species from Cambodia (both belonging to the *trang*-group and both also unusual in other ways) are exceptions: their major embolic fold (although relatively wide and short as in all other *trang*-group species) clearly points prolaterad, and this may be plesiomorphic.

- The displacement of the para-embolic plate (considered homologous with the conductor of Heptathelinae which lies very close to the embolus; Schwendinger & Ono, 2011: 618) away from the embolus proper to the ventral/retroventral edge of the embolic base is presumably derived. So is the reduction of the para-embolic plate.
- Modifications on the distal edge of the contrategulum (e.g. in the form of parallel ridges or teeth) are found in *Liphistius* and in the Heptathelinae and have probably evolved several times in parallel. The V-shaped or U-shaped row of denticles at the proventral end of this edge (Figs 4C, 6C, 8D) is a clear synapomorphy of the *malayanus*-group and unique to these species.
- A ventral process on the contrategulum is absent in the Heptathelinae. The spindle-shaped, distad-directed process on the contrategulum of *Ganthela yundingensis* Xu (in Xu *et al.*, 2015a: figs 10-12) is more likely homologous with the strongly elongate, spine-like, distad-directed contrategular denticle of species in *Ryuthela* Haupt, 1983 than with the ventrad- or proventrad-directed, blunt process in many *Liphistius* species. A distinct contrategular process is present in some (but not all) species of all groups except for the *bristowei*-group and the *linang*-group; *L. malayanus* and *L. endau* (in the *malayanus*-group) appear to have an indistinct, very low and wide contrategular process. This structure may be a synapomorphy for the genus *Liphistius* that has become lost many times, or it may be a synapomorphy for certain species groups (with subsequent loss in some of their species).

- The usually well-developed and very prominent marginal and terminal apophyses of the tegulum in Heptathelinae are much reduced in the Liphistiinae. The distal edge of the *Liphistius* tegulum (corresponding to the marginal apophysis in Heptathelinae) is completely reduced in all species treated here, but still visible as a more or less distinct and prominent edge in other species groups. The dentate proximal edge of the *Liphistius* tegulum (corresponding to the dentate edge on the dorsal extension of the terminal apophysis in Heptathelinae; Schwendinger & Ono, 2011: 619, fig. 52) is strongly or completely reduced in the *batuensis*-group, but more or less well-developed in other species groups. These different degrees of reduction are considered as apomorphic.
- The presence of a subtegular apophysis (absent in the Heptathelinae) is most likely a synapomorphy of *Liphistius* which has been independently reduced or lost in many species of all groups, completely so in all species treated here.
- A more or less elevated cumulus (often indiscernible but always identifiable by the presence of a group of bristles that are distinct from nearby bristles) is quite unique within spiders, not present in the Heptathelinae, and a clear synapomorphy for *Liphistius*. Whether the elevated or the non-elevated cumulus is apomorphic remains unclear.
- The presence of a retrolateral apophysis on the palpal tibia of males distinguishes *Liphistius* from the Heptathelinae (Platnick & Sedgwick, 1984: 3) and it is a synapomorphy for *Liphistius*, probably evolved convergently to the retrolateral tibial apophysis in other spider families. This is supported by fossil evidence. The surprisingly well-preserved male palps of *Parvithela muelleri* Wunderlich, 2017 and of *P. spinipes* Wunderlich, 2017 from mid-Cretaceous amber of northern Myanmar (= Burma) lack a tibial apophysis, and they – at least the palp of the former species – look quite similar to male palps of extant Heptathelinae (see Wunderlich, 2017a: 98-99, figs 17-18, 20). As mentioned above, this is a strong indication that copulatory organs of Heptathelinae are more primitive than those of *Liphistius*.
- The deeply divided tibial apophysis of *L. tionian* (*tionian*-group) on one hand, and that of *L. linang* sp. nov. and *L. indra* sp. nov. (*linang*-group) on the other, are unique and highly derived. Their different shapes (different length of dorsal part of apophysis), in connection with different types of female copulatory organs, show that they probably evolved in convergence. Female genital characters (which are often more conservative than male genital characters) indicate that the *tionian*-group is closer to the *malayanus*-group than to the *linang*-group.
- The vulval plate of *Liphistius* is unique among spiders and a clear synapomorphy for the genus (Platnick & Sedgwick, 1984: 3). It starts off as a small, slightly

sclerotised and lightly pigmented structure in juvenile females and becomes larger and increasingly sclerotised and pigmented with each moult. For me it is not possible to tell if the female is still immature or already adult from just looking at a vulval plate. Surprisingly small females (clearly smaller than the conspecific males) were observed to produce eggs. The only partially pigmented (and sclerotised) vulval plate of the *linang*-group and the *batuensis*-group thus suggests neoteny or an atavism linking these species to the Heptathelinae with an unsclerotised, leathery bursa copulatrix (Schwendinger & Ono, 2011: 621, figs 55-57). However, the fact that the unpigmented parts of the vulval plates in the *linang*-group and in the *batuensis*-group are found in its centre, around the base of the receptacular cluster and between the poreplate and the posterior stalk, not at the periphery as in juvenile females, is a strong indication that this is a case of apomorphic reduction. This is not just a matter of reduced pigmentation, but also of reduced sclerotisation. Cleared vulval plates dissected from specimens of these species or vulval plates on exuviae (without the surrounding tissue that keep them straight) often fold along a horizontal axis that runs through the desclerotised areas. It is thus a clear synapomorphy for the species in the *linang*-group and for the species in the *batuensis*-group, but it remains to be established if it is also a synapomorphy for both groups together.

- The unpaired receptacular cluster of *Liphistius* is most likely a derivate of the four receptacles present in primitive Heptathelinae (and in primitive Mygalomorphae). In the Heptathelinae the two pairs of receptacles show a tendency towards fusion into a single pair and further into a single receptacle, and a tendency for displacement away from the anterior margin of the bursa copulatrix onto the dorsal or onto the ventral side (less pronounced and less frequent) of the bursa (Schwendinger & Ono, 2011: 621-624). The simple digitiform receptacular cluster of a few species in the *trang*-group are most likely derived simplifications (also present in heptathelines; Schwendinger & Ono, 2011: 621, figs 42-43) of the complex receptacular cluster found in the species treated here.
- The divided receptacular cluster of the *tioman*-group is probably also derived. Considering that the divided receptacular cluster arises from a well-developed poreplate, it is unlikely to be a plesiomorphic link between the unpaired receptacular cluster in *Liphistius* and the paired receptacles of heptathelines. Early stages of a subdivision of the receptacular cluster into subclusters can be found in some females of *L. malayanus* (Fig. 5B) and *L. endau* (Fig. 7B, E, G), which indicates an evolutionary trend within the *tioman*-group and the *malayanus*-group and suggests that both are closely related.
- A character not previously recognised as being of taxonomic value in *Liphistius* is the extent and density

of the ventral scopula on leg tarsi of males (not present in females). It allows some species to be distinguished from similar (closely related) ones, e.g. *L. linang* sp. nov. from *L. indra* sp. nov., and *L. tempurung* from *L. batuensis* and from *L. priceae* sp. nov. However, the most distinctive characters in males of extant liphistiids are found in the morphology of the palp. In females there are fewer valuable morphological characters for species distinction. Most of them are found in details of the vulva, but as these show relatively high degrees of intraspecific (even within-population) variability, an identification of females based on morphology and in the absence of corresponding males is still quite unreliable. Therefore the description of new species from females without the corresponding males, or – even worse – from a single female, should be avoided. It is advisable to illustrate the copulatory organs of more than just a single female per species. If a larger series of specimens is studied, then the typical as well as the most aberrant ones should be illustrated in order to avoid somebody else later describing a “new species” from an aberrant specimen.

- As in all other *Liphistius* species, those treated here possess “tibial spurs” (*sensu* Platnick & Goloboff, 1985) in juveniles and adult females, whereas adult males (except for quite rare cases in which individual “spurs” are retained) have lost them. The statement by Wunderlich (2017a: 90), with reference to Schwendinger & Ono (2011: 603), that “tibial spurs” are absent in *Qionghela australis* (Ono, 2002) is incorrect. The corresponding observation by Schwendinger & Ono refers to males only; for females of this species “tibial spurs” are reported as “present on legs I-III”.

**Paleobiogeography:** The oldest unambiguous mesothelid fossil is *Palaeothele montceauensis* (Selden, 1996) from a late Carboniferous Lagerstätte in France. Additional fossils that clearly belong to the Mesothelae were recently described (and placed in three extinct families) from mid-Cretaceous amber of northern Myanmar by Wunderlich (2015, 2017a). Extant mesothelids (all belonging to the family Liphistiidae) are only known from East and Southeast Asia. These are the undisputed facts. Other Palaeozoic fossil taxa currently placed under “mesotheles” may not be true spiders and need re-evaluation (Dunlop *et al.*, 2017; Garwood *et al.*, 2016: 6; Penney & Selden, 2011). A discussion of these facts is given in the following.

In the late Carboniferous, when *P. montceauensis* lived, France was part of northwestern Pangaea and it was situated near the equator (Scotese, 2002). Mesothelid spiders may have originated in this period and in this region. Or they could have originated earlier, on the minor supercontinent of Euramerica, which was isolated and continuously situated at the equator (Scotese, 2002) or just south of the equator (Streel *et al.*, 2000) during the Devonian and the early Carboniferous, whereas

northwestern Gondwana was slowly moving northward from southern temperate to subtropical latitudes during the same periods. Climatic conditions for the ancestors of *P. montceauensis* would have been more favourable on Euramerica than on Gondwana, unless global temperatures in the Palaeozoic and Mesozoic were indeed much more balanced than they are today (i.e. only warm temperate and subtropical zones but no tropical zone existed) and unless the geographical ranges of animal and plant taxa in these eras were almost pan-continental (Razumovsky, 1971; Zherikhin, 1978; Eskov & Golovatch, 1986). The fossil record supports an Euramerican origin of mesothelid spiders: Devonian *Uraraneida* (an extinct arachnid order close to the Araneae; considered as an suborder of the Araneae by Wunderlich, 2015: 46-48) in North America and western Russia (see Dunlop *et al.*, 2017); Carboniferous *Idmonarachne brasieri* Garwood, Dunlop, Selden, Spencer, Atwood, Vo & Drakopoulos, 2016 (an extinct arachnid of an unspecified order; considered as the sister group of the Araneae by Garwood *et al.*, 2016) in France; Carboniferous Arthrolycosidae, Arthromygalidae and Pyritaraneidae (which may or may not represent mesothelid spiders) in North America, England, France, the Czech Republic, Poland, Ukraine – all former parts of Euramerica – but also in Siberia (see Dunlop *et al.*, 2017). No Palaeozoic spider fossils are known from areas that then belonged to Gondwana.

Whatever happened before, in the late Carboniferous mesothelid spiders were evidently present in northwestern Pangaea. In the Mesozoic this region slowly drifted further north, out of tropical and subtropical latitudes. The alternatives for tropical spiders were adaptation to the new climatic conditions (something only few extant atypid and antrodiaetid species among the primitive spiders have achieved) or gradual dispersal while tracking suitable conditions which results in a shift in the geographical range. The latter would lead to only local extinction. Too rapid or too drastic changes in climatic conditions, or new barriers to dispersal, would lead to total extinction. This happened quite often, as the fossil record clearly shows: e.g. various tropical spider families in Baltic amber, see Wunderlich, 2004; Ricinulei fossils in North America, Europe and Burma, see Selden, 1992 and Wunderlich, 2012; Onychophora in Baltic and Burmese amber, see Poinar, 1996 and Muriene *et al.*, 2014.

How did mesothelid spiders get from northwestern Pangaea to East and Southeast Asia in between the late Carboniferous and today? Four hypotheses try to explain this:

- 1) Schwendinger (2009: 1265-1266) postulates that the mesothelid spiders originated in a tropical or subtropical part of Euramerica before the late Carboniferous, possibly before it was integrated into Pangaea. When this region drifted northwards and became too cold to sustain these spiders, they migrated from their ancestral region into warmer zones. Those that stayed behind and those that spread southward became extinct (possibly due to large-scale aridification of this region during the late Palaeozoic and Mesozoic, see Rees *et al.*, 1999 and Rees *et al.*, 2000), whereas those that migrated eastwards along the southern margin of northeastern Pangaea onto accreting terranes continued to exist and evolve until today. This hypothesis, called the “northern route” by Schwendinger (2009: 1265), was called the “stepping on Middle East” hypothesis by Xu *et al.* (2015b: 7-8), who also provided molecular-based dating of the diversification events for the family Liphistiidae and its genera. All known fossils that clearly belong to the Mesothelae support this hypothesis. Long-distance migration of animals with low powers of dispersal, as in the case of mesothelid spiders, should by no means be considered as something that happened relatively quickly. It would have taken many millions of years. In this case mesothelids had about 200 million years to get from France to northern Myanmar, and about another 100 million years to get from northern Myanmar to the present locations. That is a minimal pace of about 40 mm per year, which is certainly not beyond the capability of such spiders. It is quite likely (and not in contradiction with this hypothesis) that ancestral mesothelids dispersed slightly more quickly and were already widely distributed in southeastern Laurasia by the mid-Cretaceous.
- 2) A second hypothesis implies migration from tropical and subtropical areas of western Pangaea eastwards along the northern margin of Gondwana, followed by rafting on a Cimmerian terrane that detached from the northeastern margin of Gondwana in the early Permian, drifting northwards through the Paleotethys Ocean and accreting to the southern margin of eastern Laurasia in the early Jurassic. This was called the “southern route” by Schwendinger (2009: 1265) and the “out of Gondwana” hypothesis by Xu *et al.* (2015b: 7). This scenario is rather improbable, since, in order to “catch the raft”, the spiders would have had to migrate through cold southern latitudes in a relatively short period of time. There are no fossils to support this.
- 3) Xu *et al.* (2015b: 7) proposed a third hypothesis, called the “silk road”. It puts the eastward migration route further north, through northern Laurasia, onto the North China craton. As that would have gone through quite high northern latitudes and thus through a quite cold climate, it appears less likely than the first hypothesis. It is also not supported by any fossil evidence.
- 4) Wunderlich (2017a, b) indicates that during the Palaeozoic and Mesozoic mesothelid spiders were widespread in large parts of the world [“I suppose that East Asian Palaeozoic fossils of the Mesothelae will be discovered in the future” Wunderlich, 2017a: 88; “The Mesothelae did not invade South East

Asia in the Palaeogene for the first time (see my corresponding comment below) but their members lived already in this region for million (sic) of years”, “the report of (Mesothelae) fossils from the Southern Hemisphere should be only a matter of time”, “I expect the discovery of fossil Mesothelae in the Southern Hemisphere in the future” Wunderlich, 2017b: 285-286] and that the extant species are relicts of that once vast distribution. This “relict” hypothesis would require large-scale extinction and the presence of mesothelid fossils in almost all known Palaeozoic and Mesozoic Lagerstätten. So far such fossils are only known from one locality in France (Palaeozoic) and from one locality in northern Myanmar (Mesozoic) and therefore support for this hypothesis is very weak.

In his recent publication, which also gives the description of mesothelid spiders (placed in three extinct families) from mid-Cretaceous amber of northern Myanmar, Wunderlich (2017a: 91; 2017b: 285) rejects the “stepping on Middle East” (Euramerican origin and eastward migration) hypotheses of Xu *et al.* (2015b), without referring to the same hypothesis by Schwendinger (2009). Wunderlich further states that “Mesothelae did not invade South East Asia in the Palaeogene for the first time” (Wunderlich, 2017b: 285). Yet, nobody has ever suggested that. Xu *et al.* (2015b: 4) placed the origin of the family Liphistiidae in the Palaeogene and in Southeast and East Asia, which does not exclude that now-extinct mesothelid families (as the ones described by Wunderlich) were present in this region earlier. Actually the discovery of mid-Cretaceous mesothelid fossils from northern Myanmar nicely supports the “stepping on Middle East” hypothesis, because northern Myanmar lies on the postulated migration route and it would have been suitable for accommodating mesothelid spiders. About 100 million years ago (in the mid-Cretaceous) the land that is now northern Myanmar had already accreted to the southern margin of eastern Laurasia and was lying in warm (at least subtropical) latitudes (Scotese, 2002).

The answer to the question of how and from where mesothelid spiders did get to Southeast Asia lies in the ground. The discovery of a mesothelid fossil of any age in Australia or on other islands of the Sahul Shelf would disprove the “stepping on Middle East” hypothesis. So would a find of Palaeozoic mesothelid fossils in East Asia (predicted by Wunderlich, 2017a: 88). However, the discovery of mesothelid fossils in former western Gondwana would not disprove this hypothesis, providing that they were from northern South America or from northern Africa. These lands were adjacent to former Euramerica, situated in warm latitudes during the existence of Pangea, and could have been colonized by mesothelid spiders that later became extinct.

**Biogeography:** If the paleobiogeographical hypothesis advocated above is correct, then mesothelid spiders

have come as far as they can: to the eastern and southeastern shores of tropical and subtropical Asia. Ancestors of species found on remote islands were already there before they separated from mainland Asia, as in the case of Japan (harbouring *Heptathela* Kishida, 1923 and *Ryuthela* Haupt, 1983) (see Rogers & Santosh, 2004) and Hainan (harbouring *Qionghela* Xu & Kuntner in Xu *et al.*, 2015a) (see Zhu, 2016). Taiwan, which has no mesothelids, was never connected to the mainland (Sibuet & Hsu, 2004). Islands close to the mainland were probably colonized from the mainland during one of the periods of lowered sea level in the Caenozoic. Several of these islands harbour liphistiid species, many of them are endemics (e.g. the Malaysian island of Penang even has two species: *L. desultor* which also occurs on the mainland and *L. murphyorum* which is an endemic; Platnick & Sedgwick, 1984: 16-20). The well-investigated island of Singapore, on the other hand, which is only about 1 km away from the mainland and which is much larger than Penang Island, has no resident *Liphistius* species. The same appears to be the case with less well-investigated Indonesian islands (several of which I have visited) south of Singapore. Extinction most likely occurred there, and one can expect to find Caenozoic fossils of liphistiid spiders on these and many other islands near mainland East and Southeast Asia.

Among the islands harbouring *Liphistius* species, Sumatra is the one furthest away from the mainland. It is important to note that *L. sumatranus* Thorell, 1890 is not a primitive relict species, but clearly a member of the derived and species-rich *trang*-group. It is morphologically similar to *L. desultor* (occurring on Penang Island and mainland northwestern Malaysia, facing the east coast of Sumatra), but sufficiently distinct (with a strongly autapomorphic plate-like elevation at the retrodorsal corner of the embolus complex in addition to an only slightly elevated para-embolic plate) to give evidence for a long separation from related species on the mainland. The Strait of Malacca (between Malaysia and Sumatra), which is only 65 km wide in the south and for the most part only 27 m deep (rarely more than 37 m), was probably largely dry during several periods of lowered global sea levels; not just during the Pleistocene glacial periods, but also earlier, during the Pliocene, Miocene and Oligocene (Miller *et al.*, 2005). This is a sufficiently large time frame (about 33 million years) for speciation to take place. Surprisingly no adaptive radiation appears to have occurred; but it may have, with *L. sumatranus* the only survivor.

It is suggestive that islands of the Sunda Shelf which are further away from mainland Southeast Asia harbour no liphistiid spiders. Had they ever made it to the very large and remote island of Borneo, they should have been able to successfully establish themselves and, given enough time, to radiate into a number of descendant species. One would also expect to find extant (and fossil) mesothelids

on Borneo if they had arrived from northeastern Gondwana (see “out of Gondwana” hypothesis) or if they had been present on Borneo in the Mesozoic (see “relict” hypothesis). No mesothelids (extant or fossil) are known from Borneo, and I too failed to find any there.

Most species in the Malay Peninsula appear to be short-range endemics (according to Harvey, 2002). Among the species treated here, *L. gracilis* sp. nov., *L. indra* sp. nov., *L. johore*, *L. linang* sp. nov., *L. negara* sp. nov., *L. panching* and *L. tioman* are currently only known from their type localities (the presence of *L. gracilis* sp. nov. on Gunung Belumut needs to be confirmed; *L. johore* was not found again). *Liphistius endau* is known from three localities (Fig. 1, localities 6-8) and thus has a relatively wide distribution in the southern part of peninsular Malaysia, but the most widely distributed *Liphistius* species in the country clearly is *L. malayanus*. It is confirmed from five localities which are relatively far from each other [Fig. 1, localities 1-5; additional localities near Kuala Lumpur, e.g. Klang Gates (Murphy & Murphy, 2000: pl. 2.5), need confirmation but most likely also belong to this species]. This is an exceptionally large geographical range (very few congeners in northern and northeastern Thailand may have wider ranges) and also an exceptionally large vertical distribution. *Liphistius malayanus* occurs between altitudes of 230 m near Kuala Lumpur and about 1800 m in the Genting Highlands. It was also recorded from three other localities on mountains: Gunung Angsi, Fraser’s Hill and the Cameron Highlands. This surpasses all other congeners and makes *L. malayanus* the ecologically most successful of the known *Liphistius* species.

The “cave species” have, as usual, very small geographical ranges, and their association with caves is more or less close. The “caves” in which *L. tioman* were found are not real caves but crevices under and between large boulders. Nevertheless, I could only find spiders of this species there, not anywhere else in the nearby forest, although this may just be a snapshot impression due to limited sampling. *Liphistius panching* was found in a quite large limestone cave, but only in the oligophotic zone behind the entrance and not in the completely dark portions. It was also collected at the entrance of the cave (Platnick & Sedgwick, 1984: 27-28). The quite large size and dark body colouration of this species is untypical for true cave spiders and therefore I assume that it also lives outside caves though I have not found them anywhere on Bukit Charas apart from the Caras Cave (not even in one of several smaller caves in the same hill). All three species of the *batuensis*-group have a very close association with limestone caves and have never been collected away from the entrance or the interior of caves. These are rather small spiders with a light body colouration (though without true cave adaptations) and thus they are in their somatic morphology very similar to *L. tham* Sedgwick & Schwendinger, 1990 which is only known from the dark interior of a limestone cave in

central Thailand. *Liphistius priceae* sp. nov. has the least pronounced cave association of these three species. The types were found in the dark portions of the caves and at the cave entrances, some trapdoors were actually exposed to full sunlight for a short period of the day. Such spiders were not found in the nearby forest, nor in crevices of limestone boulders away from the cliffs, nor on the steep cliffs of the hill away from the cave entrances. *Liphistius batuensis* is well-investigated and much has been written about this species. It is most probably confined to the dark portions of limestone caves, and so is *L. tempurung* (in contrast to *L. kanthan* which will be treated in the second part of this revision). Due to their very localised occurrences and to their threatened (by quarrying and tourism) habitat, *L. batuensis* and *L. tempurung* are the rarest and most vulnerable liphistiids in Malaysia.

Syntopic occurrences of two *Liphistius* species in the Malay Peninsula are not uncommon, but a locality in Malaysia with three species (as at Khlong Nakha in southern Thailand; Schwendinger, 1995: 155) is not known. *Liphistius gracilis* sp. nov. and *L. endau* can be found at the Kota Tinggi Waterfall (Fig. 1, locality 8), with burrows of both species occurring side by side. The same is the case with *L. linang* sp. nov. and *Liphistius* sp. at the Jeram Linang Waterfall (Fig. 1, locality 13), and with *L. indra* sp. nov. and *Liphistius* cf. *thaleban* in the Sankalakhierie Mountains of southern Thailand (Fig. 1, locality 14). There is a sympatric occurrence of two *Liphistius* species near Kuala Lumpur: *L. batuensis* lives in the dark portions of the Batu Cave (Fig. 1, locality 15) and of the Anak Takun Cave in the Templer Park (Fig. 1, localities 2), and *L. malayanus* lives in the nearby forests. Populations of both species may only be (or better: were) before the forest around the limestone hills were cleared; Lim & Yussof, 2009: 130) hundreds of metres apart, but the habitats are very different. Two *Liphistius* species are found near Dabong (Fig. 1, locality 18): *L. priceae* sp. nov. in the Keris Cave and the Pagar Cave, *Liphistius* cf. *rufipes* a few kilometres away in the forest at the foot of Gunung Stong. A most remarkable co-occurrence of two cave species will be reported in the second part of this revision.

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