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Le comité soumet chaque manuscrit pour évaluation à des experts d'institutions suisses ou étrangères selon le sujet étudié.

La préférence sera donnée aux travaux concernant les domaines suivants: taxonomie, systématique, faunistique, phylogénie, évolution, morphologie et anatomie comparée.

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# The European athecate hydroids and their medusae (Hydrozoa, Cnidaria): Filifera Part 3

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**The European athecate hydroids and their medusae (Hydrozoa, Cnidaria): Filifera Part 3.** - This study reviews all European hydroids belonging to the filiferan families Hydractiniidae, Rhysiidae, and Stylasteridae. Stylasterids are treated only summarily because a recent, exhaustive monograph is available.
*Stylactaria claviformis* Bouillon, 1965 and *Hydractinia calderi* Bouillon, Medel, & Peña Cantero, 1997 are both regarded as junior synonyms of *Hydractinia proboscidea* (Hincks, 1868). *Podocoryna corii* Stechow, 1929 is regarded as a new junior synonym of *H. borealis*. *Cytaeandrea polystyla* Haeckel, 1879 is perhaps a synonym of *Turritopsis polycirrha* (Keferstein, 1862). *Hydractinia areolata* Alder, 1862 is selected as type species for the genus *Cytaeandra* Haeckel, 1879. *Clavopsis adriatica* Graeffe, 1883a is an indeterminate species, perhaps belonging to *Turritopsis dohrnii* (Weismann, 1883).

**Keywords:** Cnidaria - marine - Hydrozoa - Hydractiniidae - Rhysiidae - Stylasteridae - revision - taxonomy - northeastern Atlantic - Mediterranean.

## INTRODUCTION

This study is the fourth in a series of taxonomic revisions and reviews of the European Anthoathecata (=Anthomedusae, Athecata). The previous ones are: Schuchert (2004; Oceaniidae and Pachycordylidae), Schuchert (2006; Acaulidae, Boreohydridae, Candelabridae, Cladocorynidae, Cladonematidae, Margelopsidae, Pennariidae, Protohydridae, Tricyclusidae), and Schuchert (2007; Bougainvilliidae, Cytaeididae, Rathkeidae, and Pandeidae).

## MATERIAL AND METHODS

For morphological methods see Schuchert (1996; 2004) or Bouillon *et al.* (2004). For technical terms see below and also in Boschma (1956), Millard (1975), Cornelius (1995a, b), and Bouillon *et al.* (2006).

Where possible, it was attempted to supplement the species descriptions by sequence information of the 16S mitochondrial rRNA gene. The methods to obtain DNA sequences are described in Schuchert (2005). All sequences have been submitted

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to the EMBL database. The origin and identity of the material used to obtain 16S sequence data as well as the accession numbers are given for each species in the section "Material examined". Some sequences have been determined by other laboratories using material described here.

## Definition of some Terms

ampulla: bubble-like cavity in the coenosteum of stylasterids containing the gonozooid, either at the surface or deeply buried in coenosteum, with efferent canals or pores. Female ampullae are generally larger than male ones.

blastostyle: structure carrying gonophores, often strongly reduced hydranths, but not all blastostyles are homologous.

coenosarc: living tissue of a colony.

coenosteum: calcified skeleton of stylasterids, hydrocorals, or corals.

cyclosystem: in stylasterids, concentric arrangement of dactylopores around a gastropore.

dactylopore: in stylasterids, tubular opening in the skeleton into which the dactylozooids can retract, usually smaller than the gastropore, in some genera encircling the gastropore, some dactylopores have a spine, a collar-like elevation of the rim.

dactylozooids: modified polyps with a defensive function, comprises tentaculozooids and spiral zooids.

diastema: in stylasterids, occlusion of dactylopore; some dactylopores in cyclosystems may be secondarily filled by coenosteum.

flabelliform: fan-shaped.

gastropore: tubular opening in the skeleton of stylasterids into which the gastrozooid can retract, usually larger than the dactylopore.

gastrostyle: in stylasterids, coaxial spine at base of gastropore, always ornamented with prickles.

gastrozooids: normal feeding polyps with mouth and normally with tentacles, without reproductive organs.

gonophore: reproductive structures formed during polyp stage, may develop into free medusa or remain fixed, phylogenetically derived from one medusa bud only.

gonozooids: reproductive polyps bearing gonophores, either modified gastrozooids that show various stages of reduction and loss of tentacles, or polyps that are distinct from gastrozooids from the beginning, later developing gonophores.

hydrorhiza: all structures by which polyps are attached to the substratum, usually stolons.

medusoid: reduced medusa, with umbrella, but without functional mouth and either no or only rudimentary tentacles.

nematopore: in stylasterids, small pore harbouring nematozooids.

nematozooid: similar to tentaculozooid, zooid with defensive function.

palisade, ring palisade: in stylasterids, columnar processes of lateral wall of gastropore, pointing towards the centre.

pedicel: stalk of polyp.

pseudoseptae: in cyclosystems of stylasterids the wall separating the gastropore and the surrounding dactylopores is often obliterated. With the radially arranged edges of the dactylopores, the cyclosystems thus resemble the calyces of scleractinian corals.

spine in stylasterids: elevatation of rim of dactylopore into mound- or collar-like structure.

stolonal: in stolonal colonies, polyps arise only from stolons, they may have a caulus, here used in the sense of colonies without branching stems.

sporosacs: gonophores that mostly remain fixed to the hydranth and release gametes from there; there is no further implication on its structure, but usually kept separate from attached medusoids that differ in having pulsating umbrella.

sympodial: stem axis forming a zigzag pattern through superposed lateral branches.

tentaculozooid: polyp similar to tentacle in structure, mostly with a solid core of gastrodermis and no mouth or gastric cavity. More delicate and slender than spiral zooids.

texture of coenosteum: microscopic surface texture of skeleton of stylasterids, e. g. linear-imbricate scales or reticular-granular.

unifacial: one-sided.

Abbreviations

| | |
|---|---|
| BMNH | The Natural History Museum, London, England |
| ERMS | European Register of Marine Species (Costello *et al.,* 2001) |
| FNHM | The Faroes Natural History Museum |
| MHNG | Muséum d'histoire naturelle de Genève, Switzerland |
| ICZN | International Code of Zoological Nomenclature |
| IRSN | Institut Royal des Sciences Naturelles de Belgique, Bruxelles |
| ZMO | Zoological Museum Oslo, Norway |
| ZMUC | Zoological Museum Copenhagen, Denmark |
| ZSM | Zoologische Staatssammlung, Munich, Germany |

## TAXONOMIC PART

### Family Hydractiniidae L. Agassiz, 1862

Type genus: *Hydractinia* van Beneden, 1841.

Synonyms: Podocorynidae Allman, 1864c: 353. – Stylactidae Haeckel, 1889: 79. – Hydrodendridae Nutting, 1906. – Janariidae Stechow, 1921a: 29.

Diagnosis: Polyps colonial, lacking pedicels and thus sessile, polymorphic or not; hydrorhiza either perisarc-covered stolonal tubes, or an encrusting mat resulting from the coalescence of the stolonal system, either covered by a common layer of perisarc or with naked coenosarc; in some genera the hydrorhizal mat is reinforced by a calcareous skeleton; frequently with chitinous or calcareous spines sometimes forming pillars and branches, sometimes with protective tubes overarching the hydranths. Polyps either with one or several whorls of filiform tentacles beneath hypostome, or with scattered tentacles on the upper half of the body, exceptionally with one or two tentacles only; dactylozooids, when present, with no tentacles. Gonophores typically borne on gonozooids, these with one or more whorls of filiform tentacles or without tentacles and mouth (= blastostyles), giving rise to fixed sporosacs, eumedusoids, or free medusae.

Medusa umbrella more or less bell-shaped, with or without slight apical process; manubrium tubular to sac-shaped, not extending beyond bell margin; with or without gastric peduncle; mouth with four simple or branched oral lips drawn out to form arms with terminal nematocyst clusters; four, eight, or more, solid, marginal tentacles, tentacles not in groups; with or without ocelli; four radial canals and circular canal. Gonads on manubrium, interradial, sometimes extending along basal, perradial protrusions of the manubrium.

References: Motz-Kossowska (1905), Goette (1916), Kramp (1927, 1932a), Calder (1988), Namikawa (1991), Bouillon *et al.* (1997).

Remarks: The taxonomic history and the problems of this family have been outlined by Calder (1988). The generic subdivision of the Hydractiniidae is provisional and will certainly be changed in future again. Here, the classification of Bouillon *et al.* (1997, 2006) was adopted, though with some modifications. As discussed in Schuchert (2001a), the genus *Clava* Gmelin, 1791 is also regarded as a member of the Hydractiniidae. This leads to the awkward situation that the name Hydractiniidae L. Agassiz, 1862 formally becomes a junior synonym of Clavidae McCrady, 1859 [see also Schuchert (2001a) for further details]. Even without this, the scope of the family

Hydractiniidae remains contentious [see e.g. Schuchert (2007) for *Kinetocodium* and others]. Bouillon *et al.* (2006) provide a key and diagnoses for all genera.

*Dysmorphosa minuta* Mayer, 1900b and *Cytaeis minima* Trinci, 1903 have both been included in the Hydractiniidae, either in the genus *Podocoryne* or *Hydractinia* (e. g. Kramp, 1961; Bouillon *et al.*, 2006). In my previous study (Schuchert, 2007), I argued that both belong to the family Rathkeidae. Furthermore, *Dysmorphosa minuta* Mayer, 1900b is a subjective synonym of *Lizzia blondina* Forbes, 1848, and *Cytaeis minima* was transferred to a new genus as *Podocorynoides minima* (Trinci, 1903).

As with many other hydrozoans, non-reproductive hydroids in this family are not reliably identifiable. In order to identify hydroids producing a free medusa phase, information on the mature medusa stage is usually essential. This means that only living, cultivated material is reliably identifiable. This also holds true for some species producing medusoids, as some traits – like the rudimentary tentacles – will develop only rather late.

The nematocyst types of the Hydractiniidae examined here are rather uniform and do not offer much help in reliably discriminating the species. In future, barcoding approaches (e. g. Moura *et al.*, 2008) will certainly play a decisive role to resolving some of the problems.

KEY TO THE HYDRACTINIID GENERA OF THE ERMS ZONE:

1a Polyp tentacles in 1-3 whorls confined to a narrow region ....... *Hydractinia*
1b Polyp tentacles scattered in broad region below hypostome, no polymorphism, with sporosacs .................................. *Clava*

### Genus ***Hydractinia*** van Beneden, 1841

TYPE SPECIES: *Hydractinia lactea* van Beneden, 1844, a synonym of *H. echinata.*

SYNONYMS:

*Echinochorium* Hassal, 1841; type species *Echinochorium clavigerum* Hassall, 1841, a synonym of *H. echinata.*
*Dysmorphosa* Philippi, 1842; type species *Dysmorphosa conchicola* Philippi, 1842.
*Podocoryna* M. Sars, 1846; type species *Podocoryna carnea* M. Sars, 1846, by monotypy.
*Podocoryne* Lütken, 1850, introduction of incorrect spelling that became prevalent.
*Synhydra* Quatrefages, 1843; type species *Synhydra parasites* Quatrefages, 1843, a synonym of *H. echinata.*
*Cionistes* Wright, 1861; type species: *Cionistes reticulata* Wright, 1861, an indeterminate hydractiniid species.
*Stylactis* Allman, 1864c; type species *Podocoryna fucicola* Sars, 1857, designated by Mayer (1910).
*Rhizocline* Allman, 1864c; type specis *Hydractinia areolata* Alder, 1862.
*Cytaeandra* Haeckel, 1879; type species *Hydractinia areolata* Alder, 1862.
*Hydrodendrium* Nutting, 1906; type species *Hydrodendrium gorgonoides* Nutting, 1906 by monotypy.
*Nuttingia* Stechow, 1909; type species *Hydrodendrium gorgonoides* Nutting, 1906; invalid new name for *Hydrodendrium* Nutting, 1906 as junior synonym.
*Euhydractinia* Broch, 1910; introduced as subgenus of *Hydractinia*, no type species specified.
*Hydronema* Stechow, 1921b; type species *Hydractinia dendritica* Hickson & Gravely, 1907, name preoccupied by *Hydronema* Martynow (Trichoptera).
*Stylactaria* Stechow, 1921b; type species *Stylactis inermis* Allman, 1872 after original designation by Stechow (1921b).

*Hydractomma* Stechow, 1921b; type species: *Hydractinia pruvoti* Motz-Kossowska, 1905.
*Hydrissa* Stechow, 1922; type species *Hydractinia sodalis* Stimpson, 1859.
*Podocorella* Stechow, 1921c; type species *Stylactis minoi* Alcock, 1892.
*Halorhiza* Stechow, 1962; type species *Hydractinia dendritica* Hickson & Gravely, 1907.
? *Cnidostoma* Vanhöffen, 1911; type species of *Cnidostoma fallax* Vanhöffen, 1911.
? *Archaeoceania* Picard & Rahm, 1954; type species *Archaeoceania tournieri* Picard & Rahm, 1954, synonym of *Cnidostoma fallax* Vanhoeffen, 1911.
? not *Clavopsis* Graeffe, 1883; type species *Clavopsis adriatica* Graeffe, 1883.
not *Stylactella* Haeckel, 1889, belongs to Cytaeididae.
not *Oorhiza* Mereschowsky, 1877, belongs to Cytaeididae.
not *Halerella* Stechow, 1922, belongs to Rhysiidae.

DIAGNOSIS: Hydroid arising either from a reticular hydrorhiza formed by perisarc-covered stolonal tubes, or from an encrusting mat issued through the coalescence of stolonal system, covered by a common layer of perisarc or by naked coenosarc; hydrorhizal crust can secrete a calcareous skeleton in some genera; frequently with chitinous or calcareous spines, sometimes forming erect structures. Polyps sessile, naked, usually polymorphic; gastrozooids with one or more whorls of oral filiform tentacles confined to a small region below hypostome; dactylozooids, when present, with no tentacles; gonophores borne on gonozooids; gonozooids with or without tentacles, with or without mouth, giving rise to fixed sporosacs, fixed or free medusoids, or free medusae.

Medusa umbrella more or less bell-shaped; with or without slight apical process; manubrium tubular to sac-shaped, not extending beyond bell margin; with or without gastric peduncle; perradial corners of mouth with four nematocyst clusters or drawn out into simple or branched oral lips, sometimes elongated to form arms, ending in terminal nematocyst clusters; 4, 8, or more, solitary, solid, marginal tentacles; four radial canals and circular canal; gonads on manubrium, interradial, sometimes also on basal perradial pouches of the manubrium. With or without ocelli. Medusae budding from manubrium occasionally present.

REMARKS: Following Bouillon *et al.* (1997, 2006), the genera *Stylactaria* Stechow, 1921c and *Podocoryna* M. Sars, 1846 are here regarded as synonyms of *Hydractinia* van Beneden, 1841 as they cannot be separated unambiguously. As can be seen from the list above, there are many more synonyms that can be subsumed under *Hydractinia*.

The genus *Cytaeandra* Haeckel, 1879 was established for *Hydractinia areolata* Alder, 1862 and *H. polystyla* Haeckel, 1879. Haeckel (1879) did not select a type species. *Hydractinia areolata* Alder, 1862 is herewith selected as type species for the genus *Cytaeandra*, rendering it thus a synonym of *Hydractinia* as defined here. Kramp (1959, as *Podocoryne polystyla*) regarded the medusa *Cytaeandrea polystyla* Haeckel, 1879 as a doubtful species. It is characterised by 32 simple tentacles, bulbs with an ocellus, 16 nematocyst clusters on the mouth-rim, and crescent shaped gonads with their concave side facing towards the mouth. I think Haeckel's medusa was a young *Turritopsis polycirrha* (Keferstein, 1862) (see Schuchert, 2004 for a description).

Some nominal species of *Hydractinia* in the ERMS region have long been recognized as indeterminate (Bedot, 1910) and will not be discussed here. These are: *H. littoralis* Gosse, 1855; *H. incerta* van Beneden, 1867; *H. solitaria* van Beneden, 1867; and *H. tenuissima* van Beneden, 1867. This list is perhaps not complete.

The species are discussed in the same sequence in which they appear in the following key.

KEY TO *HYDRACTINIA* SPECIES IN THE ERMS ZONE (PROBLEMATIC SPECIES EXCLUDED):

1a Gonophores released as free medusae having tentacles longer than bell when expanded . . . . . . . . 2

1b Gonophores sporosacs or medusoids with rudimentary tentacles . . . . . . . . 5

2a Manubrium of mature medusa with basal pouches bearing gonads, bell-margin with more than 40 tentacles of very unequal length . . . . . . . *H. areolata*

2b Medusa without basal manubrium pouches, mature with 4-30 tentacles . . . . . 3

3a Mature medusa with branched oral nematocyst clusters, 16-30 tentacles . . . . . . . . *H. borealis*

3b Oral nematocyst clusters simple, not branched . . . . . . . . 4

4a Mature medusa with 8-10 tentacles, newly liberated medusae 5-8 tentacles, British Isles to Norway . . . . . . . . *H. carnea*

4b Mature medusa with 4 tentacles, Mediterranean and Atlantic coast from Gibraltar to France . . . . . . . . *H. exigua*

5a Gonophores sporosacs or medusoids, in both cases with four radial canals . . . 6

5b Mature gonophores sporosacs without radial canals . . . . . . . . 10

6a Arctic species on gastropods, encrusting hydrorhiza, medusoid with 8 rudimentary tentacles, up to 100 eggs per medusoid . . . . . . . . *H. allmani*

6b Boreal or Mediterranean distribution, hydrorhiza stolonal . . . . . . . . 7

7a Gonozooids with much reduced number of tentacles (1-2, rarely 3); medusoids released, with gastric peduncle . . . . . . . . *H. pruvoti*

7b Gonozooids like smaller gastrozooids, more than 3 tentacles, produces sporosacs or medusoids without gastric peduncle . . . . . . . . 8

8b Gastrozooid tentacles in 2-3 close-set whorls. medusoids or sporosacs without distinct bulbs . . . . . . . . 9

8a Gastrozooid tentacles in one whorl, female medusoids with four small bulbs and 0-4 tentacle rudiments . . . . . . . . *H. aculeata*

9b Gastrozooid hypostome slightly necked, with or without spines, gonophores medusoid, with 4-10 tentacle rudiments, released or not . *H. proboscidea*

9b Gastrozooid hypostome not necked, no spines, gonophores sporosacs without tentacle rudiments, not released . . . . . . . . *H. inermis*

10a Gonozooids with tentacles, these fully formed or only somewhat shortened . . . . . . . . 11

10b Gonozooids without tentacles or these reduced to stumps or warts . . . . . . . . 12

11a On fixed substrata, Mediterranean to Brittany . . . . . . . . *H. fucicola*

11b On gastropod shells and other living, mobile substrates, distribution Norway to Arctic . . . . . . . . *H. sarsii*

12a Boreal shallow water occurrence, distal end of gonozooids with nematocyst buttons, spines with spiny ridges . . . . . . . . *H. echinata*

12b Predominantly arctic or deep-sea species . . . . . . . . 13

13a Growing on deep-sea ophiurid *Homalophiura tesselata,* hydrorhiza stolonal . . . . . . . . *H. ingolfi*

13b Arctic species growing on gastropod shells . . . . . . . . . . . . . . . . . . . . . . . . 14
14a Hydrorhiza stolonal, deep sea species, gonozooids with rudimentary tentacles, 10 eggs per sporosac . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *H. arctica*
14b Hydrorhiza encrusting . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 15
15a Spines high, slender . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 16
15b Spines low, conical, gonozooids 0-4 very short tentacles, 3-7 sporosacs, 5-6 eggs per female sporosac . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *H. carica*
16a 1-4 sporosacs at base of gonozooids, female sporosacs one egg, spines with four serrated ridges . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *H. serrata*
16b 1 sporosac in middle of gonozooid, female sporosacs with up to 50 eggs, spines without serrated ridges . . . . . . . . . . . . . . . . . . . . . . . . . . . *H. monocarpa*

### ***Hydractinia areolata*** Alder, 1862 Fig. 1

*Hydractinia areolata* Alder, 1862a: 144. – Alder, 1862b: 311, pl. 13 figs 1-4. – Alder, 1863: 314, pl. 14 figs 1-4. – Cornelius & Garfath, 1980: 277.
*Rhizocline areolata.* – Allman, 1864c: 11.
*Podocoryne areolata.* – Hincks, 1868: 32, pl. 6 figs 1 & 1a. – Allman, 1872: 353.
*Cytaeandrea areolata.* – Haeckel, 1879: 79.
in part *Podocoryne areolata.* – Hartlaub, 1911: 219, figs 191. [others *H. borealis*]
*Podocoryne hartlaubi* Neppi & Stiasny, 1911: 395. – Neppi & Stiasny, 1913: 25, pl. 2 fig. 14. – Russell, 1953: 130, figs 60A-D, 61A-B, pl. 6 figs 1, 4. – Kramp, 1961: 69. – Yamada, 1961: 134, figs 1-5. – Kramp, 1959: 101, fig. 66. – Brinckmann-Voss, 1970: pl. 7 fig. 2. – Edwards, 1972: 104, synonym.
not *Podocoryne areolata.* – Kramp & Damas, 1925: 268, figs 15-17.[= *H. borealis*]
*Podocoryne areolata.* – Edwards, 1972: 98, figs 1-2.
*Hydractinia areolata.* – Bouillon *et al.,* 2004: 63, figs 37B-I.

Material examined: FNHM, BIOFAR station 473; 62.603°N 05.717°W; The Faroes; 198 m; 6 June 1989; with medusa buds. – France, Brittany, Roscoff; 1 April 1998; 10 m depth; one mature medusa from plankton; material not preserved. – Norway, Raunefjord; 0-20 m; plankton net 190 $\mu$m; 19 June 2006; one mature medusa; material photographed but not preserved; 16S DNA sequence identical to **AM939651**. – MHNG INVE48749; Norway, Fanafjord, close to southern coast; fine mud; 60-80 m; 16 June 2006; triangular dredge; polyp on gastropod shell with hermit crab; liberated medusae have 16 tentacles, spines not distinctly grouped, but medusa and DNA sequences confirmed identification; 16S DNA sequence **AM939651**.

Diagnosis: Polyps relatively small (2 mm), gonozooids smaller than gastrozooids, spines when present often grouped, newly released medusa with 14-16 tentacles, mature medusa with perradial, basal pouches on manubrium bearing gonads, more than 40 tentacles of very unequal length.

Description: Hydroid growing on shells of hermit-crabs and crab carapaces. Hydrorhiza a small-meshed network of adhering stolons enclosed in perisarc, in more marginal region it can be less densely developed, in some regions network may become confluent and mat-like, layer of naked coenosarc rare or lacking. Spines present or not, presence depending on substrate and environment the host is living in. Spines rather high, slender, pointed, perisarc smooth. The spines can be arranged in a characteristic grouped pattern, either in linear arrays or small rows or groups of closely set spines, alternating with spine-free patches.

Polyps polymorphic, relatively small, differentiated into gastrozooids, gonozooids, tentaculozooids, and spiral zooids; the latter two types may be absent, their presence depending on host and environment.

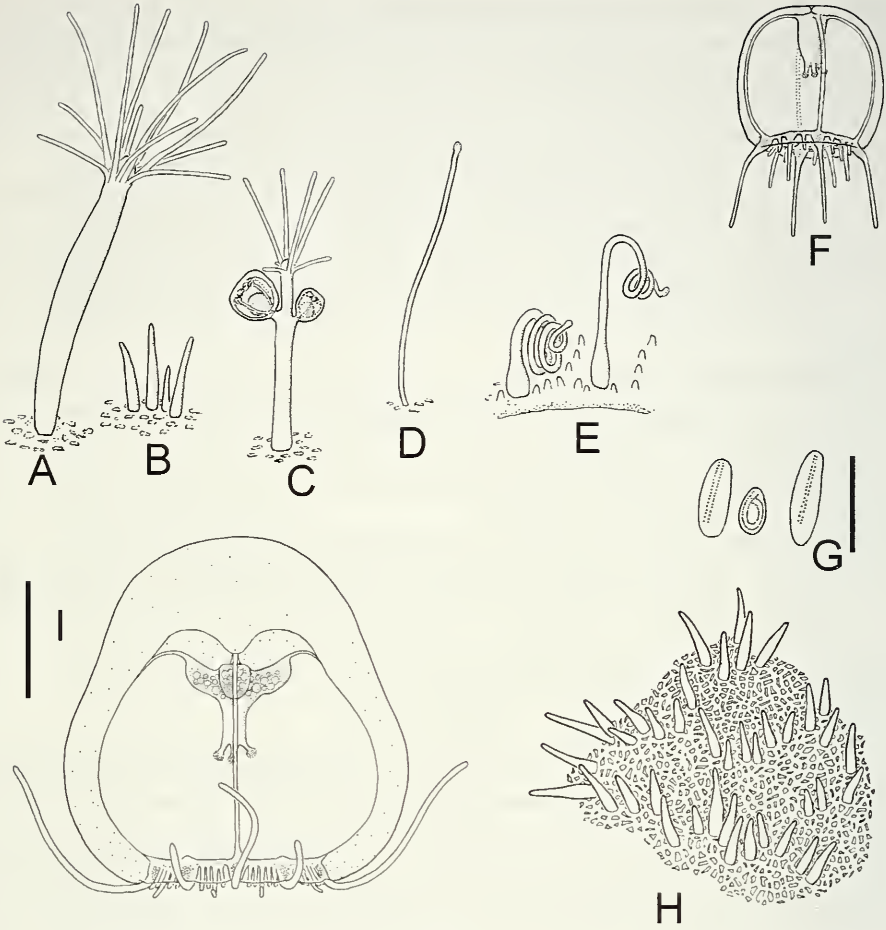

FIG. 1

*Hydractinia areolata* Alder, 1862; A-F, H modified after Edwards, 1972; G after preserved material; I after life. (A) Gastrozooid, ca 2 mm high. (B) Group of spines, same scale as A. (C) Gonozooid, same scale as A. (D) Tentaculozooid, same scale as A. This zooid-type is not always present. (E) Two spiral zooids at the margin of the colony. This zooid-type is not always present. (F) Newly released medusa. (G) Nematocysts: microbasic eurytele, desmoneme, elongate microbasic eurytele of oral lips of the medusa; scale bar 10 $\mu$m. (H) Perisarc skeleton showing mesh of stolons and the characteristically grouped spines. Note that the spines are not present in all colonies and they are sometimes evenly distributed, not grouped. (I) Lateral view of mature medusa from plankton, bell rim slightly contracted, scale bar 1 mm.

Gastrozooids with fusiform body, dome-shaped hypostome, one or two very closely set whorls of tentacles, 9-12 in number (range 4-14), unequal in length, alternately pointing upward and horizontal, base of hydranth without perisarc collar. Hypostome with scattered euryteles, but these not forming a contiguous layer.

Gonozooids smaller and more slender than feeding zooids (ca. 1/3 to 2/3 the size of the gastrozooids), 4-7 tentacles, medusa buds arising below tentacles, one to rarely five in number but usually two, when two buds occur, these opposed. Larger gonozooids are able to ingest prey. With progressing medusa-bud development, gonozooids becoming reduced to mere stumps (reproductive exhaustion), feigning development of the gonophores from stolons.

Tentaculozooids of about the size of gastrozooids, rare, very slender (1/10 of diameter of gastrozooids of similar height), not spirally coiled, uniform thickness, slightly swollen tip.

Spiral zooids sometimes present at the rim of the colony at the outer lip of the supporting gastropod shell, length comparable to large gastrozooids, base swollen, above this swelling tapering to a blunt tip armed with nematocysts, when active coiling and uncoiling frequently.

Nematocysts of polyps: oval microbasic euryteles, desmonemes. Colours: spine perisarc brown; hydranths white to pinkish.

Medusa at liberation usually with 16 tentacles or tentacle rudiments (range 14-16), four perradial tentacles well developed and each with a well developed basal bulb with red gastrodermal tissue, four interradial tentacle bulbs less developed than perradial ones, eight adradial tentacles short, without bulbs. Apical canal present, umbrella spherical, exumbrella sprinkled with numerous nematocysts, manubrium simple, about 1/2 the height of the subumbrellar cavity, square in cross-section, without any trace of gonads or basal pouches, four relatively long, unbranched oral lips.

Adult medusa bell-shaped, slightly wider than high, jelly thicker at apex, often with shallow gastric peduncle. Four radial canals and a circular canal. 40-56 tentacles (max. 66 in Mediterranean), eight tentacles (per- and interradial ones) long, others markedly shorter. Bulbs of variable size, correlated with tentacle length, without ocelli. Manubrium spans about 1/2 to entire height of subumbrella, cross-section cruciform to square, with four characteristic perradial basal pouches of variable size, pouches may reach a size of about 1/3 of radial canal length; four oral lips relatively long and tentacle-like, terminating in single, rounded mass of nematocysts. Gonads adradial on basal pouches and interradial regions between the pouches, separated perradially. Nematocysts: in tentacles shorter microbasic euryteles and desmonemes, on oral lips elongated microbasic euryteles. Medusa gastrodermis vermillion-red, yellow, or dark brown, colour probably depending on diet.

DIMENSIONS: Gastrozooids up to 2 mm, 0.22 mm diameter. Largest spines 0.7-0.9 mm. Microbasic euryteles of polyp (7-8)x(2.5x3) $\mu$m, desmonemes 5x3 $\mu$m. Newly liberated medusa 0.7-0.8 mm in diameter and height, nematocysts like in polyp plus larger euryteles on oral lips ca. 10x3 $\mu$m (for more nematocyst measurements see Yamada, 1961). Gonads mature at a diameter of 1.84 mm (Edwards, 1972). Mature medusae from plankton 3-4 mm in diameter and height. Diameter of eggs 0.15-0.22 mm (Yamada, 1961). For more measurements see Edwards (1972), who also provides a table with the correlation of size, tentacle numbers, and gonad development.

BIOLOGY: The hydroid occurs in depths of 13-275 m, on muddy grounds or mixed mud, shell, and stone bottoms, usually on shells inhabited by various hermit crabs (in the Atlantic e. g. shells of *Natica montagui* and *Turritella communis*) or on crabs like *Inachus dorsettensis* (Pennant) (Mediterranean) or *Hyas coarctatus*

(Atlantic). The medusa can be found in surface waters. It takes about two months for the medusa to reach its full size (Yamada, 1961). In British waters and in the Mediterranean, the medusa has been reported from January to November (Edwards, 1972; Brinkmann-Voss, 1987).

Distribution: Southern Norway, British Isles, Atlantic coast of Spain, western Mediterranean (Yamada, 1961; Russell, 1957, 1970; Edwards, 1972; Medel & López-González, 1996; this study). Not in southern North Sea and Baltic Sea. Type locality: England, Northumberland, Cullercoats, on shell of the gastropod *Natica alderi*.

Remarks: The synonymy and taxonomic history was outlined in detail by Edwards, (1972). Edwards also synonymized the Mediterranean *Pododcoryna hartlaubi* Neppi & Stiasny, 1911 with *H. areolata*. However, some doubts on this synonymy remain and molecular investigations should re-address the question.

The smooth, rather thin and long spines that are aggregated into groups or lines are a characteristic feature of the polyp stage of this species (Fig. 1H). However, the spines are not always present and even when spines are present, not all colonies show this grouping (own observations on material from Norway, cultivation of the medusa and sequence data allowed a reliable identification of the colony). The polyps are conspicuously smaller than *H. borealis* (factor 2). For a reliable identification of the hydroid, the newly liberated medusa must be examined. It has more tentacles (14-16) than any other European *Hydractinia* species. The mature medusa is very distinctive through its perradial stomach pouches and the large number and unequal size of the tentacles (Fig. 1I).

### ***Hydractinia borealis*** (Mayer, 1900a) Figs 2-3

? *Podocoryna tubulariae* M. Sars, 1857: 145.
*Limnorea norvegica* Broch, 1905: 5.
? *Podocoryne alderi* Hodge, 1863: 82, pl. 2 fig. 10. – Edwards, 1972: 135. – Calder, 1988: 27.
*Lymnorea borealis* Mayer, 1900a: 6, pl. 5 figs 16-18. – Mayer, 1910: 154, pl. 15 figs 1-3.
*Podocoryna corii* Stechow, 1929: 150. **new synonym**
*Podocoryne areolata*. – Kramp & Damas, 1925: 268, figs 15-17.
[not *Hydractinia areolata* Alder, 1862]
in part *Podocoryne areolata*. – Hartlaub, 1911: 219, figs 19192-194 [Fig. 191 is *H. areolata*].
*Podocoryne borealis*. – Rees, 1941: 307, fig. 1. – Russell, 1953: 125, figs 57B, 59A, C-F, pl. 6 fig. 5. – Russell, 1970: 235. – Edwards, 1972: 111, figs 4-6, synonymy.
*Hydractinia borealis*. – Schuchert, 2001a: 9, fig. 2A-B.

Material examined: MHNG INVE29474; Iceland, Sandgerdi; 11 May 2000; polyp colony on *Buccinum* inhabited by *Pagurus bernhardus*, medusa development followed to maturity; 16S sequence **AY787878**. – Scotland, Firth of Lorn, Dunstaffnage Bay; 0 m; 10 May 2004; 2 mature medusae from plankton: not preserved; 16S sequence of one specimen gave identical sequence as **AY787878**. – MHNG INVE48806; Norway, Raunefjord; 10 m; 15 June 2006; 2 mature medusae from plankton; 16S sequence of one specimen gave identical sequence as **AY787878**. – Norway, Raunefjord; 0-20 m; 19 June 2006; young medusa with beginning gonad maturation; not preserved.

Diagnosis: Polyps polymorphic, hydrorhiza encrusting, spines smooth, small, not grouped, may be absent. Newly liberated medusa with 6-8 tentacles. Mature medusa with 16 or more tentacles, oral lips divided, manubrium without basal pouches.

Description: Colonies usually growing on shells, crustaceans, *Tubularia*, and other substrates. Stolons in young colonies or at colony margin reticulate and

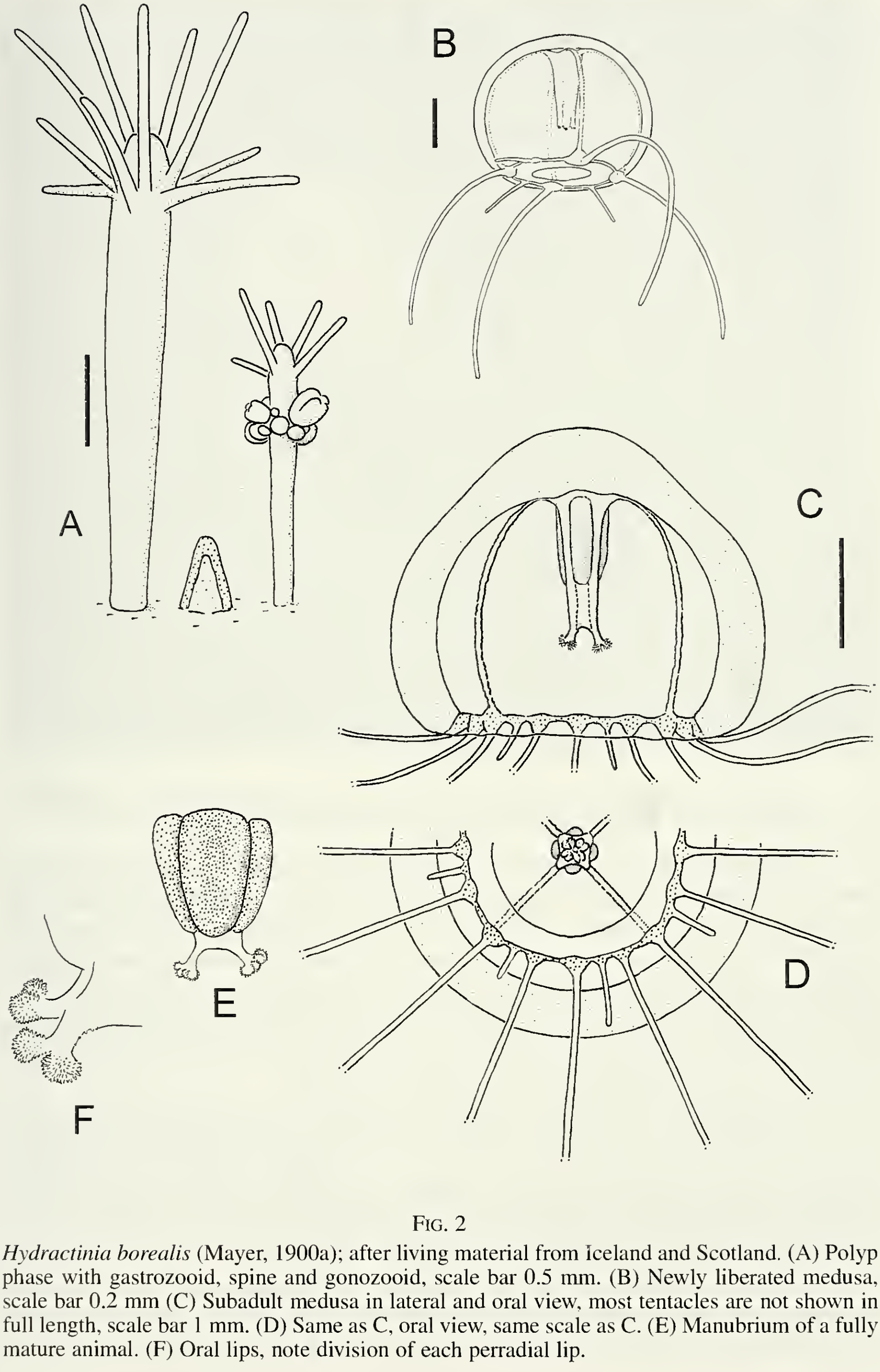

FIG. 2

*Hydractinia borealis* (Mayer, 1900a); after living material from Iceland and Scotland. (A) Polyp phase with gastrozooid, spine and gonozooid, scale bar 0.5 mm. (B) Newly liberated medusa, scale bar 0.2 mm (C) Subadult medusa in lateral and oral view, most tentacles are not shown in full length, scale bar 1 mm. (D) Same as C, oral view, same scale as C. (E) Manubrium of a fully mature animal. (F) Oral lips, note division of each perradial lip.

composed of perisarc covered tubules, later coalescing to a crust that can be covered by coenosarc tissue. Few shallow, conical spines present, not in groups. Polyps polymorphic, with gastrozooids, gonozooids and sometimes tentaculozooids.

Gastrozooids with fusiform body, large dome-shaped hypostome, hypostome with scattered euryteles, but these not forming a contiguous layer, two very closely set whorls of tentacles, 10-16 in number, unequal in length, alternately pointing upward or horizontal, base of hydranth sometimes sitting on shallow, calotte-shaped perisarc beaker, may be absent in some colonies.

Gonozooids smaller and more slender than feeding zooids (ca. 1/4 to 1/2 the size of the gastrozooids), 4-10 tentacles, below tentacles one whorl of up to 10 medusae buds; larger gonozooids able to ingest prey. Nematocysts of polyps: microbasic euryteles (of two similar size classes), desmonemes. Colours: spine perisarc brown; hydranths white to pinkish.

Medusa at liberation with 6-8 tentacles, four perradial and 2-4 short interradial ones, four perradial marginal bulbs, interradial bulbs absent or inconspicuous, manubrium simple, square in cross-section, without any trace of gonads.

Adult medusa slightly wider than high, jelly thicker at apex, no gastric peduncle. Four relatively broad radial canals and a circular canal, 16-30 tentacles of unequal length, perradial and interradial bulbs largest, without ocelli. Manubrium spans about 2/3 of subumbrella, cross-section distinctly cross-shaped to square, with four perradial, long, oral lips. Each oral lip branched at least once and ending in round clusters of cnidophores. Cnidophores are long cells bearing at distal end an elongated eurytele. Gonads oblong pads on manubrium in interradial positions. No medusae budding. Colours: marginal bulbs red-brown or reddish yellow; stomach yellowish brown. Nematocysts: in tentacles shorter microbasic euryteles and desmonemes, on oral lips elongated microbasic euryteles.

ADDITIONAL INFORMATION: Simple, rather thin tentaculozooids can be present in colonies growing on shells inhabited by hermit crabs (Edwards, 1972).

DIMENSIONS (Edwards, 1972; own data): Spines 0.2-0.6 mm high, diameter 0.12 mm. Stolon diameter 0.03-0.06 mm. Gastrozooids usually 4-5 mm high, fully extended reaching up to 15 mm, length of tentacles up to 3.2 mm. Medusa after liberation 0.8 mm, adult medusa up to 3-4 mm high (reportedly up to 5 mm in the western Atlantic), diameter up to 4 mm. Nematocysts of medusa: desmonemes (4.5-6)x(3-3.5) $\mu$m; microbasic euryteles of tentacles (8)x(3.5-4) $\mu$m; microbasic euryteles of oral lips (10-12.5)x(3) $\mu$m. More data, including the relationship of medusa size and tentacle numbers, are given in Russell (1953) and Edwards (1972).

OTHER DATA: The number of spines depends on the environment and the behaviour of the host organism. Colonies from soft muddy localities have few spines whereas those from mixed grounds are often more spiny. It appears that the presence of spines is governed by the roughness of the substratum and by the reaction of the colony to abrasive contact with hard bodies (Edwards, 1972).

BIOLOGY: *Hydractinia borealis* is not very substrate specific, it occurs most commonly on shells inhabited by a variety of hermit crabs, but also on *Tubularia indivisa,* carapaces of crustaceans, mollusc shells, and the polychaete *Aphrodite aculeata*

FIG. 3

*Hydractinia borealis* (Mayer, 1900a), mature medusa from Dunstaffnage, Scotland.

(Edwards, 1972). The hydroid can occur from the low-water mark down to depths of more than 100 m. The medusa is found in the surface waters. In the Clyde Sea Area (western Scotland) it can be found from February to November; more frequently in spring and early summer (Russell, 1953).

DISTRIBUTION (Edwards, 1972): Maine, USA; Iceland; British Isles from the Channel coast to Shetland; North Sea; southern and western Norway. The Mediterranean records are unreliable. Type locality: Eastport, Maine, USA.

REMARKS: This species was studied in detail by Edwards (1972), who provides an excellent, comprehensive report on its taxonomy, life-cycle, and biology. There is only one new synonym to add.

Stechow (1929) described *Podocoryne corii* based on an infertile colony he had obtained from off Oostende (Belgium). He did not publish a figure, but apparently left a drawing with the type material. This illustration will be shown in a forthcoming publication by Ruthensteiner *et al.* (2008). There is nothing in his description or figure that would make this species identifiable, except that it grew on the polychaete *Aphrodite aculeata* (Linnaeus). The only hydractiniid from the region that is known to occur on this substrate is *H. borealis* (see Edwards, 1972: 112). *Podocoryne corii* is therefore here regarded as a questionable synonym of *H. borealis*.

### ***Hydractinia carnea*** (M. Sars, 1846) Fig. 4

*Podocoryna carnea* M. Sars, 1846: 4, pl. 1 figs 7-18, not pl. 2 figs 5-11. [=*H. sarsii*]
*Podocoryna albida* M. Sars, 1846: 7. – Allman, 1872: 349, synonym.
*Sarsia nodosa* Busch, 1851: 17, pl. 2, figs 6-8. – Edwards, 1972: 133, synonym.
*Hydractinia echinata.* – Lovèn, 1857: 305, pl. 4. [not *Hydractinia echinata* (Fleming, 1828)]
*Podocoryne inermis* Allman, 1876: 255, pl. 10, figs 4-5.
*Podocoryne carnea.* – Hincks, 1868: 29, pl. 5. – Browne, 1896: 463. – Bonnevie, 1898: 486. – Jäderholm, 1909: 50, pl. 3 figs 1-3. – Broch, 1911: 19, fig. 15. – Kramp, 1927: 72, fig. 1. – Rees, 1941: 310, fig. 1b. – Vervoort, 1946: 126, fig 49. – Kramp, 1961: 68. – Russell, 1953: 121, Figs 57A, 58A, 59A, pl. 6 figs 2-3. – Kramp, 1959: 101, fig. 65. – Avset, 1961: 49, figs 1-4. – Edwards, 1972: 122, figs 7-9, synonymy, bibliography.
in part *Podocoryne carnea.* – Allman, 1872: 349, pl. 16 figs 1-9. – Mayer, 1910: 136, fig. 75, pl. 14.
? *Podocoryne carnea* var. *chilensis* Kramp, 1952: 4, figs 1-2.
*Hydractinia carnea.* – Naumov, 1969: 219, figs 51c & 87.

MATERIAL EXAMINED: BMHNH 1877.4.12.12, syntype material of *Podocoryne inermis* Allman 1876; 6 colonies on gastropod shells, loc. Denmark. – ZMUC, without registration number, as *Podocoryne carnea*; Denmark, Frederikshavn; 31 Jul.-11 Aug. 1933; several 100 medusae released from polyp, leg. P. Kramp. – ZMUC, without registration number, as *Podocoryne carnea*; Denmark, Middelfart Sund; 16 Jul. 909; 2 medusae from plankton, leg. Kramp. – ZMUC, without registration number, as *Podocoryne carnea*; Denmark, Hirshomene; 14 Jul. 1956; several medusae from plankton, leg. K.W. Petersen. – ZMUC, without registration number, as *Podocoryne carnea*; Denmark, Randers Fjord; 6-9 m depth; 28 Aug. 1915; polyp colony on *Nassarius reticulatus* (L.). – ZMUC, without registration number, as *Podocoryne carnea*; Denmark, Frederikshavn; 28 June 1909; polyp colony on *Nassarius reticulatus* (L.).

DIAGNOSIS: Polyps polymorphic, hydrorhiza stolonal or encrusting, spines smooth, not grouped, may be absent. Newly liberated medusa with 5-8 tentacles, with or without immature gonads. Mature medusa with 8 tentacles, oral lips undivided, without basal extensions of manubrium.

DESCRIPTION (after Edwards, 1972 and examined material): Colonies usually growing on gastropods of the genus *Nassarius* and on shells inhabited by hermit crabs. Hydrorhiza either reticulate stolons or forming an encrusting plate covered by coenosarc tissue. Spines rather shallow, not grouped, blunt, density variable, often absent, presence depends on host and exposure to abrasive contact. No perisarc collar at base of hydranths except rarely for some polyps near the colony margin. Polyps polymorphic with gastrozooids, gonozooids and sometimes tentaculozooids and spiral zooids.

Gastrozooids with fusiform to cylindrical body when relaxed, dome-shaped hypostome, hypostome with scattered euryteles not forming a contiguous layer, one whorl of 12-19 tentacles of different length, alternately pointing upward or horizontal, longest ones shorter than hydranth body height.

Gonozooids usually smaller and more slender than feeding zooids (ca. 1/4 to nearly same size as gastrozooids), 4-10 tentacles, shorter than those of gastrozooids, below tentacles one whorl of 1-10 medusa buds. With continued medusa-budding the gastrozooids may become reduced to mere stumps (reproductive exhaustion).

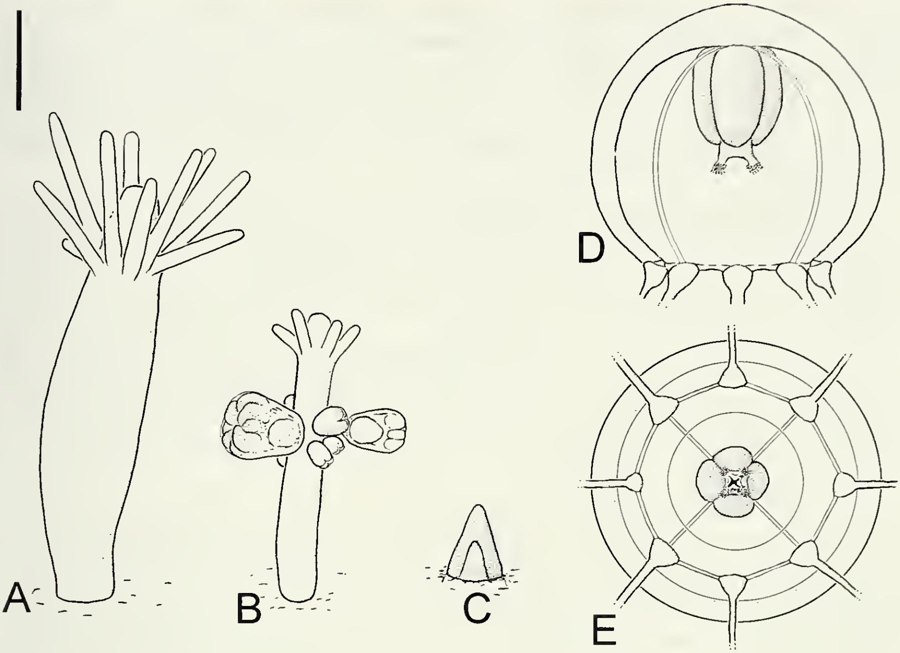

FIG. 4

*Hydractinia carnea* (M. Sars, 1846), schematic after several preserved samples, scale bar 0.5 mm. (A) Gastrozooid. (B) Gonozooid with medusa buds. (C) Spine. (D) Mature medusa from plankton in side view. (E) Oral view of medusa.

Spiral- and tentaculozooids only in colonies on hermit crabs. Spiral zooids on lip of shell opening, coiled a few times when contracted, distal end slightly swollen. Tentaculozooids very slender, within colony.

Nematocysts of polyps: microbasic euryteles of two size classes, desmonemes. Colours: spine perisarc brown; hydranths white to pinkish, variable.

Medusa at liberation with 5-8 tentacles, four perradial and 2-4 short interradial ones, four perradial marginal bulbs, interradial bulbs sometimes smaller or inconspicuous; manubrium simple, square in cross-section, with or without visible gonads (esp. oogonia are easy to see); numerous nematocysts scattered over the exumbrella.

Adult medusa slightly wider than high, jelly thicker at apex, without gastric peduncle (a slight gastric peduncle may be formed transiently in juvenile specimens). Four radial canals and a circular canal. Eight tentacles of approximately equal length, eight bulbs all of similar size, without ocelli. Exumbrella with no or few nematocysts. Manubrium spans about 1/2 of subumbrella, cross-section distinctly cross-shaped to square, mouth with four perradial unbranched tufts of long cnidophores. Cnidophores long cells bearing at distal end an elongated eurytele. Gonads oblong, vertical pads on manubrium in interradial positions. No medusae budding.

Nematocysts: in tentacles microbasic euryteles and desmonemes, on oral lips elongated microbasic euryteles.

DIMENSIONS (after Edwards, 1972 and examined material): Gastrozooids up to 5.5 mm, more commonly 2-3 mm. Spines 0.2-0.3 mm. Nematocysts of polyps (preserved): microbasic euryteles (9-10)x(2.5-3) $\mu$m, (6.5-7)x(2-2.5) $\mu$m; desmonemes (4.5-5.5)x(2.5-3) $\mu$m. Newly released medusae 0.7-0.8 mm. Medusae from plankton 1.6-1.8 mm in diameter, largest specimens 2.4 mm in diameter and 2.1 mm high. More data are provided by Edwards (1972).

OTHER DATA: Rarely some medusae may have 9 or 10 tentacles. The degree of spininess shows great variation and depends on the host species. The hydrorhizal base is also variable, either a stolonal mesh or encrusting. It is mostly encrusting on shells inhabited by hermit crabs. For additional details see Edwards (1972). Rasmussen (1973) examined and depicted the distribution of the polyps on the host shell. Some authors found that the newly liberated medusae had no gonads yet (M. Sars, 1846), while others observed medusae with incipient gonads (Lovèn, 1857, as *H. echinata*; Avset, 1961; Edwards, 1972). Avset (1961) describes the histology of the medusa-bud development and the gametogenesis.

BIOLOGY (after Edwards, 1972): Occurs on shells with living gastropods or inhabited by hermit crabs. When living on gastropods, then *Nassarius reticulatus* (L.) is the preferred host, sometimes also *N. incrassatus* (Ström). The species shows less specificity for hermit crabs (shells of *Buccinum, Nassarius, Natica, Littorina, Turritella,* hermit crabs like *Pagurus prideauxi, P. bernhardus, Anapagurus laevis*). Occurs from the low water mark (on *N. reticulatus*) to 180 m (Christiansen, 1972). Christiansen (1972, Oslofjord, Norway) found polyps with medusae buds from gonophores April to October, with a maximum June-July. Rasmussen (1973, Denmark, in Isefjord) observed medusae buds from June to October, with maximum from July to August. Edwards (1972) found the medusa in the plankton of the Clyde Sea (Scotland) from March to October. Under laboratory conditions the medusae had a life span of up to 24 days.

DISTRIBUTION: British Isles including the Channel coast, Denmark, Sweden, and Norway. In the Baltic Sea, it seems to occur only along the Danish peninsula (Stechow, 1927). Absent from Helgoland (Hartlaub, 1911); Leloup (1947) qualifies it as rare along the Belgian coast. Many records, especially those outside the region outlined above, are doubtful as information on the medusa stages was not taken into consideration (see below). Type locality: The material of Sars was collected near Florö and Manger, Norway.

REMARKS: A full description, synonymy, and revision of this species are provided by Edwards (1972). Edwards also separated the North American form of *H. carnea* (see also Mayer, 1910) as a separate species *H. americana* (Edwards, 1972). There are other very similar species like *H. selena* (Mills, 1976) in the Gulf of Mexico and *H. australis* (Schuchert, 1996) in New Zealand. These species can be distinguished only in the medusa phase and the differences are rather minute. This underlines again the opinion of Edwards (1972: 124): "...it is in general unsafe to give an identification without details of the stages of growth and maturity of the medusa." In view of the subtle differences of these species, and in contradistinction of Edwards (1972), *Hydractinia exigua* is here regarded as distinct from *H. carnea* (see Remarks for *H. exigua*).

The mature medusa is not commonly found in the plankton, although he hydroid may be rather common (Kramp, 1937; Russell, 1953; Edwards, 1972).

***Hydractinia exigua*** (Haeckel, 1880) Figs 5-6

?*Dysmorphosa conchicola* Philippi, 1842: 37.
*Podocoryna carnea*. – Krohn, 1851: 263. – M. Sars, 1857: 144. – Grobben, 1876: 455-486, pls 1-2. – Weisman, 1883: 65, pl. 19. – Goette, 1916: 455, pl. 13 figs 4-10, pl. 14 fig. 24. – Brinckmann-Voss, 1970: pl. 7 fig 3. [not *Hydractinia carnea* (M. Sars, 1846)]
*Cytaeis exigua* Haeckel, 1880: 634. – Neppi & Stiasny, 1913: 22, pl. 1 fig. 11; pl. 4 figs 1-2.
*Podocoryne conchicola*. – Hargitt, 1904: 581, pl. 22 fig. 26
*Hydractinia carnea*. – Motz-Kossowska, 1905: 85.
*Hydractinia carnea* var. *inermis*. – Motz-Kossowska, 1905: 85. [not *Podocoryne inermis* Allman, 1876]
*Hydractinia carnea* var. *mediterranea* Neppi, 1917: 39.
*Podocoryne exigua*. – Picard, 1958: 190. – Cerrano *et al*., 1998: 1101, fig. 5.
*Podocoryne exigua*. – Edwards, 1972: 131.

MATERIAL EXAMINED: MHNG INVE54615, MHNG INVE54616, MHNG INVE54625; Italy, Naples. – MHNG INVE54617; France, Roscoff; coll. 20 May-6 Jun. 1910, leg. M. Bedot. – Atlantic, France, Brittany, Roscoff; several colonies cultivated in aquariums, 1991-92, medusae mature at release; 16S sequence accession number **AM939652**. – Mediterranean, Italy, Naples; several colonies cultivated in aquariums, 1991-92, medusae reared to maturity; 16S sequence identical to **AM939652**. – Mediterranean, France, Banyuls-sur-Mer; 9 May 2002; several colonies on shells of *Nassarius* spec. (with gastropod and hermit crabs), medusa reared to maturity; not preserved; 16S sequence accession number **AM939653**. – Mediterranean, France, Banyuls-sur-Mer; 6 May 2002; several colonies on *Bolinus brandaris* (L.); not preserved. – Mediterranean, France, Roussillon, Ste Marie-la-Mer, depth 2 m; 15 July 1998, several colonies with medusa buds, on shells inhabited by hermit crabs. – Atlantic, France, Brittany, Roscoff, l'Estacade, low water level of spring tide; 14 Sept. 2004; on *Nassarius reticulatus* (L.) (gastropod); not preserved. – Atlantic, Spain, San Sebastián (Guipúzcoa), depth 6 m; collected August 2006 by Dr. A. Altuna, with medusa buds, material used to make DNA; 16S sequence **AM939654**.

DIAGNOSIS: Polyps polymorphic, hydrorhiza stolonal or encrusting, spines smooth, not grouped, may be absent. Newly liberated medusa with 4 tentacles, gonads mature or in development. Mature medusa with 4 tentacles, oral lips undivided, without basal extensions of manubrium.

DESCRIPTION: Colonies usually growing on gastropods of the genus *Nassarius* (=*Hinia*) or on shells inhabited by hermit crabs. Hydrorhiza either reticulate stolons or forming an encrusting plate covered by coenosarc tissue. Spines present or not, rather shallow, not grouped, blunt, density variable within colony. No perisarc collar at base of hydranths. Polyps polymorphic with gastrozooids, gonozooids and sometimes tentaculozooids and spiral zooids.

Gastrozooids with fusiform to cylindrical body when relaxed, dome-shaped hypostome, hypostome with scattered euryteles, but these not forming a contiguous layer, one whorl of 10-13 tentacles of different length, alternately pointing upward or horizontal, longest ones shorter than hydranth body height.

Gonozooids usually somewhat smaller and more slender than feeding zooids (ca. 1/2 to nearly same size as gastrozooids), 4-8 tentacles, shorter than those of gastrozooids, below tentacles one whorl of up to 10 medusa buds. With continued medusa budding, the gastrozooids can sometimes become reduced to mere stumps (reproductive exhaustion).

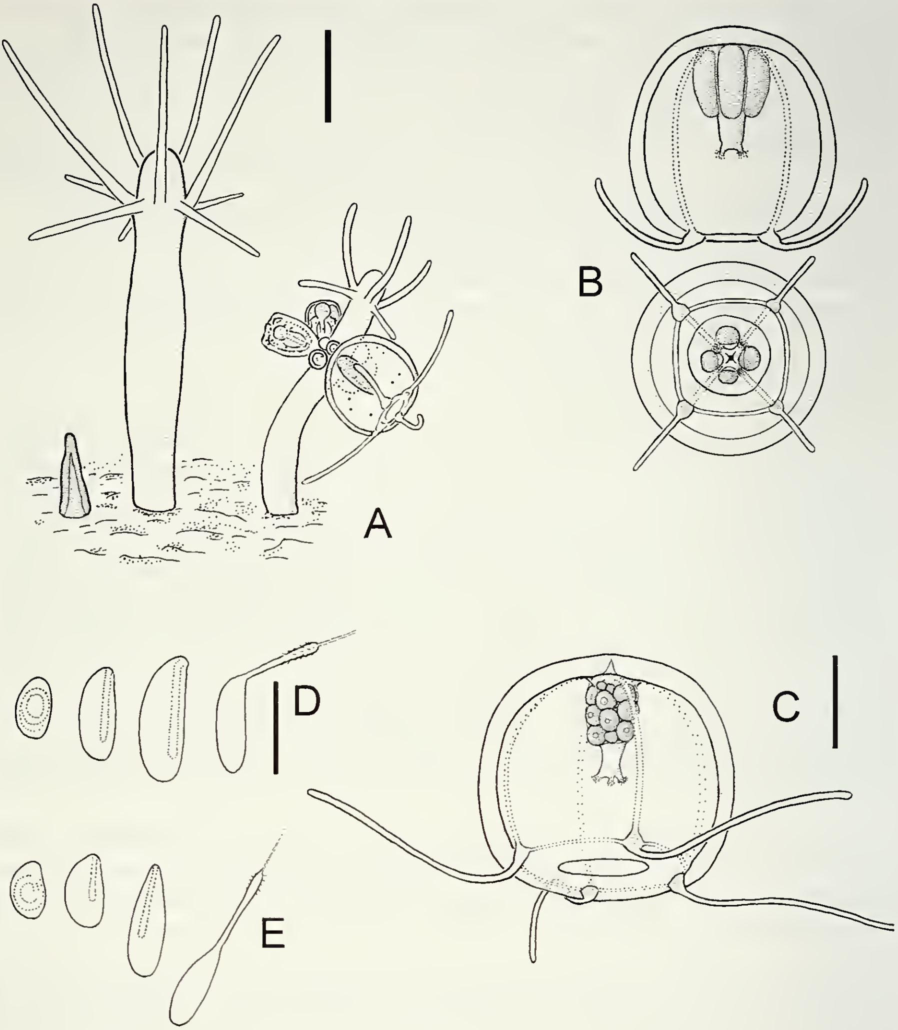

FIG. 5

*Hydractinia exigua* (Haeckel, 1880); all after life, A-B, after colony from Banyuls; C, from Roscoff; D-E, from Naples. (A) Part of colony with spine, gastrozooid, and gonozooid releasing a medusa; scale bar 0.5 mm. (B) Mature male medusa six days after release, side and oral view, same scale as A. (C) Newly liberated female medusa, note mature gonads, scale bar 0.5 mm. (D) Nematocysts of polyps: desmoneme, small microbasic eurytele, large microbasic eurytele, same discharged, scale bar 10 $\mu$m. (E) Nematocysts of newly liberated medusa: desmoneme, small microbasic eurytele from tentacles and exumbrella, elongated microbasic eurytele from mouth clusters, same discharged, magnification as in D.

Spiral- and tentaculozooids only in colonies on hermit crabs. Spiral zooids on lip of shell opening, coiled a few times when contracted, distal end slightly swollen. Tentaculozooids very slender, within colony.

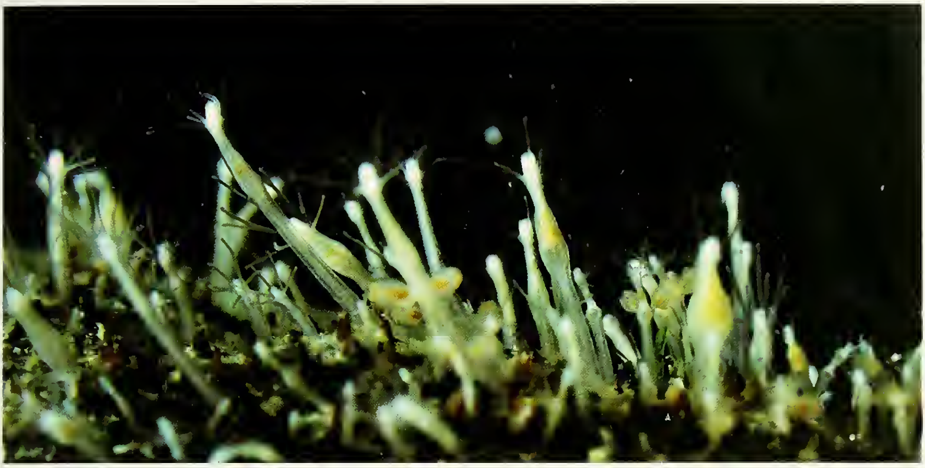

FIG. 6

*Hydractinia exigua* (Haeckel, 1880), living colony from Roscoff, showing spines, gastro-, and gonozooids.

Nematocysts of polyps: microbasic euryteles of two size classes, desmonemes. Colours: spine perisarc brown; hydranths cream to pinkish, variable.

Medusa at liberation similar to mature medusa, either with mature gonads or with immature gonads (better observable in females); numerous nematocysts scattered over the exumbrella, umbilical canal.

Fully grown medusa approximately spherical, jelly even or apex thickened, without gastric peduncle. Four radial canals and a circular canal. Four perradial tentacles of approximately equal length, four bulbs all of similar size, without ocelli. Exumbrella with no or few nematocysts. Manubrium spans about 1/2 of subumbrella, cross-section distinctly cruciform to square, mouth with four perradial tufts of cnidophores, lips unbranched. Cnidophores are long cells bearing at distal end an elongated eurytele. Gonads vertical, interradial, oblong pads on manubrium in interradial positions, perradial interruption visible in males only. No medusa-budding.

Nematocysts in tentacles microbasic euryteles and desmonemes, on oral lips elongated microbasic euryteles.

DIMENSIONS: Colonies from a few $mm^2$ up to a few $cm^2$ in size. Polyps 2-6 mm (in life), spines 0.4 mm. Newly liberated medusa 0.4-1.2 mm (correlating with gonad development); fully grown medusa 1-1.2 mm high and wide. Nematocysts (native) of polyp: small microbasic euryteles (7.5-10.5)x(3-3.5) $\mu$m, large microbasic euryteles (10.5-13)x(4-5) $\mu$m, desmonemes (6-7)x(3.5-4) $\mu$m. Nematocysts (native) of medusa: small microbasic euryteles (11-12)x(4-5) $\mu$m, microbasic euryteles from lips (14-17.5)x(4-5) $\mu$m.

OTHER DATA: At liberation, the medusae of the population in Roscoff (Brittany) possess mature gonads that can spawn gametes (induced by a change from darkness to light). Mediterranean populations produce medusae with immature gonads that take a few days (6-7) to mature (own observations based on animals taken from nature).

Rarely (one in several hundreds), the medusa has 5 or 6 tentacles, sometimes accompanied by other abnormalities (Neppi & Stiasny, 1913). Some or most populations never produce medusae with more than four tentacles (Cerrano *et al.*, 1998; own observations).

Cerrano *et al.* (1998) demonstrated that spines replace regressing polyps. Goette (1916, as *P. carnea*) examined the formation of the stolonal plate. The development of the medusa bud was investigated by e. g. Weismann (1883), Frey (1968), Schmid & Tardent (1969), and Boelsterli (1977). For the embryonic development see Bénard-Boirard, (1962) or Bodo & Bouillon (1968). This species, although under the name *Podocoryne carnea*, was also used for numerous studies in molecular- and cell-biology (e. g. by Prof. V. Schmid and his students).

BIOLOGY: Occurs from the tidal level to about 50 m (Peña Cantero & García Carrascosa, 2002), living on gastropods (mainly *Nassarius* spec., *Bolinus brandaris*, and *Aporrhais*) and on shells inhabited by hermit crabs, rarely also on other substrata (not all records are reliable). In the Atlantic, it seems to occur almost exclusively on *Nassarius reticulatus* (L.). The number of hosts bearing polyps declines from spring to summer for a factor of 10 (Cerrano *et al.*, 1998). Medusa budding can occur all year round (Cerrano *et al.*, 1998; Ligurian Sea). Teissier (1965; English Channel, as *P. carnea*) reported a budding period from May to September. Brinkmann-Voss (1987) observed the medusa in the plankton of the Gulf of Naples from January to April. Cerrano *et al.* (1998) found that medusa-budding zooids are able to detach from the colony, continue to live individually, and re-colonize new hosts.

DISTRIBUTION (some records as *P. carnea*): Western Mediterranean and Adriatic Sea (e. g. Krohn, 1851; Grobben, 1876; Motz-Kossowska, 1905; Hargitt, 1904; Neppi & Stiasny, 1913; Brinkmann-Voss, 1987; this study), Black Sea (Stantschew, 1940), perhaps also Morocco (Patriti, 1970), ? Portugal (Da Cunha, 1944), Atlantic coast of Spain (A. Altuna, pers. comm.), Brittany (Bénard-Boirard, 1962; Teissier, 1965; this study). The northernmost records are from Roscoff (southern coast of the English Channel). Surprisingly, it seems to be absent from the nearby English coast. Type locality: Naples, Italy.

REMARKS: The specific status of *H. exigua* (Haeckel, 1880) is not entirely clear. Some recent authors (Peña Cantero & García Carrascosa, 2002; Bouillon *et al.*, 2004) considered it conspecific with *H. carnea*, others regarded it as clearly distinct from this species (e. g. Hargitt, 1904; Neppi & Stiasny, 1913; Picard, 1958; Cerrano *et al.*, 1998). Edwards (1972) elegantly evaded the problem by regarding it as a subspecies. As the *carnea*- and *exigua*-form occur in disjunct areas, this is a perfectly valid hypothesis. Edwards view gains some further support by the observations of Rees (1941d), who observed intermediate forms with six tentacles in the region of Plymouth, a region where the distribution areas of both forms comes close together. The species *exigua* was here nevertheless upheld, mainly for the reason that subspecies can usually be regarded as equivalent to a full species as well. Population genetic methods must be applied to clarify the status of both forms. Another argument can be constructed using *H. selena* (Mills, 1976) and *H. australis* (Schuchert, 1996), nominal species which are distinguished based on similarly minute details from *H. carnea* as is *H. exigua*.

As outlined by Edwards (1972), *Dysmorphosa conchicola* Philippi, 1842 is likely a senior synonym of *H. exigua*, but it is was so inadequately described that is must be regarded as an indeterminate species.

***Hydractinia allmanii*** Bonnevie, 1898 Fig. 7

*Hydractinia allmanii* Bonnevie, 1898: 485, pl. 26 figs 36-37. – Bonnevie, 1899: 47, pl. 1 fig. 1. – Jäderholm, 1902: 8. – Jäderholm, 1908: 7, pl. 1 fig. 5, pl. 2 figs 2-5. – Jäderholm, 1909: 49. – Rees, 1956b: 109. – Rees, 1956a: 352, pl. 2 figs 1-7. – Naumov, 1969: 220, fig. 88. – Schuchert, 2001a: 13, fig. 3.

*Hydractinia ornata* Bonnevie, 1898: 485, pl. 26 fig. 4. – Rees, 1956b: 112, synonym.

MATERIAL EXAMINED: FNHM BIOFAR station 169; The Faroes, 62.625°N 03.546°W, 808 m, one fertile colony. – MHNG INVE27332; Eastern Greenland, 74.21°N 19.72°W, 43-53 m, 19 July 1930. More in Schuchert (2001a).

DIAGNOSIS: Arctic species, on gastropod shells, hydrorhiza encrusting, gonozooids with few tentacles and two gonophores, gonophores medusoid, large, with eight rudimentary tentacles and bulbs, up to 100 eggs.

DESCRIPTION: Colonies growing in dense and large colonies on gastropod shells, preferably *Colus* spec. Hydrorhiza coalesced into a crust with a top layer of naked coenosarc, spines either small or smooth, needle-like tubes, basal plate without prickles. Polyps dimorphic with gastrozooids and gonozooids; tentaculozooids and spiral zooids not known.

Gastrozooids very large, with a thin, shallow basal perisarc collar, body below tentacles often slightly thinner, hypostome large and dome-shaped, one whorl of 10-16 tentacles, hypostome with a broad band of contiguous euryteles.

Gonozooids only about half the height of the gastrozooids, with 4 (range 0-6) short tentacles, region above gonophores often thinner, hypostome densely studded with nematocysts. Gonozooids also have a shallow perisarc collar at base. Gonophores arise in upper third of gonozooid, normally two in opposite position, one small and one advanced. Mature gonophores spherical or slightly oblong.

Gonophores are medusoids, presumably remaining fixed. Medusoids with thin jelly, swollen manubrium with a length of 2/3 of the bell, velum present, four distinct radial canals and eight rudimentary marginal bulbs or tentacles. Fully mature gonophores have eight rudimentary tentacles, four perradial larger and four smaller interradial ones. Gonads cover manubrium and nearly entirely fill the subumbrella. Mature females with up to 100 eggs in one layer. Nematocysts: larger capsules on hypostome of both zooid types; heteronemes on tentacles of both zooid types; desmonemes, on tentacles of gastrozooids only.

DIMENSIONS: Colonies can cover several cm$^2$, gastrozooids 5-10 mm (max. 15 mm, Jäderholm, 1902), spines up to 1 mm, but usually much smaller. Mature gonophores about 1.0-1.2 mm in length. Nematocysts: large capsules on hypostome (14-16)x(4-5) $\mu$m; heteronemes in tentacles (9-11)x(3-4) $\mu$m; desmonemes (6-7)x (3-4) $\mu$m.

DISTRIBUTION: An arctic species, occurring in deep waters off northern Norway, eastern Greenland, Spitsbergen, Iceland, Arctic seas north of Russia, Sea of Okhotsk, Kuriles (Rees, 1956a; Naumov, 1969). Along the European coasts, it occurs as far

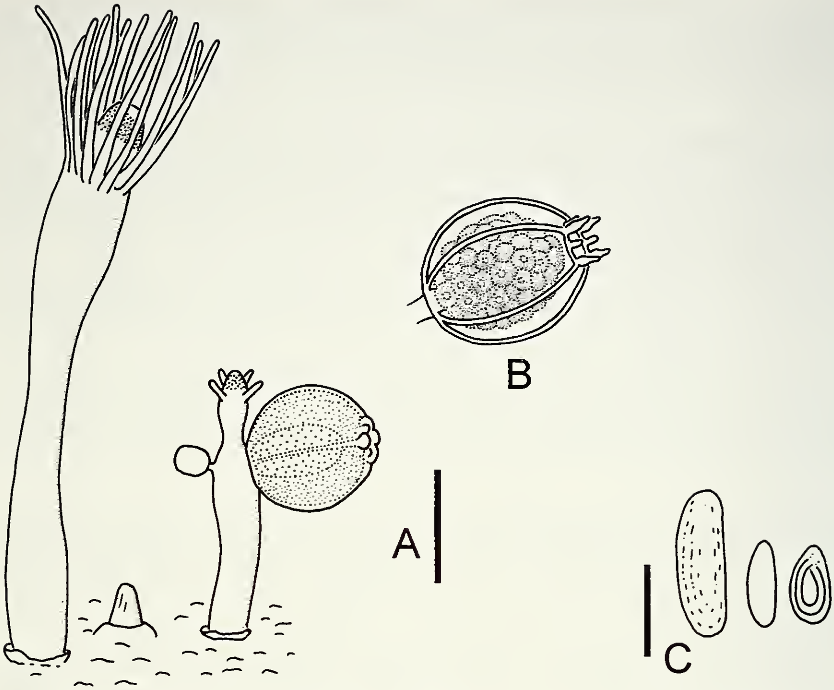

FIG. 7

*Hydractinia allmanii* Bonnevie, 1898; from Schuchert (2001a). (A) Part of colony with gastrozooid (left), spine (middle), and male gonozooid (right), scale bar 1 mm. (B) Female medusoid, same scale as A. (C) Nematocysts (preserved material): large capsule from hypostome, small capsule from tentacles, desmonemes, scale bar 10 $\mu$m.

south as in deep waters near the Faroe Islands (this study). Type locality: off Norway, 67.40°N 8.97°E, 827 m.

BIOLOGY: Epizooic on gastropod shells inhabited by molluscs, preferably of the genus *Colus* (syn. *Sipho*) (Family Buccinidae), in depths of 3-1500 m, mainly between 40 and 250 m. Water temperatures -1.2 to 2.7 °C (Rees, 1956a).

REMARKS: A distinct and unproblematic species, the synonymy and history of which has been outlined by Rees (1956a, 1956b). The morphology is rather variable, the gonozooids are very prone to reproductive exhaustion. Male and female medusoids can occur in the same colony (Rees, 1956a).

It is not known whether the medusoids are released.

The species resembles *Hydractinia hooperi* Sigerfoos, 1899, but which does not form an encrusting hydrorhiza.

### ***Hydractinia pruvoti*** Motz-Kossowska, 1905 Fig. 8

*Hydractinia pruvoti* Motz-Kossowska, 1905: 89, figs 12-13. – Neppi, 1917: 40, figs 5-6, pl. 4 figs 12-13. – Iwasa, 1934: 260, figs 13-14. – Bouillon *et al.*, 1997: 480. – Bavestrello *et al.*, 2000: 361, fig. 1. – Bouillon *et al.*, 2004: 66, fig. 39H-I.

*Stylactis pruvoti*. – Behner, 1914: 407, fig. 13-18, pl. 7 fig. 7-8. – Kramp, 1959: 103, fig. 74. – Kramp, 1961: 71.

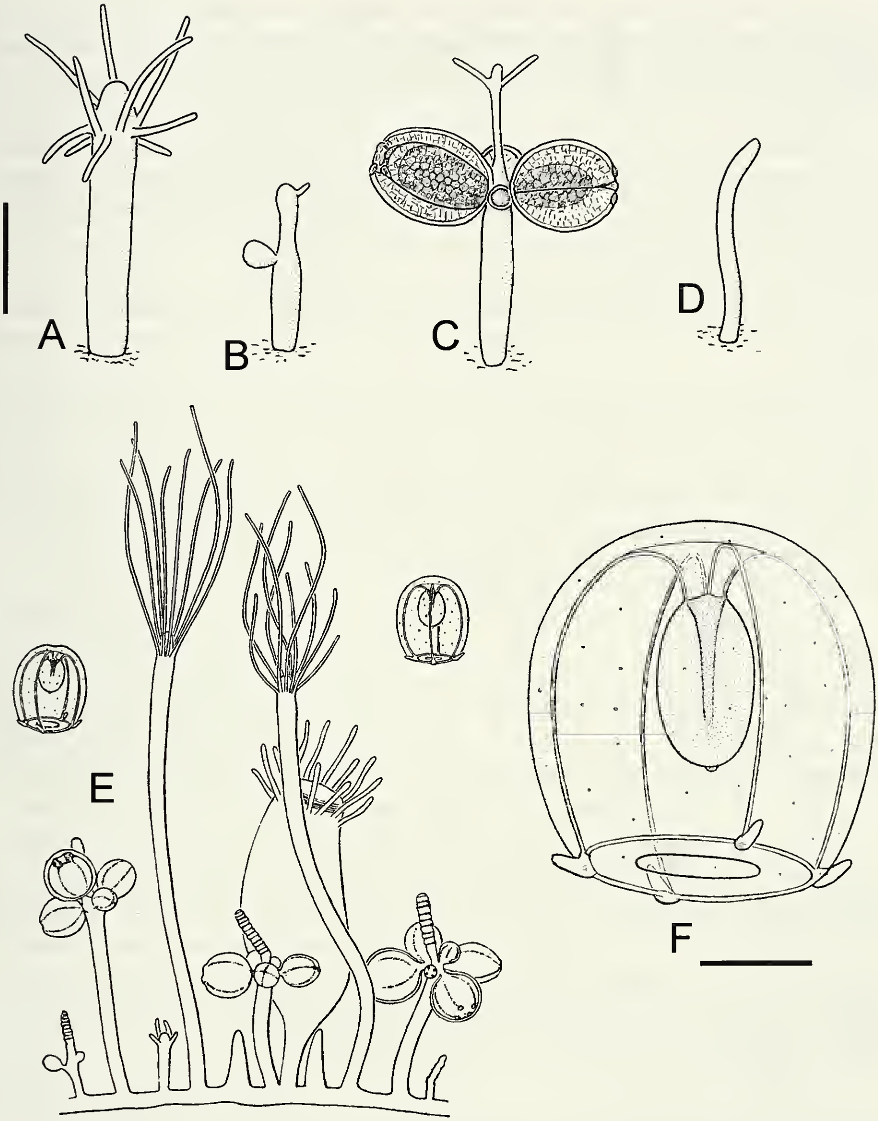

Fig. 8

*Hydractinia pruvoti* Motz-Kossowska, 1905; A-D after living material from Banyuls-sur-Mer, E-F modified from Behner (1914). (A) Gastrozooid, scale bar 0.5 mm (valid also for B-D). (B) Developing gonozooid with one tentacle. (C) Gonozooid with two tentacles and four medusa buds. (D) Tentaculozooid or other, modified zooid. (E) part of colony, showing gonozooids of various developmental stages, gastrozooids, spines, two free medusoids. (F) Liberated male medusoid, scale bar 0.5 mm.

Material examined: MHNG INVE32973; Mediterranean, France, off Banyuls-sur-Mer, depth 62 m, bottom type sand-mud-gravel; 42.506°N 03.167°E; 15 May 2002, on *Nassarius pigmaeus* (Lamarck) (Gastropoda), examined alive, some polyps used to extract DNA, 16S sequence will be published elsewhere by Dr M. P. Miglietta.

Diagnosis: Encrusting or stolonal hydrorhiza, gastrozooids 10-12 tentacles in one whorl, gonozooids smaller and only 1-2 tentacles, no functional mouth, short-lived medusoids with mature gonads, with gastric peduncle, released or not, > 100 eggs, four tentacles stumps.

Description (after literature and examined material): Colonies growing on various gastropod shells inhabited by molluscs or hermit crabs. Hydrorhiza variable, either reticulate stolons or encrusting with top-layer of coenosarc (covered by filmy perisarc), small spines present or not, smooth. Polyps polymorphic, gastrozooids, gonozooids, and tentaculozooids.

Gastrozooids with dome-shaped hypostome, without band of contiguous nematocysts; 8-14 tentacles in one whorl, unequal in length, alternately pointing upward and horizontal.

Gonozooids smaller and more slender than feeding zooids (ca. 1/3 to same size as gastrozooids), upper part above medusa buds narrow, without mouth, only with one or two thin tentacles, rarely three tentacles, tentacles very contractile, can be contracted to short stumps; in upper third one whorl of 3-5 (max. 8) medusa buds. mature buds large, globular to oblong, filled with gametes, radial canals and bulbs well visible.

Nematocysts: desmonemes and two (?) heteronemes of different size, the larger ones in groups of 20-30 on hydranth body.

Gonophores short-lived medusoids that can be released or which remain attached to the gonozooid. Liberated medusoid spherical to slightly higher than wide, jelly thin and even, covered by nematocysts, with gastric peduncle (ca. 1/5 of subumbrella height), wide circular canal and velum present. Four radial canals, four small perradial tentacle bulbs, four short tentacle stumps. Manubrium spanning about half the subumbrellar height, thin, without mouth, surrounded by a very thick gonad without perradial interruptions, females with numerous (>100) eggs. Colonies unisexual.

Dimensions: Gastrozooids in observed material 1-2 mm high (also Bavestrello *et al.*, 2000), others observed larger polyps. Motz-Kossowska (1905) gives a maximum of 15 mm but in her figures they are 2.7 mm high; Behner (1914) 4-5 mm; Neppi (1917) up to 6 mm. Gonozooids with mature medusae half to same size as gastrozooids. Spines 0.2-0.3 mm (Bavestrello *et al.*, 2000) or 0.5-0.6 mm (Behner, 1917). Mature gonophores 0.5 mm long (examined material), Neppi (1917) gives 0.84 mm. Released medusoid 1 mm and 0.6-0.7 mm wide (Behner, 1917).

Other Data: Bavestrello *et al.* (2000) found that water currents induce all polyp types to pinch off fragments of their body. These propagules can settle on other substrates – also inorganic ones – and produce new colonies. The medusoids can swim and spawn for several days (Bavestrello *et al.*, 2000).

Biology: Grows on gastropod shells of various species and sizes, either inhabited by a hermit crab or mollusc Motz-Kossowska (1905) found it on *Galeodea rugosa* (L.) inhabited by *Dardanus arrosor* (Herbst) [as *Pagurus striatus*]. Behner (1914) found his colony on a *Cerithium* shell, Bavestrello *et al.* (2000) on *Monodonta turbinata* [now *Osilinus turbinatus* (Von Born)] inhabited by *Clibanarius erythropus.* The present material was on the gastropod *Nassarius pigmaeus* (Lamarck). Depth range 10-62 m. Gonophores were observed from May to September.

DISTRIBUTION: Endemic to the western Mediterranean. It is quite a rare species, mostly reported as single findings only. Type locality: Balearic Islands, Mediterranean.

REMARKS: This species is usually portrayed as having gonozooids with a single tentacle only, although already Motz-Kossowska (1905) mentioned that some might have up to three tentacles. The gonozooids of colony examined for this study had mostly two tentacles, a few had one only (see Fig. 8B-C). Behner (1914), Neppi (1917), and Bavestrello *et al.* (2000) observed that the medusoids are released and are able to swim for some days. The colony observed by me developed pulsating medusoids with four tentacle rudiments, just as observed by the other authors, but they remained attached to the polyp while they spawned. These differences can certainly be attributed to intraspecific variation. Allowing some more tentacles on the gonozooids brings *H. pruvoti* rather close to *H. aculeata*, especially as it was described by Wagner (1833)(see Fig. 9A-D). The differences of the gonozooids are clearly gradual and might in other species fall within the range of intraspecific variation. *Hydractinia pruvoti* appears nevertheless to differ in the development of the gonozooids. These develop as reduced polyps with one tentacle only and they produce medusae buds at a very early stage (Fig. 8E). They differ from the gastrozooids at all stages. In *Hydractinia aculeata,* the gonozooids appear to be derived from gastrozooids that develop medusa buds and may then reduce the tentacle number.

### ***Hydractinia aculeata*** (Wagner, 1833) Fig. 9

*Hydra* ovipara s. *aculeata* Wagner, 1833: 256, pl. 11 figs 1-10.
*Coryne aculeata.* – Ehrenberg, 1834: 294.
*Hydra aculeata.* – M. Sars, 1846: 8.
*Hydractinia aculeata.* – Allman, 1872: 352. – Motz-Kossowska, 1905: 86, fig. 10. – Herberts, 1964: 161. – Herberts, 1969: 351. – Bouillon *et al.*, 2004: 63, fig. 37A.
*Stylactis aculeata.* – Bavestrello, 1985: 351, fig. 2.

MATERIAL EXAMINED: Mediterranean, Banyuls-sur-Mer, one colony collected January 1992, on small *Nassarius* spec. (*incrassata* or *pygmaeus*), examined alive, no material preserved. – MHNG INVE39471; Mediterranean, Corsica, Coti-Chiavari, 18 Jul. 1946, few polyps without substrate, identification somewhat uncertain.

DIAGNOSIS: Encrusting or stolonal hydrorhiza, gastrozooids up to 5 mm, with 8-12 tentacles in one whorl, gonozooids smaller, 3-7 tentacles, with mouth. Short-lived medusoid with mature gonads, released or not, > 40 eggs, four tentacle bulbs, with or without four tentacles stumps.

DESCRIPTION (after literature and examined material): Colonies growing on various gastropod shells inhabited by molluscs or hermit crabs. Hydrorhiza variable, either reticulate stolons or encrusting, small spines present or not, smooth. Polyps polymorphic, with gastrozooids, gonozooids, and tentaculozooids.

Gastrozooids with dome-shaped hypostome, with band of contiguous nematocysts; 8-12 tentacles in one whorl (range 5-18).

Gonozooids resembling gastrozooids and derived from them, size smaller (ca. 1/2 to same size as gastrozooids), with mouth, 4-7 tentacles; in upper third of body one whorl of 1-6 medusa buds, globular to oblong, filled with gametes, radial canals and bulbs well visible.

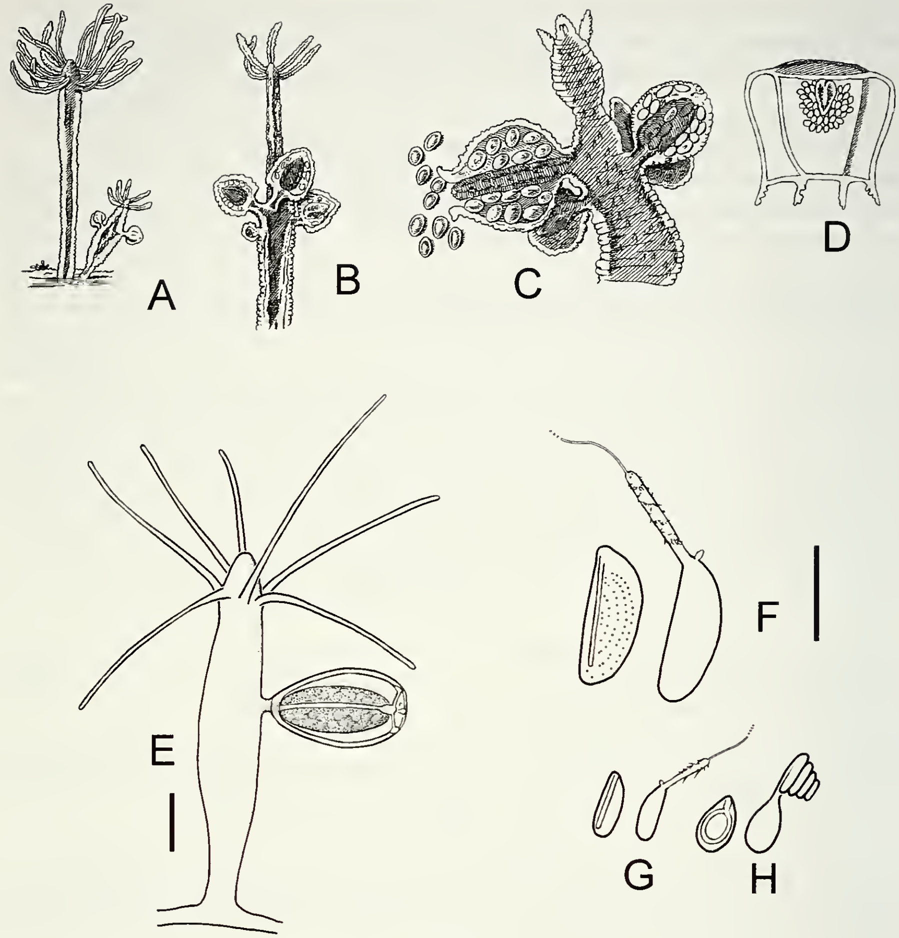

Fig. 9

*Hydractinia aculeata* (Wagner, 1833); A-D from Wagner (1833), E-F after living material from Banyuls-sur-Mer. (A) Part of colony with nutritive- and reproductive zooid. (B) Gonozooid with young medusa buds. (C) Gonozooid with spawning medusoid still attached to polyp. (D) Freely swimming medusoid. (E) Gonozooid with an advanced medusa bud, scale bar 0.2 mm. (F) Intact and discharged large heteronemes, scale bar 10 µm. (G) Smaller microbasic euryteles, same scale as F. (G) Desmonemes, same scale as F.

Nematocysts, large microbasic heteronemes (mastigophores or euryteles with faint swelling of shaft) on hypostome and body; smaller microbasic euryteles and desmonemes on body.

Gonophores short-lived medusoids that can be released or that remain attached. Liberated medusoid rather inactive, spherical, jelly thin and even, exumbrella without nematocysts, with velum, four small perradial bulbs, with or without tentacle stumps. Manubrium spanning about half the subumbrellar height, without mouth, surrounded by a very thick gonad without perradial interruptions, females with numerous (>40) eggs. Colonies unisexual.

DIMENSIONS: Gastrozooids about 2 mm (this study), Wagner (1833) gives 5 mm, Motz-Kossowska (1905) depicts them in figure as 1.2 mm high; gonozooids smaller. Free medusoid 0.6-0.8 mm in diameter (Herberts, 1964). Nematocysts (native): larger heteronemes (14-17)x(3.5-4) $\mu$m, microbasic euryteles (6.5-8)x(2.5-3) $\mu$m, desmonemes (5-7.5)x(3.5-4) $\mu$m.

BIOLOGY: Grows on various gastropod shells, inhabited either by molluscs or hermit crabs. Wagner (1833) found it on gastropods of the genera *Cerithium, Trochus,* and *Buccinum*; Motz-Kossowska (1905) on *Bolinus* (=*Murex*); Herberts (1964) on *Nassarius pygmaeus* (Lamarck); Bavestrello (1985) on shells of *Nassarius incrassatus* inhabited by the hermit crab *Catapaguroides timidus* (Rows). Depth range 0.5-20 m (Herberts, 1964; Boero & Fresi, 1986). Fertile specimens have been reported from January to November (this study; Herberts, 1964; Boero & Fresi, 1986). Wagner (1833) found his specimens in May. Herberts (1964, 1969) found that the population from Marseilles reproduced from April to August, more than 55% of the collected *N. pygmeus* were colonized by the hydroid during any month of the year. This contrasts with the observations of Bavestrello (1985) made in the adjacent Ligurian Sea. He found reproductive animals in winter only, but he examined a different host. Herberts (1964) noted that the planulae are able to settle on glass, indicating that they have no strict substrate preference (confirming the observations of Wagner (1833), but see Morri *et al.* (1991) for a different view).

DISTRIBUTION: Mediterranean. Type locality: Adriatic Sea, Trieste.

REMARKS: The description of Wagner (1833) is surprisingly precise and complete for its time (see also Fig. 9A-D). Although he noted the resemblance of the gonophores to planktonic medusae, he stopped just short of concluding that medusae and polyps are just life stages of the same animal. This was shortly afterwards recognized by M. Sars (1835). Wagner did not introduce the name as a strict binomen, he used *Hydra* ovipara s. *aculeata*. The s. likely stands for "species" and his intention, however, to name his animals *H. aculeata* is obvious. The first author to use the correct binomial nomenclature was Ehrenberg (1834) as *Coryne aculeata*.

Motz-Kossowska (1905) observed medusoids that lacked tentacle rudiments. This, and also its different host, led Herberts (1964) suspect that she had in fact a different species. The tentacle rudiments were also absent in the material examined here. This difference likely represents intraspecific variation. Also other hydroids with fixed medusoids show this variation, e. g. *Sarsia lovenii* (M. Sars, 1846) (see Schuchert, 2001b). The medusoids of this species remain always attached to the hydroid, but the tentacles are reduced to a variable degree. Some populations of *S. lovenii* produce medusoids without any tentacles, while others develop medusoids with short tentacle rudiments.

Some important details remain unknown. It is unclear whether the medusoid has a gastric peduncle and also the number of eggs per medusoid is not precisely known. Wagner (1833) depicts an animal with more than 40 eggs, likewise also Bavestrello (1985). The animals examined here had clearly more than 100 eggs, but the gonophores were perhaps not fully ripe yet (the egg number decreases during maturation in many hydrozoans). It also not known whether there is always a contiguous band of nematocysts on the hypostome.

Spineless *H. aculeata* with not fully developed medusoids are perhaps not readily distinguishable from *H. inermis*, but both forms differ in their substrate preference and the number of tentacle whorls.

As discussed under *H. pruvoti*, the morphology of this species and *H. aculeata* appear to intergrade somewhat, but both are distinct species.

***Hydractinia proboscidea*** (Hincks, 1868) Figs 10-11

*Podocoryne proboscidea* Hincks, 1868: 317, pl. 23 fig. 4. – Allman, 1872: 351.
? *Hydractinia michaelseni* Broch, 1914b: 21, fig. 1a-b.
*Stylactis claviformis* Bouillon, 1965: 54. **new synonym**
*Stylactis claviformis.* – Bouillon, 1971: 347, figs 8-9, pls 5-6.
*Stylactaria claviformis.* – Ramil *et al.*, 1994: 104, figs 2-3.
*Hydractinia calderi* Bouillon, Medel & Peña Cantero, 1997: 477, figs 1-2, 3A-B. **new synonym**
*Hydractinia calderi.* – Peña Cantero & Garcia Carrascosa, 2002: 39.
? *Hydractinia calderi.* – Vervoort, 2006: 201.
? *Hydractinia hooperii.* – Bouillon *et al.*, 1997: 478. – Peña Cantero & García Carrascosa, 2002: 41, fig. 8c-e.
Not *Stylactis hooperii* Sigerfoos, 1899: 806, figs 1-5.

MATERIAL EXAMINED: BMNH 1899.5.1.132, Syntype colony of *Podocoryne proboscidea* Hincks, 1868; Ilfracombe, England. – BMNH 1982.9.21.2, as *Stylactis claviformis* topotype material; approx. 7 km north of Roscoff, 16 Aug. 1982, det. L. Cabioch and P. F. S. Cornelius, on pebble, fertile female. – Syntype specimen of *H. calderi*, obtained through Dr. A. L. Peña (University of Valencia, Spain); loc. Chafarinas Islands, Arrastre Baños de la Reina; fertile female colony on *Bolma rugosa* (Linnaeus) [Gastropoda], some polyps as permanent slide preparations deposited as MHNG INVE60720. – *Hydractinia hooperii* material of Peña Cantero & García Carrascosa (2002), obtained as loan from Dr A. L. Peña Cantero; loc. Mediterranean, Chafarinas Islands, Baños de la Reina, no collection date, fertile female, on *Cerithium* species (45 mm high).

DIAGNOSIS: Hydrorhiza stolonal, polyps large, gastrozooids with 10-32 tentacles in 2-3 whorls, hypostome usually slightly necked; gonozooids smaller, fewer tentacles; gonophores medusoids, liberated or not, with 4-10 tentacle stumps when fully mature, females with 20-70 eggs.

DESCRIPTION (after examined material; Hincks, 1868; and Bouillon, 1971): Colonies growing on various substrates like pebbles, laminarian holdfasts, and large gastropod shells. Hydrorhiza a network of perisarc covered stolons, smooth spines present or not. Polyps polymorphic, gastrozooids, gonozooids, and tentaculozooids.

Gastrozooids distinctly club-shaped, with very prominent, hypostome large (1/6 to 1/4 of total height, variable), usually somewhat necked, upper part ellipsoid to barrel-shaped, covered by a band of contiguous nematocysts; 2-3 close set whorls of 10-32 tentacles (usually 14-22); base of hydranth can be surrounded by a shallow, filmy perisarc collar.

Gonozooids similar like gastrozooids but smaller (1/2 to 3/4 their height), 6-12 tentacles in one whorl, hypostome elongated, with band of contiguous nematocysts. 2-10 gonophores in one whorl in upper third of polyp, hydranth body above tentacles thinner.

Tentaculozooids rare, smaller than gastrozooids, solid gastrodermis, smooth, end may be slightly swollen.

Gonophores are ovoid medusoids with rudimentary tentacles issued from a thin ring-canal with a narrow diameter, no distinct bulbs, four radial canals, large manu-

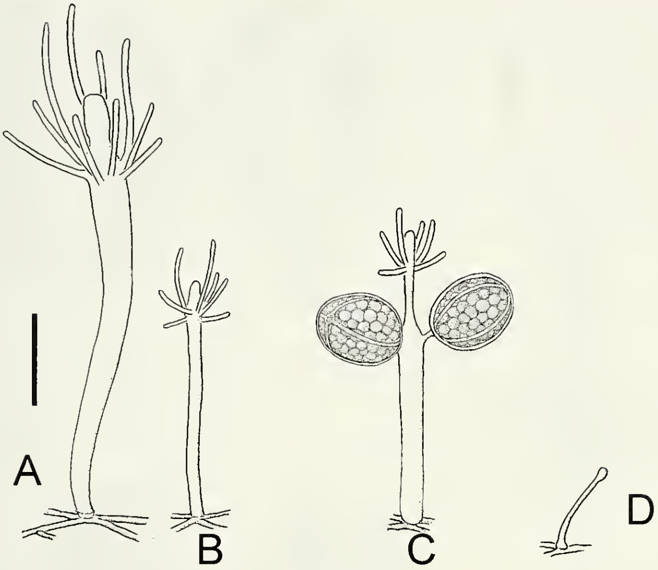

FIG. 10

*Hydractinia proboscidea* (Hincks, 1869); A-D after preserved material from the English Channel («topotype» material) identified as *H. claviformis*, scale bar 1 mm. (A) Gastrozooid. (B) Smaller, perhaps younger polyp. (C) Gonozooid with two female medusoids, their umbrella not yet inflated. (D) Tentaculozooid.

brium without mouth spanning the whole subumbrella, with narrow velum when fully mature, gametes fill subumbrella. Female gonophores are only rarely liberated, 4-8 tentacle stumps, egg number 16-70, larviparous. Male gonophores may be liberated into plankton or may remain attached, 8-10 thin tentacle stumps of unequal length, gonads large and filling subumbrella, encircling manubrium without perradial separation.

Nematocysts: microbasic euryteles and desmonemes. Colour: orange-brown or pink-salmon.

DIMENSIONS: Gastrozooids 1-5 mm (preserved material), Bouillon (1971) observed that the polyps can extend to 16 mm, but those in his figures are a few mm in height. Gonozooids somewhat smaller. Gonophores ca 0.7 mm long. Medusoids from plankton 1.5 mm high and 1 mm wide (Bouillon, 1971). Nematocysts (Bouillon, 1871; for *H. claviformis*): microbasic euryteles (12)x(3-4) $\mu$m, desmonemes (8-9)x(4) $\mu$m. The type specimens of *H. proboscidea* and *H. calderi* have capsules that fall within this range.

BIOLOGY: Grows on pebbles (Hincks, 1868; Bouillon, 1971), laminarian holdfasts (Hincks, 1868; Ramil *et al.,* 1994), gastropods. Depth range 0-70 m. Mature colonies were observed in the months of April, August, and September. Polyps have been observed from February to November.

DISTRIBUTION: Bristol Channel (Hincks, 1868), English Channel (Bouillon, 1971; *as S. claviformis*), Galicia in Spain (Ramil *et al.,* 1994; *as S. claviformis*), and

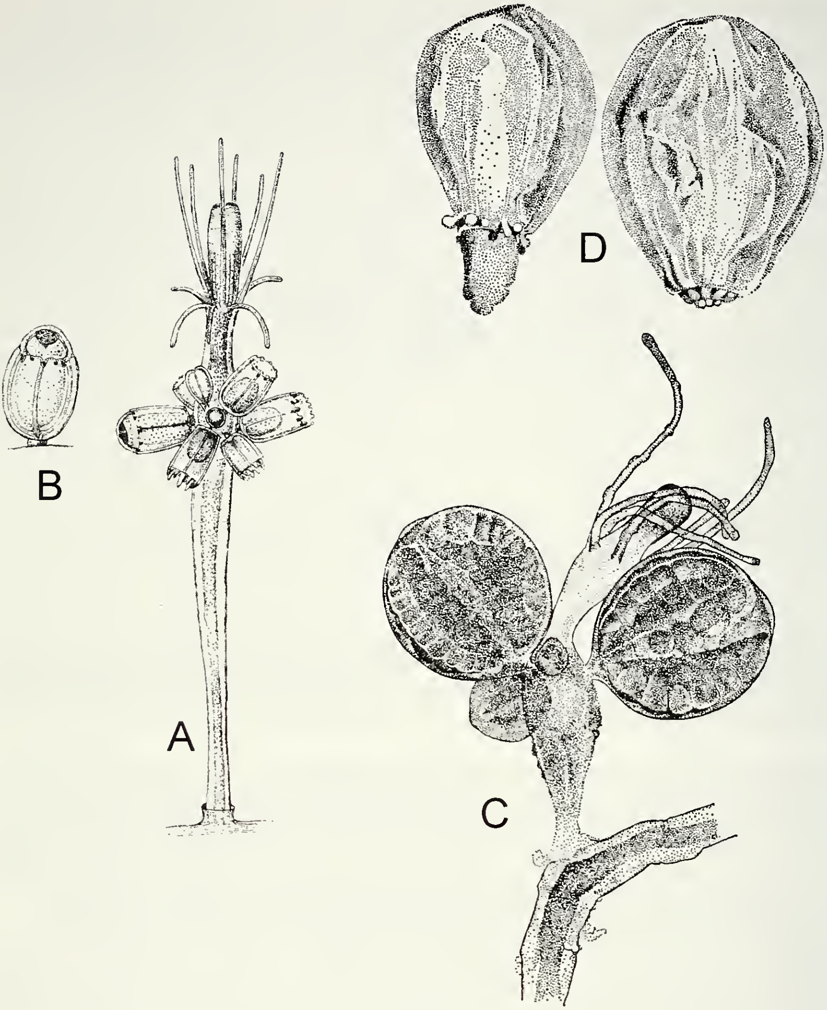

FIG. 11

*Hydractinia proboscidea* (Hincks, 1869); A-B from Hincks (1868); C-D from Bouillon (1971, as *S. claviformis*). (A) Gonozooid with male medusoids. (B) Male medusoid with bulging sperm mass (C) Gonozooid with female medusoids. (D) Two free, male medusoids.

Alborean Sea (Bouillon *et al.*, 1997; as *Hydractinia calderi*).Type locality: Bristol Channel, Devon, Ilfracombe, Capstone.

REMARKS: When describing *S. claviformis*, Bouillon (1971) did not discuss its relationship to *H. proboscidea* (Hincks, 1868). The latter species was described in an appendix of Hincks's book and placed in the genus *Podocoryne*. It has thus perhaps escaped the attention of Bouillon. Comparing Hincks's figures (Fig. 11A-B) of *H. proboscidea* – in particular the male medusoids – with *H. claviformis* (Fig. 11C-D), it is rather evident that they are indistinguishable and both species are here regarded as conspecific.

The type material of *H. proboscidea* is not well preserved, but its examination confirmed the accuracy of the original description. The polyp-tentacles are lost, but their remaining bases are clearly in two close-set whorls, the hydrorhiza is stolonal, the gastrozooids are of a similar size as the gonozooids. This material could be compared with a female colony of *H. claviformis* originating from the type locality ("topotype"). The gastrozooids are indistinguishable from *H. proboscidea*, the only apparent difference being the higher number of medusa buds of the gonozooids of *H. proboscidea* (up to 10 versus 4). The difference is considered as insignificant and both nominal species are regarded as conspecific.

The figures and description of *H. calderi* Bouillon, Medel & Peña Cantero, 1997 appear also hardly distinguishable from the concept of *H. proboscidea* (=*H. claviformis*) given above. The only differences according to the literature are: it was observed on gastropod shells, it has some rare spines, and the female medusoid has also small interradial marginal bulbs. A re-examination of the type material of *H. calderi* showed that the bulbs are in fact small, rudimentary tentacles. I regard the remaining differences as insignificant and both species are likely conspecific. The presence of spines is usually related to the substrate, which might also be that case for *H. calderi*. Bouillon *et al.* (1997) list the following differences allowing a distinction of *H. claviformis* and *H. calderi*: the dimorphism of its gonophores by having free male medusoids with ten tentacles instead of eight and the cnidome of the gonozooids. These arguments are not so convincing and there are no apparent differences of the cnidomes.

*Hydractinia hooperii* was recorded for the Mediterranean by Bouillon *et al.* (1997). The same specimen was then described and depicted in Peña Cantero & García Carrascosa (2002) and it was also kindly made available for this study. The material is very similar to *H. proboscidea*, differing principally only in the number of tentacle whorls. The gastrozooids have the same necked hypostome as *H. proboscidea*, but in contracted polyps the tentacles are in two close set whorls, while in expanded ones they appear to be arranged in one whorl only. The tentacle number is somewhat lower (12-20). The gonophores are medusoids with eight very short tentacle rudiments. I think that these differences are due to environmental influences or that they reflect intraspecific variation. This material is therefore also assigned to *H. proboscidea*, although with some doubts.

*Hydractinia proboscidea* is not easily separable from *H. inermis,* but differs by the presence of spines, the tentacle rudiments of the medusoids, the necked hypostome, and a higher egg number per gonophore.

*Hydractinia michaelseni* Broch, 1914b from Nigeria, western Africa, was originally found on a shell inhabited by a hermit crab, but it remains insufficiently known. Its gonophores are apparently medusoids with four bulbs, but they might not have been fully developed. Perhaps the record of *H. calderi* from the Cape Verde Islands by Vervoort (2006) is better referred to this species.

There are actually a number of nominal *Hydractinia* species resembling *Hydractinia proboscidea* and their relationships and validity are not resolved satisfactorily. In the examined region or adjacent to it, there are also *Hydractinia aculeata, H. hooperii, H. inermis,* and *H. michaelseni* that resemble *Hydractinia proboscidea*. Considering also more remote regions, more similar species have to be added to this list (comp. e. g. Millard, 1975; Calder, 1988; Hirohito, 1988). *Hydractinia* species offer far too few diagnostic characters and it seems almost impossible to disentangle the complicated situation, only molecular data and detailed investigations on their biology have the potential to do so.

### ***Hydractinia inermis*** (Allman, 1872) Fig. 12

*Stylactis inermis* Allman, 1872: 305, fig. 79. – Du Plessis, 1888: 541.
? *Clava nana* Motz-Kossowska, 1905: 62, fig 3. – Stechow, 1919: 10, synonym.
not *Stylactis inermis*. – Goette, 1916: 451, fig. A, pl. 13 fig. 3, pl 14 figs 25-37. [= *H. fucicola*]
*Stylactis inermis*. – Stechow, 1919: 23. – Iwasa, 1934: 251. – Boero, 1981: 188, fig. 3. – Gili & Castello, 1985: 11, fig. 2E. – Namikawa, 1991: 810.
*Stylactaria inermis*. – Stechow, 1921c: 250.
*Stylactella inermis*. – Stechow, 1923: 63.
? *Hydractinia inermis*. – Bouillon, Medel & Peña Cantero, 1997: 478. – Peña Cantero & García Carrascosa, 2002: 41, fig. 8f. – Bouillon *et al.*, 2004: 65, fig. 39C.

MATERIAL EXAMINED: ZSM 20040316, 20000684, 20000685, as *Stylactis inermis*, alcohol and slide preparations; Italy, Naples; collected end of April 1911; on *Sargassum vulgare*; fertile males; part of material described by Stechow (1919). – MHNG INVE 32950; Adriatic Sea, Italy, Brindisi; 23 March 1997; fertile female on *Cystoseira* spec. – Mediterranean, Banyuls-sur-Mer; 8 May 2002; small male colony on sponge growing on coralligenous concretions, depth likely more than 10 m, not preserved, used to make DNA (tissues turned intensely blue in concentrated alcohol), 16S sequence **AM940002**.

DIAGNOSIS: On algae and other fixed substrates, hydrorhiza stolonal network, without spines, gastrozooids with 12-20 tentacles in two close-set whorls, broad and dense band of nematocysts on hypostome, gonozooids smaller and with 8-16 tentacles, several gonophores, gonophores fixed sporosacs with four radial canals, no bulbs or tentacle rudiments, 10-20 eggs.

DESCRIPTION: Colonies usually growing on algae, barnacles and other fixed substrates, but not on shells and crabs. Stolons tightly reticulate and composed of tubules covered by perisarc, spines absent.

Polyps only slightly polymorphic, gastrozooids and gonozooids similar.

Gastrozooids relatively large, extensile, club-shaped to fusiform body; hypostome large, dome- to barrel-shaped, with a broad band of contiguous nematocysts; 12-22 tentacles (usually 16-18) in two close set whorls, unequal in length, alternately pointing upward or horizontal; base of hydranth often with filmy perisarc collar (needs examination with compound microscope).

Gonozooids smaller and more slender than feeding zooids (ca. 1/3 to 1/4 the size of the gastrozooids), 6-16 tentacles, hypostome with a broad band of contiguous nematocysts, in middle of body or below one whorl of four to eight gonophores.

Gonophores fixed sporosacs, initially spherical, fully mature with slight distal thickening, with radial canals and a narrow ring canal, no tentacle bulbs, no tentacle rudiments, no velum. Sporosacs not medusoid (no umbrella) and gametes appear to be released from the attached sporosacs. Colonies unisexual. Female sporosacs with 10-20 eggs. Nematocysts: microbasic euryteles of two size classes, desmonemes. Colours: hydranths pale pink to brownish.

DIMENSIONS: Colonies size is variable from a few hydranths to many cm$^2$ (Boero, 1981), gastrozooids 1.5-6 mm (usually 2-3 mm); sporosacs 0.4 mm. Nema-

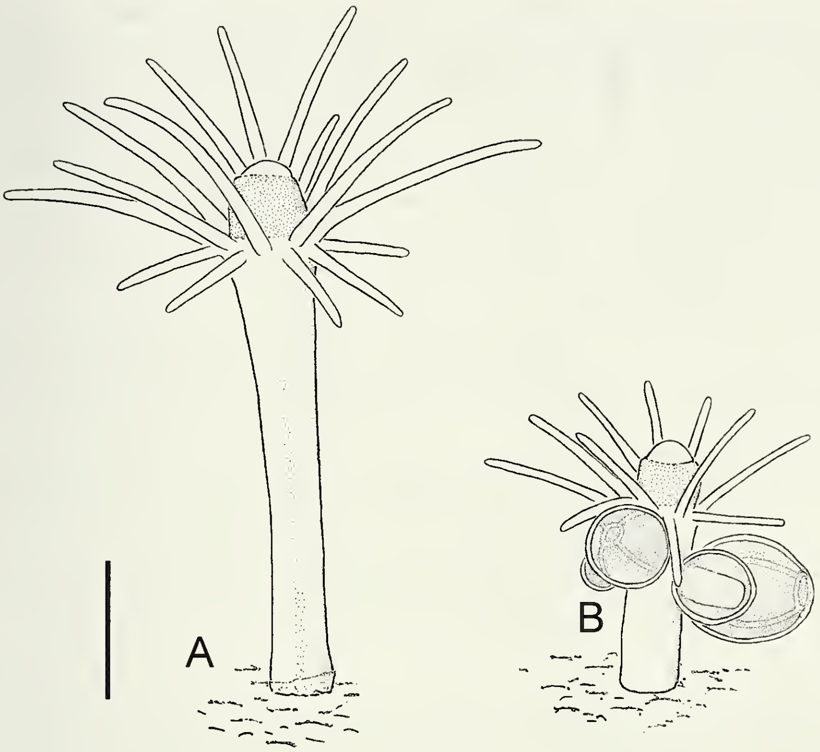

FIG. 12

*Hydractinia inermis* (Allman, 1872), after preserved material from Naples, tentacles partially contracted, scale bar 0.5 mm. (A) Gastrozooid. (B) Gonozooid with male gonophores.

tocysts (preserved material): euryteles on hypostome (9)x(3) $\mu$m, euryteles on tentacles (7.5-8)x(2.5) $\mu$m, desmonemes (4.5-5)x(2.5) $\mu$m.

OTHER DATA: Boero (1981) also found very small anisorhiza-type nematocysts. This type could not be found in the preserved material examined here.

BIOLOGY: Locally common on rocky coasts, occurs from a few meters to 30 m depth (Boero, 1981; Boero & Fresi, 1986; Gili & Castello, 1985) from October to May, very abundant from March to May; on algae, sponges, hydroids, barnacles; reproduction from April to May. In the three months of its maximum occurrence, it can cover almost everything forming a temporary facies (Boero & Freesi, 1986). Dormant in hydrorhiza in summer and autumn.

DISTRIBUTION: Mediterranean (western Mediterranean and Adriatic Sea). Type locality: Nice, Ligurian Sea.

REMARKS: Allman (1872) described *Stylactis inermis* based on material sent to him by G. Du Plessis (professor of Zoology, Lausanne, Switzerland). The specimens available to Allman were colonies – certainly preserved – that had developed on aquarium cultivated seaweeds collected near Nice. Du Plessis (1888), who must have seen the living type material, qualifies the species as "planulipare" (as opposed to producing medusae). Allman (1872) gives no precise details on the nature of the gonophores, but qualifies them as sporosacs (p. 306) and he does not mention radial canals. These radial canals can be very difficult to see in preserved material and he may have overlooked them. Unfortunately, the type material seems to be lost. Allman's description nevertheless contains some distinct features that allow *H. inermis* to be distinguished from the similar *H. fucicola*, a species that also occurs on the same substrates: about 20 tentacles in two close set whorls, polyps up to 5 mm high, hydrorhiza stolonal, without spines, base of polyp with perisarc collar, female sporosacs with more than 10 eggs (taken from figure).

Bouillon *et al.* (1997: 478) characterized the gonophores as eumedusoids with eight tentacular bulbs. In the material examined here, there were no marginal bulbs. As bulbs are normally quite obvious in mature gonophores, they would most likely not have escaped the attention of Allman.

The material identified by Goette (1916) as *Stylactis inermis* was more likely *H. fucicola*. His polyps had 12 or less tentacles and the mature sporosacs had no radial canals.

The nematocyst band on the hypostome has also not been reported so far. It is somewhat less refringent and thus less obvious than the one in *H. fucicola*. Preserved material must be examined at high magnifications by transmitted light microscopy.

Allman (1876) also described *Podocoryne inermis* as a new species based on material from Denmark, distinct from *Stylactis inermis* Allman, 1872. This species produces medusae and is evidently conspecific with *H. carnea* (see discussion there).

Spineless, immature stages of *H. aculeata* with not fully developed medusoids are perhaps not distinguishable from *H. inermis*, but both forms apparently differ in their substrate preference. More details on the development of the gonophores and the reproductive biology of *H. inermis* are nevertheless needed to allow a better separation.

### ***Hydractinia fucicola*** (M. Sars, 1857) Figs 13-14

*Podocoryna fucicola* Sars, 1857: 145, pl. 2 figs 6-13.
? *Podocoryne Haeckelii* Hamann, 1882: 519, pl. 5 figs 15-16.
*Stylactis fucicola*. – Allman, 1872: 304.
*Hydractinia fucicola*. – Bonnevie, 1898: 486. – Motz-Kossowska, 1905: 87, fig. 11, pl. 3 fig. 20.
*Stylactis inermis*. – Goette, 1916: 451, fig. A, pl. 13 fig. 3, pl 14 figs 25-37. [not *Hydractinia inermis* (Allman, 1872)]
*Hydractinia fucicola*. – Stechow, 1919: 13. – Castric-Fey, 1970: 2, figs 1-9. – Bouillon, Medel & Peña Cantero, 1997: 479. – Bouillon *et al.*, 2004: 65, fig. 39A.
*Stylactis fucicola*. – Iwasa, 1934: 249, fig. 1. – Boero & Freesi, 1986: 140.

MATERIAL EXAMINED: Syntype, ZMO B1348; as *Hydractinia fucicola*; leg. & det. M. Sars, loc. Messina; several excellently preserved, fertile colonies on *Cystoseira compressa*. – MHNG INVE36838; Mediterranean, France, Port of Villefranche-sur-Mer France, 0 m depth, 5 May 2005, fertile male colony on *Cystoseira* spec. (Fig. 14). – Mediterranean, France, Cassis, Presque île, Plage Bleue, 0-1 m depth, 23 April 2003, fertile female colony on barnacles, examined alive, not preserved.

DIAGNOSIS: On algae and other fixed substrates, hydrorhiza encrusting, with smooth spines, gastrozooids up to 12 tentacles in one whorl, broad band of nema-

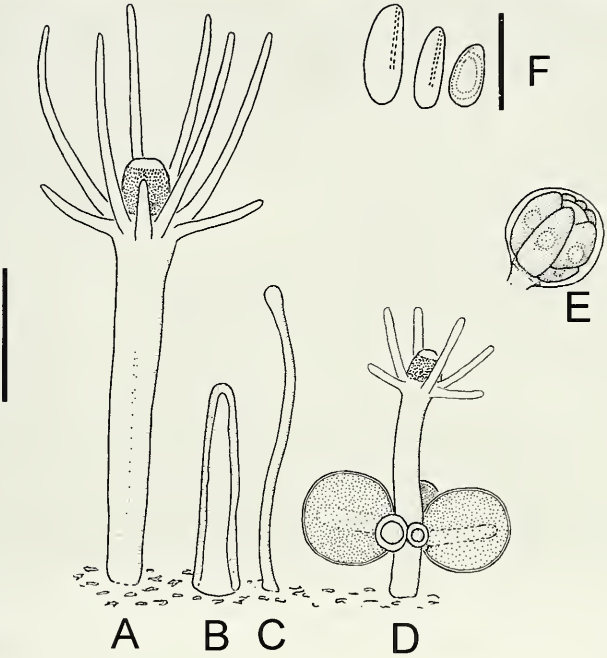

FIG. 13

*Hydractinia fucicola* (M. Sars, 1857), after living material from the Mediterranean, scale bar 0.5 mm for A-E, 10 $\mu$m for F. (A) Gastrozooid. (B) Spine. (C) Tentaculozooid (not always present). (D) Gonozooid with male sporosacs. (E) Female gonophore with mature eggs. (F) Nematocysts: two microbasic euryteles, desmoneme.

tocysts on hypostome, gonozooids smaller and only up to 8 tentacles, several gonophores, gonophores fixed sporosacs without radial canals or bulbs, 6-12 eggs.

DESCRIPTION: Dense colonies usually growing on algae, barnacles and many other fixed substrates, but not on shells or crabs. Stolons in young colonies or at colony periphery tightly reticulate and composed of tubules covered by thin perisarc, in older colonies and in centre usually coalescing into a thick crust covered by coenosarc tissue. Spines rare to frequent, slender, pointed, perisarc smooth or undulated.

Polyps polymorphic, composed of gastrozooids, gonozooids, and sometimes tentaculozooids.

Gastrozooids with fusiform to cylindrical body; hypostome dome-, barrel-, or ball-shaped, with a broad, refringent band of contiguous nematocysts; one whorl of 6-12 tentacles, distinctly unequal in length, alternately pointing upward or horizontal, terminal region of tentacles can be transiently swollen, base of hydranth without perisarc collar.

Gonozooids usually smaller and more slender than feeding zooids (ca. 1/2 the size of the gastrozooids, but in some population sizes equal), up to eight tentacles, hypostome with a broad, refringent band of contiguous nematocysts, in middle of body or below one whorl of four to eight gonophores.

FIG. 14

*Hydractinia fucicola* (M. Sars, 1857); photograph of living male colony from Villefranche-sur-Mer, Mediterranean.

Gonophores fixed sporosacs, covered by numerous nematocysts, spherical, without radial canals or tentacle rudiments (heteromedusoid), spadix present. Colonies unisexual. Female sporosacs with 6-12 eggs, frequently arranged in a circle around spadix.

Nematocysts: microbasic euryteles of two size classes, desmonemes. Colours: spine perisarc brown; hydranths orange or pink.

DIMENSIONS: Colonies can spread several cm$^2$, gastrozooids 1-2 mm (max. 3 mm in Atlantic), spines up to 0.7 mm, diameter of sporosacs 0.3-0.4 mm.

OTHER DATA: The very young sporosacs develop anlagen of the radial canals which are rapidly lost in later development (Motz-Kossowska, 1905; Castric-Fey, 1970). The presence of spines depends on the substrate. Motz-Kossowska (1905) observed a colony that was spreading from barnacles onto a stem of *Sertularella* spec. While the part on the barnacle had no spines, these were abundant on the *Sertularella* substrate.

BIOLOGY: In the Mediterranean, *H. fucicola* occurs only in very shallow waters (0-4 m), between 5 and 20 m in the Atlantic (Castric-Fey, 1970; Boero & Fresi, 1986). It can occur on a variety of substrata, most commonly on algae, barnacles, and hydroids. It seems not to occur on mobile substrata like gastropods or hermit crabs. In the Mediterranean it is fertile from April to August (Boero & Fresi, 1986), in the Atlantic from July to September (Castric-Fey, 1970).

DISTRIBUTION: Western Mediterranean, Southern Brittany (Castric-Fey, 1970). Type locality: Messina, Italy.

REMARKS: Contrary to the data given in Iwasa (1934), the gonophores of this species are cryptomedusoid sporosacs and not eumedusoids (see Motz-Kossowska, 1905; Castric-Fey, 1970).

The type material of Sars was re-examined for this study. It is composed of several, perfectly preserved colonies. The hypostomes of the polyps have a band of contiguous nematocysts as found in other samples and the type material was indistinguishable from the other samples from the Mediterranean examined for this study.

The hypostome of *H. fucicola* is densely studded with euryteles. These were only described relatively late by Castric-Fey (1970). This band of nematocysts is very refringent and well visible in living material, but in preserved and contracted material it can get almost invisible and requires an examination by transmitted light microscopy. Such a nematocyst band is found in several species and it is not diagnostic for *H. fucicola*.

*Stylactis inermis* Allman, 1872 was regarded as a junior synonym of *Hydractinia fucicola* by Picard (1958b: 190). However, I believe they are distinct, even though they can be difficult to distinguish in being similar morphologically and in occurring on the same substrates. *Hydractinia inermis* differs in the following aspects from *H. fuciola*: spines are absent, hydrorhiza mostly stolonal and not forming crust covered by coenosarc, gastrozooids about two times larger and more extensile, more tentacles (up to 22, mostly more than 12) and these in two whorls, basal perisarc collar frequent, gonozooids also with about twice as many tentacles, mature sporosacs with four radial canals, females with more eggs.

*Hydractinia fucicola* also closely resembles *Hydractinia sarsii*, the latter differing only by its preference for mobile substrata, like crustaceans and gastropod shells, and the higher tentacle numbers. Tentacle numbers are admittedly usually only a poor taxonomic character for hydractiniids, but *H. fucicola* gastrozooids seem to have a tentacle number (8-12) that shows relatively little variation.

The material identified by Goette (1916) as *Stylactis inermis* was more likely *H. fucicola.* His polyps had 12 or less tentacles and the mature sporosacs had no radial canals.

*Clava nana* Motz-Kossowska, 1905 is an indeterminable species based on a juvenile hydractiniid. Stechow (1919) regarded it as conspecific with *H. inermis*, while Picard (1958) treated it as a synonym of *H. fucicola*. As *H. fucicola* has only one whorl of tentacles, Stechow's assumption is more likely correct.

### ***Hydractinia sarsii*** (Steenstrup, 1850) Fig. 15

in part *Podocoryna carnea* M. Sars, 1846: 7, pl. 2 figs 5-11, not pl. 1 figs 7-18.
*Podocoryna Sarsii* Steenstrup, 1850: 33, new name.
*Stylactis Sarsii*. – Allman, 1864c: 66. – Allman, 1872: 303. – Iwasa, 1934: 230.
*Hydractinia sarsii*. – Bonnevie, 1898: 486, pl. 26 fig. 42. – Bonnevie, 1899: 45. – Broch, 1916: 45, fig. M, pl. 1 fig. 12. – Schuchert, 2001a: 18, fig. 8.

MATERIAL EXAMINED: ZMO, no. B1347, as *Hydractinia sarsii* Steenstrup, identified by M. Sars, locality and collection date unknown; sample comprises three shells of *Littorina* spec. (up to 18 mm size), one inhabited by a juvenile *Pagurus pubescens* Krøyer, shells covered by encrusting hydrorhiza, most coenosarc lost, a few gastrozooids remain, some also detached. Although this material is not explicitly marked as type material, the fact that it was identified

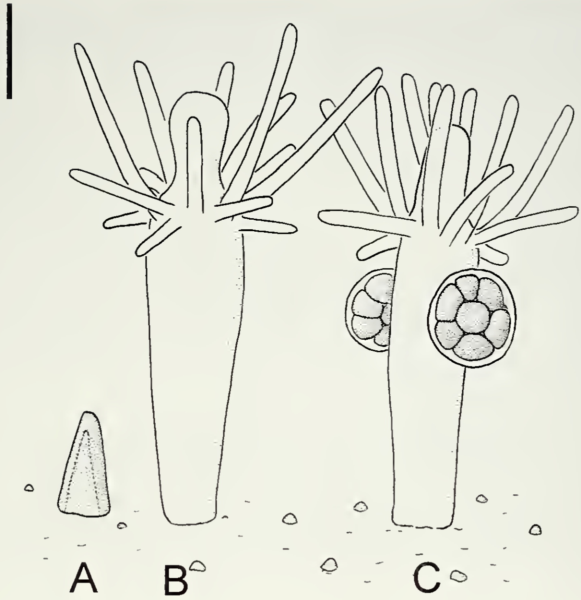

FIG. 15
*Hydractinia sarsii* Steenstrup, 1850; after preserved material from Greenland growing on a crab leg; scale bar 0.5 mm. (A) Spine. (B) Gastrozooid. (C) Gonozooid with female sporosacs.

(labelled) by M. Sars and that it was part of the collection that includes also the other type specimens of species described by M. Sars, this material must be regarded as the type material. (conf. also Bonnevie, 1898). – Another colony was examined for the study of Schuchert (2001a).

DIAGNOSIS: On gastropod shells and other mobile substrates, hydrorhiza encrusting, with smooth spines, gastrozooids and gonozooids identical, up to 30 tentacles in two close-set whorls, usually with broad band of nematocysts on hypostome, several gonophores, gonophores fixed sporosacs without radial canals or bulbs, up to 10 eggs.

DESCRIPTION: Colonies on crustaceans or on gastropod shells inhabited by hermit crabs. Hydrorhiza an encrusting plate, covered by coenosarc tissue; spines present, conical rounded tip, perisarc smooth or undulated; numerous small prickles penetrating coenosarc layer. Gastrozooids and gonozooids not much different, the latter ones may be somewhat smaller, hypostome high, usually with a broad, refringent band of contiguous nematocysts; up to 30 tentacles in two close-set whorls, distinctly unequal in length. Gonozooids with one whorl of 2-6 gonophores in upper third of hydranth. Gonophores spherical, fixed sporosacs without ring- or radial canals, spadix present, females with 2-10 eggs, larviparous. Nematocysts: heteronemes and desmonemes.

DIMENSIONS: Polyps 1-3 mm; spines 0.5-1 mm high. Nematocysts: desmonemes, (5-6)x(3-3.5) $\mu$m; heteronemes (8-11)x(3-4.5) $\mu$m.

Biology: Christiansen (1972) found several colonies of this species in the Oslo Fjord, growing on the crab *Geryon trispinosus* collected in depths of 80-100 m on mud bottom [reported as *Gerion tridens*, a junior synonym of *Geryon trispinosus* (Herbst)]. The colony described by M. Sars was growing on gastropod shells used by hermit crabs.

Distribution: A northern boreal to arctic species, known from Norway, the Faroes, Iceland, and Greenland (Broch, 1916; Kramp, 1942; Christiansen, 1972; Schuchert, 2001a). Type locality: south-western Norway.

Remarks: This species has been recorded only a few times and its biology remains inadequately known. A re-examination of the type material provided few new data besides an observation that the hypostome has a belt of contiguous nematocysts. No such belt was found in the material from Greenland growing on a crab, in addition to the somewhat lower tentacle numbers (up to 20). Perhaps this indicates that we are dealing with a species complex. The morphology of *H. sarsii* is very similar to *H. fucicola*, the latter differing mainly only in the lower tentacle number and the smaller gonozooids. Both species differ in their substrate preference: while *H. fucicola* grows on fixed substrata like algae, *H. sarsii* occurs on mobile substrata like crustaceans. Their disjunct distributions also help to separate the two.

See also remarks under *H. carica*.

### ***Hydractinia echinata*** (Fleming, 1828) Fig. 16

*Alcyonium echinatum* Fleming, 1828: 517.
*Coryne squamosa* var. Johnston, 1938: pl. 2 figs 4-5. – Allman, 1872: 345, synonym.
*Hydractinia rosea* van Beneden, 1844: 41, 63, pl. 6 figs 1-6. – van Beneden, 1867: 134, synonym.
*Hydractinia lactea* van Beneden, 1844: 41, 64, pl. 6 figs 7-14. – van Beneden, 1867: 134, synonym.
*Echinochorium clavigerum* Hassall, 1841: 371, pl. 10 fig. 5. – Hincks, 1868: 23 synonym.
*Coryne Hassalli* Forbes, 1843: 189. – Bedot, 1905, synonym.
*Synhydra parasites* Quatrefages, 1843: 230, pls 8-9. – Hincks, 1868: 23, synonym.
*Clava capitata* Thompson, 1844: 283.
*Hydractinia grisea* Leuckart, 1847: 138.
not *Hydractinia polyclina* Agassiz, 1862: 227. – Buss & Yund, 1989: 869, figs 1-2.
*Hydractinia echinata* – Hincks, 1868: 23, pl. 4 figs 1-6. – Allman, 1871: 220. – Allman, 1872: 345, pls 15 and 16 figs 10-12. – Weismann, 1883: 73, pl. 23. – Jäderholm, 1909: 48, pl. 2 figs 6-9. – Broch, 1911: 18, fig. 14, pl. 2 fig 3. – Goette, 1916: 464, text fig. C, pl. 13 figs 1-2, 11-19, pl. 14 figs 20-22, pl. 15 figs 56-59. – Vervoort, 1946: 130, fig 51. – Naumov, 1969: 223, fig. 91. – Buss *et al.*, 1989: 862. – Schuchert, 2001a: 15, fig. 6A-G.

Material examined: MHNG INVE29281; France, Roscoff; intertidal pool; 2 June 2000; on shells of hermit crabs; several fertile colonies, examine alive. – MHNG INVE49491; France, Roscoff; 18 Sept. 2006; on hermit crab shells; several fertile colonies. – MHNG INVE60166; France, Brittany, Baie de Morlaix, Ile Callot, 25 Oct. 2007; part of fertile colony; 16S sequence accession number **AM939655.**

Diagnosis: Polyps strongly polymorphic, distal end of gonozooids with nematocyst buttons, without tentacles, gonophores sessile sporosacs without radial canals or tentacles, 6-8 eggs, hydrorhiza encrusting, covered by naked tissue, spines with spiny ridges.

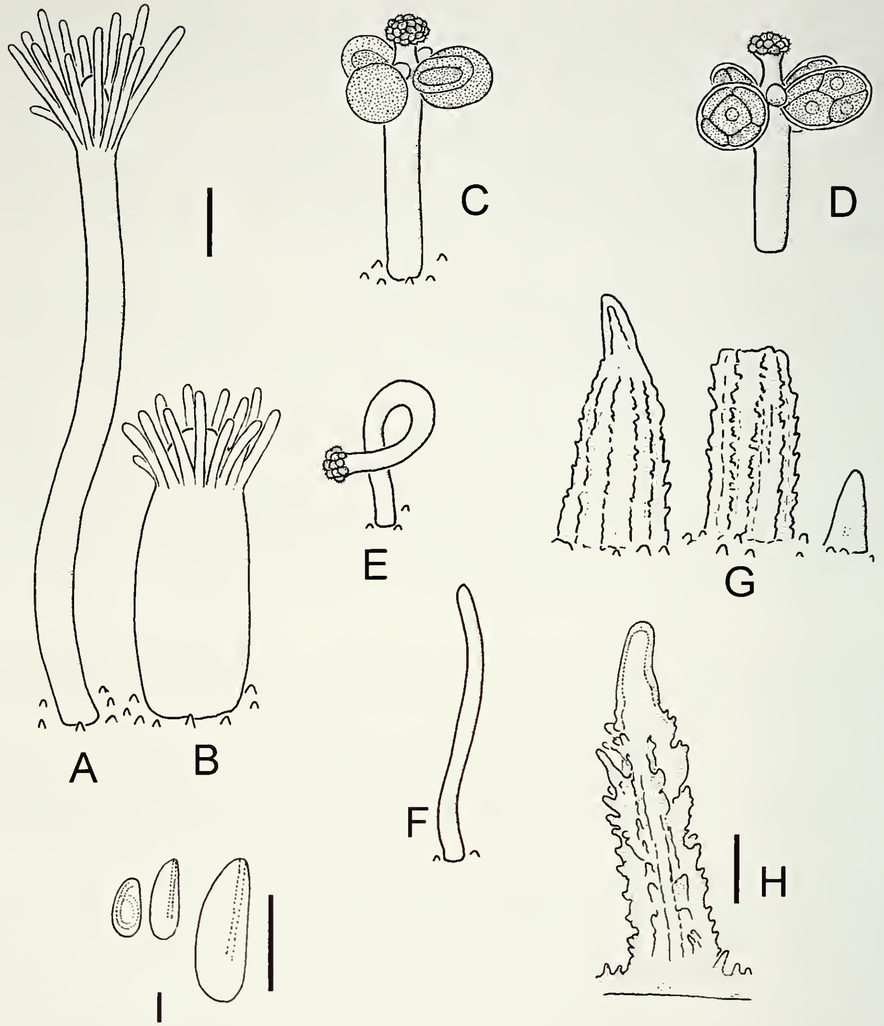

FIG. 16

*Hydractinia echinata* Fleming, 1820; A-G, I after life, H after preserved material (A) Extended gastrozooid, scale bar 0.5 mm. (B) Contracted gastrozooid, same scale as A. (C) Male gonozooid, same scale as A. (D) Female gonozooid, same scale as A. (E) Spiral zooid, same scale as A. (F) Tentaculozooid, same scale as A. (G) Different spine forms, same scale as A. (H) Typical spine, coenosarc removed, scale bar 0.1 mm. (I) Undischarged nematocysts: desmoneme, small microbasic eurytele from gastrozooids, large eurytele from gonozooids, scale bar 10 $\mu$m.

DESCRIPTION: Hydroid normally growing on gastropod shells inhabited by hermit crabs. Hydrorhiza initially a network of adhering stolons enclosed in perisarc, later forming a thick, crust-like layer, covered by coenosarc from which spines, prickles and polyps emerge. Perisarc spines frequent but not always present, dispersed, some regions of colony lacking spines (depends on contact with substratum), size and shape variable but usually rather large, filled with coenosarc, usually with several irregularly spiny ridges running from base to upper regions, top of spines pointed or blunt, smooth or rough; smaller spines smooth. Numerous small prickles rise through the coenosarc of the stolonal plate. Larger spines partly covered by naked coenosarc, mostly in the longitudinal grooves, sometimes even bearing polyps.

Polyps dense, polymorphic, composed of gastrozooids, gonozooids, tentaculozooids, and spiral zooids; the latter two types may be absent, their presence depending on host and environment.

Gastrozooids with cylindrical to fusiform body, large dome-shaped hypostome, two very closely set whorls of tentacles, 15-20 in number (max. 30), unequal in length, alternately pointing upward and horizontal, lower ones shorter, base of hydranth without perisarc collar. Hypostome with scattered euryteles, but these not forming a contiguous layer. Colour pinkish to white.

Gonozooids much smaller and more slender than feeding zooids (ca. 1/5 to 1/3 the size of the gastrozooids), without tentacles, these reduced to wart-like nematocyst buttons tightly clustered into a calotte or band at top of gonozooid. Polyp body somewhat narrowing in diameter below nematocyst buttons and above gonophores, up to 12 gonophores in one whorl in upper region of gonozooid. Gonozooids do not feed. With progressing gonophore development, the gonozooids may become reduced to mere stumps (reproductive exhaustion).

Tentaculozooids may occur or not at margin of colony, smaller then gastrozooids, slender, not spirally coiled, uniform thickness, no tentacles.

Spiral zooids sometimes present at the rim of the colony at the outer lip of the supporting gastropod shell, shorter than gastrozooids, roughly isodiametric, distal end swollen and with nematocyst buttons like in gonozooids.

Gonophores are fixed sporosacs without any canal system or tentacle rudiments, spherical to oblong, male ones white, female ones orange, mature with 4-8 eggs. Colonies unisexual.

Nematocysts: two types of microbasic euryteles, and desmonemes, larger euryteles found on gonozooids.

DIMENSIONS: Colonies can cover several cm$^2$, living gastrozooids up to 5-12 mm when extended, size depends to some degree on environment, spines up to 2 mm, gonophores about 0.4 mm, the stolonal mat can reach 3 mm of thickness. Desmonemes (5-6)x(3)$\mu$m; microbasic euryteles (7-9)x(2.5-3)$\mu$m; larger microbasic euryteles of gonozooids, (14-16)x(5-6)$\mu$m.

OTHER DATA: Sometimes a few sporosacs can also arise from the hydrorhiza (Goette, 1916). For details on the hydrorhiza and spines see Goette (1916), for gonophores see Weismann (1883), Goette (1916), Avset (1959, 1960) and Hertwig & Hündgen (1984). There exist many more publications on the development, ultrastructure, cell biology, and experimental biology of *Hydractinia echinata*, too many to give a comprehensive overview in this more taxonomically oriented review.

BIOLOGY: Quite common in shallow waters around the British Isles, most frequently found on various gastropod shells inhabited by the hermit crab *Eupagurus bernhardus*, but also other hermit crabs possible. Apparently it can also grow rarely on other substrates (e. g. pieces of wood, Hamond, 1963). The depth range is from intertidal pools to more than 100 m, but it is scarce below 100 m (Jäderholm, 1909; Vervoort, 1946; Rees & Rowe, 1969; Christiansen, 1972). Fertile colonies can be found all year round, but more frequently in spring and early summer (Robson, 1914; Teissier, 1965; Hamond, 1957; Christiansen, 1972). Aspects of its feeding biology were investigated by Christensen (1967).

DISTRIBUTION: Northeastern Atlantic from the Arctic Seas south to NW Africa (Patriti, 1970). Includes also the North Sea (Hartlaub, 1894; Rasmussen, 1973) and parts of the Baltic Sea (Schönborn *et al.,* 1993). Its distribution is treated in e. g. Hincks (1868), Allman (1872), Jäderholm (1909), Broch (1911), Da Cunha (1944, 1950), Vervoort, 1946; Leloup (1947), Hamond (1957), Teissier (1965), Naumov (1969), Rees & Rowe (1969), Fey (1970), Christiansen (1972). It also occurs at Iceland (Schuchert, 2001a).

*Hydractinia echinata* has also been recorded in the Mediterranean a few times (e. g. Du Plessis, 1888; Lo Bianco, 1909; Rossi, 1950; Gili, 1986 cited in Medel & López-González, 1996). However, these records give no figures and no voucher material is known. Goette (1916) thinks that Lo Bianco's *H. echinata* from Naples were in fact *H. inermis* [more likely *H. fucicola,* as Goette misidentified his *H. fucicola* as *H. inermis*]. Therefore, there remain some doubts on the correct identification and the presence of *H. echinata* in the Mediterranean needs confirmation.

The species has also been recorded from the western Atlantic, but these records refer to other species as has been shown by Buss & Yund (1989). Type locality: British Isles.

REMARKS: In the NE Atlantic this is a characteristic and easily identifiable species. In contradistinction, Buss and Yund (1989) demonstrated that in the western Atlantic the *H. echinata*-like hydroids belong to a complex of sibling species. Traditional morphometric characters are largely inadequate to distinguish between species. Each of the three *Hydractinia* species is predominantly, but not exclusively, associated with a single host hermit crab species. The species are best distinguished using molecular methods.

### ***Hydractinia ingolfi*** Kramp, 1932 Fig. 17

*Hydractinia* (*Stylactis*) *ingolfi* Kramp, 1932: 13, figs 5-6.
*Stylactis ingolfi*.– Iwasa, 1934: 266, figs 20-21.
*Hydractinia ingolfi*. – Svoboda *et al*., 1995: figs 1b, 2d. – Svoboda *et al*., 1997: figs 3.1b, 3.2d, 3.4. – Schuchert, 2001a: 16.

DIAGNOSIS: Growing on the deep-sea ophiurid *Homalophiura tesselata*, hydrorhiza a stolonal network; gastrozooids with large hypostome, 15-17 tentacles; gonozooids reduced, without tentacles. Gonophores cryptomedusoids, females with > 50 eggs.

DESCRIPTION (Kramp, 1932): Colonies growing on the deep-sea ophiurid *Homalophiura tesselata*. Hydrorhiza a stolonal network, not coalescing into plate, perisarc very thin, no spines, perisarc collar at base of hydranths. Polyps polymorphic with gastrozooids and gonozooids.

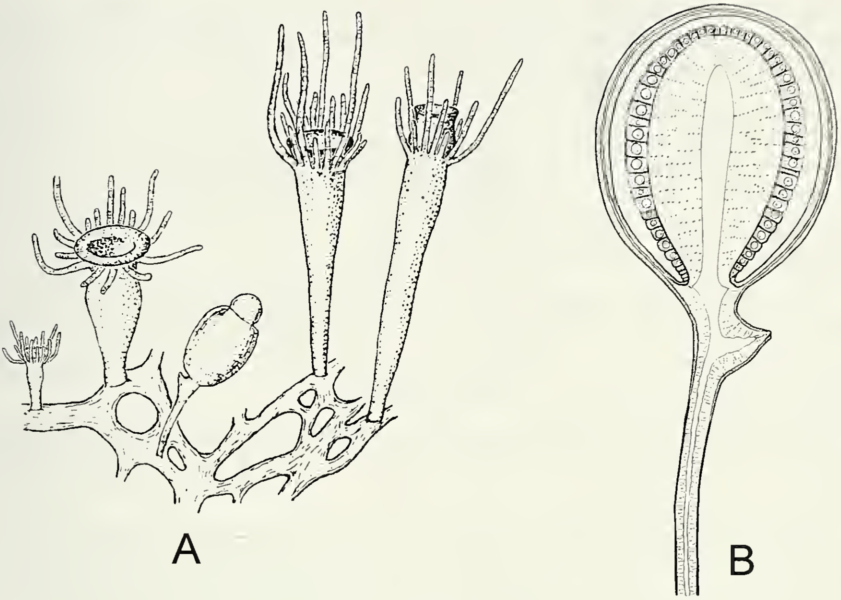

FIG. 17

*Hydractinia ingolfi* Kramp, 1932; modified after Kramp (1932a), for sizes see text. (A) Part of colony with four gastrozooids and a gonozooid. (B) Schematic, longitudinal, optical section of a gonozooid bearing one female sporosac; note the high number of eggs and also the alignment of the sporosac axis as a continuation of the polyp axis; the hypostome is a conical protrusion pointing towards the right side.

Gastrozooids club-shaped, base narrow, hypostome large and trumpet-shaped, surrounded by a whorl of 15-17 tentacles, some tentacles very long and reaching length of hydranth height, others short, short and long ones not alternating regularly.

Gonozooids small and slender, without tentacles, bearing one or rarely two sporosacs, sporosac axis and body of gastrozooid in one line, hypostome a small protuberance below the sporosac, directed sideways.

Gonophores are sessile sporosacs, ovoid, without radial or ring canal, with large spadix covered by single layer of much more than 50 small eggs.

DIMENSIONS: Gastrozooids up to 2.5 mm; sporosacs about 0.5 mm.

DISTRIBUTION AND BIOLOGY: A deep-sea arctic to northern boreal species, species living on the ophiurid *Homalophiura tesselata* (Verrill). Only known from its original descriptions based on several samples from south of Greenland and Iceland (Kramp, 1932). Depth range ca. 2100-3200 m. Type locality: North Atlantic, 58°20'N 40°48'W, 3192 m depth, on *Homalophiura tesselata* (Verrill) (Echinodermata, Ophiuridae).

REMARKS: Contrary to the opinion of Bouillon *et al.* (1997), *H. ingolfi* is most likely not conspecific with *H. arctica* (see Schuchert, 2001a). Judging from its rather unusual, specific, association with a deep-sea ophiurid it appears as a distinct species.

The large, trumpet shaped hypostome seems to be a characteristic trait of the species. The significance of such an enlarged hypostome and the epizoism on ophiurids was outlined by Svoboda *et al.* (1995, 1997).

**Hydractinia arctica** (Jäderholm, 1902) Fig. 18

*Stylactis arctica* Jäderholm, 1902: 5, pl. 1 figs 1-2. – Iwasa, 1934: 258, fig. 10.
*Hydractinia arctica*. – Bouillon *et al.*, 1997: 467, table 1. – Schuchert, 2001a: 14, fig. 4.

MATERIAL EXAMINED: SMNH, Syntypes, 72°42'N 14°49'W, 3 colonies on gastropod shells, some with gonozooids (see also Schuchert, 2001a).

DIAGNOSIS: Arctic, deep-sea species, usually on buccinid gastropods, hydrorhiza stolonal, gastrozooids with basal perisarc collar, hypostome cylindrical, with nematocysts, tentacles in 2-3 whorls, gonozooids smaller, tentacles rudimentary, 2 sporosacs, with ring canal, about 10 eggs per sporosac.

DESCRIPTION: Colonies usually growing on gastropod shells, stolons forming a loose mesh, not coalescing or encrusting, covered by perisarc, without spines. Polyps polymorphic with gastrozooids and gonozooids.

Gastrozooids with shallow basal perisarc collar, club-shaped, broadest in region of tentacles, hypostome high, thick, cylindrical to trumpet-shaped, with a broad band of contiguous euryteles, below hypostome 18-22 filiform tentacles in 2-3 whorls.

Gonozooids much smaller than gastrozooids (1/4), tentacles reduced to a few stumps, with 2 spherical gonophores. Gonophores with ring canal and perhaps also radial canals. Female gonophores with about 10 eggs.

Nematocysts: desmonemes, on tentacles; microbasic euryteles, on tentacles; microbasic mastigophores or euryteles with faint swelling, on hypostome.

DIMENSIONS: Gastrozooids about 2 mm high. Desmonemes 6x4 $\mu$m, smaller microbasic euryteles, on tentacles (8.5-9.5)x(2.5-3.0) $\mu$m, discharged shaft ~0.9 of capsule length; microbasic mastigophores on hypostome, (12-14)x(4-5) $\mu$m, discharged shaft ~0.9 of capsule length.

BIOLOGY: Deep-sea species. The type material grew on gastropod shells. Kramp (1932a) attributed a sterile colony growing on a *Eudendrium* species to *H. arctica*, but this identification should be regarded with much caution.

DISTRIBUTION: An arctic species, reliable records are confined to type locality east of Greenland. Type locality: 72.70°N 14.82°W, depth 2000 m, on shell of the buccinid gastropod *Mohnia mohni* Friele.

REMARKS: See Schuchert (2001a) for a discussion of the species. The high cylindrical hypostome is likely a characteristic trait of this species (Kramp, 1932), but similar hypostomes can also be found in e. g. *H. ingolfi* and *H. fucicola*.

**Hydractinia carica** Bergh, 1887 Fig. 19

*Hydractinia carica* Bergh, 1887: 331, pl. 28, fig. 1. – Jäderholm, 1908: 8. – Jäderholm, 1909: 48, pl. 2 figs 10-11. – Broch, 1916: 48, pl. 1 fig. 11. – Fraser, 1944: 77, pl. 13 fig. 53. – Rees, 1956a: 355, figs 1-2, synonymy, bibliography. – Naumov, 1969: 221, fig. 89. – Calder, 1972: 223, pl. 2 fig. 2. – Schuchert, 2001a: 15, fig. 5.
*Hydractinia minuta* Bonnevie, 1898; 487, pl. 26 fig. 38. – Rees, 1956a: 355.

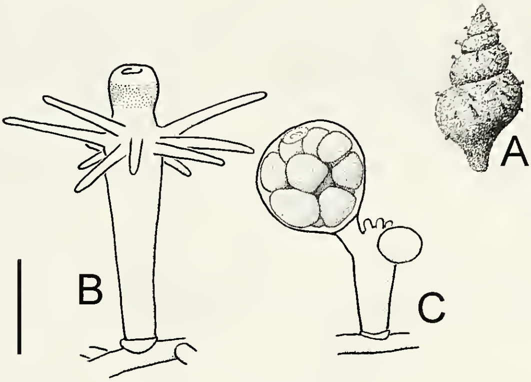

Fig. 18

*Hydractinia arctica* (Jäderholm, 1902); A, after Jäderholm (1902), B-C after type material. (A) Colony on *Mohnia mohni* Friele, shell height 22 mm. (B) Gastrozooid, scale bar 0.5 mm. (C) Female gonozooid, same scale as B.

Material examined: Syntypes, ZMUC, no registration number, leg. Dijmpha, loc. Petuchoffskoi Schar, Kara Sea, on *Buccinum groenlandicum*.

Diagnosis: Usually on gastropods of the genus *Buccinum*, encrusting hydrorhiza, smooth spines, no prickles, gastrozooids with one whorl of 12-16 tentacles, gonozooids much reduced, no tentacles or 2-4 very short ones, 3-7 sporosacs without radial canals, 5-6 eggs per sporosac.

Description: Colonies preferentially on gastropods of the genus *Buccinum*, forming encrusting hydrorhiza covered by coenosarc layer, few conical spines, smooth, tip rounded, stolonal plate without prickles. Gastrozooids with a single whorl of 12 to 16 (max. up 22) tentacles; hypostome without belt of nematocysts, high, nipple-shaped. Spiral zooids and tentaculozooids unknown.

Gonozooids thinner than gastrozooids, size variable but usually much smaller than gastrozooids, sometimes initially of same height as gastrozooids and with up to eight tentacles, gonozooids usually becoming gradually reduced to short stumps lacking tentacles or with few (2-4) short tentacles, degree of reduction of mature gonozooids quite variable; hypostome tightly beset with nematocysts; 3-7 gonophores in one whorl in upper 2/3 of gonozooid.

Gonophores cryptomedusoids, spherical, relatively small, without ring- and radial canals, with spadix, distal calotte sometimes thickened and containing nematocysts, females with 5-6 eggs.

Nematocysts: desmonemes and two other types, probably heteronemes.

Dimensions: Spines 0.3-0.7 mm; extended gastrozooids up to 2.5 mm; diameter of sporosacs 0.25-0.4 mm. For additional measurements see Rees (1956a).

Distribution: A predominantly arctic species, recorded from Norway, Arctic Sea north of Russia, Spitsbergen, western Greenland, and NE Canada (Jäderholm, 1909; Fraser, 1944; Rees, 1956a; Naumov, 1969; Calder, 1972). Naumov (1969) recorded it also from the Bering Sea, Sea of Okhotsk, and Japan Sea. Along the

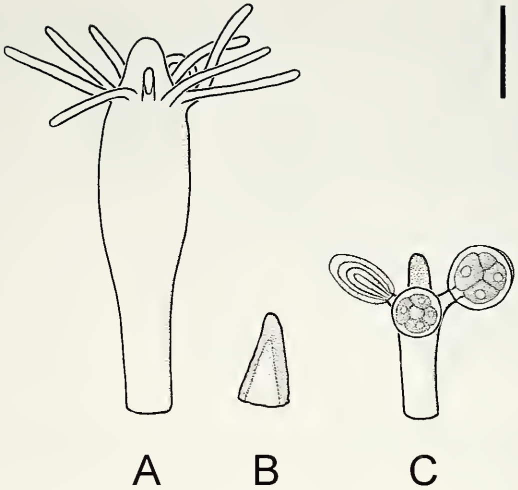

Fig. 19

*Hydractinia carica* Bergh, 1887; after type material, scale bar 0.5 mm. (A) Gastrozooid. (B) Spine. (C) Female gonozooid with three sporosacs of different developmental stages.

European costs, it can rarely be found as far south as Bergen in Norway (Bonnevie, 1901; as *H. minuta*). Most records are from Spitsbergen. Type locality: Petuchoffskoi Schar, Kara Sea, 15 m.

BIOLOGY: The species favours as substratum the shells of the various northern species of *Buccinum* (like *B. undatum, B. scalariforme, B. glaciale, B. ovum, B. groenlandicum, B. ciliatum*; all still used by the gastropod and not by hermit crabs) (Jäderholm, 1909; Rees, 1956a). Jäderholm (1909) also found it also on *Boreotrophon clathratus* (family Muricidae). The bathymetric range is 0 to 120 m.

REMARKS: Broch (1916) and Rees (1956a) re-examined type material of *Hydractinia carica* Bergh, 1887 and *H. minuta* Bonnevie, 1898. Both authors concluded that the two species must be conspecific. Rees (1956a) re-described *H. carica*, but unfortunately made contradictory statements. In his diagnosis (p. 356) he describes the gonophores as "... with 4 radial canals and rudiments of tentacles...", while later (pp. 358 and 359) he describes the female gonophores of the type material as having no radial canals. Bonnevie (1899: 48) and Jäderholm (1908) describe the gonophores as devoid of radial canals. I was also unable to see any indication of radial canals in the type material and it appears that Rees's (1956a) diagnosis contains a typographic error. The male sporosacs have apparently not yet been described.

*Hydractinia carica* can be distinguished from *H. echinata* by its smaller polyps (about half the size), the smooth spines, and the absence of wart-like nematocyst clusters on the gonozooids, the absence of small perisarc prickles on the hydrorhiza, and its host preference.

It even more resembles *H. sarsii*, the most obvious difference being the more reduced gonozooids. However, this can sometimes be a character of limited value for discriminating *Hydractinia* species (Bouillon *et al.*, 1997). Other differences are the absence of small perisarc prickles on the hydrorhiza, gastrozooids with somewhat fewer tentacles, and – likely the most significant difference – its host preference: shells of the genus *Buccinum* still inhabited by the gastropod and not by hermit crabs.

*Hydractinia monocarpa* can easily be confounded with *H. carica*, but it has significantly more eggs per sporosac (50 versus 5-6), fewer gonophores (1-2 versus 3-7), and has more pointed and longer spines.

### ***Hydractinia serrata*** Kramp, 1943 Fig. 20

*Hydractinia monocarpa*. – Kramp, 1932: 16. [not *Hydractinia monocarpa* Allman, 1867]
*Hydractinia serrata* Kramp, 1943: 9, figs 1-3. – Naumov, 1969: 223, fig. 92. – Schuchert, 2001a: 18, fig. 9.

MATERIAL EXAMINED: ZMUC, Godthaab station 107, near Cape Aholl, 76.41°N 69.63°W, 165 m, 15 Aug. 1928, on living *Buccinum* shell; labelled *Hydractinia monocarpa,* described by Kramp (1932a). – ZMUC, Just & Vibe station 35, as *Hydractinia serrata* Kramp, 1943; 76.447°N 69.705°W, western Greenland, Bylot Sound, 260 m, 14 Aug. 1968, fertile colony on gastropod shell.

DIAGNOSIS: Arctic species, encrusting hydrorhiza, spines slender and with four serrated ridges, gonozooids small with few short tentacles, sporosacs pyriform originating from base of gonozooids, female sporosacs with one egg.

DESCRIPTION (in part after Kramp, 1943b): Dense colonies growing on arctic gastropods of the genus *Buccinum,* forming encrusting hydrorhiza covered by coenosarc. Spines numerous, not grouped, high and slender, usually with four longitudinal ridges, their edges irregularly serrated, overgrown by living tissue except for the tip. Polyps polymorphic, differentiated into gastrozooids and gonozooids.

Gastrozooid fusiform to cylindrical, hypostome short and dome-shaped, 8-12 tentacles in one whorl.

Gonozooids small, tentacles in one whorl, reduced to 0-8 short stumps. Gonophores develop near base of gonozooid or even from stolonal plate close to gonozooid, 1-4 per gonozooid, pear-shaped, colonies unisexual. Gonophores develop into sessile sporosacs without canal system (cryptomedusoid), spadix present, females with one egg only. Nematocysts: desmonemes, microbasic euryteles with discharged shaft longer than capsule.

DIMENSIONS: Colonies several cm$^2$, gastrozooids up to 3 mm, gonozooids up to 0.5 mm, sporosacs up to 0.5 mm, spines 0.45-1.2 mm. Preserved microbasic euryteles ca. (10.5-12)x(3.5-4) $\mu$m.

BIOLOGY: Grows on arctic gastropods of the genus *Buccinum* (e. g. *Buccinum belcheri* Reeve, *Buccinum hydrophanum* Hancock, and *Buccinum glaciale* [syn *B. groenlandicum*]), depth range 15-300 m (Naumov, 1969).

DISTRIBUTION: Strictly Arctic; reported from eastern- and western Greenland, Barents Sea (Kramp, 1943; Naumov, 1969; Schuchert, 2001a). Type locality: eastern Greenland, Lindenows Fjord, 20-35 m, on *Buccinum glaciale* Linnaeus (by designation of Kramp, 1943).

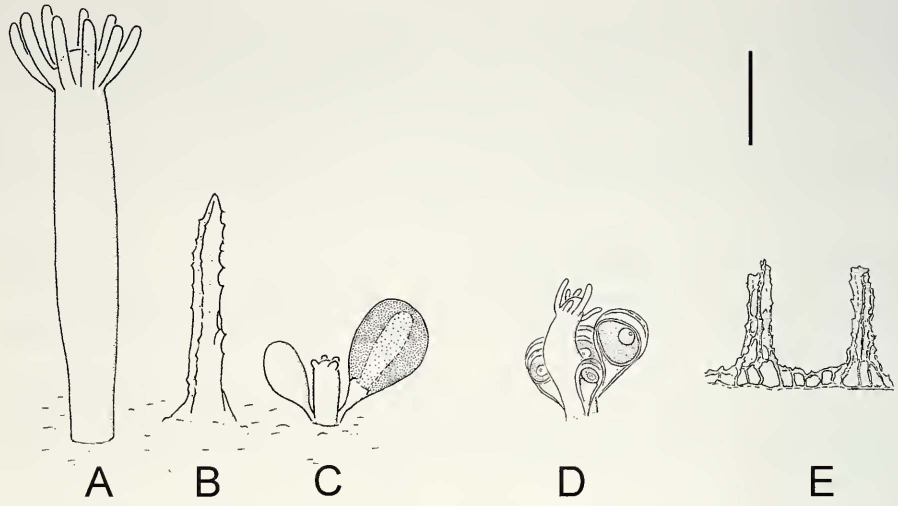

FIG. 20

*Hydractinia serrata* Kramp, 1943; A-C after preserved material, D-E redrawn from Kramp (1943b), scale bar 0.5 mm. (A) Gastrozooid. (B) Spine, note serrated ridges. (C) Male gonozooid, note origin of sporosacs near base of hydranth or from basal plate. (D) Female gonozooid. (E) Section of perisarc skeleton with two spines and basal plate.

## ***Hydractinia monocarpa*** Allman, 1876 Fig. 21

*Hydractinia monocarpa* Allman, 1876: 254, pl. 10 figs 1-3. – Jäderholm, 1909: 49, pl. 2 figs 12-13. – Schuchert, 2001a: 17, fig. 7.
? *Hydractinia monocarpa*. – Calder, 1972: 225, pl. 2 fig. 3.
not *Hydractinia monocarpa*. – Jäderholm, 1908: 8, pl. 1 fig. 6, pl. 2 figs 6-9. – Kramp, 1932: 16 [= *H. serrata*]. – Rees, 1956a: 359, pl. 12 figs 8-11. – Naumov, 1969: 222, fig. 90.

MATERIAL EXAMINED: Syntype, ZMUC, without registration number; loc. Spitsbergen, on 2 cm shell. – Syntype, BMNH 1877.4.12.28; Spitzbergen; on shell of gastropod *Boreotrophon* inhabited by mollusc; female colony.

DIAGNOSIS: Arctic species, usually on *Boreotrophon* gastropods, hydrorhiza encrusting with coenosarc on top, spines tall and pointed, overgrown by coenosarc, gonozooids with no or very reduced tentacles, only one sporosac fully developed, female sporosacs with up to 50 eggs.

DESCRIPTION: Colonies usually growing on gastropod shells of the genus *Boreotrophon*, forming encrusting hydrorhiza covered by coenosarc. Spines numerous, not grouped, high and slender, often needle-like, hollow, straight or curved, very few branched, either smooth or some with undulated or warty ridges, spines overgrown by living tissue except for the tip.

Polyps polymorphic, differentiated into gastrozooids and gonozooids. Gastrozooid fusiform to cylindrical, hypostome short and dome-shaped, about 12 tentacles in one whorl.

Gonozooids much smaller than gastrozooids, rod-shaped, without tentacles or with a few stumps only, usually only one large gonophore, sometimes two opposite but

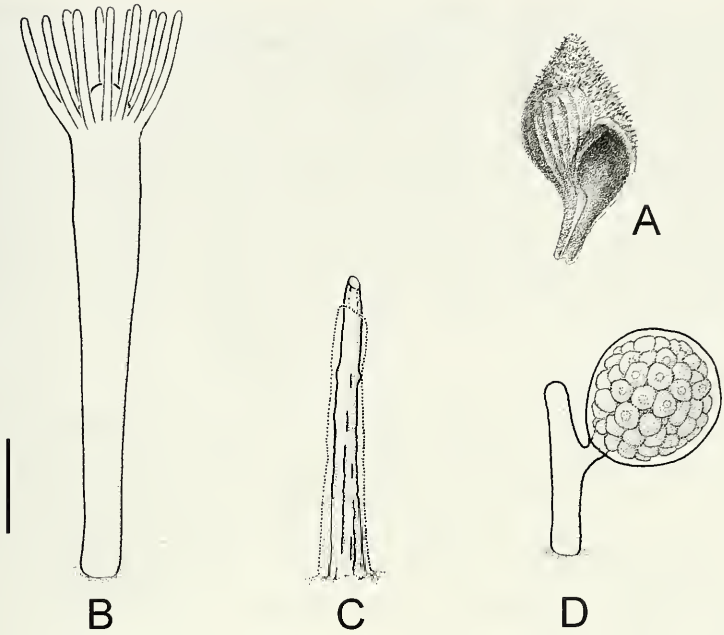

FIG. 21
*Hydractinia monocarpa* Allman, 1876; A, from Allman (1876), B-D, after type material, scale bar 0.5 mm. (A) Colony on *Boreotrophon* shell, size about 2 cm. (B) Gastrozooid. (C) Spine, overgrown by coenosarc. (D) Gonozooid with female sporosac.

one very small, developing near middle of gonozooid. Gonophores spherical, sessile sporosacs without canal system, spadix present, females with about 50 eggs.

DIMENSIONS: Colonies several cm$^2$, limited by shell surface, gastrozooids up 3 mm, gonozooids up to 1 mm, spines up to 1.5 mm, gonophore diameter up to 0.6 mm.

BIOLOGY: The type colony grew on gastropod shells of the species *Boreotrophon clathratus* (L.)[identification by Allman, 1876], Jäderholm (1909) reported it also on a *Bela* spec. (Gastropoda). Calder (1972) recorded it on a sertularian hydroid, which is perhaps an unusual substrate for this species.

DISTRIBUTION: High Arctic species, known from Spitsbergen and Canada (Calder, 1972), perhaps more widespread. Type locality: Spitsbergen.

REMARKS: This is a rarely reported species that has been misidentified several times. An examination of the type specimens showed that some gonozooids have stumps of tentacles and sometimes two opposite sporosacs of very different size.

The species very much resembles *H. carica*, but has significantly more eggs per sporosac (50 versus 5-6), fewer gonophores (1-2 versus 3-7), and has more pointed and longer spines.

The non-type material examined by Jäderholm (1908), Rees (1956), and Naumov (1969) had sporosacs with radial canals. However, I was unable to find any radial canals in the female gonophores of the type material. Also Allman (1876) and Calder (1972) do not mention radial canals. Jäderholm (1908) identified material from the Russian Arctic Seas as *H. monocarpa,* although he initially thought that it could be a new species. His material differed from typical *H. monocarpa* by sporosacs arising from the base of the gonozooids (comparable to *H. serrata*), the presence of four radial canals, and the branched, stout spines. I therefore think that Jäderholm's specimens cannot be referred to *H. monocarpa.* They also do not belong to *H. serrata* due to the sporosacs with radial canals and the high number of eggs. It is rather probable that the material of Jäderholm, Rees, and Naumov belonged to different, probably new species. New investigations on Arctic hydractiniids using living material must be made to clarify the situation.

## Genus ***Clava*** Gmelin, 1788

TYPE SPECIES: *Clava parasitica* Gmelin, 1788 = *Clava multicornis* (Forsskål, 1775).

DIAGNOSIS: Hydroids sessile, not polymorphic, rising directly from hydrorhiza, naked, with or without a low perisarcal collar round base, with conical to dome-shaped hypostome, filiform tentacles scattered or in indistinct whorls, confined to upper third or less of the hydranth; gonophores fixed sporosacs, on hydranth body below tentacles.

REMARKS: This is currently a monotypic genus.

### ***Clava multicornis*** (Forsskål, 1775) Figs 22-23

*Hydra multicornis* Forsskål, 1775: 131. – Forsskål, 1776: pl. 26, fig. B b.
*Hydra squamata* Müller, 1776. 230.
*Clava parasitica* Gmelin, 1788: 3131.
*Tubularia affinis* Gmelin, 1788: 3834.
*Clava repens* Wright, 1857: 227, pl. 11 fig. 1.
*Clava membranacea* Wright, 1857: 228, pl. 11 figs 2-3.
*Clava cornea* Wright, 1857: 228. – Hincks, 1868: 5, pl. 1 figs 3, 3a.
*Clava discreta* Allman, 1859: 369.
*Clava leptostyla* L. Agassiz, 1862: 218, pl. 20 figs 11-16, pl. 21. – Hincks, 1868: 6, pl. 2 fig. 1. – Nutting, 1901: 327, fig 1.
*Clava diffusa* Allman, 1863: 8. – Allman, 1872: 247, pl. 2 figs 3-4. – Hincks, 1868: 9.
*Clava nodosa* Wright, 1863: 378. – Hincks, 1868: 9.
*Clava glomerata* Lönneberg, 1899: 45, fig. – Jäderholm, 1909: 44, synonym.
*Clava multicornis.* – Hincks, 1868: 2, pl. 1 fig. 1. – Allman, 1872: 246, pl. 2 figs 1-2. – Broch, 1916: 38, fig. K, pl. 1 fig. 5. – Weill, 1934: 382. – Vervoort, 1946: 116, figs 24a & 46. – Naumov, 1969: 195, fig. 65. – Edwards & Harvey, 1975: 879, synonymy. – Barnes, 1994: 62, fig . – Broch, 1916: 38, fig. K, pl. 1 fig. 5. – Schuchert, 2001a: 9, fig. 1.
not *Clava multicornis.* – Bedot, 1911: 202. [= *Rhizogeton* spec.]
*Clava squamata.* – Hincks, 1868: 4, pl. 1 fig. 2. – Allman, 1872: 243, pl. 1. – Lönneberg, 1899: 17. – Bedot, 1911: 202. – Broch, 1911: 12, fig. 8. – Kramp, 1914: 976. – Weill, 1934: 381.
? not *Clava multicornis*? – Wedler & Larson, 1986: 82, fig. 5A.
? not *Clava multicornis.* – Peña Cantero & García Carrascosa, 2002: 25, fig. 3d. [?= *Rhizogeton* spec.]

MATERIAL EXAMINED: MHNG INVE54612; Atlantic, France, Roscoff; 15 June 1910, material *Clava multicornis* of Bedot (1911). – MHNG INVE27333; Scotland, Kames Bay; 3 June 1992, on *Ascophyllum* and *Fucus.* – MHNG INVE35753; Scotland, Argyll, Connel Bridge rapids; 4 May 2004, numerous living colonies growing mainly on *Ascophyllum nodosum.* – Atlantic, France, Roscoff; April-May 1998 and 2000, numerous living colonies growing on

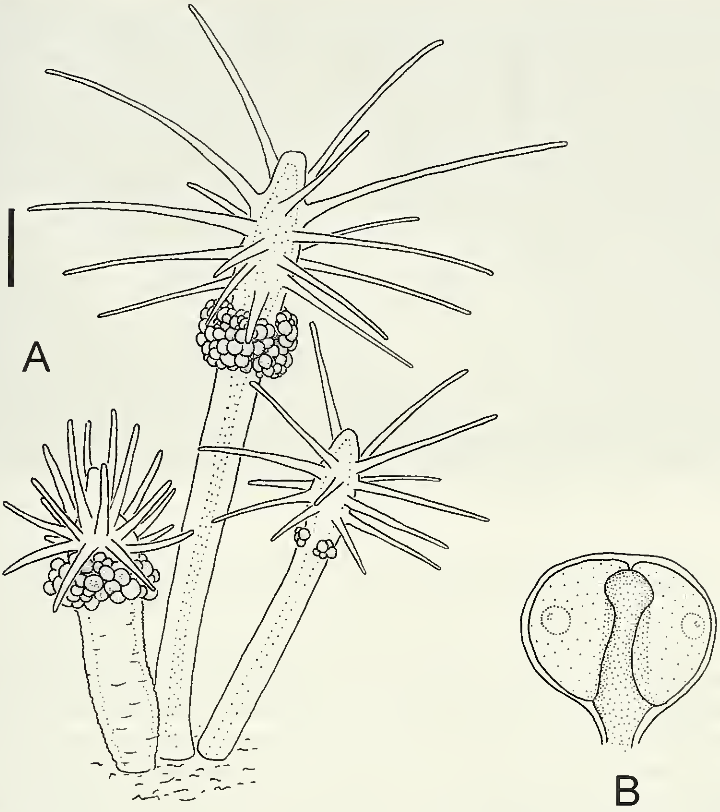

FIG. 22
*Clava multicornis* (Forsskål, 1775), after living material from Scotland. (A) Part of colony, scale bar 1mm. (B) Female sporosac, diameter ca. 0.2 mm.

*Ascophyllum nodosum* and other substrates; not preserved; several independent colonies gave the same 16S DNA sequence as EMBL/GenBank number **EU272552**. – MHNG INVE54079; Atlantic, Spain, Basque Country, San Sebastián (Guipúzcoa), Punta de Mompás; May 2006, one colony; leg. A. Altuna; 16S DNA sequence identical to **EU272552**. – Iceland, Sandgerdi, south of harbour, intertidal, 4 May 2000, numerous fertile colonies on *Fucus* spec. and other substrates, included *multicornis* and *squamata* form, examined alive and used for DNA extraction, not preserved, 16S DNA sequence identical to **EU272552**.

DIAGNOSIS: As for genus.

DESCRIPTION: Mainly growing on fucoid algae, but also on other substrata. Colony form variable, either densely clustered polyps borne on a compact hydrorhizal base of anastomosing stolons that give the impression of a crust (*squamata* form), or scattered polyps arising from an open hydrorhizal network of creeping stolons (*multicornis* form). Intermediate forms also frequent. Stolons always covered by perisarc, without spines. Polyps not polymorphic, in fertile colonies almost all polyps with gonophores, except for the smallest ones.

FIG. 23
*Clava multicornis* (Forsskål, 1775); Dunstaffnage, Scotland, contracted.

Hydranths very large for the family, club-shaped, thickest in region of tentacles and gonophores, very contractile, slender when expanded, base with or without collar of thin perisarc, base sometimes with a constriction (*leptostyla* form). Hypostome dome-shaped, without concentration of nematocysts; 20-40 tapering tentacles, confined to distal 1/3 to 1/6 of hydranth body, scattered or in four indistinct whorls, very contractile. Gonophores small, up to 50 per hydranth, initially separated into groups of several small gonophores, later contiguous in a dense collar below tentacles, sometimes also spreading and thinning out towards base (*diffusa* form).

Gonophores are simple, sessile sporosacs without canal system. Female sporosacs produce mostly 1 or 2 eggs, occasionally 3 eggs. Eggs develop into planula in sporosac, thus larviparous. Colonies unisexual, but some colonies have male and female polyps due to gregarious settlement of several larvae.

Nematocysts: microbasic euryteles and desmonemes. Colours: hydranth pink to cream, spadix dark orange, eggs white.

DIMENSIONS: Colonies from a few hydranths to several $cm^2$. Polyps up to 30 mm if fully expanded, usually shorter and about 10 mm, diameter when fully expanded 0.5 mm. Sporosacs about 0.2 mm. Nematocysts (preserved): microbasic euryteles (7-8)x(2.5-3) $\mu$m, desmonemes (4.5-5)x(3) $\mu$m.

OTHER DATA: The histology of the sporosacs and the gametogenesis were examined by Weismann (1883) and Brien (1942). The influence of environmental factors on the morphology of the polyp was examined in detail by Kinne & Paffenhöfer (1965, 1966), Thiel (1970), and Edwards & Harvey (1975). The colony form and hydranth size and shape are determined by a range of environmental factors such as substratum type, tidal exposure, food availability and water movement.

BIOLOGY: Usually a very common species in the boreal NE Atlantic, abundant at places with good tidal flow. Occurs preferentially on Phaeophyta (*Fucus*, *Ascophyllum*), but is also able to colonize a number of other solid substrata, like rock, timber, barnacles. Its main depth range lies between the mean tide level and the low-water mark of ordinary spring tides, and accordingly it is adapted to aerial exposure twice daily for several hours. Some deeper records are also known (e. g. Rasmussen, 1973: 20 m), but deeper findings should be regarded with suspicion. When exposed to the air during low water, the colonies form compact jelly-like masses, able to withstand desiccation (Edwards & Harvey, 1975). Under good conditions it is perennial (English Channel, Teissier, 1965; Scotland, Edwards & Harvey, 1975). Christiansen (1972) observed gonophores in the Oslofjord (Norway) from May to September. It can live in estuaries and in reduced salinities down to 6 ppt (Barnes, 1994; Schönborn *et al.*, 1993). Its diet appears not to be very selective. It has been observed to feed on small crustaceans, annelids, molluscs, small fish larvae (Kinne & Paffenhöfer, 1965). Additional aspects of its biology can be found e. g. in: Allman (1872), Harm (1902), Ephrussi (1923), Föyn (1927a, 1927b, 1929), Williams (1965), Aldrich *et al.* (1980), Orlov & Marfenin (1993), Orlov (1996), and Rossi *et al.* (2000).

DISTRIBUTION: Mainly North-eastern Atlantic, ranging from the Arctic Sea south to Portugal, including also the North Sea and the Baltic Sea (Hincks, 1868; Allman, 1872; Hartlaub, 1894; Naumov, 1969; Bonnevie, 1901; Jäderholm, 1909; Bedot, 1911; Robson, 1914; Philbert, 1935; Kramp, 1942; Vervoort, 1946; Leloup, 1947; Rees, 1952; Hamond, 1957; Russell, 1957; Teissier, 1965; Castric-Fey, 1970; Christiansen, 1972; Rasmussen, 1973; Schönborn *et al.*, 1993; Medel & López-González, 1996). Also present along the Atlantic coast of North America (Fraser, 1944, as *Clava leptostyla*). Occurs also along the coasts of Iceland, but it is not known to occur in Greenland (Schuchert, 2001a). It has also repeatedly been reported from the Mediterranean (Peña Cantero & García Carrascosa, 2002; Bouillon *et al.*, 2004), but see remarks below. Wedler & Larson (1986) found it in the tropical Atlantic, but due to its occurrence in tropical waters they think that their find might belong to a separate species, an opinion I share with them. The figure given by them, however, looks like *C. multicornis*. Type locality: Øresund (Denmark or Sweden), on bottom between *Fucus*.

REMARKS: In the northern Atlantic, *Clava multicornis* can locally be the most abundant and most conspicuous hydroid. Its morphology is modulated by environmental factors and it is therefore not surprising that it was given numerous different names. The synonymy has fortunately been worked out by the authoritative work of Edwards & Harvey (1975), on which also the synonymy of this study is based.

So far, I have seen no convincing evidence (e. g. museum samples, unambiguous figures) that this species also occurs in the Mediterranean. If it is present in the Mediterranean, it is a rather rare species there. It could be that many Mediterranean records refer actually to an undescribed *Rhizogeton* species. This species has been observed repeatedly in the western Mediterranean (Ligurian Sea, pers. com H. Galea; Banyuls-sur-Mer, own observations), but also along the northern coast of Spain (A. Altuna, pers. com.), and the English Channel (Brittany and Normandy, own observations). The sample identified by Bedot (1911) as *Clava multicornis* belongs also to this *Rhizogeton* species. The polyps resemble somewhat *Clava multicornis*, but they are much smaller (2 mm), are more delicate, they have their tentacles (20-30) more widely spaced and they spread over the distal half or more of the hydranth. The polyps are almost indistingishable from *Rhizogeton nudus* Broch, 1910 (see Schuchert, 2004), but 16S sequence data show that it is distinct from it (unpublished). The naming and description of this species has to wait until some fertile material becomes available.

## Problematic Hydractinidae species

### ***Hydractinia humilis*** Bonnevie, 1898

*Hydractinia humilis* Bonnevie, 1898: 486, pl. 26 figs 39-40. – Rees, 1956b: 109.
[Not *Podocoryne humilis* Hartlaub, 1905: 523, fig. E.]

DIAGNOSIS: Encrusting hydrorhiza, gastrozooids 1-2 mm, 20 tentacles in two close set whorls, gonozooids somewhat smaller and fewer tentacles; sporosacs hermaphroditic, few eggs.

DISTRIBUTION: Only known from the type locality at Manger in Norway.

REMARKS: This is a somewhat problematic species that has never been found again since its original description. It was based on a colony originally collected by M. Sars, but described only in 1898 by Bonnevie. She made histological sections and found spermatids and eggs in the same sporosacs. If not based on a misinterpretation, this is likely a distinct species. Rees (1956b) re-examined the type material, but was unable to investigate the hermaphroditic gonophores. He found the specimen much resembled *Hydractinia carica*. The validity of the species depends on the confirmation of C. Bonnevie's observations.

### ***Hydractinia reticulata*** (Wright, 1861)

*Cionistes reticulata* Wright, 1861: 123, fig. 1. – Hincks, 1868: 135. – Allman, 1872: 309.
[not *Stylactis reticulata* Hirohito, 1988: 139, fig. 51d-f]
[not *Podocoryne reticulata* Fraser, 1938: 24, fig. 23]

REMARKS: This is an indeterminate species. Already Hincks (1868) and Allman (1872) considered its description as insufficient. Its origin and the fixed sporosacs indicate that it is perhaps referable to *H. echinata*. Note that when applying the concept of *Hydractinia* as used here, then *Stylactis reticulata* Hirohito, 1988 and *Podocoryne reticulata* Fraser, 1938 will become secondary homonyms of *H. reticulata* Wright, 1861a.

### ***Clavopsis adriatica*** Graeffe, 1883) Fig. 24

*Clavopsis adriatica* Graeffe, 1883: 84, plate. – Stechow, 1913: 21. – Picard, 1958: 190.

DIAGNOSIS: Hydrorhiza perisarc covered stolons, continued as thin film over basal part of hydranth, hydranths club-shaped, up to 7 mm, 8-14 tentacles in 1-2 whorls, hypostome trumpet-shaped, gonophore producing polyps with fewer tentacles, 5-7 gonophores per polyp, developing well below tentacles, gonophores released as sac-shaped medusoids, gonads not yet formed, four radial canals, four tentacle rudiments, bulbs with pigment spot.

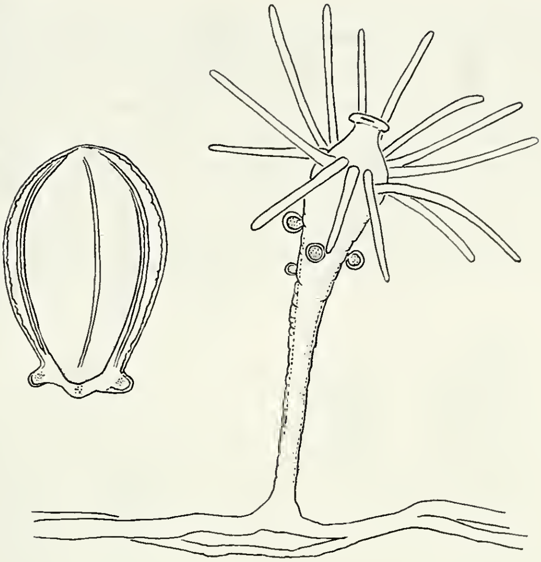

FIG. 24
*Clavopsis adriatica* Graeffe, modified after Graeffe (1883). At right a polyp with gonophores. Left, at higher magnification, a released medusoid.

BIOLOGY: Colonizes tubes of the polychaete *Spirographis spallanzani* and old *Eudendrium* stems.

DISTRIBUTION: Only known from type locality, Harbour of Trieste, Adriatic Sea.

REMARKS: *Clavopsis adriatica* Graeffe, 1883 is only known from its first description. No type material could be located, it is likely lost. Stechow (1923) included it in the Hydractiniidae, Picard (1958b) considered it even as conspecific with *Hydractinia areolata,* which is very unlikely.

Graeffe described the polyps as naked, although there was a thin, filmy perisarc covering at least part of the base and hydranth. This perisarc is also indistinctly indicated in Graeffe's figure and Calder's (1988) conclusion is therefore correct that this species is likely not a hydractiniid, but more likely a member of Pandeidae or Bougainvilliidae.

Some, so far neglected details, allow a re-assessment of this species. Graeffe made his observations on colonies he cultivated in an aquarium. He qualified the polyps as identical with *Clava* and placed it into a new genus solely for the gonophores that did not match this genus. Each bulb of the medusoid had a pigment spot, thus perhaps an ocellus. The gonads of the released medusoids were not yet developed as must be concluded from a passage in Graeffe on page 84: "...ist die medusoide Generation dadurch ausgezeichnet, dass ihr die Erzeugung von Geschlechtsprodukten abgeht..." [the medusoid generation of this species is distinguished by the absence of the production of gametes]. The sentence following this is even more revealing. Graeffe summarizes how the medusoids fell to the bottom of the jar and reverted into the polyp phase again. This unique feature of a life-cycle reversion has been observed for some *Turritopsis* medusae (Piraino *et al.*, 1996). Only the Mediterranean *Turritopsis dohrnii* (Weismann, 1883) is actually able to so (see Schuchert, 2004), a process that is initiated by adverse conditions. Taken also into account the perisarc covered pedicels of the polyps and the medusoids lacking gonads, this makes me suspect that *Clavopsis adriatica* was actually *Turritopsis dohrnii*. Graeffe's colonies were perhaps not kept under good conditions and produced medusae with shrivelled bells and reduced tentacles that then re-differentiated back to the polyp stage. If Graeffe had indeed *Turritopsis dohrnii*, then his illustration of the polyp-tentacles must be incorrect (comp. Fig. 24).

## Family Rhysiidae Brinckmann, 1965

Type Genus: *Rhysia* Brinckmann, 1965.

Diagnosis: Hydroids polymorphic, with gastrozooids, with or without distinct gonozooids, with or without dactylozooids. Polyps issuing from creeping stolons, these covered with perisarc. Gastrozooids naked, sessile, columnar, one whorl of filiform tentacles, large nematocysts on hypostome. Tentaculozooids in perisarc sheath, with swollen naked end studded with nematocysts. Gonozooids naked, sessile, either derived by reduction from gastrozooids or developing as distinct type with fewer or no tentacles; with sexual dimorphism. Gonophores absent, gonad develops on one side of the polyp between the epidermis and gastrodermis, females producing a single large egg only that develops in situ. Cnidome of microbasic euryteles and desmonemes.

Remarks: Hirohito (1988) regarded the Rhysiidae as part of the Hydractiniidae. I agree with Brinckmann-Voss *et al.* (1993) that this family should be kept separate. The extreme reduction of the gonophore makes it impossible to find convincing synapomorphies. The Rhysiidae could be related to the Hydractiniidae as well as to the Cytaeididae. For the moment, they are thus best kept separate. There is only one genus in this family.

## Genus ***Rhysia*** Brinckmann, 1965

Type species: *Rhysia autumnalis* Brinckmann, 1965, by original designation.

Diagnosis: As for the family.

Remarks: There is only one *Rhysia* species in the in the ERMS zone.

### ***Rhysia autumnalis*** Brinckman, 1965 Fig. 25

*Rhysia autumnalis* Brinckmann, 1965: 942, figs 1-15. – Boero & Fresi, 1986: 139. – Bouillon *et al.*, 2004: 78, fig. 44I.
not *Stylactis halecii* Hickson & Gravely, 1907: 8 pl. 1 figs 5-6, pl. 4 fig. 33. – Iwasa, 1934: 262, figs 15-16.
not *Stylactaria halecii*. – Hirohito, 1988: 131, fig. 48a-b. – Namikawa. 1991: 810.

Material examined: Holotype, BMNH 1965.8.31.1; Italy, Vico Equense; 30 m; 18.11.1961; male colony on *Vermetus* and the algae *Flabellia petiolata* (syn. *Udotea petiolata*). – Paratype, BMNH 1965.8.31.2; Italy, Vico Equense; 30 m; 12.12.1961; colony on *Vermetus*.

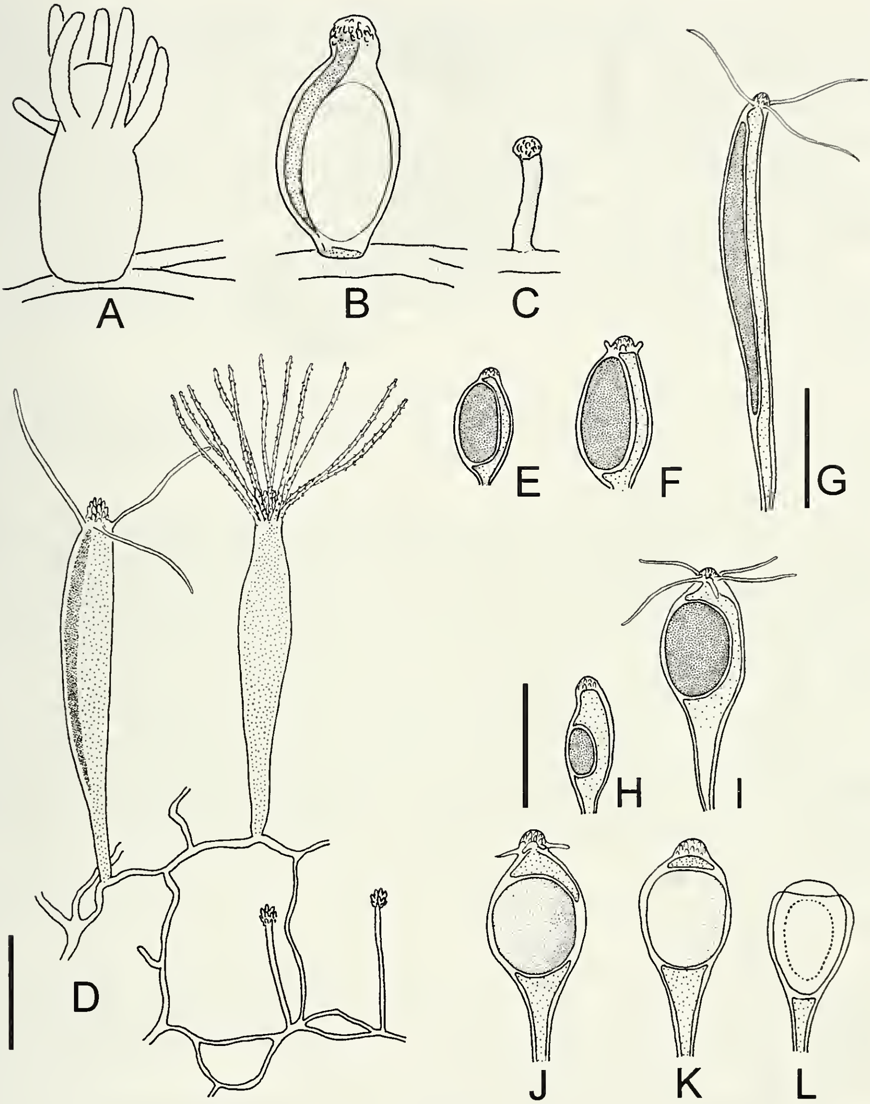

FIG. 25

*Rhysia autumnalis* Brinckman, 1965; A-C after preserved type material, D-L modified from Brinckmann (1965). (A) Contracted nutritive zooid, size about 0.5 mm. (B) Contracted male gonozooid lacking tentacles. (C) Tentaculozooid. (D) Part of colony with gonozooid, gastrozooid, two tentaculozooids, scale bar 0.5 mm. (E) Young gonozooid, same scale as G. (F) More advanced stage of male gonozooid, same scale as G. (G) Extended mature male gonozooid, scale bar 0.5 mm. (H) Young female gonozooid, scale bar 0.5 mm. (I) Mature female gonozooid, same scale as H. (J-L) Development of planula and concomitant reduction of polyp, same scale as H.

DIAGNOSIS: Polyps sessile, polymorphic, tentaculozooids with perisac sheath, gonozooids with few or no tentacles, without gonophores, gametes develop in bodywall.

DESCRIPTION (after Brinckmann, 1965, own observations): Colonies small, polyp issuing from an open hydrorhizal network of creeping stolons. Stolons covered by thin perisarc. Polyps polymorphic, with gastro-gonozooids and tentaculozooids.

Tentaculozooids composed of a thin stem and a terminal spherule beset with nematocysts. Stem enveloped in tube of thin perisarc.

Hydranths naked, sessile, spindle-shaped, with short, rounded or conical hypostome, hypostome covered by large nematocysts. Tentacles filiform, 8-12 in one whorl, nematocysts concentrated in irregular patches.

Gonozooids with bilateral symmetry, develop as small, tentacle-less polyps, the incipient gametes already visible at an early stage, hypostome with large nematocysts, some tentacles may form in later stages. Gonozooids not feeding, male and female polyps in separate colonies.

Male polyps produce a gonad on one side of the polyp between the epidermis and gastrodermis. The gonad is elongated, almost as long as the height of the polyp. The male polyps grow to about the same size as nutritive polyps, but have fewer (0-4), shorter, and thinner tentacles.

Female polyps produce a single, large egg on one side of the polyp between the epidermis and gastrodermis. Egg surrounded by a layer of cells. Mature polyps with 6-10 thin tentacles, nematocysts confined to tentacle tips. Fertilisation and embryonic development takes place in situ, the tentacles and gastrodermis of the gonozooid are concomitantly reduced. Planula becomes free by rupture of the polyp. Colours: male gonads white when young, whitish-blue when completely ripe.

Nematocysts: Microbasic euryteles of three size classes, desmonemes.

DIMENSIONS: Nutritive hydranths extended 1-1.7 mm high, 0.13 mm wide, contracted about 0.4 mm. Tentaculozooids 0.5 mm high. Largest type of euryteles (29-31)x(11) $\mu$m, medium sized eurytels on hypostome (16)x(5-6) $\mu$m, small euryteles on tentacles ca (8)x(4-5) $\mu$m, desmonemes ca (4-5)x(3) $\mu$m.

OTHER DATA: For more details on the histology of the polyps and their gonads see Brinckmann (1965).

BIOLOGY: Occurs on the tubes of the sedentary gastropods of the genus *Vermetus*, spreading also to neighbouring algae. Depth range 7-50 m (Brinckmann, 1965; Boero & Fresi, 1986). Fertile colonies have been found from October to January (Brinckmann, 1965; Boero & Fresi, 1986).

DISTRIBUTION: Western Mediterranean (Gulf of Naples and Ligurian Sea). Type locality: Mediterranean, Italy, Gulf of Naples, Vico Equense.

## FAMILY STYLASTERIDAE GRAY, 1847

TYPE GENUS: *Stylaster* Gray, 1831.

DIAGNOSIS: Hydroid colony erect, branched, usually flabellate, more rarely encrusting, with a thick calcareous skeleton (coenosteum); polyps polymorphic and retractile; gastrozooids and dactylozooids retractable into special skeletal depressions: gastropores and dactylopores; bottom of gastropores and dactylopores with or without an upright pointed or rounded toothed spine (gastrostyle or dactylospine); gastro- and

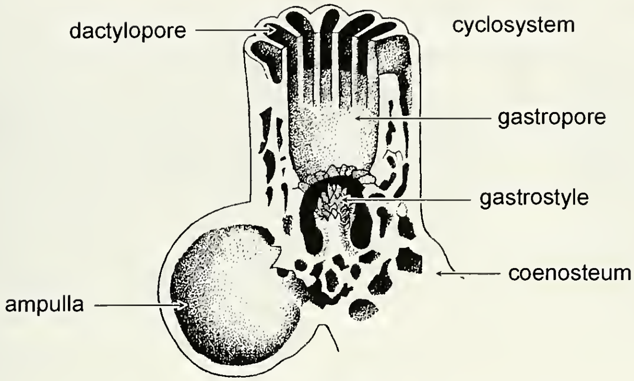

FIG. 26

Schematic longitudinal section of through the skeleton of a stylasterid cyclosystem and an ampulla, modified after Moseley (1879).

dactylozooids either irregularly distributed over colony, or limited to certain regions of colony, or arranged in circles (cyclosystems) where one gastrozooid is surrounded by several dactylozooids. Gastrozooids with one whorl of filiform tentacles, exceptionally without tentacles; dactylozooids filiform, without tentacles. Gonophores fixed sporosacs and developed inside vesicles (ampullae) covered by or buried in coenosteum.

REMARKS: The European species of this family have been revised and monographed in detail by Zibrowius & Cairns (1992). Therefore, only a summary of the species found in the ERMS region is given here and only a few species that also occur in more shallow waters are illustrated. Some important technical terms necessary for the usage of the keys are explained under Material and Methods and in Fig. 26. For introductions to the Stylasteridae see Moseley (1879), Boschma (1956b) and Cairns (1983b).

KEY TO THE GENERA FOUND IN THE ERMS ZONE (AFTER ZIBROWIUS & CAIRNS, 1992):

1a Gastro- and dactylopores independent, not arranged in cyclosystems . . . . . . . 2
1b Gastro- and dactylopores arranged in cyclosystems . . . . . . . . . . . . . . . . . . . . 4
2a Gastropore without gastrostyle . . . . . . . . . . . . . . . . . . . . . . . . . . . ***Pliobothrus***
2b Gastropore with gastrostyle . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 3
3a Dactylopores are low, apically perforated cones (Fig. 27B) . . . . . . ***Lepidopora***
3b Dactylopores surrounded by U-shaped collar (spine with slit, see Fig. 28C) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . ***Errina***
4a Cyclosystem (partially) overarched by fixed lid; gastropore double chambered; gastro- and dactylostyles absent . . . . . . . . . . . . . . . . . ***Cryptothelia***
4b Cyclosystem without lid; gastropore tube cylindrical; gastro-and dactylostyles present . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 5
5a Cyclosystems on anterior branch face; gastropore tube long and curved; ampullae usually clustered near cyclosystems . . . . . . . . . . . . . . . . . ***Stenohelia***
5b Cyclosystems randomly or sympodially arranged; gastropore tube (usually) short and (nearly) straight; ampullae scattered randomly over coenosteum . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . ***Stylaster***

## Genus *Pliobothrus* Pourtalès, 1868

Type species: *Pliobothrus symmetricus* Pourtales, 1868.

Diagnosis: Gastro- and dactylopores randomly arranged. Coenosteal texture linear-imbricate; coenosteal pores large. Gastropore tube double-chambered; no gastrostyles. Dactylopore spines conical or tubular; dactylopore tubes quite long; no dactylostyles. Ampullae usually internal (females external *P. gracilis*).

### Key to the *Pliobothrus* species of the ERMS region

1a Female ampullae internal, gastropores 0.30-0.45 mm in diameter . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *P. symmetricus*

1b Female ampullae superficial mounds, gastropores 0.18-0.25 mm in diameter . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *P. gracilis*

### ***Pliobothrus symmetricus*** Pourtalès, 1868 Fig. 27

*Pliobothrus symmetricus* Pourtalès, 1868: 141. – Pourtalès, 1871: 57, pl 4 figs 7-8. – Cairns, 1983: 439, figs 3A-H, 24G, 25G, 27B. – Boschma, 1956b: F104, fig. 85.1a-b. – Boschma, 1967: 333, pl. 1 figs 5-6. – Zibrowius & Cairns, 1992: 38, figs 5A-G & 6A-G.
*Hornera gravierei* Calvet, 1911: 7, fig 5.

Diagnosis: See keys to genera and species.

Description: See Zibrowius & Cairns (1992).

Dimensions: Colonies in eastern Atlantic around 6 cm, gastropores 0.30-0.45 mm in diameter (developing ones smaller, 0.2 mm), more data in Zibrowius & Cairns (1992).

Distribution: In the western Atlantic from South Carolina through the Lesser Antilles, depths 150-400 m. In the eastern Atlantic southeast of Iceland, east of The Faroes, between Faroes and Hebrides, Norway, west of Ireland, Celtic Sea, Bay of Biscay, Galicia and Josephine Seamounts, ? Madeira, Azores, ranging from 80 to 1600 m, usually below 250 m. Type locality: Off Sand Key, Key West, Florida.

### ***Pliobothrus gracilis*** Zibrowius & Cairns, 1992

*Pliobothrus gracilis* Zibrowius & Cairns, 1992: 44, Fig. 5H-N, 8A-G.

Diagnosis: See keys to genus and species.

Description and Illustration: Zibrowius & Cairns (1992)

Distribution: Known from type locality only, Hyères Seamount, west of Morocco, depth 620-700 m.

## Genus *Lepidopora* Pourtalès, 1871

Type species: *Errina glabra* Pourtalès, 1867.

Diagnosis: Coordination of gastro- and dactylopores usually random; however, in some species dactylopores serially arranged on branch edges, and gastropores serially arranged on anterior or antolateral branch faces. Coenosteal texture quite

FIG. 27

*Pliobothrus symmetricus* Pourtalès, 1868; from Pourtalès (1871). (A) Colony. (B) Part of branch. The flush, larger holes are the gastropores, the smaller holes on round tubercules are the dactylopores, scale bar 2.5 mm

variable. Gastropores often bordered by proximal lip, gastro- and dactylore tubes long. Gastrostyles usually not ridged; height:width ratio high. Dactylopores apically perforate mounds; no dactylostyles.

REMARKS: Only *Lepidopora eburnea* is present in the ERMS zone.

***Lepidopora eburnea*** (Calvet, 1903)

*Horneara eburnea* Calvet, 1903: 162, pl. 18 fig 5a-c.
*Errina* (*Lepidopora*) *hicksoni* Boschma, 1963: 339, fig. 1, pl. 1 figs 1-3.
*Lepidopora eburna*. – Zibrowius & Cairns, 1992: 27, figs 1A-F, 2A-J.

DIAGNOSIS: See genus diagnosis.

DESCRIPTION AND ILLUSTRATIONS: See Zibrowius & Cairns (1992).

DISTRIBUTION: Azores, depth range 480-983 m. Type locality: 38°22'N 28°14.4'W, 736 m (Azores).

Genus ***Errina*** Gray, 1835

TYPE SPECIES: *Millepora aspera* Linnaeus, 1767.

DIAGNOSIS: Gastro- and dactylopores usually randomly arranged. Coenosteal texture reticulate-granular or linear-imbricate. Proximal gastropore often with lip-like process (hood); gastrostyles present, having a moderate height: width ratio. Dactylopore spines U-shaped, with groove directed proximally; walls of dactylopore spine thick; no dactylostyles. Ampullae superficial or internal.

KEY TO THE *ERRINA* SPECIES FOUND IN THE ERMS ZONE:

1a Colony branches with rather blunt ends; gastropore with lip . . *Errina dabneyi*
1b Branches taper gradually; gastropore without lip . . . . . . . . . . . . . . . . . . . . . . 2
2a Colony uniplanar to slightly bushy, dactylopore spines high (up to 0.65 mm), some dactylopores without spines . . . . . . . . . . . . . . . *Errina aspera*
2b Colony bushy, sparsely branched, dactylopore spines shallow 0.14-0.16 mm . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Errina atlantica*

For a more elaborate table of differences see Zibrowius & Cairns (1992).

**Errina dabneyi** (Pourtalès, 1871)

*Lepidopora dabneyi* Pourtalès, 1871: 41, pl. 7 figs 10-11.
*Hornera verrucosa* Calvet, 1903: 161, pl. 18 fig. 6a-c.
*Errina amoena* Boschma, 1956a: 281, figs 1-3, pls 1-2, pl. 3 figs 1-4.
*Errina dabneyi*. – Zibrowius & Cairns, 1992: 53, figs 11A-I, 12A-F, 13A-B.

DIAGNOSIS: See keys to genera and species.

DESCRIPTION: See Zibrowius & Cairns (1992).

DIMENSIONS: Colonies up to 30 cm, branches tapering to about 0.6 mm, gastropores 0.15-0.20 mm in diameter, dactylopore spines up to 0.15 mm high.

DISTRIBUTION: Azores, and Mid-Atlantic Ridge southwest of the Azores, 140-2200 m. Type locality: Azores, Faial.

**Errina aspera** (Linnaeus, 1767) Fig. 28

*Millepora aspera* Linnaeus, 1767: 1282.
*Errina aspera* – Fol, 1885: 668. – Boschma, 1954: 143, fig. 1a-c, pls 1-3. – Cairns, 1983: 459, fig. 11A-G. – Zibrowius & Cairns, 1992: 46, figs 9A-I & 10A-H, synonymy. – Bouillon *et al.*, 2004: 79, fig. 45B-C.
*Errina aspera mascarina* Boschma, 1965: 3, figs 1-2, pl. 1-2.

MATERIAL EXAMINED: MHNG INVE55452 and INVE55453; Mediterranean, Italy, Messina; several colonies or fragments; no collection date, material mentioned in Fol (1885) and Zibrowius & Cairns (1992).

DIAGNOSIS: See keys to genera and species.

DESCRIPTION: See Zibrowius & Cairns (1992).

DIMENSIONS: Colonies up to 20 cm, branches tapering to about 0.7 mm, gastropores 0.18-0.25 mm in diameter, dactylopore spines up to 0.65 mm high.

DISTRIBUTION: Mediterranean Sea (mainly Strait of Messina), Strait of Gibraltar, off Morocco, ? off Cape Verde Islands, depth range 80-226 m. Type locality: Mediterranean.

**Errina atlantica** Hickson, 1912

*Errina atlantica* Hickson, 1912: 464. – Boschma, 1967: 331, fig. 3a-b, pl. 1 fig. 7-10. – Zibrowius & Cairns, 1992: 58, figs 14A-F, G-I?, 15 A-G.

DIAGNOSIS: See keys to genera and species.

DESCRIPTION: See Zibrowius & Cairns (1992).

DIMENSIONS: Colonies up to 12 cm, branches tapering to about 0.7 mm, gastropores 0.22-0.30 mm in diameter, dactylopore spines 0-0.16 mm high.

DISTRIBUTION: Azores, 610-938 m. Type locality: Azores, 38°07'N 27°11.75'W, 983 m.

Genus ***Stylaster*** Gray, 1831

TYPE SPECIES: *Madrepora rosea* Pallas, 1766: 312.

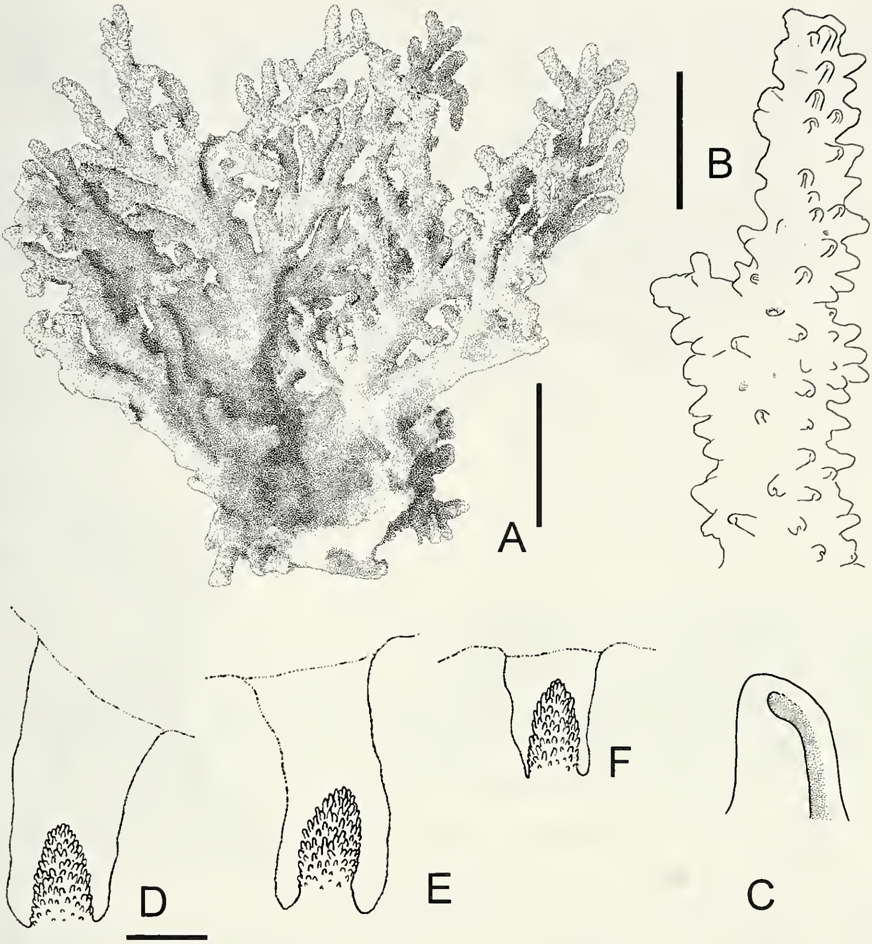

FIG. 28

*Errina aspera* (Linnaeus, 1767); A-C after MHNG INVE55452, D-F from Boschma (1954). (A) Colony, scale bar 2 cm. (B) Terminal branch, scale bar 5 mm. (C) Characteristic dactylopore spine, height about 0.6 mm. (D-F) Transversal sections of gastropore, showing gastrostyle and variability of gastropore depth, scale bar 0.2 mm.

DIAGNOSIS: Gastro- and dactylopores arranged in cyclosystems. Cyclosystems variable in location, ranging from uniform coverage of all branch surfaces (Group A) to a strictly sympodial arrangement (Group C), with many intermediate arrangements (Group B). Coenosteal colour and texture variable: most common textures reticulate-granular and linear imbricate. Gastro- and dactylostyles present, the latter robust in Group A, more moderate to rudimentary in Groups B and C. Gastrostyles usually ridged and bearing long, pointed spines. Ring palisade often present; gastropore inner shelf sometimes present in Group C. Ampullae usuallly superficial, usually with distinct efferent pores.

REMARKS: The differences of the *Stylaster* species and subspecies found in the ERMS zone do not easily lend themselves to construct a robust, reliable identification key. For identifications use preferably the detailed table in Zibrowius & Cairns (1992).

KEY TO THE *STYLASTER* SPECIES FOUND IN THE ERMS ZONE

1a Cyclosystems dispersed, tips of branch diameter larger than cyclosystems, coenosteum smooth ........................ *Stylaster norvegicus*
1b Cyclosystems primarily on sides of branches, some on anterior and posterior sides, branch tips usually tapering to diameter of cyclosystems, coenosteum rough or smooth ........................................ 2
2a Cyclosystems flared (Fig. 30C), coenosteum rough .... *Stylaster gemmascens*
2b Cyclosystems not flaring, coenosteum rough or smooth ................. 3
3a Smooth, porcellanous coenosteum ...................... *Stylaster ibericus*
3b Coenosteum granulate, rough ........................................ 4
4a Cyclosystems sympodial and on anterior face, colonies small (1 cm), gastrostyle elongate cylindrical .................... *Stylaster maroccanus*
4b Cyclosystems primarily on sides of branches, some on anterior and posterior sides, colonies 1-15 cm ...................... *Stylaster erubescens*

**_Stylaster norvegicus_** (Gunnerus, 1768) Fig. 29

*Millepora norvegica* Gunnerus, 1768: 64, pl. 2 figs 20-22.
? *Allopora oculina* Ehrenberg, 1834: 147.
*Stylaster* (*Allopora*) *norvegicus* forma *atlantica* Broch, 1936: 49, fig. 14, pl. 7 figs 20-21.
Not *Stylaster* (*Allopora*) *norvegicus* forma *pacifica* Broch, 1936: 52, fig. 15, pl. 6 figs 18-19.
*Stylaster norvegicus*. – Zibrowius & Cairns, 1992: 62, figs 16A-G & 17A-I.

DIAGNOSIS: See key to the *Stylaster* species.

DESCRIPTION: See Zibrowius & Cairns (1992).

DIMENSIONS: Colonies up to 10 cm high and 15 cm wide, diameter of branches at tip 2-3 mm, cyclosystems 0.9-1.1 mm in diameter.

DISTRIBUTION: Known from a wide area of the North Atlantic: from Denmark Strait, the northwest, southwest, and southeast of Iceland, Faroes and Hebrides, Rockall, and along the coast of Norway. In Norway it is common in depths of 80-300 m, frequently found together with the bank-forming scleractinian *Lophelia pertusa*. Elsewhere the shallowest records are from 75 m in the Faroes. In the Iceland-Faroes area, this species has been obtained as deep as 1400 m. Type locality: Nordmør, Norway.

REMARKS: See under *Stylaster gemmascens*.

**_Stylaster gemmascens_** (Esper, 1794) Fig. 30

*Madrepora gemmascens* Esper, 1790: pl. 55 figs 1-2; corresponding text 1794: 60.
*Stylaster gemmascens*. – Broch, 1914a: 8, fig. C, pl. 1 figs 4-7, pl. 2 fig. 16, pl. 3 figs 21, 24-26, 30-31, pl. 4 fig. 32-33, pl. 5 figs 46, 49-50. – Zibrowius & Cairns, 1992: 79, figs 23A-H, 24A-F, synonymy.
not *Stylaster gemmascens alascanus* Fisher, 1938: 500, pls 47-48, pl. 54 fig. 1. – Naumov, 1969: 584, figs 430-431, pl. 27 fig. 1.
*Stylaster gemmascens*. – Boschma, 1955: 22, figs 1-3, pls 1-2.

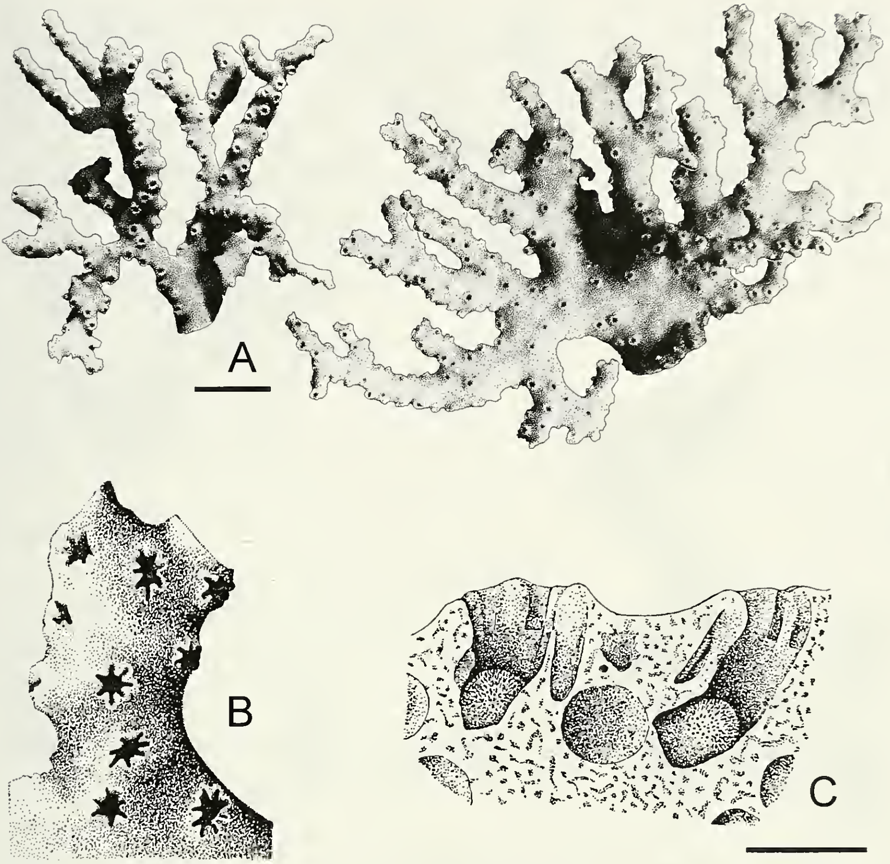

FIG. 29

*Stylaster norvegicus* (Gunnerus, 1768); A redrawn after photographs in Zibrowius & Cairns (1992), B from Boschma (1956b), C from Broch (1934). (A) Parts of two colonies, scale bar 1 cm. (B) Branch of colony in higher magnifications. (C) Longitudinal section through the coenosteum showing two gastropores and their gastrostyles, in-between them an ampulla; scale bar 1 mm.

DIAGNOSIS: See key to the *Stylaster* species.

DESCRIPTION: See Zibrowius & Cairns (1992).

DIMENSIONS: Colonies up to 11 cm high and wide, terminal branch width about as diameter of cyclosystems (1.3 mm, oval ones 1.6 x 0.7 mm).

DISTRIBUTION: North Atlantic from Denmark Strait, east of Greenland, north-west of Iceland through Faroes-Hebrides area to Norway and Rockall. Along the Norwegian coast the species is common in depths of about 40 to 400 m, frequently found together with the bankforming scleractininan *Lophelia pertusa*. Depth range elsewhere down to depths of 665 m. Type locality: Norway (see Zibrowius & Cairns, 1992 for details).

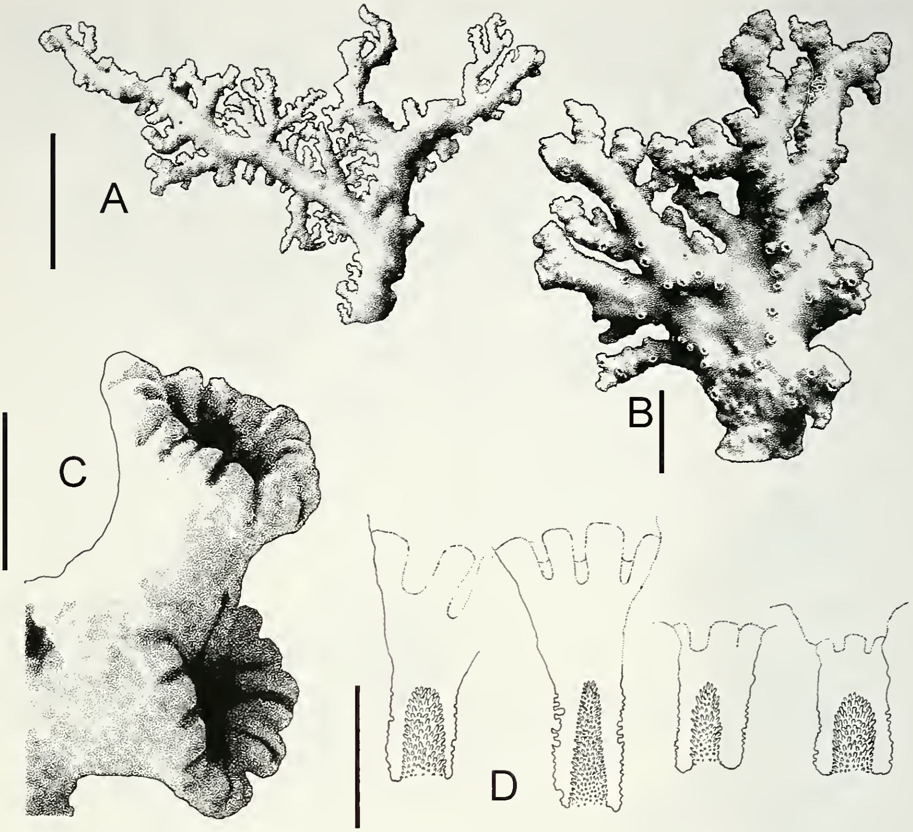

FIG. 30

*Stylaster gemmascens* (Esper, 1794) A-C modified and redrawn from Zibrowius & Cairns (1992), D from Boschma (1955). (A-B) Colonies, scale bar 1 cm. (C) Terminal region of branch with two cyclosystems, note flaring openings; scale bar 1 mm. (D) Longitudinal sections of gastropores, note variability of gastrostyle and pore length, scale bar 0.5 mm.

REMARKS: *Stylaster gemmascens* (Esper, 1794) and *Stylaster norvegicus* (Gunnerus, 1768) are the most common stylasterids in the north-eastern Atlantic, although both still occur in deeper waters (below 40 m depth, while most other NE Atlantic species occur below 200 m). The two species can occur together and have been confused repeatedly. *Stylaster gemmascens* can be distinguished by its flared cyclosystems (Fig. 30C), the rough surface, the narrow gastropore tubes (Fig 30D), and a male ampulla with a crest. In *S. norvegicus* the skeleton surface is smooth and the cyclosystems are scattered evenly over the colony (Fig. 29A), while in *S. gemmascens* they tend to be concentrated on the lateral branch edges (but some do also occur on posterior and anterior faces) (Fig. 30A-B)

**Stylaster ibericus** Zibrowius & Cairns, 1992

*Stylaster ibericus* Zibrowius & Cairns, 1992: 84, figs 25A-O, 26A-G.

DIAGNOSIS: See key to the *Stylaster* species.

DESCRIPTION: See Zibrowius & Cairns (1992).

DISTRIBUTION: Off north-western Spain, depth range 490-620 m. Type locality: 44°01.6N 08°40.6'W, 500 m.

***Stylaster maroccanus*** Zibrowius & Cairns, 1992

*Stylaster maroccanus* Zibrowius & Cairns, 1992: 76, figs 21A-D & 22A-G.

DIAGNOSIS: See key to the *Stylaster* species.

DESCRIPTION: See Zibrowius & Cairns (1992).

DISTRIBUTION: Only known from type locality, off Atlantic coast of Morocco, 34°24.7'N 07°39.3W, 1378 m.

***Stylaster erubescens britannicus*** Zibrowius & Cairns, 1992

*Stylaster erubescens britannicus* Zibrowius & Cairns, 1992: 92 figs 29A-G, 30A-G.

DIAGNOSIS: *Stylaster erubescens* with coarse, granular surface of coenosteum, granules rounded.

DESCRIPTION: See Zibrowius & Cairns (1992).

DISTRIBUTION: Southeast of Iceland through the Faroes-Hebrides area and the Rockall Trough to the Celtic Sea, depth range 350-1080 m. Type locality: Southeast of Iceland, 64°16'N 11°15' W, 350 m.

***Stylaster erubescens groenlandicus*** Zibrowius & Cairns, 1992

*Stylaster roseus*. – Broch, 1914a; 12, pl. 1 figs 8-9, pl. 2 figs 10-11, 17, pl. 3 fig. 22, pl. 4 fig. 36, 39, pl. 5 fig. 43, 47-48.
[not *Stylaster roseus* (Pallas, 1766)]
*Stylaster erubescens groenlandicus* Zibrowius & Cairns, 1992: 89, figs 27A-H, 28A-H.

DIAGNOSIS: *Stylaster erubescens* of Greenland.

DESCRIPTION: See Zibrowius & Cairns (1992).

DISTRIBUTION: East of Greenland to northwest of and southeast of Iceland, all north of 60°, depth range 263-1440 m. Type locality: Denmark Strait, northwest of Iceland, 66°18'N 25°59'W, 621 m.

***Stylaster erubescens meteorensis*** Zibrowius & Cairns, 1992

*Stylaster erubescens meteorensis* Zibrowius & Cairns, 1992: 96, figs 31A-H, 32A-H.

DIAGNOSIS: *Stylaster erubescens* with bushy colony, coenosteum texture reticulate-smooth, strips with numerous symmetrical lateral protuberances.

DESCRIPTION: See Zibrowius & Cairns (1992).

DISTRIBUTION: Great Meteor Seamount, 29°59'N 28°33'W, 290 m (type locality).

Genus ***Stenohelia*** Saville Kent, 1870

TYPE SPECIES: *Allopora maderensis* Johnson, 1862.

DIAGNOSIS: Gastro- and dactylopores arranged in cyclosystems, which occur exclusively on the anterior branch face. Cyclosystems without lips or lids. Coenosteum white or light brown, either linear-imbricate or reticular-granular in texture. Gastropores long and usually curved; gastrostyles present, usually encircled by a robust ring palisade. Dactylostyles rudimentary. Ampullae superficial, often clustered around base of cyclosystem. Ampullar efferent pores of both sexes usually well distinguished.

REMARKS: There occurs only one named *Stenohelia* species in the ERMS zone, but a second, unnamed species is present (Zibrowius & Cairns, 1992).

### ***Stenohelia maderensis*** (Johnson, 1862)

*Allopra maderensis* Johnson, 1862: 196, figs 1-3.
*Stenohelia maderensis*. – Cairns, 1983: 487, fig. 20A-B, D-G. – Zibrowius & Cairns, 1992: 99, figs 33A-L & 34A-J. – Alvarez, 1995: 263, fig 1.
Not *Stylaster maderensis* – Boschma, 1964b: 64, pl. 1 figs 13-14 [= *S. profunda*].

DIAGNOSIS: See key to the genera and genus diagnosis.

DESCRIPTION: See Zibrowius & Cairns (1992).

DISTRIBUTION: The Faroes and Hebrides (665 m), north-western Spain and southern Bay of Biscay (490-910 m), Galicia Seamount, Madeira, Cape Verde Islands; depth range 110-1125 m. Type locality: Madeira.

### Genus ***Crypthelia*** Milne Edwards & Haime, 1849

TYPE SPECIES: *Crypthelia pudica* Milne Edwards & Haime, 1849.

DIAGNOSIS: Gastro- and dactylopores arranged in cyclosystems, which usually occur exclusively on anterior branch face. Cyclosystems partially or entirely covered by one or more fixed lids. Coenosteum white or light brown, linear imbricate in texture, and often spinose as well. Nematopores usually present, especially on cyclosystem lids, pseudoseptae, and ampullae. Gastropores double-chambered; no gastro- or dactylostyles. Ampullae usually superficial and large, occurring in various position and with a variety of efferent pore location.

REMARKS: The lid over the cyclosystem makes this genus quite easily recognizable. See Zibrowius & Cairns (1992) for a table to distinguish the species of the ERMS zone.

### ***Crypthelia affinis*** Moseley, 1879

*Crypthelia affinis* Moseley, 1879: legend on pl. 42. – Zibrowius & Cairns, 1992: 106, figs 36A-I, 37A-I.
*Crypthelia moseleyi* Hickson & England, 1905: 21.

DISTRIBUTION: Azores, depth range 712-1557 m, perhaps as deep as 2790 m. Type locality: uncertain, Southwest of the Canary Islands, 25°45'N 20°12'W, 2790 m.

### ***Crypthelia medioatlantica*** Zibrowius & Cairns, 1992

*Crypthelia medioatlantica* Zibrowius & Cairns, 1992: 112, figs 36J-M, 38A-H.

DISTRIBUTION: Azores, Azores and Mid-Atlantic Ridge, depth range 861-2644 m. Type locality: Mid-Atlantic Ridge, 36°50.9'N 32°57.9'W, 1400-2200 m.

***Crypthelia tenuiseptata*** Cairns, 1986

in part *Crypthelia tenuiseptata* Cairns, 1986a: 115, figs 52A-G, 53K.
*Crypthelia vascomarquesi*.– Zibrowius & Cairns, 1992: 117, figs 41A-J, 42A-I.

DISTRIBUTION: Virgin Islands, Lesser Antilles, and Azores; depth range 761-1557 m. Type locality: Grenada, 12°03.25'N 61°48.50E, 761 m.

***Crypthelia vascomarquesi*** Zibrowius & Cairns, 1992

*Crypthelia vascomarquesi* Zibrowius & Cairns, 1992: 114, Figs 39A-J, 40A-J.

DISTRIBUTION: Azores, Hyères Seamount, Madeira, depth range 390-1520 m. Type locality: 38°07'N 27°11.75'W, 983 m.

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## REFERENCES

AGASSIZ, L. 1862. Contributions to the Natural History of the United States of America. Vol. IV. *Little Brown, Boston*, pp. 1-380, pls 1-19.

ALCOCK, A. 1892. A case of commensalism between a gymnoblastic anthomedusoid and a scorpaenoid fish. *Annals and Magazine of Natural History* (6)10: 207-214.

ALDER, J. 1862a. Observations on British Zoophytes. *Edinburgh new philosophical Journal (N. S.)* 14: 144.

ALDER, J. 1862b. Descriptions of some new and rare zoophytes found on the coast of Northumberland and Durham. *Annals and Magazine of Natural History* (3)9: 311-317, plates 13-15.

ALDER, J. 1863. Observations on British Zoophytes. 1. *Hydractinia areolata* n. sp. 2 *Atractylis arenosa*, n. sp. *Proceedings of the Royal Society of Edinburgh* 2: 314-316.

ALDRICH, J. C., CROWE, W., FITZGERALD, M., MURPHY, M., MCMANUS, C., MAGENNIS, B. & MURPHY, D. 1980. Analysis of environmental gradients and patchiness in the distribution of the epiphytic marine hydroid *Clava squamata*. *Marine Ecology Progress Series* 2: 293-301.

ALLMAN, G. J. 1859. Notes on the hydroid zoophytes. *Annals and Magazine of natural History* (3) 4: 137-144.

ALLMAN, G. J. 1864. On the construction and limitation of genera among the Hydroida. *Annals and Magazine of Natural History* (3) 13: 345-380.

ALLMAN, G. J. 1871. A monograph of the gymnoblastic or tubularian hydroids. In two parts. 1. The Hydroida in general. *Ray Society, London*, pp. 1-154.

ALLMAN, G. J. 1872. A monograph of the gymnoblastic or tubularian hydroids. Conclusion of Part I, and Part II, containing descriptions of the genera and species of Gymnoblastea. *Ray Society, London*, pp. 155-450, plates 1-23.

ALLMAN, G. J. 1876. Diagnoses of new genera and species of Hydroida. *Journal of the Linnean Society of London* 12: 251-284, plates 9-23.

ALVAREZ, C. C. 1995. *Stenohelia maderensis* (Johnson, 1862) (Cnidaria, Hydrozoa, Athecatae, Stylasteridae) en el Golfo de Vizcaya (N de Espana). *Miscellania Zoologica* 17: 263-264.

AVSET, K. 1959. The gonophore development in the genus *Hydractinia* van Beneden. I. *Hydractinia echinata* Flem. *Nytt magasin for zoologi* 8: 25-33.

AVSET, K. 1960. The gonophore development in the genus *Hydractinia* van Beneden. II. Further studies on *Hydractinia echinata* Flem. *Nytt magasin for zoologi* 9: 23-27.

AVSET, K. 1961. The development of the medusa *Podocoryne carnea* M. Sars. *Nytt magasin for zoologi* 10: 49-56.

BARNES, R. S. K. 1994. The brackish-water fauna of northwestern Europe: an identification guide to brackish-water habitats, ecology and macrofauna for field workers, naturalists and students. *Cambridge University Press, Cambridge*, pp. XVI & 287.

BAVESTRELLO, G. 1985. Idroidi simbionty di paguri e gastropodi nella riviera ligure di levante. *Oebalia* 11: 349-362.

BAVESTRELLO, G., PUCE, S., CERRANO, C., CASTELLANO, L. & ARILLO, A. 2000. Water movement activating fragmentation: a new dispersal strategy for hydractiniid hydroids. *Journal of the Marine Biological Association of the United Kingdom* 80: 361-362.

BEDOT, M. 1905. Matériaux pour servir à l'histoire des hydroïdes. 2me période (1821-1850). *Revue suisse de Zoologie* 13: 1-183.

BEDOT, M. 1911. Notes sur les hydroïdes de Roscoff. *Archives de Zoologie Expérimentale et Générale* 6: 201-228.

BEHNER, A. 1914. Beitrag zur Kenntnis der Hydromedusen. *Zeitschrift für wissenschaftliche Zoologie* 111: 381-427, pl. 7.

BÉNARD-BOIRARD, J. 1962. Développement embryonnaire de *Podocoryne carnea* (Sars) de Roscoff. *Cahiers de Biologie Marine* 3: 137-155.

BERGH, R. S. 1887. Goplepolyper (Hydroider) fra Kara-Havet (pp. 329-338, pl. 28). *In*: *Dijmphna-Togtets zoologisk-botaniske Udbytte,* Copenhagen, ed. CHR. FR. LÜTKEN, pp. xxi & 515, 41 pls, 1 map.

BODO, F. & BOUILLON, J. 1968. Etude histologique du développement embryonnaire de quelques hydroméduses de Roscoff: *Phialidium hemisphaericum* (L.), *Obelia* sp. Péron et Lesueur, *Sarsia eximia* (Allman), *Podocoryne carnea* (Sars), *Gonionemus vertens* Agassiz. *Cahiers de Biologie Marine* 9: 69-104.

BOELSTERLI, U. 1977. An electron microscopic study of early developmental stages, myogenesis, oogenesis and cnidogenesis in the Anthomedusa, *Podocoryne carnea* M.Sars. *Journal of Morphology* 154: 259-289.

BOERO, F. 1981. Systematics and ecology of the hydroid population of two *Posidonia oceanica* Meadows. *Marine Ecology* 2: 181-197.

BOERO, F. & FRESI, E. 1986. Zonation and evolution of a rocky bottom hydroid community. *Marine Ecology* 7: 123-150.

BONNEVIE, K. 1898. Zur Systematik der Hydroiden. *Zeitschrift für Wissenschaftliche Zoologie* 63: 465-495, plates 25-27.

BONNEVIE, K. 1899. Hydroida. *Norske Nordhavs-Expedition 1876-1878, Zoologi* 26: 1-104, pls. 1-8, map.

BONNEVIE, K. 1901. Hydroiden. *Die Meeresfauna von Bergen* 1: 1-15.

BOSCHMA, H. 1954. Stylasterina in the collection of the Amsterdam Museum. I. *Errina aspera* (L.). *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen. Series C, Biological and medical sciences* 57: 143-150.

BOSCHMA, H. 1955. The type specimen of *Stylaster gemmascens* (Esper, 1794). *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen. Series C, Biological and medical sciences* 58: 22-31.

BOSCHMA, H. 1956a. Stylasterina in the collection of the Paris Museum. II. *Errina amoena* nov. spec. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen. Series C, Biological and medical sciences* 59: 281-289.

BOSCHMA, H. 1956b. Milleporina and Stylasterina (pp. F99-F106). *In*: R. C. MOORE (ed). *Treatise on Invertebrate Paleontology, part F, Coelenterata.* University of Kansas Press, Kansas.

BOSCHMA, H. 1963. On the Stylasterine genus *Errina*, with the description of a new species. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen. Series C, Biological and medical sciences* 66: 331-344.

BOSCHMA, H. 1965a. On stylasterine corals of the genus *Errina* from the island Mauritius. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen. Series C, Biological and medical sciences* 68: 1-7.

BOSCHMA, H. 1967. Comments upon Hickson's notes on Stylasterina in the collection of the Paris Museum. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen. Series C, Biological and medical sciences* 70: 324-337.

BOUILLON, J. 1965. Diagnoses préliminaires de trois hydroides de Roscoff. *Travaux de la Station Biologique de Roscoff* 16: 54.

BOUILLON, J. 1971. Sur quelques hydroides de Roscoff. *Cahiers de Biologie Marine* 12: 323-364.

BOUILLON, J., MEDEL, D. & PENA CANTERO, A. L. 1997. The taxonomic status of the genus *Stylactaria* Stechow, 1921 (Hydroidomedusae, Anthomedusae, Hydractiniidae), with the description of a new species. *Scientia Marina* 61: 471-486.

BOUILLON, J., GRAVILI, C., PAGÈS, F., GILI, J.-M. & BOERO, F. 2006. An introduction to Hydrozoa. *Mémoires du Muséum national d'Histoire naturelle* 194: 1-591.

BOUILLON, J., MEDEL, M. D., PAGÈS, F., GILI, J. M., BOERO, B. & GRAVILI, C. 2004. Fauna of the Mediterranean Hydrozoa. *Scientia Marina* 68 (Suppl. 2): 1-448.

BRIEN, P. 1942. Etude sur deux hydroïdes gymnoblastiques *Cladonema radiatum* (Duj.) et *Clava squamata* (O.F. Müller) (Origine des cellules blastogénétiques, sexuelles, des cnidoblastes et des cellules glandulaires. Le polype, la méduse, le gonophore). *Mémoires de l'Académie royale de Belgique, Classe des sciences* 20: 1-116.

BRIEN, P. 1943. Etude de la régénération et de la rénovation de l'appareil sexuel chez les hydroïdes (*Clava squamata* O.F. Müller). *Archives de Biologie, Paris* 54: 409-475.

BRINCKMANN, A. 1965. The biology and development of *Rhysia autumnalis* gen. nov., sp. nov. (Anthomedusae-Athecatae, Rhysiidae fam. nov.). *Canadian Journal of Zoology* 43: 941-952.

BRINCKMANN-VOSS, A. 1970. Anthomedusae/Athecata (Hydrozoa, Cnidaria) of the Mediterranean. Part I. Capitata. *Fauna e Flora Golfo di Napoli* 39: 1-96, pls 1-11.

BRINCKMANN-VOSS, A. 1987. Seasonal distribution of hydromedusae (Cnidaria, Hydrozoa) from the Gulf of Naples and vicinity, with observations on sexual and asexual reproduction in some species (pp. 133-141). *In*: BOUILLON, J., BOERO, F., CICOGNA, F. & CORNELIUS, P.F.S. (eds). *Modern trends in the systematics, ecology, and evolution of hydroids and hydromedusae.* Clarendon Press, Oxford, 328 pp.

BRINCKMANN-VOSS, A., LICKEY, D. M. & MILLS, C. E. 1993. *Rhysia fletcheri* (Cnidaria, Hydrozoa, Rhysiidae), a new species of colonial hydroid from Vancouver Island (British Columbia, Canada) and the San Juan Archipelago (Washington, U.S.A.). *Canadian Journal of Zoology* 71: 401-406.

BROCH, H. 1905. Zur Medusenfauna von Norwegen. *Bergens Museum Aarbog* 11: 1-8.

BROCH, H. 1910a. Die Hydroiden der Arktischen Meere. *Fauna Arctica* 5: 127-248, plates 2-4.

BROCH, H. 1911. Fauna droebachiensis. I. Hydroider. *Nyt Magazin for Naturvidenskaberne* 49: 3-47, pls 1-2.

BROCH, H. 1914a. Stylasterina. *Danish Ingolf Expedition* 5: 1-25, 5 pls.

BROCH, H. 1914b. Hydrozoa benthonica (pp. 19-50, plate 1). *In*: MICHAELSEN, W. (ed). *Beiträge zur Kenntnis der Meeresfauna Westafrikas*. Friedrichsen, Hamburg.

BROCH, H. 1916. Hydroida. (Part I). *Danish Ingolf Expedition* 5: 1-66.

BROCH, H. 1936. Untersuchungen an Stylasteriden (Hydrokorallen). Teil I. *Skrifter utgitt av det Norske Videnskaps-Akademi i Oslo. 1, Mathematisk-naturvidenskapelige klasse* 1936: 1-103, pls 1-13.

BROWNE, E. T. 1896. On British hydroids and medusae. *Proceedings of the Zoological Society of London* 1896: 459-500, pls 16-17.

BUSCH, W. 1851. Beobachtungen über Anatomie und Entwicklung einiger wirbellosen Seethiere. *August Hirschwald, Berlin*, 143 pp., pls 1-17.

BUSS, L. W. & YUND, P. O. 1989. A sibling species group of *Hydractinia* in the north-eastern United States. *Journal of the Marine Biological Association of the U. K.* 69: 857-874.

CAIRNS, S. D. 1983. A generic revision of the Stylasterinae (Coelenterata: Hydrozoa). Part 1. Description of the genera. *Bulletin of Marine Science* 33: 427-508.

CALDER, D. R. 1972. Some athecate hydroids from the shelf waters of northern Canada. *Journal of the Fisheries Research Board of Canada* 29: 217-228.

CALDER, D. R. 1988. Shallow-water hydroids of Bermuda. The Athecatae. *Royal Ontario Museum Life Sciences Contributions* 148: 1-107.

CALVET, L. 1903. *In*: JULLIEN & L. CALVET, Bryozoaires provenant des campagnes de l'Hirondelle (1886-1888). *Résultats des campagnes scientifiques accomplies sur son yacht par Albert Ier, Prince Souverain de Monaco* 23: 1-188, 18 pls.

CALVET, L. 1911. Diagnoses de quelques espèces nouvelles de bryozoaires cyclostomes provenant des campagnes scientifiques accomplies par S.A.S. le Prince de Monaco, à bord de la Princesse-Alice (1889-1910). *Bulletin de l'Institut Océanographique* 8: 1-9.

CASTRIC-FEY, A. 1970. Sur quelques hydraires de l'Archipel de Glénan (Sud-Finistère). *Vie et Milieu* 21: 1-23.

CERRANO, C., BAVASTRELLO, G., PUCE, S. & SARÀ, M. 1998. Biological cycle of *Podocoryna exigua* (Cnidaria: Hydrozoa) from a sandy bottom of the Ligurian Sea. *Journal of the Marine Biological Association of the U. K.* 78: 1101-1111.

CHRISTENSEN, H. E. 1967. Ecology of *Hydractinia echinata* (Fleming) (Hydroidea, Athecata). I. Feeding biology. *Ophelia* 4: 245-275.

CHRISTIANSEN, B. O. 1972. The hydroid fauna of the Oslo Fjord in Norway. *Norwegian Journal of Zoology* 20: 279-310.

CLARKE, S. F. 1882. New and interesting hydroids from Chesapeake Bay. *Memoirs of the Boston Society of Natural History* 3: 135-142, pls 7-9.

CORNELIUS, P. F. S. & GARFATH, J. B. 1980. The coelenterate taxa of Joshua Alder. *Bulletin of the British Museum* 39: 273-291.

CORNELIUS, P. F. S. 1995a. North-west European thecate hydroids and their medusae. Part 1. Introduction, Laodiceidae to Haleciidae. *Synopses of the British Fauna New Series* 50: 1-347.

CORNELIUS, P. F. S. 1995b. North-west European thecate hydroids and their medusae. Part 2. Sertulariidae to Campanulariidae. *Synopses of the British Fauna New Series* 50: 1-386.

DA CUNHA, A. X. 1944. Hidropólipos das costas de Portugal. *Memorias e Estudos de Museu Zoologico da Universidade de Coimbra* 161: 1-101.

DA CUNHA, A. X. 1950. Nova contribuição para o estudo dos Hidropólipos das costas de Portugal (Colecção do Museu Bocage). *Arquivos do Museu Bocage* 21: 121-144.

DU PLESSIS, G. 1888. Faune des hydraires littoraux gymnoblastes observés à Villefranche sur Mer. *Recueil de zoologie suisse* 4: 525-544.

EDWARDS, C. S. & HARVEY, M. 1975. The hydroids *Clava multicornis* and *Clava squamata*. *Journal of the Marine Biological Association of the U. K.* 55: 879-886.

EDWARDS, C. 1972. The hydroids and the medusae *Podocoryne areolata*, *P. borealis* and *P. carnea*. *Journal of the Marine Biological Association of the U. K.* 52: 97-144.

EHRENBERG, C. G. 1834. Beiträge zur physiologischen Kenntniss der Corallenthiere im allgemeinen, und besonders des rothen Meeres, nebst einem Versuche zur physiologischen Systematik derselben. *Abhandlungen der Königlichen Akademie der Wissenschaften, Berlin* 1: 225-380.

EPHRUSSI, B. 1923. Sur la sexualité d'un hydraire *Clava squamata. Comptes rendus hebdomadaires des séances de l'Académie des sciences de Paris* 176: 1766.

ESPER, E. J. C. 1788-1830. Die Pflanzenthiere in Abbildungen nach der Natur mit Farben erleuchtet nebst Beschreibungen. *Raspe, Nürnberg*. 3 volumes.

ESPER, E. J. C. 1794-1806. Fortsetzungen der Pflanzenthiere in Abbildungen nach der Natur mit Farben erleuchtet nebst Beschreibungen. *Raspe, Nürnberg*. 2 volumes.

FISHER, W. K. 1938. Hydrocorals of the North Pacific Ocean. *Proceedings of the United States National Museum* 84: 493-554.

FLEMING, J. 1828. A history of British animals, exhibiting the descriptive characters and systematical arrangements of the genera and species of quadropeds, birds, reptiles, fishes, Mollusca, and Radiata of the United Kingdom. *Bell and Bradfute, Edinburgh*, 565 pp.

FOL, H. 1885. Zur Mittelmeerfauna. *Zoologischer Anzeiger* 8: 667-670.

FORBES, E. 1843. Note in reply to Mr. Hassall. *Annals and Magazine of Natural History* 12: 188-190.

FORBES, E. 1848. A monograph of the British naked-eyed medusae: with figures of all the species. *Ray Society, London*, 104 pp., 13 plates.

FORSSKÅL, P. 1775. Descriptiones animalium avium, amphibiorium, piscium, insectorum, vermium; quae in itinere orientali observavit Petrus Forskål. Post mortem auctoris edidit Carsten Niebuhr. *Mölleri, København*, pp. 164.

FORSSKÅL, P. 1776. Icones rerum naturalium, quas in itinere orientali depingi curavit Petrus Forskål, Prof. Haun. Post mortem auctoris ad Regis mandatum æri incisas edidit Carsten Niebuhr. *Mölleri, København*, pp. 15, pls 43.

FÖYN, B. 1927a. Studien über Geschlecht und Geschlechtszellen bei Hydroiden I. Ist *Clava squamata* (Müller) eine gonochoristische oder hermaphrodite Art? *Wilhelm Roux' Archiv für Entwicklungsmechanik der Organismen* 109: 513-534.

FÖYN, B. 1927b. Studien über Geschlecht und Geschlechtszellen bei Hydroiden. II. Auspressungsversuche an *Clava squamata* (Müller) mit Mischung von Zellen aus Polypen desselben oder verschiedenen Geschlechts. *Wilhelm Roux' Archiv für Entwicklungsmechanik der Organismen* 110: 89-148.

FÖYN, B. 1929. Studien über Geschlecht und Geschlechtszellen bei Hydroiden III. Bemerkungen über die Entstehung der Keimzellen und die Entwicklung der Gonophoren bei *Clava squamata* (Müller). *Wilhelm Roux' Archiv für Entwicklungsmechanik der Organismen* 114: 501-511.

FRASER, C. M. 1938. Hydroids of the 1934 Allan Hancock Pacific Expedition. *Allan Hancock Pacific Expeditions* 4: 1-105.

FRASER, C. M. 1944. Hydroids of the Atlantic coast of North America. *The University of Toronto Press, Toronto*, 451 pp., pls 1-94.

FREY, H. & LEUCKART, R. 1847. Beiträge zur Kenntniss wirbelloser Thiere mit besonderer Berücksichtigung der Fauna des Norddeutschen Meeres. *Vieweg & Sohn, Braunschweig*, 170 pp.

FREY, J. 1968. Die Entwicklungsleistungen der Medusenknospen und Medusen von *Podocoryne carnea* M. Sars nach Isolation und Dissoziation. *Wilhelm Roux' Archiv für Entwicklungsmechanik der Organismen* 160: 428-464.

GILI, J.-M. & CASTELLO, G. 1985. Hidropolipos de la costa norte del Cabo de Creus (N.E. Cataluna). *Miscellania Zoologica* 9: 7-24.

GMELIN, J. F. 1788. Caroli a Linné ... *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis / cura Jo. Frid. Gmelin.* Tom. 1, Pars. 6. *Impensis Georg. Emanuel. Beer, Lipsiae*, pp. 3021-3909.

GOETTE, A. 1916. Die Gattungen *Podocoryne, Stylactis* und *Hydractinia. Zoologische Jahrbücher, Abteilung für Systematik und Geographie der Tiere* 39: 443-510.

GOSSE, P. H. 1855-1856. A manual of marine zoology for the British Isles. 2 vols. *J. Van Voorst, London.*

GRAEFFE, E. 1883. Biologische Notizen über Seethiere der Adria. Zur Fortpflanzung der Hydroidpolypen. *Bollettino della Società Adriatica di Scienze Naturali in Trieste* 8: 79-89, pls 1-2.

GRAY, J. E. 1831. Description of a new genus of star-bearing corals. *The Zoological Miscellany* 36-37.

GRAY, J. E. 1835. [no title; Corals — Characters of two new genera of corals, *Errina* and *Anthophora*]. *Proceedings of the Zoological Society of London* 1835: 85-86.

GRAY, J. E. 1847. An outline of an arrangement of stony corals. *Annals and Magazine of Natural History (1)* 19: 120-128.

GROBBEN, C. 1876. Über *Podocoryne carnea* Sars. *Sitzungsberichte der mathematisch-naturwissenschaftlichen Classe der kaiserlichen Akademie der Wissenschaften Wien* 72: 455-486, pls 1-2.

GUNNERUS, J. E. 1768. Om nogle Norske coraller. *Kongelige Norske Videnskabers-Selskabs Skrifter* 4: 38.

HAECKEL, E. 1879. Das System der Medusen. Erster Teil einer Monographie der Medusen. *Denkschriften der Medicinisch-Naturwissenschaftlichen Gesellschaft zu Jena* 1: I-XX & 1-360, 20 plates.

HAECKEL, E. 1880. Das System der Acraspeden. 2te Hälfte des Systems der Medusen. Acht Nachträge zur Vervollständigung des Systems. *Denkschriften der Medicinisch-Naturwissenschaftlichen Gesellschaft zu Jena* 2: 361-672, plates 21-40.

HAECKEL, E. 1889. Report on the deep-sea Keratosa collected by H.M.S. Challenger during the years 1873-76. *Report of the Scientific Results of the Voyage of H.M.S. Challenger during the years 1873-76* 82: 1-92, pls 1-8.

HAMANN, O. 1882. Der Organismus der Hydroidpolypen. *Jenaischen Zeitschrift für Naturwissenschaft* 15: 473-544.

HAMOND, R. 1957. Notes on the Hydrozoa of the Norfolk coast. *Journal of the Linnean Society of London* 43: 294-324.

HAMOND, R. 1963. A preliminary report on the marine fauna of the North Norfolk Coast. *Transactions of Norfolk and Norwich Naturalists' Society.* 20: 1-31.

HARGITT, C. W. 1904. Notes on some Hydromedusae from the Bay of Naples. *Mitteilungen der Zoologischen Station zu Neapel* 16: 553-585.

HARM, K. 1902. Die Entwicklungsgeschichte von *Clava squamata. Zeitschrift für wissenschaftliche Zoologie* 73: 115-165, pls 7-9.

HARTLAUB, C. 1894. Die Coelenteraten Helgolands. Vorläufiger Bericht. *Wissenschaftliche Meeresuntersuchungen* n. ser. 1: 161-206.

HARTLAUB, C. 1905. Die Hydroiden der magalhaenischen Region und der chilenischen Küste. *Zoologische Jahrbücher, Supplement Band* 6: 497-714.

HARTLAUB, C. 1911. Craspedote Medusen. Teil 1, Lief. 2, Margelidae. *Nordisches Plankton* 6: 137-235.

HASSALL, A. H. 1841. Supplement to a catalogue of Irish Zoophytes. *Annals and Magazine of Natural History* 7: 276-287, 363-374, pls 6-10.

HERBERTS, C. 1964. Note au sujet de la reproduction de l'hydraire *Hydractinia aculeata* (Wagner, 1833). *Recueil des travaux de la Station marine d'Endoume* 34(50): 161-165.

HERBERTS, C. 1969. Note au sujet du développement de *Nassa pygmaea* Lamarck et *Hydractinia aculeata* (Wagner) 1833. – *Recueil des travaux de la Station marine d'Endoume* 45(61): 351-357.

HERTWIG, I. & HÜNDGEN, M. 1984. Gonophorenbildung und Keimzellentwicklung bei *Hydractinia echinata* Fleming 1828 (Hydrozoa, Athecata). *Zoologische Jahrbuecher Abteilung fuer Anatomie und Ontogenie Der Tiere* 112: 113-136.

HICKSON, S. J. & ENGLAND, H. M. 1905. The Stylasterina of the Siboga Expedition. *Siboga-Expeditie* 8: 1-26, pls 1-3.

HICKSON, S. J. & GRAVELY, F. H. 1907. II Hydroid Zoophytes. *National Antarctic Expedition* 34: 1-33, plates1-4.

HICKSON, S. J. 1912. Notes on some Stylasterina in the Muséum d'Histoire Naturelle de Paris. *Bulletin du Muséum d'Histoire Naturelle, Paris* 18: 461-466, pl. 8.

HINCKS, T. 1868. A history of the British hydroid zoophytes. *John van Voorst, London.* Volume 1: i-lxvii + 1-338, volume 2, pls 1-67.

HIROHITO, EMPEROR OF JAPAN 1988. The hydroids of Sagami Bay collected by His Majesty the Emperor of Japan. *Biological Laboratory of the Imperial Household, Tokyo*, pp. 179, plates 1-4.

HODGE, G. 1863. On a new hydroid zoophyte (*Podocoryne Alderi*). *Transactions of the Tyneside Naturalists' Field Club* 5: 82-84, pl. 2.

IWASA, M. 1934. Revision of *Stylactis* and its allied genera, with description of *Stylactella* (*Stylactis*) *yerii* n. sp. *Journal for the Faculty of Science Hokkaido Imperial University* 2: 241-277.

JÄDERHOLM, E. 1902. Die Hydroiden der Schwedischen Zoologischen Polarexpedition 1900. *Bihang till Kungliga Svenska Vetenskaps-akademiens Handlingar* 28: 1-11, pl. 1.

JÄDERHOLM, E. 1908. Die Hydroiden des sibirischen Eismeeres, gesammelt von der Russischen Polar-Expedition 1900-1903. *Mémoires de l'Académie des Sciences de St.-Petersbourg* 18: 1-26, plates.

JÄDERHOLM, E. 1909. Northern and arctic invertebrates in the collection of the Swedish state museum (Riksmuseum). IV Hydroiden. *Bihang till Kungliga Svenska Vetenskaps-akademiens Handlingar* 45: 1-24.

JOHNSON, J. Y. 1862. Description of some new corals from Madeira. *Proceedings of the Zoological Society of London* 1862: 194-197.

JOHNSTON, G. 1838. A history of the British zoophytes. *Lizars, Edinburgh*, pp. i-xii & 1-341, pls 1-44.

KEFERSTEIN, W. 1862. Untersuchungen über niedere Seethiere. *Zeitschrift für Wissenschaftliche Zoologie* 12: 1-147.

KINNE, O. & PAFFENHÖFER, G. A. 1965. Hydranth structure and digestion rate as a function of temperature and salinity in *Clava multicornis* (Cnidaria, Hydrozoa). *Helgoländer wissenschaftliche Meeresuntersuchungen* 12: 329-341.

KINNE, O. & PAFFENHÖFER, G. A. 1966. Growth and reproduction as a function of temperature and salinity in *Clava multicornis* (Cnidaria, Hydrozoa). *Helgoländer wissenschaftliche Meeresuntersuchungen* 13: 62-72.

KRAMP, P. L. 1914. Hydroider. Conspectus Faunae Groenlandicae. *Meddelelser om Grønland* 23: 953-1080.

KRAMP, P. L. 1927. The hydromedusae of the Danish waters. *Kongelige Danske Videnskabernes Selskab Biologiske Skrifter* 12: 1-290.

KRAMP, P. L. 1932. Hydroids. *In*: The Godthaab expedition 1928. *Meddelelser om Grønland* 79: 1-86.

KRAMP, P. L. 1942. Marine Hydrozoa. *Zoology of the Faroes* 1: 1-59.

KRAMP, P. L. 1943. The Zoology of East Greenland. Hydroida. *Meddelelser om Grønland* 121: 1-52.

KRAMP, P. L. 1952. Medusae collected by the Lund University Chile Expedition 1948-49. Reports of the Lund University Chile Expedition 1948-49. *Lunds Universitets Årsskrift, N. F. Avd. 2* 47: 1-19.

KRAMP, P. L. 1959. The Hydromedusae of the Atlantic Ocean and adjacent waters. *Dana Report* 46: 1-283.

KRAMP, P. L. 1961. Synopsis of the medusae of the world. *Journal of the Marine Biological Association of the U. K.* 40: 1-469.

KRAMP, P. L. & DAMAS, D. 1925. Les Méduses de la Norvège. Introduction et partie spéciale. *Videnskabelige meddelelser fra Dansk naturhistorik Forening* 80: 217-323.

KROHN, A. 1851. Ueber *Podocoryna carnea* Sars und die Fortpflanzungsweise ihrer medusenartigen Sprösslinge. *Archiv für Naturgeschichte* 17: 263-268.

LELOUP, E. 1947. Les Coelentérés de la faune Belge. Leur bibliographie et leur distribution. *Mémoires du Musée royal d'histoire naturelle de Belgique* 107: 1-73.

LEUCKART, R. 1847. Verzeichniss der zur Fauna Helgolands gehörenden wirbellosen Seethiere (pp. 136-168). *In*: *H. Frey & R. Leuckart*, 1847. F. Vieweg und Sohn, Braunschweig, 170 pp., 2 pls.

LINNAEUS, C. 1767. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species cum characteribus, differentiis, synonymis, locis. Tomus I. Pars II. Editio duodecima, reformata. *Laurentii Salvii, Holmiae*, pp. 533-1317.

LO BIANCO, S. 1909. Notizie biologiche riguardanti specialmente il periodo di maturità sessuale degli animali del golfo di Napoli. Hydromedusae. *Mitteilungen der Zoologischen Station von Neapel* 19: 538-545.

LÖNNBERG, E. 1899. *Clava glomerata* mihi, eine anscheinend neue Hydroide. *Zoologischer Anzeiger* 22: 45-46.

LOVÉN, C. 1857. Till utvecklingen af *Hydractinia*. *Oefversigt af Kongliga Vetenskaps-Akademiens Förhandlingar, Stockholm* 14: 305-313, pl. 4.

LÜTKEN, C. 1850. Nogle Bemaerkninger om Medusernes systematiske Inddeling, navnlig med Hensyn til Forbes's History of British Naked-eyed Medusae. *Videnskabelige meddelelser fra Dansk naturhistorik Forening* 1850: 15-35.

MAYER, A. G. 1900a. Descriptions of new and little-known medusae from the western Atlantic. *Bulletin of the Museum of Comparative Zoology of Harvard* 37: 1-9, plates 1-6.

MAYER, A. G. 1900b. Some medusae from the Tortugas, Florida. *Bulletin of the Museum of Comparative Zoology of Harvard* 37: 13-82, pls 1-44.

MAYER, A. G. 1910. Medusae of the world. Hydromedusae, Vols. I & 11. Scyphomedusae, Vol. 111. *Carnegie Institution, Washington*, 735 pp., plates 1-76.

MCCRADY, J. 1859. Gymnopthalmata of Charleston Harbor. *Proceedings of the Elliott Society of Natural History* 1: 103-221.

MEDEL, D. & LOPEZ GONZALEZ, P. J. 1996. Updated catalogue of hydrozoans of the Iberian Peninsula and Balearic Islands, with remarks on zoogeography and affinities. *Scientia Marina* 60: 183-209.

MERESCHKOWSKY, C. 1877. On a new genus of hydroids from the White Sea with a short description of other new hydroids. *Annals and Magazine of natural History (4)* 20: 220-228.

MIGOTTO, A. E. 1996. Benthic shallow-water hydroids (Cnidaria, Hydrozoa) of the coast of São Sebastião, Brazil, including a checklist of Brazilian hydroids. *Zoologische Verhandelingen, Leiden* 306: 1-125.

MILLARD, N. A. H. 1975. Monograph on the Hydroida of southern Africa. *Annals of the South African Museum* 68: 1-513.

MILLS, C. E. 1976. *Podocoryne selena*, a new species of hydroid from the Gulf of Mexico, and a comparison with *Hydractinia echinata*. *Biological Bulletin* 151: 214-224.

MILNE EDWARDS, H. & HAIME, J. 1849. Mémoire sur les Polypes appartenant à la famille des Oculinides, au groupe intermédiaire des Pseudastréides et à la famille des Fongides. *Comptes rendus hebdomadaires des Séances de l'Académie des Sciences, Paris* 29: 67-73.

MOSELEY, H. N. 1879. On the structure of the Stylasteridae, a family of the hydroid stony corals. *Philosophical Transactions of the Royal Society of London* 169: 425-503.

MOTZ-KOSSOWSKA, S. 1905. Contribution à la connaissance des hydraires de la Méditerranée occidentale. I. Hydraires gymnoblastiques. *Archives de Zoologie Expérimentale et générale, 4me série* 3: 39-98.

Moura, C. J., Harris, D. J., Cunha M. R. & Rogers, A. D. 2008. DNA barcoding reveals cryptic diversity in marine hydroids (Cnidaria, Hydrozoa) from coastal and deep-sea environments. *Zoologica Scripta* 37:93-108.

Müller, O. F. 1776. Zoologiae Daniae prodromus seu animalum Daniae et Norvegiae indigenarum characteres, nomina et synonyma. *Hallageriis, Hauniae*, pp. 282.

Namikawa, H. 1991. A new species of the genus *Stylactaria* (Cnidaria, Hydrozoa) from Hokkaido, Japan. *Zoological Science* 8: 805-812.

Naumov, D. V. 1969. Hydroids and Hydromedusae of the USSR. *Israel Program for scientific translation, Jerusalem*, 463 pp., 30 plates.

Neppi, V. 1917. Osservazioni sui polipi idroidi del golfo di Napoli. *Pubblicazioni della Stazione Zoologica di Napoli* 2: 29-65.

Neppi, V. & Stiasny, G. 1911. Die Hydromedusen des Golfes von Triest. *Zoologischer Anzeiger* 38: 395-399.

Neppi, V. & Stiasny, G. 1913. Die Hydromedusen des Golfes von Triest. *Arbeiten des Zoologischen Institutes der Universität Wien* 20: 23-92.

Neppi, V. & Stiasny, G. 1911. Die Hydromedusen des Golfes von Triest. *Zoologischer Anzeiger* 38: 395-399.

Nutting, C. C. 1901. The Hydroids of the Woods Hole region. *Bulletin of the U. S. Fish Commission for 1899* 19: 325-386.

Nutting, C. C. 1906 (1905). Hydroids of the Hawaiian Islands collected by the steamer Albatross in 1902. *Bulletin of the United States Fish Commission for 1903* 23: 931-959, pls 1-13.

Orlov, D. 1996. Observations on the settling behaviour of planulae of *Clava multicornis* Forskal (Hydroidea, Athecata). *Scientia Marina* 60: 121-128.

Orlov, D. V., & Marfenin, N. N. 1993. Behavior and settlement of the White Sea hydroid *Clava multicornis* (Athecata, Hydrozoa). *Vestnik Moskovskogo Universiteta Seriya Xvi Biologiya* 4: 24-30.

Pallas, P. A. 1766. Elenchus zoophytorum sistens generum adumbrationes generaliores et specierum cognitarium succinctas descriptiones cum selectis auctorum synonymis. *Fransiscum Varrentrapp, Hagae*, 451 pp.

Patriti, G. 1970. Catalogue des cnidaires et cténaires des côtes Atlantiques marocaines. *Travaux de l'Institut scientifique chérifien, Série zoologie* 35: 1-149.

Peña Cantero, A. L. & Garcia Carrascosa, A. M. 2002. The benthic hydroid fauna of the Chafarinas Islands (Alboran Sea, western Mediterranean). *Zoologische Verhandelingen* 337: 1-180.

Philbert, M. 1935. Les hydraires de la région malouine. *Bulletin de l'Institut Océanographique, Monaco* 673: 1-36.

Philippi, A. 1842. Zoologische Beobachtungen. (4. *Dysmorphosa conchicola*, ein neues *Coryne*-artiges Zoophyten Genus). *Archiv für Naturgeschichte* 8: 33-45, pl. 1.

Picard, J., & Rahm, U. 1954. *Archaeooceania* n. gen. *tournieri* n. sp. Une nouvelle Anthoméduse de la famille des Oceaniidae provenant de la lagune Ebrié (Côte d'Ivoire). *Acta Tropica* 11: 303-307.

Picard, J. 1958. Origines et affinités de la faune d'hydropolypes (Gymnoblastes et Calyptoblastes) et d'hydroméduses (Anthoméduses et Leptoméduses) de la Méditerranée. *Rapports et procès verbaux des Réunions de la Commission Internationale pour l'Exploration Scientifique de la Mer Méditerranée Monaco* 14: 187-199.

Piraino, S., Boero, F., Aeschbach, B., & Schmid, V. 1996. Reversing the life cycle: medusae transforming into polyps and cell transdifferentiation in *Turritopsis nutricula* (Cnidaria, Hydrozoa). *Biological Bulletin* 190: 302-312.

Pourtalès, L. F. de 1867. Contributions to the Fauna of the Gulf Stream at great depths. *Bulletin of the Museum of comparative Zoölogy of Harvard College* 1: 103-120.

POURTALÈS, L. F. DE 1868. Contributions to the fauna of the Gulf Stream at great depths (2nd series) (with a note by L. Agassiz). *Bulletin of the Museum of comparative Zoölogy of Harvard College* 1: 121-142.

POURTALÈS, L. F. DE 1871. Deep-sea corals. *Illustrated catalogue of the museum of Comparative Zoölogy at Harvard College* 4: 1-93, 8 pls.

QUATREFAGES, A. DE 1843. Mémoire sur la Synhydre parasite (*Synhydra parasites* Nob.) nouveau genre de Polypes voisin des Hydres. *Annales des Sciences naturelles* (2) 20: 230-248, pls 8-9.

RAMIL, F., ANSIN, J. A. & PULPEIRO, E. F. 1994. Aportaciones al conocimiento de *Stylactaria claviformis* (Bouillon, 1965) (Cnidaria, Hydrozoa, Anthomedusae). Galicia, Espana. *Boletin de La Real Sociedad Espanola de Historia Natural Seccion Biologica* 91: 103-107.

RASMUSSEN, E. 1973. Systematics and ecology of the Isefjord marine fauna (Denmark). With a survey of the eelgrass (*Zostera*) vegetations and its communities. *Ophelia* 11: 1-495.

REES, W. J. 1941. On the life history and developmental stages of the medusa *Podocoryne borealis*. *Journal of the Marine Biological Association of the U. K.* 25: 307-316.

REES, W. J. 1956a. On three northern species of *Hydractinia*. *Bulletin of the British Museum (Natural History)* 3: 351-362.

REES, W. J. 1956b. A revision of some northern gymnoblastic hydroids in the Zoological Museum, Oslo. *Nytt Magasin for Zoologi* 4: 109-120.

REES, W. J. & ROWE, M. 1969. Hydroids of the Swedish west coast. *Acta regiae Societatis scientiarum et litterarum Gothoburgensis. Zoologica* 3: 1-23.

ROBSON, J. H. 1914. Catalogue of the Hydrozoa of the north-east coast (Northumberland and Durham). *Report of the Dove marine Laboratory, n. ser.* 3: 87-103.

ROSSI, L. 1950. Celenterati de Golfe di Rapallo (Rivieri Ligure). *Bollettino dei Musei di zoologia ed anatomia comparata della R. Università di Torino* 2: 193-235.

ROSSI, S., GILI, J. M. & HUGHES, R. G. 2000. The effects of exposure to wave action on the distribution and morphology of the epiphytic hydrozoans *Clava multicornis* and *Dynamena pumila*. *Scientia Marina* 64: 135-140.

RUSSELL, F. S. 1953. The medusae of the British Isles. *Cambridge University Press, London*, 530 pp., 35 pls.

RUSSELL, F. S. 1957. Coelenterata (pp. 37-69). *In*: *Plymouth marine fauna.* Marine Biological Association of the United Kingdom, Plymouth, 457 pp.

RUSSELL, F. S. 1970. The medusae of the British Isles. Pelagic Scyphozoa with a supplement to the first volume on Hydromedusae. *Cambridge University Press, Cambridge*, 284 pp.

RUTHENSTEINER, B., REINICKE, G.-B. & STRAUBE, N. 2008. The type material of Hydrozoa described by Eberhard Stechow in the Zoologische Staatssammlung München. *Spixiana*, in press.

SARS, M. 1846. Fauna littoralis Norvegiae, I Heft: Ueber die Fortpflanzungsweise der Polypen. *Johann Dahl, Christiania*, 94 pp., plates.

SARS, M. 1857. Bidrag til kundskaben om middelhavets Littoral-Fauna, Reisebemaerkninger fra Italien. I Classis: Polypi. *Nyt Magazin for Naturvidenskaberne* 9: 110-164.

SAVILLE KENT, W. 1870. On some new and little-known species of madrepores, or stony corals, in the British Museum collection. *Annals and Magazine of Natural History (4)* 5: 120-123.

SCHMID, V. & TARDENT, P. 1969. Zur Gametogenese von *Podocoryne carnea* M. Sars. *Revue suisse de Zoologie* 76: 1071-1078.

SCHÖNBORN, C., ARNDT, E. A. & GOSSELCK, F. 1993. Bestimmungsschlussel der benthischen Hydrozoen der Ostsee. *Mitteilungen aus dem Zoologischen Museum in Berlin* 69: 201-253.

SCHUCHERT, P. 1996. The marine fauna of New Zealand: athecate hydroids and their medusae (Cnidaria: Hydrozoa). *New Zealand Oceanographic Institute Memoir* 106: 1-159.

SCHUCHERT, P. 2001a. Hydroids of Greenland and Iceland (Cnidaria, Hydrozoa). *Meddelelser om Grønland, Bioscience* 53: 1-184.

SCHUCHERT, P. 2001b. Survey of the family Corynidae (Cnidaria, Hydrozoa). *Revue suisse de Zoologie* 108: 739-878.

SCHUCHERT, P. 2004. Revision of the European athecate hydroids and their medusae (Hydrozoa, Cnidaria): Families Oceanidae and Pachycordylidae. *Revue suisse de Zoologie* 111: 315-369.

SCHUCHERT, P. 2005. Species boundaries in the hydrozoan genus *Coryne*. *Molecular Phylogenetics and Evolution* 36: 194-199.

SCHUCHERT, P. 2006. The European athecate hydroids and their medusae (Hydrozoa, Cnidaria): Capitata Part 1. *Revue suisse de Zoologie* 113: 325-410.

SCHUCHERT, P. 2007. The European athecate hydroids and their medusae (Hydrozoa, Cnidaria): Filifera part 2. *Revue suisse de Zoologie* 114: 195-396.

SIGERFOOS, C. P. 1899. A new hydroid from Long Island Sound. *American Naturalist* 33: 801-807.

STANTSCHEW, V. 1940. Das Vorkommen von *Podocoryne carnea* Sars im Golf von Varna und sein verhalten ausserhalb des Wassers. *Trudove na Cernomorskata biologicna stancija v" Varna [= Arbeiten aus der Biologischen Meerestation am Schwarzen Meer in Varna, Bulgarien]* 9: 11-17.

STECHOW, E. 1909. Hydroidpolypen der japanischen Ostküste. I. Teil: Athecata und Plumularidae. In: F. Doflein, Beiträge zur Naturgeschichte Ostasiens. *Abhandlungen der Mathematisch-Phyikalische Klasse der Königlichen Bayerischen Akademie der Wissenschaften, Supplement Band* 1: 1-111, plates 1-7.

STECHOW, E. 1913. Hydroidpolypen der japanischen Ostküste. II. Teil: Campanularidae, Halecidae, Lafoeidae, Campanulinidae und Sertularidae, nebst Ergänzungen zu den Athecata und Plumularidae. *In*: DOFLEIN, F., Beiträge zur Naturgeschichte Ostasiens. *Abhandlungen der Mathematisch-Physikalische Klasse der Königlichen Bayerischen Akademie der Wissenschaften, Supplement Band* 3: 1-162.

STECHOW, E. 1919. Zur Kenntnis der Hydroidenfauna des Mittelmeeres, Amerikas und anderer Gebiete, nebst Angaben über einige Kirchenpauer'sche Typen von Plumulariden. *Zoologische Jahrbücher. Abteilung für Systematik, Geographie und Biologie der Tiere* 42: 1-172.

STECHOW, E. 1921a. Neue Ergebnisse auf dem Gebiete der Hydroidenforschung. III. *Münchener medizinischen Wochenschrift* 1: 30.

STECHOW, E. 1921b. Neue Gruppen skelettbildender Hydrozoen und Verwandtschaftsbeziehungen rezenter und fossiler Formen. *Verhandlungen der deutschen zoologischen Gesellschaft* 26: 29-31.

STECHOW, E. 1921c. Neue Genera und Species von Hydrozoen und anderen Evertebraten. *Archiv für Naturgeschichte* 87: 248-265.

STECHOW, E. 1923. Zur Kenntnis der Hydroidenfauna des Mittelmeeres, Amerikas und anderer Gebiete. II. Teil. *Zoologische Jahrbücher, Abteilung für Systematik, Geographie und Biologie der Tiere* 47: 29-270.

STECHOW, E. 1929. Ueber Symbiosen von Hydrozoen mit Polychaeten. *Zoologischer Anzeiger* 86: 150-153.

STECHOW, E. 1927. Die Hydroidenfauna der Ostsee. *Zoologischer Anzeiger* 70: 304-313.

STECHOW, E. 1962. Ueber skelettbildende Hydrozoen. *Zoologischer Anzeiger* 169: 416-428.

STEENSTRUP, J. 1850. *In*: LÜTKEN, C. Nogle Bemaerkinger om Medusernes systtematiske Indeeling, navnlig med Hensyn til Forbes's History of British naked-eyed Medusae. *Videnskabelige Meddelelser fra Dansk naturhistorisk Forening i København* (1850): 15-35.

STIMPSON, W. 1859. Prodromus descriptionis animalium evertebratorum, quae in Expeditione ad Oceanum Pacificum Septentrionalem, a Republica Federata missa, Cadwaladaro Ringgoid et Johanne Rodgers Ducibus, observavit et descripsit W. Stimpson. P. VII, Crustacea anomoura. *Proceedings of the Academy of Natural Sciences of Philadelphia* 1858: 225-252.

SVOBODA, A., STEPANJANTS, S. & SMIRNOV, I. 1995. Zwei polare Hydractiniden-Arten (Hydroida, Cnidaria) als Symbionten nahe verwandter Schlangensterne (Ophiolepididae, Echinodermata) - ein okologisches Beispiel fur Bipolaritat. *Berichte zur Polarforschung* 155: 86-89.

SVOBODA, A., STEPANJANTS, S. & SMIRNOV, I. 1997. Two polar *Hydractinia* species (Cnidaria), epibiotic on two closely related brittle stars (Echinodermata): an example for a taxonomic and ecological bipolarity (pp. 22-25). *In*: BATTAGLIA *et al.* (ed). *Antarctic Communities.* Cambridge University Press.

TEISSIER, G. 1965. Inventaire de la faune marine de Roscoff. Cnidaires-Cténaires. *Travaux de la Station Biologique de Roscoff* 16: 1-53.

THIEL, H. 1970. Beobachtungen an den Hydroiden der Kieler Bucht. *Berichte der Deutschen Wissenschaftlichen Kommission für Meeresforschung., n. ser* 21: 474-493.

THOMPSON, W. 1844. Report on the fauna of Ireland. Div. Invertebrata. *Report on the British Association for the Advancement of Science* 13: 245-291.

TRINCI, G. 1903. Di una nuova specie di *Cytaeis gemmante* del Golfo di Napoli. *Mitteilungen aus der Zoologischen Station zu Neapel* 16: 1-34, pl. 1.

VAN BENEDEN, P. J. 1841. Recherches sur la structure de l'œuf dans un nouveau genre de polype (Genre Hydractinie). *Bulletin de la classe des sciences de l'Académie royale de Belgique* 8: 89-93.

VAN BENEDEN, P. 1844. Recherches sur l'embryogenie des tubulaires, et l'histoire naturelle des différents genres de cette famille qui habitent la Côte d'Ostende. *Nouveaux Mémoires de l'Académie Royale des Sciences et Belles-Lettres de Bruxelles* 17: 1-72.

VAN BENEDEN, P. J. 1867. Recherches sur la faune littorale de Belgique (polypes). *Mémoires de l'Académie Royale des Sciences et Belles-Lettres de Belgique* 36: 1-207.

VANHÖFFEN, E. 1911. Die Anthomedusen und Leptomedusen der Deutschen Tiefsee Expedition 1898-1899. *Wissenschaftliche Ergebnisse der deutschen Tiefsee Expedition Valdivia* 19: 193-233.

VERVOORT, W. 1946. Hydrozoa (C 1) A. Hydropolypen. *Fauna van Nederland* 14: 1-336.

VERVOORT, W. 2006. Leptolida (Cnidaria: Hydrozoa) collected during the CANCAP and Mauritania-II expeditions of the National Museum of Natural History, Leiden, the Netherlands (Anthoathecata, various families of Leptothecata and addenda). CANCAP-project. Contributions, no. 128. *Zoologische Mededelingen, Leiden* 80: 181-318.

WAGNER, R. 1833. Ueber eine neue im adriatischen Meere gefundene Art von nackten Armpolypen und seine eigenthümliche Fortpflanzungsweise. *Isis oder encyclopädische Zeitung* 1833: 256-260.

WEDLER, E. & LARSON, R. 1986. Athecate hydroids from Puerto Rico and the Virgin Islands. *Studies on Neotropical Fauna and Environment* 21: 69-101.

WEILL, R. 1934. Contribution à l'étude des Cnidaires et de leurs nématocystes. II. Valeur taxonomique du cnidôme. *Travaux de la Station zoologique de Wimereux* 11: 349-701.

WEISMANN, A. 1883. Die Entstehung der Sexualzellen bei den Hydromedusen. Zugleich ein Beitrag zur Kenntnis des Baues und der Lebenserscheinungen dieser Gruppe. *Gustav Fischer, Jena*, pp. i-xiii & 1-295.

WILLIAMS G. B. 1965. Observations on the behaviour of the planulae larvae of *Clava squamata. Helgoländer wissenschaftliche Meeresuntersuchungen* 45: 257-273.

WRIGHT, T. S. 1857. Observations on British Zoophytes. *Edinburgh new Philosophical Journal (new series)* 6: 79-90, pls 2-3 (also *Proceedings of the Royal Physical Society of Edinburgh* (1854-58) 1: 226-237, pls 11-12).

WRIGHT, T. S. 1861. Observations on British Protozoa and zoophytes. *Annals and Magazine of Natural History (3)* 8: 120-135.

Wright, T. S. 1863. Observations on British Zoophytes. *Proceedings of the Royal Physical Society of Edinburgh* 2: 91, 216-221, 250-253, 270-286, 349-352, 378-381, 439-442, plates 9-12, 15, 17, 22.

YAMADA, M. 1961. Polyp and medusa of *Podocoryne hartlaubi* Neppi & Stiasny (Hydrozoa) from the Gulf of Naples. *Pubblicazioni della Stazione Zoologica di Napoli* 32: 134-143.

ZIBROWIUS, H. & CAIRNS, S. D. 1992. Revision of the northeast Atlantic and Mediterranean Stylasteridae (Cnidaria: Hydrozoa). *Mémoires du Museum National d'Histoire Naturelle Serie A Zoologie* 153: 1-136.

## INDEX

Revue suisse de Zoologie 115 (2): 303-309; juin 2008

# Additions to the Cosmopterigidae (Lepidoptera) of the Galapagos Islands, Ecuador, with description of a new species of *Stilbosis* Clemens

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**Additions to the Cosmopterigidae (Lepidoptera) of the Galapagos Islands, Ecuador, with description of a new species of *Stilbosis* Clemens.** - The Cosmopterigidae (including Chrysopeleiinae) of the Galapagos Islands are briefly reviewed in terms of their distribution and 10 new island records are given for seven of the eight previously reported species. *Stilbosis schmitzi* Landry is described as new from the islands of San Cristobal and Santa Cruz. The female of *Periploca darwini* Landry is described and illustrated for the first time; this species was reared as a leaf miner on *Dodonea viscosa* (L.) Jacq. (Sapindaceae) on Isabela Island.

**Keywords:** Cosmopterigidae - Chrysopeleiinae - new species - *Stilbosis* - female of *Periploca darwini* Landry - *Dodonea viscosa* - Sapindaceae.

## INTRODUCTION

The Cosmopterigidae (inclusive of the Chrysopeleiinae) of the Galapagos Islands were reviewed by Landry (2001). Since then more than 125 specimens of cosmopterigids were collected on the archipelago by the authors, Patrick Schmitz, and staff of the Charles Darwin Research Station, Santa Cruz Island, Galapagos (CDRS), mostly with the help of an ultra-violet light held inside a tower of white gauze. Among this material there is a series belonging to the genus *Stilbosis* Clemens, which was first collected only in 2004 despite numerous previous collecting efforts, especially in 1989, 1992, and 2002 by the first author (BL). All of the other eight species of Galapagos Cosmopterigidae were found again since 2001, except *Pyroderces rileyi* (Walsingham) although some previous records of this species (see below) in the CDRS were not incorporated in Landry (2001). Described from two males, *Periploca darwini* Landry was discovered in 2004 on Volcan Alcedo, including two specimens of the previously unknown female, which is described below.

## MATERIAL AND METHODS

The manner of giving the label data of the holotype and paratypes is presented in Landry (2006) as are the methods used for specimen collecting. Paratypes of the new

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species are deposited in the Natural History Museum, London, UK (BMNH), the CDRS, the Muséum d'histoire naturelle, Geneva (MHNG), and the National Museum of Natural History, Washington, DC, USA (USNM).

## DESCRIPTIONS

### *Stilbosis schmitzi* B. Landry, sp. n. Figs 1-4

Material examined: Holotype male: 'ECU[ADOR]. Galápagos, Santa Cruz | casa L. Roque-Albelo & | V. Cruz, G[lobal]P[ositioning]S[ystem]: 137 m elev[ation]. | S 00°42.595', W 090°19.196' | u[ltra]v[iolet]l[ight], 20.ii.2005, *leg*. B. Landry' [white, printed]; 'HOLOTYPE | Stilbosis | schmitzi Landry' [red card stock, hand written]. Deposited in the MHNG.

Paratypes: 5 ♂, 22 ♀, from the Galapagos Islands, Ecuador. Deposited in BMNH, CDRS, MHNG, and USNM.

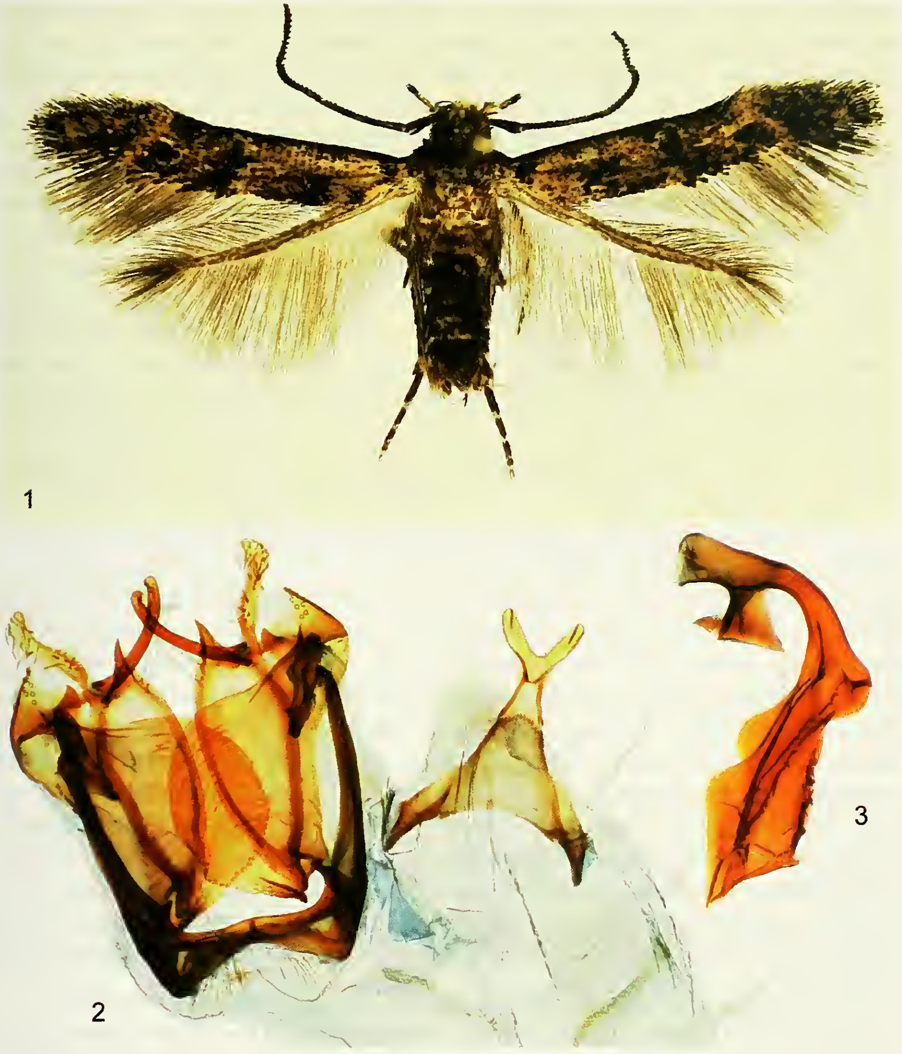
*San Cristobal*. 1 ♀, antiguo botadero, ca. 4 km SE P[uer]to Baquerizo, G[lobal]P[ositioning]S[ystem]: 169 m elev[ation]., S 00°54.800', W 89°34.574', 25.ii.2005, u[ltra]v[iolet]l[ight] (B. Landry). – 1 ♀, transition zone, SW El Progreso, GPS: elev. 75 m, S 00°56.359', W 89°32.906', 15.iii.2004, uvl (B. Landry, P. Schmitz). – 1 ♂ (Slide MHNG ENTO 4687), 1 ♀ (Slide MHNG ENTO 4671), near Loberia, GPS: elev. 14 m, S 00°55.149', W 89°36.897', 16.iii.2004, uvl (B. Landry, P. Schmitz).

*Santa Cruz*. 3 ♂ (one with Slide MHNG ENTO 4669), 10 ♀ (one with Slide MHNG ENTO 4670), same data as holotype. – 1 ♂, 8 ♀, same data as holotype except date: 27.ii.2005. – 1 ♀, transition zone, house of L. Roque, same GPS data as holotype, 11.iii.2004, white light (B. Landry, P. Schmitz).

Etymology: The species name honors Patrick Schmitz of Geneva. During his doctoral work he collected or helped to collect some of the specimens of the type series of this species and several other micromoths in the Galapagos in 2004, 2005, and 2006.

Diagnosis: *Stilbosis schmitzi* is a small species with a distinct colouration. It is most similar to *S. lonchocarpella* Busck in size and forewing colour, but the latter is still larger (forewing length: 3.3 to 3.8 mm) and its genitalia strongly differ (compare with Hodges, 1978: 122, pl. 5 fig. 38; text figs 36 c, 49 d). In the Galapagos there are no other gelechioid species with such small size and conspicuous patches of raised scales.

Description: *MALE* (n=6) (Fig. 1): Forewing length 2.8–3.03 mm (holotype 2.86 mm). Head with greyish brown white-tipped scales converging towards midline on occiput and vertex. Haustellum with pale greyish brown, white-tipped scales. Labial palpus with greyish brown, white-tipped scales, paler medially and dorsally, with short, blackish brown ring subapically on third palpomere followed by 2-3 short, pointed white scales. Antenna blackish brown; scape with scales shortly white-tipped, also with white spot apicomedially. Thorax mostly with brown white-tipped scales, darker, blackish brown at base of tegulae, metascutellum dirty white, shiny. Foreleg with blackish brown, white-tipped scales, with narrow white rings at tips of tibia and tarsi. Midleg as foreleg, but also with narrow white rings on tibia postbasally and postmedially. Hindleg mostly with dark brown, white-tipped scales, with white rings at bases of spurs on tibia, and tips of tarsi; apical spurs of tibia and tarsi darker, blackish brown. Forewing mostly chestnut brown, with paler-tipped scales; patches of raised scales blackish brown, white tipped, glossy; black to blackish brown at base as triangle not reaching dorsal margin, along costa until 3/4, subapically, and along dorsal margin



FIGS 1-3

*Stilbosis schmitzi* Landry, sp. n. (1) Holotype (MHNG). (2) Male genitalia without phallus (Slide MHNG ENTO 4687). (3) Phallus (same slide as Fig. 2; not to scale with Fig. 2).

mostly following raised scale patches; fringe apically with greyish brown and blackish brown, white tipped scales and narrower, unicolorous, greyish brown scales, dorsal margin with hair-like scales, unicolorous greyish brown. Hindwing greyish brown with concolorous fringe. Abdomen dorsally greyish brown with single row of white at apex of tergites; ventrally white, with tuft of long scales on each side of genitalia pale beige.

Male genitalia (n=2) (Figs 2, 3). Uncus well-developed, Y-shaped, with stem and arms of equal lengths, stem wider toward base. Tegumen dorsoventrally flattened, triangular, with arms moderately wide, as moderately sclerotized as uncus. Vinculum arms long, narrow, tightly connected to dorsal edge of valva, ventrally forming narrow bridge at right angle. Small, elongate sclerite at connection of tegumen arm and apex of vinculum arm. Valvae symmetrical; each with medial, eye-shaped part with thickly sclerotized margins, ventrally terminating in short point, with 4-5 setae subapically on ventral margin; laterally with wide, ventrally-rounded flange produced ventrally and curved medially; dorsoapically with short, medially setose, lightly sclerotized projection with wider base; ventroapically with longer, rod-like, thickly sclerotized projection directed apicomedially, with short setae at apex. Juxta flattened, triangular, fused subbasally to phallus. Phallus asymmetrical, thickly sclerotized, curved at right angle from middle; basal half narrowly tube-like; terminal half laterally enlarged, through-like with sub-parallel lateral margins, with cuticle reticulated along margins ventrally; with two short, rounded carinae ventrally: more basal carina along mid-line, other situated on right side subapically; apically narrowing to pointed apex; opening at base of through on right side.

*FEMALE* (n=22). Forewing length 2.74-3.2 mm. Frenulum with 3 acanthae. Otherwise externally like male.

Female genitalia (n=2) (Fig. 4). Papillae anales lightly sclerotized and setose, apically rounded narrowly. Posterior and anterior apophyses thin, straight, subequal in length; anterior apophyses reaching middle of segment VII in fully extended abdomen, joined by bow-shaped bridge postmedially. Sternite VII basal two-thirds forming triangular depression, with lateral margins thickly sclerotized as elongate, tongue-like bands possibly not fused at apical point of connection, forming hood over antrum; inside surface of depression well sclerotized, with tiny, downward point anterad from apex of depression; ventral surface of sternite, outside depression, scaled until before apex, with low and narrow furrow medially; apex truncated. Apical margin of sternite VI well sclerotized, forming internal fold supporting antrum. Antrum forming wide, thickly sclerotized, goblet-like pocket with rounded bottom, about 2/3 width of segment VI, reaching basal margin of segment V, with bottom spiculate. Ductus bursae short, coiled once, of medium girth, spiculate. Corpus bursae circular, of medium size, spiculate on most of surface but more strongly so around signa; signa a pair of short spines on lightly sclerotized base of indistinct shape.

REMARKS: Genus *Stilbosis* includes 39 species mostly distributed in the Nearctic and Neotropical regions, with three species in the Oriental region and four in the Afrotropics (S. Sinev, pers. comm.). Fourteen species have been described from the Neotropical region by Meyrick (9 spp.), Walsingham (2 spp.), and Busck, Forbes, and Walker (1 sp. each). *Stilbosis tesquella* Clemens, described from the United States of America, also occurs in the Neotropics (Becker, 1984). However, *Stilbosis polygoni* (Zeller) mentioned in Robinson *et al.* (2007) from the Neotropical region actually belongs in *Mompha* Hübner (Momphidae) (S. Koster, S. Sinev, pers. comm.). The 15 Neotropical species were all compared with *S. schmitzi* to conclude that it was new. The Meyrick, Walker, and Walsingham types at the BMNH were compared with our new species by Sergey Sinev and Sjaak Koster, and the Meyrick types were also checked against the illustrations provided by Clarke (1965). The Busck and Clemens species also belong to the Nearctic fauna and so they were treated and well illustrated by Hodges (1978), with which all other Nearctic species were also checked. *Stilbosis phaeoptera* Forbes (1931) from Puerto Rico, differs in being twice as large as based on the original description.

*Stilbosis schmitzi* is known only from the Galapagos Islands of San Cristobal and Santa Cruz. The biology is unknown. Other *Stilbosis* species feed on *Ostrya* (Corylaceae), *Amphicarpaea*, *Lespedeza*, *Lonchocarpus*, and *Rhynchosia* (Fabaceae), *Quercus* (Fagaceae), *Carya* (Juglandaceae), and *Epilobium* (Onagraceae) (Hodges, 1978; Robinson *et al.*, 2007). Corylaceae and Fagaceae do not occur in the Galapagos, but the other three families do (Lawesson *et al.*, 1987).

***Periploca darwini*** Landry, 2001 Fig. 5

NEW MATERIAL EXAMINED: 1 ♂, 1 ♀ (dissected, Slide MHNG ENTO 4688) 'ECU[ADOR]. Gálapagos, Isabela | NE slope Alcedo, G[lobal]P[ositioning]S[ystem]: elev[ation]. | 292 m, S 00°23.829' W 091° | 01.957', 30.iii.2004, u[ltra]v[iolet]l[ight] | *leg.* B. Landry, P. Schmitz' (MHNG). – 1 ♀ (dissected, slide LR 188) 'ECU[ador]. GALAPAGOS | Isabela, V[olcan] Alcedo, [zona] A[rida] Baja | Minador de hojas [de] *Dodonea viscosa* | 19 X 1999, emergio 25 XI 1999 | L [azaro] Roque' (CDRS).

DESCRIPTION: *FEMALE* (n=1): Antenna slightly thinner than male's at basal flagellomeres. Forewing length 3.31 mm. Wing pattern and colouration as in males'. Frenulum with two acanthae.

Female genitalia (n=1) (Fig. 5). Papillae anales dorsoventrally compressed, moderately sclerotized, apically fused and blunt. Apophyses long, thin; posteriores slightly longer; anteriores not bridged, reaching anterior margin of segment VII when abdomen fully extended. Apical margin of sternite VI extended beyond margin of tergite VI, broadly rounded. Antrum at apical margin of sternite VI, forming pocket slightly wider than long, slightly less than half as wide as segment VI, covered inside on dorsal and ventral walls by drop-shaped spicules partly concentrated to form pair of nearly circular, dense patches. Ductus bursae short, wide, widening toward corpus bursae, with short bulbous extension subbasally on right side and with small spicules along right wall. Corpus bursae elongate, spiculate on most of surface except near ductus bursae, with pair of small, circular signa adorned medially with short spine.

REMARKS: The female genitalia of *P. darwini* differ strongly from those of *P. longipenis* Landry, the other Galapagos species of *Periploca* (see Landry, 2001: pp. 534, 535, fig. 25). For example, in *P. darwini* the papillae anales are not strongly sclerotized, the apophyses are thin, the anteriores apparently are not bridged (the unique specimen could not be cleaned properly along the apophyses), the antrum is lined with small spicules, the ductus bursae is short and unsclerotized, and the corpus bursae is adorned with a pair of signa. Given the strong differences in male and female genitalia of the two species of *Periploca* in the Galapagos, it seems most likely that they belong to two separate phylogenetic lines and that they are not the result of a speciation event that would have occurred in the Galapagos.

*Dodonea viscosa* (L.) Jacq. (Sapindaceae) is represented by two varieties in the Galapagos, one endemic and the other native. It is present on Fernandina, Isabela, Pinta, and Santiago (Lawesson *et al.*, 1987). Sapindaceae were not known to be associated with *Periploca* species previously (Hodges, 1978; Robinson *et al.*, 2007).

Figs 4-5

Female genitalia. (4) *Stilbosis schmitzi* Landry, sp. n. (Slide MHNG ENTO 4670). (5) *Periploca darwini* Landry (Slide MHNG ENTO 4688).

## NEW ISLAND RECORDS

New island records were found for *Cosmopterix attenuatella* (Walker) (Marchena, Pinzon), *C. galapagosensis* Landry (Pinta), *Cosmopterix madeleinae* Landry (Floreana), *Cosmopterix yvani* Landry (Marchena), *Ithome volcanica* Landry (Fernandina, Pinzon), *Periploca longipenis* Landry (Marchena, Pinzon), and *Pyroderces rileyi* (Walsingham) (Isabela: Alcedo, Sierra Negra). The voucher specimens for these records are in the CDRS and MHNG.

## ACKNOWLEDGEMENTS

We thank the authorities of Parque Nacional Galapagos and CDRS for allowing and facilitating field work and for permits to export specimens. We thank Sergey Sinev and Sjaak Koster for checking our new species of *Stilbosis* with the types of *Stilbosis* in the BMNH. We are grateful to Stewart B. Peck (Carleton University, Ottawa) for inviting BL to participate in his inventory of the Galapagos insects, for organizing his first two expeditions, and for companionship in the field. Furthermore, BL wishes to thank LR's family for hospitality, and N. Castillo, P. Schmitz, B. Sinclair, and E. Vilema for companionship and help in the field, as well as Sergey Sinev (St. Petersburg, Russia) for sharing unpublished data from his World Catalogue of Chrysopeleiinae in press.

## REFERENCES

BECKER, V. O. 1984. Cosmopterigidae (pp. 43-44). *In*: HEPPNER, J. B. (ed.). Atlas of Neotropical Lepidoptera, Checklist: Part 1, Micropterigoidea - Immoidea. *Dr. W. Junk Publishers. The Hague*, xxvii + 112 pp.

CLARKE, J. F. G. 1965. Catalogue of the type specimens of Microlepidoptera in the British Museum (Natural History) described by Edward Meyrick. Volume V. Timyridae, Hyponomeutidae, Ethmiidae, Metachandidae, Cosmopterigidae, Walshiidae, Blastodacnidae, Scythridae. *Trustees of the British Museum (Nat. Hist.), London*, 581 pp.

FORBES, W. T. M. 1931. Scientific survey of Porto Rico and the Virgin Islands. Volume XII (Supplementary Part). Insects of Porto Rico and the Virgin Islands. Supplementary report of the Heterocera or moths of Porto Rico. *Journal of the Department of Agriculture of Porto Rico* 4: 339-394.

HODGES, R. W. 1978. Cosmopterigidae. *In*: DOMINICK, R. B. *et al.* (eds). The Moths of America North of Mexico, Fasc. 6.1, Gelechioidea (part). *E. W. Classey Ltd. and the Wedge Entomological Research Foundation, London*, 166 pages + x.

LANDRY, B. 2001. The Cosmopterigidae (Lepidoptera) of the Galápagos Islands, Ecuador. *Revue suisse de Zoologie* 108: 513-539.

LANDRY, B. 2006. The Gracillariidae (Lepidoptera, Gracillarioidea) of the Galapagos Islands, Ecuador, with notes on some of their relatives. *Revue suisse de Zoologie* 113: 437-485.

LAWESSON, J. E., ADSERSEN, H. & BENTLEY, P. 1987. An updated and annotated check list of the vascular plants of the Galapagos Islands. *Reports from the Botanical institute, University of Aarhus*. No 16: 74 pp.

ROBINSON, G. S., ACKERY, P. R., KITCHING, I. J., BECCALONI, G. W. & HERNÁNDEZ, L. M. 2007. HOSTS - a Database of the World's Lepidopteran Hostplants. http://www.nhm.ac.uk/research-curation/projects/hostplants/. *The Natural History Museum, London*. Last checked: 5 December, 2007.

## APPENDIX

**Resumen. Adicion al conocimiento de los Cosmopterigidae (Lepidoptera) de las islas Galápagos, Ecuador, con descripcion de una nueva especie de *Stilbosis* Clemens. -** Los Cosmopterigidae (incluyendo Chrysopeleiinae) de las islas Galapagos son brevemente revisados desde el punto de vista de la distribucion donde 10 nuevos registros para islas son dados para siete de las ocho especies previamente registradas. *Stilbosis schmitzi* Landry es descrita como nueva especie y fue registrada para las islas San Cristobal y Santa Cruz. La hembra de *Periploca darwini* Landry es descrita e ilustrada por primera vez; esta especie fue criada minando las hojas de *Dodonea viscosa* (L.) Jacq. (Sapindaceae) en la isla Isabela.

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# A review of the spider genus *Hygropoda* in Thailand (Araneae, Pisauridae)

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**A review of the spider genus *Hygropoda* in Thailand (Araneae, Pisauridae).** - Three species belonging to the spider genus *Hygropoda* Thorell are recorded from Thailand. All of them have previously been reported from Yunnan Province, southern China. The males of *H. argentata* Zhang, Zhu & Song, 2004 and *Hygropoda yunnan* Zhang, Zhu & Song, 2004 are described and illustrated here for the first time from specimens collected in northern Thailand. The female of *H. campanulata* Zhang, Zhu & Song, 2004 is redescribed and illustrated from a specimen collected in western Thailand.

**Keywords:** Taxonomy - conspecific sex - zoogeography - new record - *H. argentata* - *H. campanulata* - *H. yunnan*.

## INTRODUCTION

Most documented information on the spider family Pisauridae occurring in Thailand comes from lists of taxa obtained in the course of faunistic surveys. Okuma (1968) first recorded two *Dolomedes* species collected from paddy fields in northern and northeastern Thailand. In the result of her next expedition to several other localities, she recorded the genus *Hygropoda* for the first time from Thailand (Okuma & Wongsiri, 1973), although the specimens were identified only to generic level. Unfortunately, we were unable to locate the specimens examined by Okuma. Dankittipakul (2002) reported *Hygropoda argentata* Zhang, Zhu & Song, 2004 to occur in relatively high abundance along a river running through dry deciduous dipterocarp forests in the Doi Inthanon National Park of northern Thailand. When examining a spider collection deposited at Chiang Mai University, the so far unknown males of two *Hygropoda* species described from southern China were identified. These are treated here. Earlier records of pisaurid spiders from Thailand refer only to a male of *Perenethis venusta* L. Koch collected in central Thailand and to males of *Polyboea vulpina* Thorell collected in the Khao Yai National Park and in the Chantaburi Province, eastern Thailand (Sierwald, 1997). The unusually low number of species

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previously recorded from the country suggests that its pisaurid fauna is still superficially known and that further basic taxonomic and faunistic work is required.

To date, the following representatives of the genus *Hygropoda* are known from Thailand: *H. argentata* Zhang, Zhu & Song, 2004, *Hygropoda yunnan* Zhang, Zhu & Song, 2004 and *H. campanulata* Zhang, Zhu & Song, 2004. All of them were previously reported from Yunnan Province in southern China. Their taxonomic treatment is presented below.

## MATERIAL AND METHODS

External morphology was examined, measured and drawn with an Olympus SZX-9 stereomicroscope equipped with a drawing tube. Measurements of leg segments were taken from the dorsal side. All measurements are in millimeters. Vulvae were drawn in cleared state after immersion in 90% lactic acid for 10-30 minutes.

The material examined will be deposited in the collections of the Muséum d'histoire naturelle de la Ville de Genève, Switzerland (MHNG, curator: P. J. Schwendinger) and in the Thailand Natural History Museum, National Science Museum, Pathumthani Province, Thailand (TNHM, curator: J. Nabhitabhata).

Abbreviations used in the text and in the figures are as follows: AER, anterior eye row; ALE, anterior lateral eyes; AME, anterior median eyes; BE, basal projection of embolus; C, conductor; Cy, cymbium; DTA, distal tegular apophysis; E, embolus; FD, fertilization duct; ID, insemination duct; juv., juvenile; LL, lateral lobe of epigyne; MA, median apophysis; MOQ, median ocular quadrangle; PER, posterior eye row; PLE, posterior lateral eyes; PME, posterior median eyes; RTA, retrolateral tibial apophysis; S, spermathecae; T, tegulum.

In the text 'Fig.' and "Figs" refer to figures herein, while 'fig.' and "figs" refer to figures published elsewhere.

## TAXONOMY

### Family **PISAURIDAE** Simon, 1890

### Genus ***Hygropoda*** Thorell, 1894

*Hygropoda* Thorell, 1894: 4; Simon, 1898: 315; Pocock, 1900: 245; Hu, 1984: 260; Yaginuma, 1986: 176.

Type species: *Tegenaria dolomedes* Doleschall, 1859 by original designation.

Diagnosis: Representatives of the genus *Hygropoda* can be recognized by morphological and genitalic structures which are considered synapomorphic: Tarsi of legs long and slender (except for leg III), highly flexible (Fig. 1); anterior eye row slightly procurved, posterior one strongly recurved (Figs 2-4); conductor and distal tegular apophysis of the male palp membranous (Figs 5, 12) (conductor sclerotized in *Eurychoera* Thorell). Further SEM examination by Zhang *et al.* (2004) revealed an additional diagnostic character: Posterior lateral and posterior median spinnerets provided with cylindrical gland spigots (*sensu* Zhang *et al.*, 2004: 381, figs 209, 211-213). However, cylindrical gland spigots produce egg sac silk, and as nearly all spider species construct egg sacs, nearly all female spiders will possess cylindrical spigots. Accordingly, this character cannot be considered an apomorphy for the genus *Hygropoda* (P. Sierwald, pers. comm.).

DESCRIPTION: Prosoma generally flattened, in profile slightly higher in cephalic part (Figs 1, 2). Carapace yellowish, with two dark parallel bands and a pair of dark marginal bands; often with a thin narrow line of dark brown colour between PME and fovea. Fovea longitudinal, deep (Figs 2-4). Chelicerae with three teeth each on promargin and retromargin of fang groove. Clypeus not as high as the ocular quadrangle. AER slightly procurved or straight, shorter than PER; PER strongly recurved; PME largest. Legs more or less distinctly annulated, long and slender, provided with erect spines; tarsi of legs I, II and IV distinctly elongate, highly flexible. Opisthosoma elongate oval, covered with fine pubescence; dorsum yellowish posteriorly, dark median band anteriorly bifurcated, followed by a series of transverse lines. Male palp (Figs 5-7, 12-14) with palpal tibia curved dorsad; retrolateral tibial apophysis broad at base, tapering distally, pointing ventrally; cymbium digitiform, usually elongate; bulb more or less rounded; distal tegular apophysis petal-shaped, membranous; median apophysis strongly sclerotized, often with denticle; conductor membranous, situated retrolaterally; embolus needle-shaped, originating prolaterally; basal extension of embolus forming a sclerotized plate, accommodating the embolus. Epigyne (Figs 8, 10, 15) often with median field; lateral lobes well-developed in some species; vulva simple (Figs 9, 11, 16), with more or less straight insemination ducts descending to strongly sclerotized, posteriorly located spermathecae.

NATURAL HISTORY: Almost all *Hygropoda* species are riparian spiders that can be found close to the edge of running streams and rivers. They build sheet webs on the upper side of large leaves (Cerveira & Jackson, 2002). A male specimen collected by sweeping vegetation overhanging a river in northern Thailand showed its first tarsus winding around a small dried stick. This suggests that the flexible tarsi of *Hygropoda* have an anchoring function (personal observations).

DISTRIBUTION: The fishing spider genus *Hygropoda* currently comprises 21 valid species distributed throughout the topics, ranging from South America, Africa to Australia, with a small radiation into China and Japan (Barrion & Litsinger, 1995; Davies, 1985; Kishida, 1936; Platnick, 2008; Pocock, 1897; Reimoser, 1934; Strand, 1907; Thorell, 1877, 1895; Yaginuma, 1986; Zhang *et al.*, 2004). It is highly unlikely that the South American species assigned to *Hygropoda* are congeneric. According to all we know at this time, the family Pisauridae does not occur in South America. Thus, South American species assigned to *Hygropoda* most likely belong to the family Trechaleidae (P. Sierwald, pers. comm.).

### ***Hygropoda argentata*** Zhang, Zhu & Song, 2004 Figs 1, 2, 4-9

*Hygropoda argentata* Zhang, Zhu & Song, 2004: 381, figs 71-73 (description of ♀).

MATERIAL EXAMINED: Northern Thailand, Chiang Mai Province, Chomthong District, Doi Inthanon National Park, near kilometer marker 20, 510 m: 2♂ [MHNG-HA1, TNHM], 2♀ [MHNG-HA2, TNHM], 24.vi.2000. – 1 juv. [TNHM], 27.xi.1999; 1 juv. [TNHM], 25.ix.1999; 3 juv. [TNHM], 29.i.2000. – 4 juv. [TNHM], 23.x.1999. – 2 juv. [TNHM], 29.iv.1999, all leg. P.

Dankittipakul; Doi Inthanon National Park, near Sirithарn Waterfall, 980 m, 1♂, 1♀ [TNHM], 9.v.2007, leg. N. Likhitrakarn & A. Lewvanich; Doi Inthanon National Park, Pha Mon, 1010 m, 1♀ [TNHM], 24.vi.2000, leg. P. Dankittipakul.

EXTENDED DIAGNOSIS: Males of *Hygropoda argentata* resemble those of *H. higenaga* (Kishida, 1936) in having a palp with similar shape of distal tegular apophysis, conductor and embolus, but can be distinguished by the sickle-shaped median apophysis lacking a mesal process. The median apophysis of *H. higenaga* is apically hooked and provided with a mesal process (Zhang *et al.*, 2004: fig. 72). Females of *H. argentata* can be recognized by their epigyne with an anterior hood, with short insemination ducts, and by spermathecae being divided into two parts: Anterior spermathecal head and posterior spermathecal base.

DESCRIPTION: Male (MHNG-HA1). Total length 7.26. Carapace 2.95 long, 2.31 wide. Opisthosoma 4.31 long, 1.72 wide.

Carapace slightly wider than long (Fig. 4); higher behind than in front, gradually lowering towards cephalic area. Fovea a deep longitudinal furrow located posteriorly. Carapace yellow, with two dark parallel bands running from behind PME and PLE to posterior margin; a thin mesal line running between PME and fovea; dusky stripes on both lateral margins. AER slightly recurved; PER strongly recurved, much wider than AER; MOQ longer than wide, wider behind than in front. Eye sizes and interdistances: AME 0.22, ALE 0.18, PME 0.25, PLE 0.27; AME-AME 0.15, AME-ALE 0.10, PME-PME 0.34, PME-PLE 0.48; MOQ 0.64 long, front width 0.60, back width 0.92. Chelicerae orange-brown, fangs reddish brown; three small promarginal and three larger retromarginal teeth on cheliceral fang grooves. Sternum yellow.

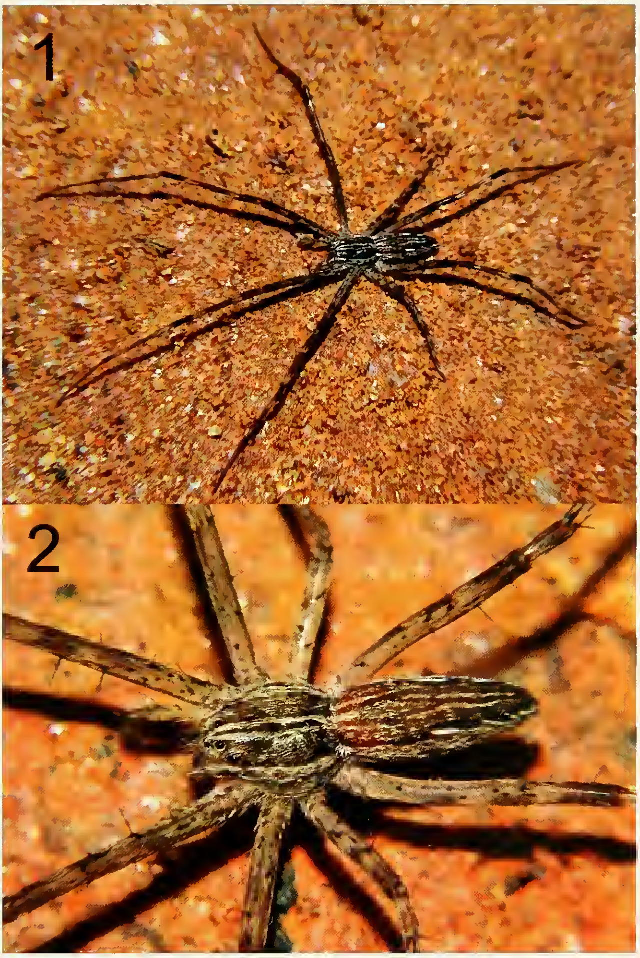
Leg measurements:

| | I | II | III | IV |
|---|---|---|---|---|
| Femur | 10.57 | 9.58 | 5.12 | 10.36 |
| Patella + Tibia | 10.05 | 10.56 | 5.17 | 9.89 |
| Metatarsus | 9.12 | 8.24 | 4.34 | 9.03 |
| Tarsus | 5.89 | 6.63 | 2.05 | 5.62 |
| Total length | 35.63 | 35.01 | 16.68 | 34.90 |

Opisthosoma oblong (Fig. 4); dorsum yellow, provided with dark brown median band, with black pigments and white spots laterally; cardiac area brown, with dark brown margins and a pair of black spots.

Male palp (Figs 5-7): Palpal tibia distinctly curved. Retrolateral tibial apophysis (RTA) broad at base, with sharply pointed apex, directed ventrally. Cymbium (Cy) elongate distally, approximately twice as long as tegulum (T). Tegulum more or less spherical, with superficial furrow on prolateral side. Distal tegular apophysis (DTA) membranous, petal-shaped. Median apophysis (MA) strongly sclerotized, sickle-shaped, without mesal projection. Conductor (C) membranous, forming a concave socket apically. Embolus (E) dark brown, needle-shaped, originating antero-prolaterally, accommodated by basal projection of embolus (BE).

Female (Siritharn Waterfall). Total length 12.77. Carapace 4.26 long, 3.74 wide. Opisthosoma 8.51 long, 3.63 wide.

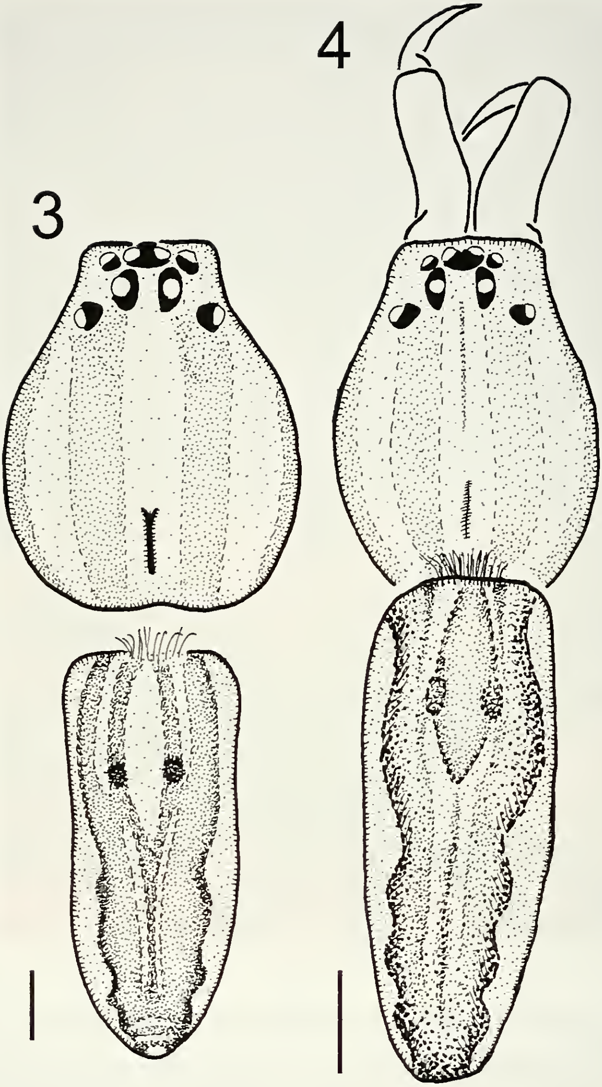


FIGS 1-2
*Hygropoda argentata*, adult female in typical resting posture.

Pattern and colouration as in males but larger in size (Figs 1, 2). Eye sizes and interdistances: AME 0.19, ALE 0.17, PME 0.22, PLE 0.24; AME-AME 0.14, AME-ALE 0.06, PME-PME 0.31, PME-PLE 0.45; MOQ 0.63 long, front width 0.58, back width 0.82.

Leg measurements:

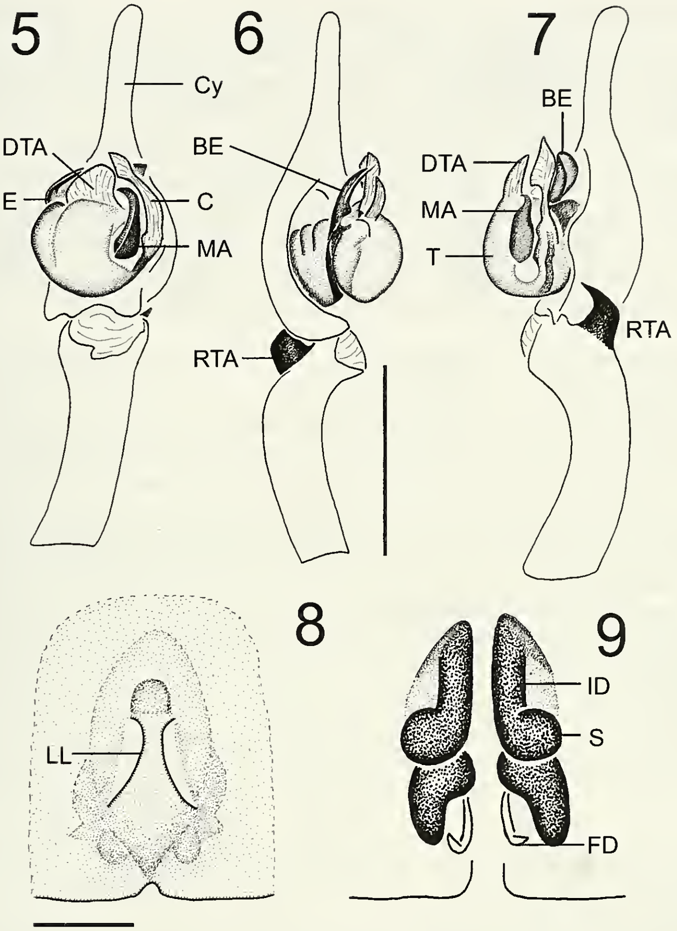
| | I | II | III | IV |
|---|---|---|---|---|
| Femur | 10.32 | 9.22 | 4.95 | 10.05 |
| Patella + Tibia | 9.87 | 10.40 | 4.99 | 9.51 |
| Metatarsus | 8.84 | 8.01 | 4.03 | 8.76 |
| Tarsus | 5.56 | 6.49 | 1.72 | 5.39 |
| Total length | 34.59 | 34.02 | 15.69 | 33.71 |



FIGS 3-4

(3) *Hygropoda yunnan* and (4) *H. argentata*, habitus of male, dorsal view. Scale line = 1.0 mm.

Epigyne and vulva (Figs 8, 9): Epigyne deeply excavated; with a bell-shaped epigynal hood located anteriorly; lateral lobes (LL) poorly developed, broadest posteriorly; median field of epigyne represented by a space between LL; insemination ducts (ID) relatively short, leading to modified spermathecae (S) that are divided into two parts: Rounded anterior spermathecal heads, and tubular posterior spermathecal bases, the latter slightly excavated on the inner side. Fertilization ducts (FD) originating posteriorly.



Figs 5-9

*Hygropoda argentata*. (5) Left palp of male, ventral view. (6) Ditto, prolateral view. (7) Ditto, retrolateral view. (8) Epigyne, ventral view. (9) Vulva, dorsal view. Scale lines = 1.0 mm (5-7); 0.25 mm (8-9).

Remarks: There is considerable variation in the shape of the genitalia. The female holotype possesses tubular spermathecal heads (see Zhang *et al.*, 2004: 380, fig. 73), which are not as round as in the female described here. The median field of the epigyne in the female examined (Fig. 8) slightly differs from that of the holotype; there it is represented by a rhomboidal groove (Zhang *et al.*, 2004: 380, fig. 72).

Natural History: *Hygropoda argentata* inhabits dry deciduous dipterocarp forest and mixed evergreen-deciduous forest dominated by pine trees between 510-1010 m elevation in the Doi Inthanon National Park.

Distribution: Thailand (Chiang Mai Province, new record) and China.

***Hygropoda campanulata*** Zhang, Zhu & Song, 2004 Figs 10, 11

*Hygropoda campanulata* Zhang, Zhu & Song, 2004: 382, figs 74-76 (description of ♀).

MATERIAL EXAMINED: 1♀, western Thailand, Khanchanaburi Province, Thong Pha Phum District, Huay Kha-Khaeng Wildlife Sanctuary, Ban [Thai: Village] Patsadu Klang, 300 m, dry dipterocarp forest, 19.x.2002, leg. T. Promi [MHNG-HC1].

EXTENDED DIAGNOSIS: Females of *Hygropoda campanulata* resemble those of *H. argentata* in having a deeply excavated epigyne with its median field narrowed, longer than wide. The former species can be easily recognized by the presence of large anterior lateral lobes on the epigyne (Fig. 10) and by long parallel insemination ducts descending to bi-lobed, posteriorly situated spermathecae (Fig. 11).

DESCRIPTION: Female (MHNG-HC1). Total length 10.32. Carapace 3.51 long, 2.76 wide. Opisthosoma 6.81 long, 2.33 wide.

Carapace longer than wide; cephalic part higher than thoracic part, highest just behind ocular area. Fovea a deep longitudinal furrow located posteriorly. Carapace dark yellow, with a pair of dark brown longitudinal bands running from behind PER to posterior margin; dusky stripes on both lateral margins. Eye sizes and interdistances: AME 0.24, ALE 0.20, PME 0.23, PLE 0.26; AME-AME 0.18, AME-ALE 0.08, PME-PME 0.35, PME-PLE 0.46; MOQ 0.70 long, front width 0.62, back width 0.85.Chelicerae brown, fangs reddish brown; three small promarginal and three larger retromarginal teeth on cheliceral fang grooves. Sternum yellow.

Leg measurements:

| | I | II | III | IV |
|---|---|---|---|---|
| Femur | 9.86 | 8.30 | 5.41 | 9.10 |
| Patella + Tibia | 11.94 | 9.21 | 5.33 | 8.62 |
| Metatarsus | 9.62 | 8.98 | 4.35 | 7.93 |
| Tarsus | 10.13 | 6.46 | 2.38 | 5.54 |
| Total length | 41.55 | 32.95 | 17.47 | 31.19 |

Opisthosoma oblong; dorsum with distinctive pattern, provided with dark brown median band, with black pigments and white silvery spots laterally; cardiac area brown, with dark brown margins, background yellowish brown.

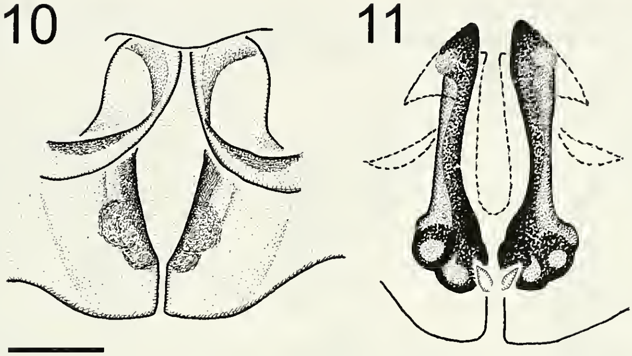
Epigyne and vulva (Figs 10, 11): Epigyne with lateral lobes occupying anterior half of epigyne, diverging from each other posteriorly; median field of epigyne longer than wide; insemination ducts long, leading to bi-lobed, heavily sclerotized spermathecae situated posteriorly.

Male unknown.

REMARKS: In the specimen examined the lateral lobes of the epigyne are distinctly larger than in the female holotype (see Zhang *et al.*, 2004: 380, fig. 75) and its insemination ducts are clearly divided into lightly sclerotized and strongly sclerotized parts, whereas in the female holotype they are not discernible.

NATURAL HISTORY: The specimen examined was collected in a lowland dry dipterocarp forest.

DISTRIBUTION: Thailand (Khanchanaburi Province, new record) and China.



FIGS 10-11

*Hygropoda campanulata*. (10) Epigyne, ventral view. (11) Vulva, dorsal view. Scale line = 0.25 mm.

**Hygropoda yunnan** Zhang, Zhu & Song, 2004 Figs 3, 12-16

*Hygropoda yunnan* Zhang, Zhu & Song, 2004: 385, figs 92-96 (description of ♀).

MATERIAL EXAMINED: Northern Thailand, Chiang Mai Province and District, Doi Suthep-Pui National Park, Pha Ngoeb, 400-500 m, 1♂, 3♀, 2 juv. [MHNG-HY1-6], 24.ix.2002, leg. P. Thamsenanupap. – 2♂ [TNHM], 8.x.2002, leg. P. Thamsenanupap. – Doi Suthep-Pui National Park, near Monthatharn Waterfall, 650-800 m: 2♀, 5 juv. [TNHM], 9.viii.2002, leg. P. Thamsenanupap. – 2♀ [MHNG], 8.x.2002, leg. P. Thamsenanupap. – Chiang Mai Province, Chomthong District, Doi Inthanon National Park, Huay Sai Lueang Waterfall, 1080 m, 1♀ [TNHM-HY], 6.x.-15.xi.2002, Malaise trap, leg. P. Thamsenanupap. – Mae Hong Son Province, Namtok Mae Surin National Park, Huay [Thai: Stream] Mae Surin, 1♀ [TNHM], 15.x.2002, leg. P. Thamsenanupap.

EXTENDED DIAGNOSIS: Males of *Hygropoda yunnan* can be recognized by the bifurcated retrolateral tibial apophysis (Fig. 13) and by the peculiar median apophysis provided with a thin mesal spike (Figs 12, 13) (represented by a small tubercle in *H. higenaga* but absent in *H. argentata*). Females of this species can be identified by the epigyne with a triangular anteriormedian tubercle flanked by large anterolateral lobes (Fig. 15). The median field of the epigyne is triangular and provided with longitudinal ridges, the insemination ducts are long and curved, leading to rounded spermathecae situated posteriorly (Fig. 16).

DESCRIPTION: Male (MHNG-HY1). Total length 6.94 Carapace 3.33 long, 2.61 wide. Opisthosoma 3.61 long, 1.52 wide.

Carapace longer than wide (Fig. 3), slightly higher in cephalic part, gradually lowering towards thoracic part. Fovea a deep longitudinal furrow located posteriorly. Carapace pale yellow, with two dark parallel bands running from behind PME and PLE to posterior margin; a thin mesal line running between PME and fovea; dusky stripes on both lateral margins. Eight eyes arranged into two rows: AER slightly recurved; PER distinctly recurved, much wider than AER; MOQ longer than wide, wider behind than in front. Eye sizes and interdistances: AME 0.28, ALE 0.18, PME 0.30, PLE 0.30; AME-AME 0.15, AME-ALE 0.10, PME-PME 0.36, PME-PLE 0.46; MOQ 0.75 long, front width 0.59, back width 0.84. Chelicerae orange, fangs brown; three small promarginal and three larger retromarginal teeth on cheliceral fang grooves. Sternum yellow.

Leg measurements:

| | I | II | III | IV |
|---|---|---|---|---|
| Femur | 8.91 | 7.40 | 4.62 | 8.21 |
| Patella + Tibia | 11.18 | 8.32 | 4.53 | 7.78 |
| Metatarsus | 8.73 | 6.17 | 3.51 | 7.16 |
| Tarsus | 9.16 | 5.69 | 1.52 | 4.75 |
| Total length | 37.98 | 27.58 | 14.18 | 27.90 |

Opisthosoma (Fig. 3) elongate, tapering posteriorly; dorsum yellow, with a broad longitudinal dark brown band, anteriorly marked with pale cardiac area, laterally striated with distinct black pigments on margins, followed by a series of transverse pale patches.

Male palp (Figs 12-14): Palpal tibia slightly curved. Retrolateral tibial apophysis with a small triangular proximal branch and a larger distal branch reaching about 1/4 of cymbial length. Cymbium with digitiform apex, relatively short, approximately of the same length as the tegulum. Tegulum orange-brown, with a distinct anterior, slightly sclerotized excavation at the base of the triangular distal tegular apophysis. Median apophysis with a thin and long mesal spike pointing upwards. Conductor membranous. Embolus black, needle-shaped, originating baso-prolaterally, accommodated by a strongly sclerotized basal projection of the embolus.

Female (TNHM-HY). Total length 10.77. Carapace 4.58 long, 3.54 wide. Opisthosoma 6.19 long, 2.28 wide.

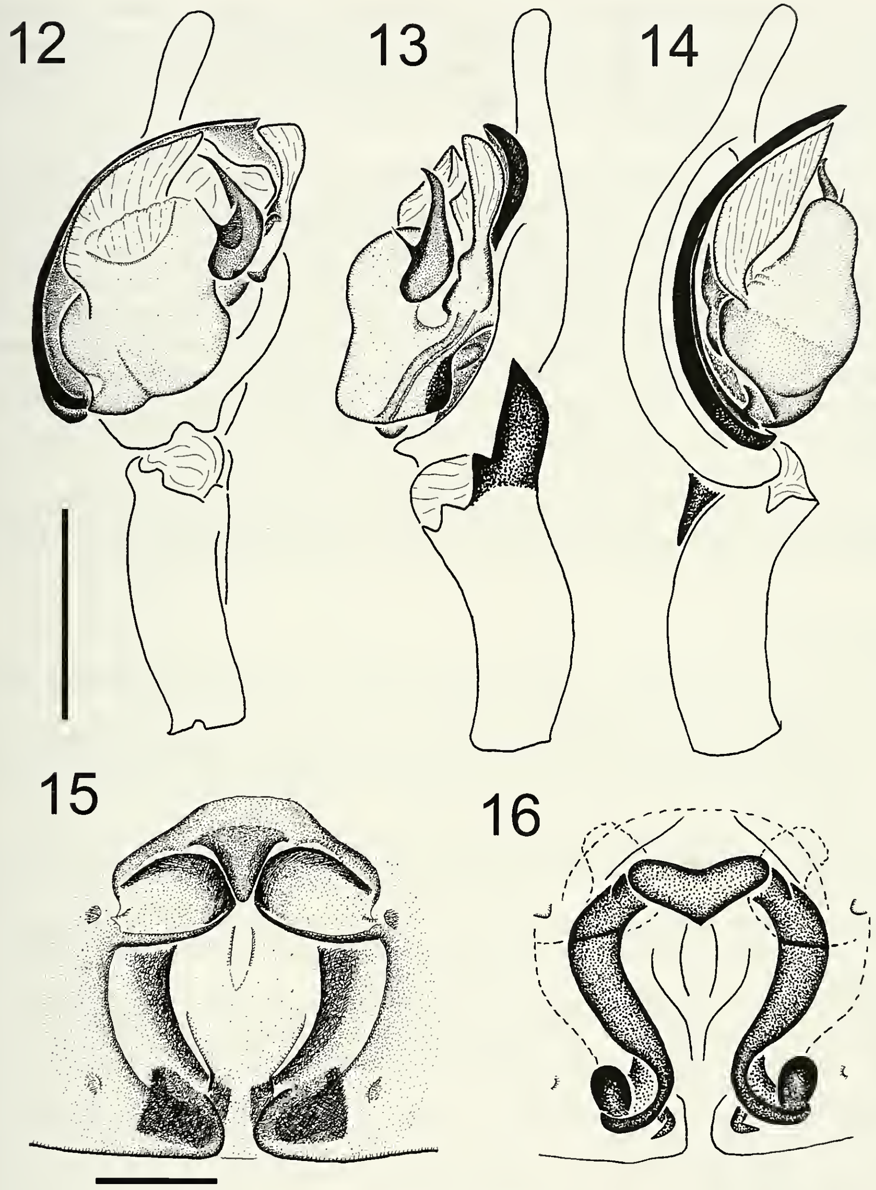
Colouration and pattern as in males but larger in size. Eye sizes and interdistances: AME 0.24, ALE 0.18, PME 0.26, PLE 0.25; AME-AME 0.12, AME-ALE 0.08, PME-PME 0.34, PME-PLE 0.45; MOQ 0.70 long, front width 0.55, back width 0.81.

Leg measurements:

| | I | II | III | IV |
|---|---|---|---|---|
| Femur | 8.62 | 7.21 | 4.41 | 8.10 |
| Patella + Tibia | 10.95 | 8.13 | 4.40 | 7.58 |
| Metatarsus | 8.56 | 5.97 | 3.30 | 6.95 |
| Tarsus | 8.98 | 5.43 | 1.42 | 4.61 |
| Total length | 37.11 | 26.74 | 13.53 | 27.24 |

Epigyne and vulva (Figs 15, 16): Epigyne with a strongly sclerotized, anteriorly located triangular tubercle surrounded by a pair of large anteriorly situated lateral lobes; large postero-lateral lobes very distinct; median field of epigyne with a longitudinal ridge, anteriorly broad, gradually narrowing posteriorly. Vulva with a sclerotized, more or less triangular distal plate; insemination ducts strongly sclerotized, extending to posterior spermathecae; spermathecal heads rounded.

REMARKS: The holotype possesses a lateral tubercle on the spermathecal head (see also Zhang *et al*., 2004: 384, fig. 96) which is indistinct in the specimens examined from northern Thailand.



FIGS 12-16

*Hygropoda yunnan*. (12) Left palp of male, ventral view. (13) Ditto, retrolateral view. (14) Ditto, prolateral view. (15) Epigyne, ventral view. (16) Vulva, dorsal view. Scale lines = 1.0 mm (12-14); 0.25 mm (15, 16).

NATURAL HISTORY: Specimens of *H. yunnan* were obtained by sweeping vegetation along streams running through dry deciduous dipterocarp forest, mixed deciduous forest and gallery evergreen forest between 400-1080 m elevation.

Distribution: Thailand (Chiang Mai and Mae Hong Son Provinces, new record) and China. Judging from the relatively wide distribution range of *H. yunnan*, this species presumably occurs all over the northern part of the kingdom.

## ACKNOWLEDGEMENTS

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## REFERENCES

Barrion, A. T. & Litsinger, J. A. 1995. Riceland Spiders of South and Southeast Asia. *CAB International, Wallingford*, xix + 700 pp.

Cerveira, A. & Jackson, R. 2002. Prey, predatory behaviour, and anti-predator defences of *Hygropoda dolomedes* and *Dendrolycosa* sp. (Araneae: Pisauridae), web-building pisaurid spiders from Australia and Sri Lanka. *New Zealand Journal of Zoology* 29: 119-133.

Dankittipakul, P. 2002. Diversity, distribution and occurrence of spiders in Doi Inthanon National Park, Chiang Mai Province. *Unpublished M. Sc. thesis, Chiang Mai University, Chiang Mai*, 325 pp.

Davies, V. T. 1985. Araneomorphae in part (pp. 49-125). *In:* Walton, D. W. (ed.). Zoological Catalogue of Australia, vol. 3. Arachnida. *Australian Government Publishing, Canberra,* 444 pp.

Doleschall, L. 1859. Tweede Bijdrage tot de Kenntis der Arachniden van den Indischen Archipel. *Acta Societatis Scientiarum Indo-Neerlandicae, Batavia* 5: 1-60.

Hu, J. L. 1984. The Chinese spiders collected from the fields and the forests. *Tianjin Press of Science and Techniques*, 482 pp.

Kishida, K. 1936. A synopsis of the Japanese spiders of the genus *Dolomedes*. *Acta arachnologica, Tokyo* 1: 114-127.

Okuma, C. 1968. Preliminary survey on the spider-fauna of the paddy fields in Thailand. *Mushi* 42(8): 89-118.

Okuma, C. & Wongsiri, T. 1973. Second report on the spider-fauna of the paddy fields in Thailand. *Mushi* 47(1): 1-17.

Platnick, N. I. 2008. The world spider catalog, version 8.5. *American Museum of Natural History, online at http://research.amnh.org/entomology/spiders/catalog/index.html* (accessed January 20, 2008).

Pocock, R. I. 1897. Spinnen (Araneae). *In*: Kükenthal, W. (ed.). Ergebnisse einer zoologischen Forschungsreise in den Molukken und Borneo. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft* 23: 591-629.

POCOCK, R. I. 1900. The fauna of British India, including Ceylon and Burma. Arachnida. *Taylor & Francis, London*, 279 pp.

REIMOSER, E. 1934. Araneae aus Süd-Indien. *Revue suisse de Zoologie* 41: 465-511.

SIERWALD, P. 1997. Phylogenetic analysis of pisaurine nursery web spiders, with revisions of *Tetragonophthalma* and *Perenethis* (Araneae, Lycosoidea, Pisauridae). *The Journal of Arachnology* 25: 361-407.

SIMON, E. 1890. Etudes arachnologiques. 22$^{e}$ Mémoire. XXXIV. Etudes sur les Arachnides de l'Yemen. [Remarques sur la classification des araignées, pp. 79-82]. *Annales de la Société entomologique de France* 6(10): 77-124.

SIMON, E. 1898. Histoire naturelle des Araignées, vol. 2, pt 2, pp. 163-380. *Roret, Paris.*

STRAND, E. 1907. Diagnosen neuer Spinnen aus Madagaskar und Sansibar. *Zoologischer Anzeiger* 31: 725-748.

THORELL, T. 1877. Studi sui Ragni Malesi e Papuani. I. Ragni di Selebes raccolti nel 1874 dal Dott. O. Beccari. *Annali del Museo civico di Storia Naturale di Genova* 10: 341-637.

THORELL, T. 1894. Decas aranearum in ins. Singapore a Cel. Th. Workman inventarum. *Bullettino della Società Entomologica Italiana* 26(3): 321-335.

THORELL, T. 1895. Descriptive catalogue of the spiders of Burma. *Taylor & Francis, London*, 406 pp.

YAGINUMA, T. 1986. Spiders of Japan in color (new edition). *Hoikusha Publ. Co., Osaka*, 135 pp.

ZHANG, J. X., ZHU, M. S. & SONG, D. X. 2004. A review of the Chinese nursery-web spiders (Araneae, Pisauridae). *The Journal of Arachnology* 32: 353-417.

REVUE SUISSE DE ZOOLOGIE 115 (2): 325-330; juin 2008

# Neue *Edaphus* aus Sri Lanka (Coleoptera: Staphylinidae)
# 97. Beitrag zur Kenntnis der Euaesthetinen

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**New *Edaphus* from Sri Lanka (Coleoptera: Staphylinidae) 97th Contribution to the knowledge of Euaesthetinae. -** Six new *Edaphus* from Sri Lanka are described: *E. incommodus* sp. n., *E. languidus* sp. n., *E. marginifrons* sp. n., *E. mussardianus* sp. n., *E. taprobanensis* sp. n. and *E. umbifons* sp. n.

**Keywords**: Coleoptera - Staphylinidae - *Edaphus* - new species - taxonomy - Sri Lanka.

## EINLEITUNG

Die *Edaphus*-Arten der Ausbeuten des Genfer Museums in Sri Lanka sind 1977 von A. Comellini bearbeitet worden. Einige wenige Stücke, die damals nicht berücksichtigt wurden, habe ich jungst untersucht und dabei neben dem ersten Beleg vom in der Orientalis weit verbreiteten *E. fauveli* Puthz sechs neue Spezies identifiziert, die im folgenden beschrieben werden. Die Holotypen aller dieser Arten befinden sich im Muséum d'histoire naturelle, Genf.

Als Abkürzungen gelten: DE = distance between eyes/Augenabstand; Dlbc = distance between basolateral carinae of pronotum/Abstand zwischen den basalen Seitenfältchen des Pronotums; EL = elytral length/Elytrenlänge; EW = elytral width/ Elytrenbreite; GL = length of genae/Wangenlänge; HT = holotype; HW = head width/Kopfbreite; LE = length of eyes/Augenlänge; PL = pronotal length/Pronotumlänge; PM = proportional measurements/Proportionsmasse (1 unit = 0.085 mm); PT = paratype; PW = pronotal width/ Pronotumbreite; SL = sutural length/ Nahtlänge; SpP = sperm pump/ Spermapumpe; TL = length of temples/ Schläfenlänge; VS = vesica seminalis.

## TAXONOMIE

### *Edaphus mussardianus* sp. n.

MATERIAL: ♂-Holotypus; SRI LANKA, Central, Hasalaka près de Weragamtota, env. 250 m, Undawattekele Sanctuary, tamisages en forêt, 11. II. 1970, Mussard, Besuchet, Löbl.

BESCHREIBUNG: Länge: 1,0 mm (Vorderkörperlänge: 0,6 mm). Makropter, rötlichbraun, glänzend, mässig grob (Pronotum) bis fein (Elytren) punktiert, dünn, anliegend beborstet.

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PM des HT: HW: 22,5; DE: 13; LE: 7,5; TL: 0; GL: 3; PW: 25; PL: 22; Dlbc: 19; EW: 36; EL: 35; SL: 29.

Männchen. 8. Sternit (Fig. 2). SpP doppelt so lang wie der Medianlobus, VS höchstens so lang wie die Apikalpartie des Medianlobus. Aedoeagus (Fig. 1), sehr klein, Medianlobus spitzwinklig verengt, Parameren so lang wie der Medianlobus, mit zwei relativ kurzen Borsten (apikal und subapikal).

Kopf deutlich schmäler als die Elytren, Augen sehr gross, grob facettiert, keine Schläfen, hintere Querfurche der Stirn und vordere Längsfurchen (diese nach vorn konvergent) deutlich eingeschnitten, vorderer Stirnmittelteil dreieckig, vollständig eingesenkt-flach, etwa so breit wie die vorderen Seitenteile, zwischen diesen vorn ganz schmal auslaufend; Stirn vorn mit mehreren deutlichen Punkten. Fühler mit zweigliedriger Keule, 10. Glied etwas breiter als lang, 11. Glied knapp 1,5 mal so breit wie lang. Pronotum breiter als lang, seitlich in den vorderen zwei Dritteln, leicht konvergent, gerade, hinten kräftig eingeschnürt, an der Basis mit deutlichen Seitenfältchen, einem kurzen, bis zur Basis durchgehenden Mittelkiel sowie 4 Grübchen, die äusseren quer; Punktierung mässig grob und dicht, Punkte etwa so gross wie der basale Querschnitt der Vorderschienen, Punktzwischenräume deutlich kleiner als die Punkte, nur in der Längsmitte gut punktgross. Elytren etwa quadratisch, kaum breiter als lang, ohne besondere Merkmale; Punktierung deutlich feiner als am Pronotum, etwa halb so fein, die Punktzwischenräume aber meist etwas grösser als die Punkte. Der basale Mittelkiel des 3. Tergits erreicht die Tergitmitte.

Bemerkungen: Diese neue Art ist dem *E. tamoul* Comellini ähnlich, besitzt jedoch viel grössere Augen und ist erheblich gröber punktiert. In meiner Bestimmungstabelle der Arten Vorder- und Hinterindiens (1979) müsste sie bei Leitziffer 126 eingeordnet werden: von *E. leileri* Puthz (der hierher gehört) unterscheidet sie sich sofort durch viel geringere Grösse, fehlende Schläfen und viel feiner punktierte Elytren, von abweichenden *E. densipennis* Cameron ebenfalls durch viel feiner punktierte Elytren, grössere Augen und geringere Grösse.

Etymologie: Mit ihrem Namen ehre ich Monsieur Robert Mussard (Genf), der sich um die Erforschung der Käferfauna Sri Lankas verdient gemacht hat.

***Edaphus incommodus*** sp. n.

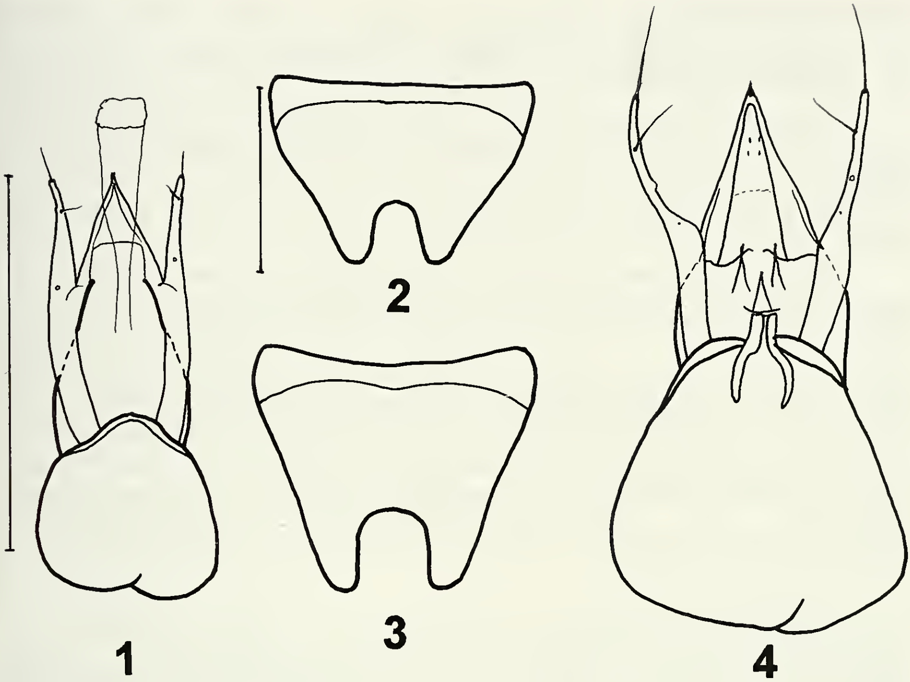
Material: ♂-Holotypus und 1 ♀-Paratypus; SRI LANKA, Polonuaruwa, 13. I. 1965, R. Mussard.

Beschreibung: Länge: 1,0 mm (Vorderkörperlänge: 0, 55 mm). Makropter, rötlichbraun, glänzend, bis auf die Insertionspunkte der feinen Beborstung unpunktiert, Beborstung anliegend.

PM des HT: WH: 23; DE: 13,5; LE: 7; TL:1; G: 3; PW: 26,5; PL: 24; Dlbc: 20; EW: 40; EL: 34; SL: 29.

Männchen. 8. Sternit (Fig. 3). SpP gut 1,5 mal so lang wie der Medianlobus, VS sehr klein. Aedoeagus (Fig. 4), Medianlobus spitzwinklig verengt, Parameren fast so lang wie der Medianlobus, mit einer langen Apikalborste und einer kürzeren Subapikalborste.

Kopf schmäler als das Pronotum, Augen ziemlich gross, mässig grob facettiert, Schläfen sehr klein, aber gerade noch erkennbar, hintere Querfurche der Stirn und vor-



Figs 1-4
Dorsalansicht des Aedoeagus (1, 4) und 8. Sternit der Männchen (2, 3) von *Edaphus mussardianus* sp n. (1, 2, HT) und *E. incommodus* sp. n. (3, 4, HT). Massstab = 0,1 mm.

dere, konvergente Längsfurchen deutlich ausgeprägt, vorderer Stirnmittelteil deutlich breiter als jedes der Seitenstücke, sehr flach gewölbt, ohne Absetzung in den Clypeus übergehend. Fühler mit deutlich abgesetzter zweigliedriger Keule, 10. Glied so lang wie breit (beim § etwas breiter als lang), 11. Glied 1,5 mal so lang wie breit. Pronotum breiter als lang, seitlich in den vorderen zwei Dritteln konvex, hinten deutlich eingeschnürt, an der Basis mit kräftigen Seitenfältchen, einem kurzen, bis zur Basis durchgehenden Mittelkiel sowie mit 6 etwa gleichgrossen Grübchen. Elytren breiter als lang, ohne besondere Merkmale. Der basale Mittelkiel des 3. Tergits befindet sich in der Vorderhälfte des Tergits.

Bemerkungen: Diese äusserlich wenig auffällige Art müsste in meiner Tabelle (1979), je nachdem wie man die Deutlichkeit ihrer Schläfen beurteilt, entweder bei Leitziffer 171 eingeordnet werden (von *E. plicatulus* (Schaufuss) unterscheidet sie sich durch erheblich schmäleres Pronotum und die Sexualcharaktere) oder bei Leitziffer 180 (von *E. minutus* Puthz unterscheidet sie sich durch nicht unterbrochene vordere Stirnseitenteile und die Sexualcharaktere).

Etymologie: Wegen der grossen Schwierigkeit der Identifizierung dieser äusserlich recht einförmigen Art nenne ich sie „*incommodus*" (lat.) = unbequem.

***Edaphus languidus*** sp. n.

MATERIAL: ♀-Holotypus; SRI LANKA, Uva, Inginiyagala, tamisages en forêt, 12. II. 1970, Mussard, Besuchet, Löbl.

BESCHREIBUNG: Länge: 0,95 mm (Vorderkörperlänge: 0, 5 mm). Makropter, helbraun, matt-schimmernd, mit äusserst feiner Grundskulptur; Beborstung dicht, anliegend.

PM des HT: WH: 19; DE: 14; LE: 5,5; TL: 2; L: 3,5; PW: 22; PL: 21,5; Dlbc: 15; EW: 28; EL: 25; SL: 22.

Kopf deutlich schmäler als das Pronotum, Augen klein, fein facettiert, keine deutlich eingeschnittene hintere Stirnquerfurche zwischen den Ozellen, vordere Längsfurchen mässig flach und nach vorn erlöschend, vorderer Stirnmittelteil schmäler als jedes der Seitenstücke, zum Clypeus verbreitert und ohne Absetzung in diesen übergehend. Fühler mit zweigliedriger Keule, 10. Glied erheblich breiter als lang, 11. Glied fast doppelt so lang wie das 10. Glied. Pronotum wenig breiter als lang, seitlich in den vorderen zwei Dritteln konvex, hinten deutlich eingeschnürt, an der Basis mit deutlichen Seitenfältchen und 6 wenig deutlichen winzigen Grübchen. Elytren wenig breiter als lang, ohne besondere Merkmale. Der Mittelkiel des 3. Tergits nur im basalen Viertel.

Männchen unbekannt.

BEMERKUNGEN: Diese neue Art ist dem *E. chalcographus* Puthz (aus Maharashtra) sehr ähnlich, unterscheidet sich von ihm aber durch geringere Grösse, fehlende hintere Querfurche der Stirn und breitere Fühlerkeule. In meiner Tabelle (1979) müsste sie bei Leitziffer 197 eingefügt werden.

ETYMOLOGIE: Wegen fehlenden Glanzes nenne ich diese neue Art „*languidus*“ lat.) = matt.

***Edaphus taprobanensis*** sp. n.

MATERIAL: ♀-Holotypus und 2 ♀♀-Paratypen; SRI LANKA, Central, Mululla, tamisage en forêt au-dessus de Mululla, à env. 750 m, 4. II. 1970, Mussard, Besuchet, Löbl.- HT und 1 PT im Museum Genf, 1 PT in meiner Sammlung.

BESCHREIBUNG: Länge: 1,0-1,1 mm (Vorderkörperlänge: 0,55 mm). Brachypter, braun, glänzend, fein punktiert; Beborstung dünn, anliegend.

PM des HT: WH: 20,5; DE: 14; LE: 6; TL: 0,8; GL: 3,5; PW: 24,5; PL: 23,5; Dlbc: 17: EW: 33; EL: 27; SL: 22.

Kopf erheblich schmäler als das Pronotum, Augen ziemlich gross, grob facettiert, Schläfen kaum erkennbar, hintere Querfurche der Stirn und vordere Längsfurchen deutlich eingeschnitten, vorderer Stirnmittelteil so breit wie jedes der Seitenstücke, flachbeulig erhoben, zum Clypeus verflacht und ohne Absetzung in diesen übergehend; vordere Stirnseitenteile mit wenigen feinen Punkten. Fühler mit zweigliedriger Keule, 10. Glied breiter als lang, 11. Glied etwa 1,5 mal so lang wie breit. Pronotum etwas breiter als lang, seitlich in den vorderen zwei Dritteln konvex, hinten deutlich eingeschnürt, an der Basis mit deutlichen Seitenfältchen sowie 6 kleinen Grübchen; Punktierung fein und dicht, Punkte fast so gross wie eine Augenfacette, Punktzwischenräume kleiner als die Punkte; die Pronotummitte vor dem basalen

Mittelkiel (der nicht die Basis erreicht) schmal punktfrei. Elytren trapezoid, viel breiter als lang, ohne besondere Merkmale; Punktierung etwas feiner als am Pronotum, dicht. Der basale Mittelkiel des 3. Tergits befindet sich im basalen Tergitdrittel.

Männchen unbekannt.

Bemerkungen: Diese neue Art müsste in meiner Tabelle (1979) bei Leitziffer 68 eingefügt werden: sie unterscheidet sich von *E. densus* Bernhauer durch geringere Grösse, nicht längs-ausgezogene Pronotumpunktierung und viel feiner punktierte Elytren. Habituell ähnelt sie dem *E. tamoul* Comellini, ist jedoch brachypter und hat keinen durchgehenden basalen Mittelkiel am Pronotum.

Etymologie: Ich wähle für diese Art die alte Bezeichnung für die Insel Ceylon.

***Edaphus marginifrons*** sp. n.

Material: ♀-Holotypus; SRI LANKA, Central, Kandy, à env. 600 m, Udawattekele Sanctuary, tamisages en lisière de forêt, 22. I. 1970, Mussard, Besuchet, Löbl.

Beschreibung: Länge: 1,5 mm (Vorderkörperlänge: 0,75 mm). Brachypter, rötlichbraun, glänzend, Pronotum und Elytren flach punktiert, Beborstung dicht, halb erhoben.

PM des HT: WH: 28,5; DE: 19; LE: 8; TL: 1,5; GL: 3; PW: 34; PL: 32; Dlbc: 21,5; EW: 48; EL: 40; SL: 34.

Kopf viel schmäler als das Pronotum, Augen ziemlich gross, mässig grob facettiert, Schläfen deutlich, schräg eingezogen, hintere Querfurche der Stirn deutlich eingeschnitten, vordere Seitenfurchen vor dem eingesenkten, flachen Stirnmittelteil miteinander verbunden, vorderer Stirnmittelteil breiter als jedes der Seitenstücke, mit 4 flachen Punkten versehen, Clypeus durch einen kräftigen Querwulst vom Stirnmittelteil abgesetzt. Fühler mit zweigliedriger Keule, 10. Glied so lang wie breit, 11. Glied gut 1,5 mal so lang wie breit. Pronotum breiter als lang, seitlich in den vorderen zwei Dritteln stark konvex, hinten stark eingezogen, an der Basis mit deutlichen Seitenfältchen und 4 mässig grossen Grübchen, die äusseren leicht quer; die Pronotumskulptur besteht aus erlöschenden, mässig feinen Punkten. Elytren viel breiter als lang, trapezoid, ohne besondere Merkmale; auch die Elytren sind sehr flach, mässig dicht punktiert. Der basale Mittelkiel des 3. Tergits reicht etwas über die Tergitmitte hinaus.

Männchen unbekannt.

Bemerkungen: In meiner Tabelle (1979) müsste diese neue Art bei Leitziffer 188 eingefügt werden: sie unterscheidet sich von *E. cameroni* Puthz sofort durch den vorn wulstförmig abgesetzten Clypeus.

Etymologie: Der Name bezeichnet das auffälligste Merkmal dieser neuen Art, ihren Querwulst auf der vorderen Stirn: „*marginifrons*“ (lat.) = mit gerandeter Stirn.

***Edaphus umbifrons*** sp. n.

Material: ♀-Holotypus; SRI LANKA, Uva, s/Wellawaya, 300 m, tamisages en forêt, 25. I. 1970, Mussard, Besuchet, Löbl.

Beschreibung: Länge: 0,95 mm (Vorderkörperlänge: 0,5 mm). Brachypter, hellbraun, glänzend, bis auf die Insertionspunkte der feinen Beborstung unpunktiert; Beborstung anliegend.

PM des HT: WH: 22; DE: 15,5; LE: 6,5; TL: 0; GL: 4; PW; 25; PL: 21; Dlbc: 18; EW: 35; EL: 26; SL: 21.

Kopf schmäler als das Pronotum, Augen mässig gross, mässig fein facettiert, keine deutlichen Schläfen, Stirn ohne hintere Querfurche, vordere Längsfurchen zum Vorderrand der Stirn flach erlöschend, Mittelteil der Stirn längsbeulig kräftig erhoben, ohne Absetzung in den Clypeus übergehend. Fühler mit zweigliedriger Keule, 10. Glied breiter als lang, 11. Glied kaum 1,5 mal so lang wie breit. Pronotum deutlich breiter als lang, seitlich in den vorderen zwei Dritteln konvex, hinten kräftig eingeschnürt, an der Basis mit kräftigen Seitenfältchen, einem kurzen, bis zur Basis durchgehenden Mittelkiel sowie 6 kleinen Grübchen. Elytren trapezoid, viel breiter als lang, ohne besondere Merkmale. An dem flachen Teil des 3. Tergits befindet sich ein wenig breiter, schmaler Quereindruck, kein Mittelkiel.

Männchen unbekannt.

BEMERKUNGEN: Diese neue Art ist eng mit *E. mussardi* Comellini und *E. puthzi* Comellini verwandt. Wegen ihrer kurzen Elytren müsste sie in meiner Tabelle (1979) bei Leitziffer 43 eingefügt werden: sie unterscheidet sich von *E. benicki* Puthz durch fehlende hintere Querfurche der Stirn und das Fehlen eines basalen Mittelkiels am 3. Tergit. Wenn man wegen ihrer Elytrenlänge im Zweifel zu Leitziffer 133 gelangte, so liesse sie sich von den eingangs genannten Arten durch geringere Grösse und stärker erhobenen, schmäleren Stirnmittelteil unterscheiden.

ETYMOLOGIE: Wegen ihrer gewölbten Stirn nenne ich diese neue Art „*umbifrons*“ (lat.) mit beuliger Stirn.

## LITERATUR

COMELLINI, A. 1977. Nouvelles espèces d'*Edaphus* Motsch. du Sri Lanka (Coleoptera Staphylinidae). *Mitteilungen der schweizerischen entomologischen Gesellschaft* 50: 251-268.

PUTHZ, V. 1979. Die vorder- und hinterindischen Arten der Gattung *Edaphus* Motschulsky (Coleoptera, Staphylinidae). *Annales historico-naturales Musei Nationalis Hungarici* 71: 107-160.

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# A revision of the New Guinean genus *Novopsocus* Thornton (Psocoptera, Pseudocaeciliidae) with the description of two new species

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**A revision of the New Guinean genus *Novopsocus* Thornton (Psocoptera, Pseudocaeciliidae) with the description of two new species. -** The New Guinean endemic genus *Novopsocus* Thornton was previously known from six specimens, all attributed to the type species *N. stenopterus* (Thornton & Smithers). The genus is here revised in the light of nine newly collected individuals. Examination of published and of new material shows that individuals previously attributed to the type species belong to two different species, *N. stenopterus* itself and *N. magnus* sp. n. A third species, *N. caeciliae* sp. n., is described on the base of a single male. The new data show that the strong sexual dimorphism reported in *Novopsocus* is most pronounced in *N. magnus*, and absent in *N. stenopterus* (the incompletely known *N. caeciliae* seems to be intermediate with respect to this character). The autapomorphies previously postulated for the genus are not all valid, although the validity of the genus itself is not questioned.

**Keywords**: Psocodea - *Zelandopsocinae* - new species - New Guinea endemic - sexual dimorphism.

## INTRODUCTION

Thornton & Smithers (1977) described *Zelandopsocus stenopterus* on the basis of one female caught in the mountains near Woitape, Papua New Guinea (PNG). The species was described as very peculiar, with narrow, strap-like wings, and a head with a sharp vertex. The species was later transferred to *Austropsocus* by Thornton (1981), who deemed it "highly abberrant [sic]". After having examined five specimens found in the collections of the Bishop Museum, Thornton (1984) placed *A. stenopterus* as the type species of the new, monotypic genus *Novopsocus*. He attributed the five new specimens (two of which were males) to *Novopsocus stenopterus* (Thornton & Smithers), and redescribed the species as strongly dimorphic sexually, due to the particular antennal morphology (first flagellar segment simple in female, massive and flattened in male). Enquiries to the staff of the Bishop Museum by the author of the present paper have revealed that the specimens mentioned by Thornton (1984) are no longer in this collection. However, it was possible to locate three of them at the Australian Museum, together with the holotype of *N. stenopterus*. In addition to these four specimens, nine additional specimens were collected in PNG in 1993. The material examined indicates the actual presence of three species in the genus, two of which are described as new.

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## MATERIAL AND METHODS

Specimens were collected on the branches of small trees and shrubs in the understorey and at the edge of undisturbed to moderately disturbed rainforest, using the branch-beating technique (Lienhard, 1998). These specimens are deposited in the Muséum d'histoire naturelle de Genève, Switzerland (MHNG). The other specimens examined belong to the Australian Museum, Sydney (AMS).

The following abbreviations are used in the descriptions. BL: body length; FW: forewing length; HW: hindwing length; fF: fore femur length and maximum width; F: length of hind femur; T: length of hind tibia; t1, t2, t3: length of hind tarsomeres (from condyle to condyle); f1: length and maximum width of first antennal flagellomere; f2: length of second flagellomere; IO/D: shortest distance between compound eyes divided by antero-posterior diameter of compound eye in dorsal view of head. – For standard abbreviations concerning wing venation, see Yoshizawa (2005).

## TAXONOMIC PART

### SPECIES LIMITS

Thornton (1984) concluded that the six specimens examined by him were conspecific. The present sampling, broader despite its small size, shows that males of *Novopsocus* belong to three different species, which are easily identified by the antennal shape and the structure of the hypandrium. Moreover, they have notable size differences (Fig. 1, Tab. 1), with the male of *N. magnus* sp. n. being almost twice as large as that of *N. caeciliae* sp. n. (see below for species description and key). Females are more difficult to distinguish, but comparison of measurements shows that all individuals are clustered in three non-overlapping classes (Tab. 1 and Fig. 2), and females can thus be unambiguously associated with males of a similar size. Additional information is given by the two cases where two individuals were found in the same sample (1 ♂ of *N. magnus* and 1 ♀, 1 ♂ of *N. stenopterus* and 1 ♀). In each case the female belongs to the same size-class as the male. No other sample contained more than one individual. Individuals of different size-classes were therefore never found together. For all these reasons, the species are defined as done below.

### DESCRIPTIONS

### ***Novopsocus*** Thornton

*Novopsocus* Thornton, 1984: 379 (type species: *Zelandopsocus stenopterus* Thornton & Smithers).

REVISED DIAGNOSIS (modified from Thornton, 1984): Belonging to the Zelandopsocinae. Subgenital plate bilobed, lobes not overlapping, each with group of 2-3 apical setae; epiproct with dorsal setose flap; first flagellar segment of male antenna massive and distinctly flattened, or slightly flattened but only weakly thickened, or neither flattened nor thickened; hypandrium 3-lobed, or with a single median lobe; phallosome with massive sclerites, no ribbon sclerite, pair of membranous (not spinous) sacs; wings long and narrow, straplike; head capsule flattened, vertex sharp-edged.

DISCUSSION: See General Discussion at the end of this paper.

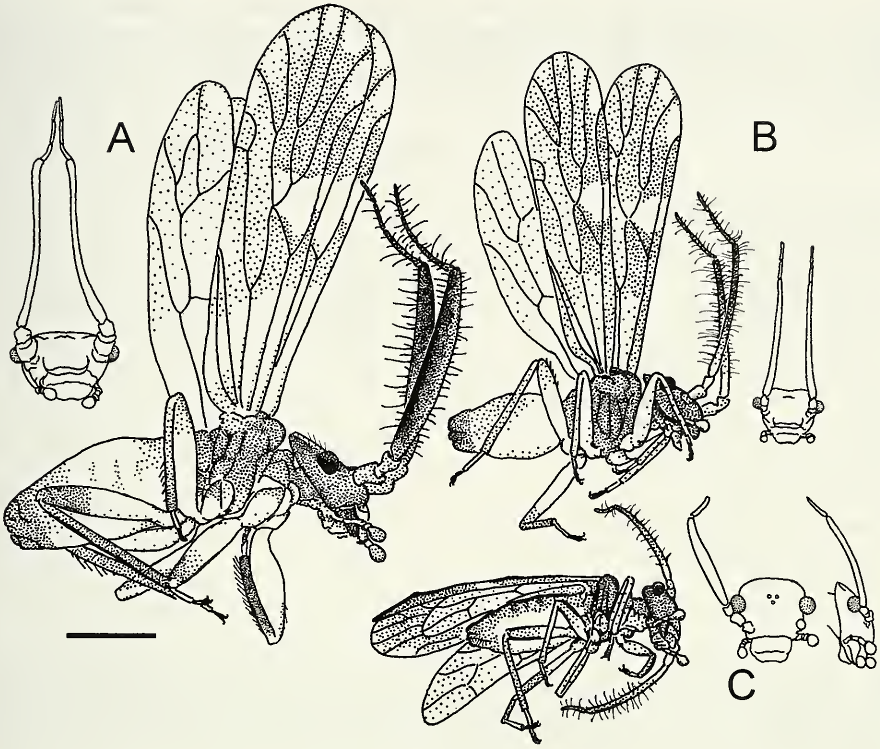

Fig. 1

Habitus of the *Novopsocus* males. (A) *N. magnus* sp. n., holotype, with antennae broken after fourth flagellar segment. Inset: head in frontal view (pilosity not figured). (B) *N. stenopterus* (Thornton & Smithers), male collected 10.6.1993, with antennae broken after third flagellar segment. Inset: head in frontal view (pilosity not figured). (C) *N. caeciliae* sp. n., holotype, with antennae broken after the second flagellar segment. Inset: head in frontal (left) and lateral (right) views (pilosity not figured, left antenna omitted). Drawing after a photograph of the three specimens taken together. Scale bar = 1mm (insets not exactly to same scale). Wing pilosity not figured. NOTE: The wing venation of the holotype of *N. magnus* is anomalous in the right forewing (Rs three-branched and M two-branched) and in the right hindwing (M two-branched with M1 distally fused to R4+5).

## ***Novopsocus magnus*** sp. n. Figs 1A, 3A, 3B

*Novopsocus stenopterus*. – Thornton, 1984: 380 (in part).

Material examined: MHNG, holotype ♂, PNG, Morobe Province, Mt Kaindi, 1400m, 22.6.1993, leg. Ph. Cuénoud. – MHNG, paratypes: 1 ♀ allotype, same data as for holotype (1 slide with terminalia, PC93.6.22.2, remaining parts in alcohol). – 1 ♀, ibidem, 16.08.1993, leg. Ph. Cuénoud. – AMS, paratypes: 1 ♂, PNG, Southern Highlands province, Koroba, 1650m, 40 km west of Tari, 17.9.1963, leg. R. Straatman, mentioned and illustrated (fore wing, antenna, paraproct, epiproct, hypandrium and phallosome) in Thornton (1984) under the name *N. stenopterus,* associated slides now missing. – 1 ♀, ibidem, 19.9.1963, leg. R. Straatman, mentioned and illustrated (subgenital plate) in Thornton (1984) under the name *N. stenopterus*, associated slide now missing. – 1 ♀, PNG, Morobe Province, Bulolo River, 1130m, 17.9.1969, leg. A. B. Mirza, mentioned in Thornton (1984) under the name *N. stenopterus*, terminalia missing.

TABLE 1. Forewing length (mm), head width (i.e. greatest width of head capsule measured at vertex, mm) and the IO/D ratio for all specimens available. Only forewing length and head width are used in the graph of Fig. 2. The IO/D ratio is less informative than the two other measurements, since it varies between sexes, and thus shows some overlapping when the sexes are pooled.

| | Forewing length [mm] | Head width [mm] | IO/D ratio |
|---|---|---|---|
| *Novopsocus magnus* sp. n. | | | |
| Male, holotype | 4.80 | 1.36 | 3.5 |
| Male, Koroba | 4.61 | 1.17 | 3.5 |
| Female, Koroba | 4.29 | 1.37 | 4.4 |
| Female, Bulolo River | 4.21 | 1.26 | 3.8 |
| Female, Mt Kaindi, 16.8.1993 | 3.98 | 1.38 | 4.4 |
| Female, Mt Kaindi, 22.6.1993 | 3.98 | 1.41 | 4.3 |
| *Novopsocus stenopterus* (Thornton & Smithers) | | | |
| Male, Mt Kaindi, 10.6.1993 | 3.78 | 0.87 | 2.7 |
| Male, Mt Kaindi, 6.6.1993 | 3.74 | 0.95 | 3.1 |
| Female, Mt Kaindi, 6.6.1993 | 3.74 | 1.02 | 3.4 |
| Female, holotype | 3.74 | 1.01 | 3.6 |
| Female, Mt Kaindi, 24.6.1993 | 3.50 | 0.95 | 3.6 |
| *Novopsocus caeciliae* sp. n. | | | |
| Male, holotype | 2.68 | 0.75 | 3.2 |

OTHER MATERIAL: Published material (Thornton, 1984) that could not be located. 1 ♀, PNG, East Sepik Province, Sepik River, Ambunti, 200m, 4.5.1963, leg. R. Straatman (*N. magnus* or *N. stenopterus*) . – 1 ♂, PNG, Morobe Province, Ulap, 800-1100m, 9.1968, leg. N. L. H. Krauss (probably *N. magnus*, since male antennal morphology seems too conspicuous to allow misidentification; see Fig. 2 in Thornton, 1984).

ETYMOLOGY: The species epithet refers to the comparatively large body size of the species: magnus (Latin) = large.

DESCRIPTION OF MALE: As in Thornton (1984) where the male is erroneously attributed to *N. stenopterus*. Since none of the mounted parts used by Thornton could be found, it was decided to choose the complete male as the holotype. Although the specimen was not dissected, its hypandrium matches Thornton's description, with its two lateral prongs and a broad median lobe. The antenna is strongly modified, with the first flagellar segment strongly broadened and flattened (Fig. 1A). The holotype also has a broadened fore femur, and the dorsal surface of the head capsule (frons, vertex) is flat with a slightly concave area on each side. Thornton (1984) mentions that the Rs and M veins are separated in the forewing of the male specimen that he examined, but this is not true for the remaining forewing of this specimen (preserved in alcohol), where the veins are joined by a short crossvein (the mounted wing illustrated by Thornton is now missing). These veins are meeting in a point in both forewings of the holotype (which has normal venation in left fore- and hindwing but somewhat anomalous venation in both right wings, see Fig. 1A and corresponding legend).

*Measurements* (holotype). BL: 4.2 mm; FW: 4.8 mm; HW: 4.3 mm; fF: 1.12 x 0.39 mm; F: 1.32 mm; T: 1.58 mm; t1: 380 $\mu$m; t2: 100 $\mu$m; t3: 110 $\mu$m; f1: 2.32 x 0.29 mm; f2: 0.53 mm; IO/D: 3.5. – Male from Koroba. FW: 4.6 mm, fF: 0.89 x 0.30 mm; IO/D: 3.5.

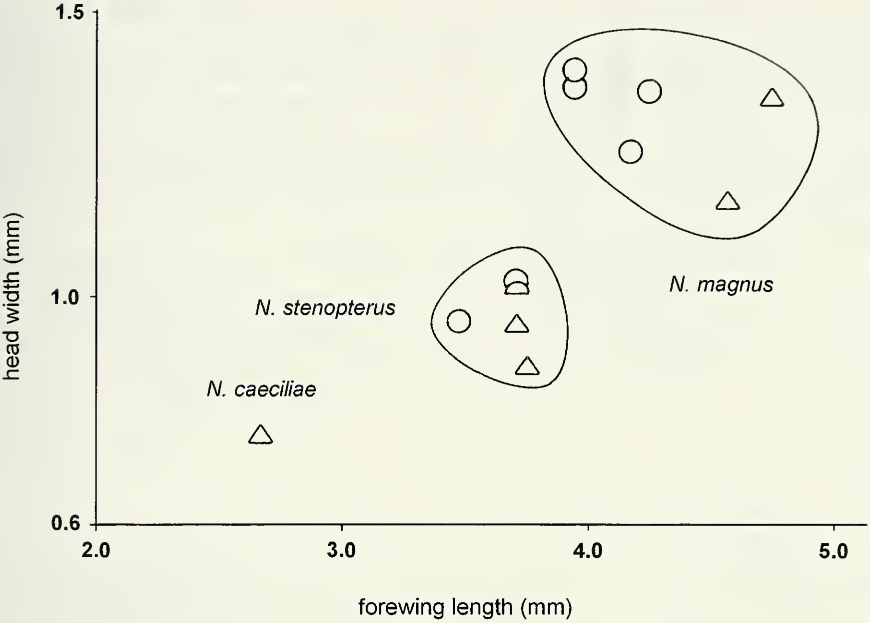

FIG. 2

Scatter plot of the *Novopsocus* specimens examined arranged by their forewing length (horizontal axis, mm) and head width (vertical axis, mm). Triangles: males; circles: females; semicircle: female holotype of *N. stenopterus* (Thornton & Smithers). It is to be noted that dimensions do not overlap across species. The data used for this graph are presented in Table I.

DESCRIPTION OF FEMALE: *Colouration*. Similar to male (see Fig. 1A). Head dark brown, frons somewhat lighter. Compound eye black, antenna light brown, maxillary palp light brown, the two basal segments darker. Thorax dark brown, coxae dark brown, trochanters very pale buff, femora dark brown, very pale buff at base (middle legs) or in basal half (hind legs). Tibiae and first tarsal segments very pale buff, second and third tarsal segments dark brown. Abdomen light brown with diffuse, darker hypodermal colouration on the dorsal side. Forewing with dark veins, its membrane brown with three hyaline areas (one at base of wing, one from base of pterostigma to Rs + M junction and one around the nodulus), and lighter zones also in the marginal cells between the pterostigma and the areola postica. Hindwing with a similar pattern, simpler and attenuated.

*Morphology*. In general similar to male (see Fig. 1A) except for antenna and terminalia. Head dorsally slightly convex, broad with a sharp vertex. Maxillary palp with a short and broadly rounded apical segment. Antenna similar to that of female *N. stenopterus*, i.e. first flagellar segment not flattened and only very slightly thicker than more distal flagellar segments. Claw without a preapical tooth. Forewing narrow; veins bearing two rows of setae, CuP bare; Rs and M linked by a short crossvein, or meeting in a point. Hindwing with bare veins, margin setose from the tip of R1 to anal cell. Epiproct with a dorsal setose flap bearing two particularly long setae.

Trichobothrial field of paraproct with 14-20 trichobothria. Subgenital plate posteriorly slightly bilobed (Fig 3A; Fig. 7 of Thornton, 1984, illustrates the subgenital plate of the female from Koroba), each lobe with two or three setae (distance between left and right external seta 0.133 mm, thus one third larger than in the holotype of *N. stenopterus* - 0.100 mm). Gonapophyses (Fig 3B): ventral valve narrow and pointed, with short recurrent microtrichia at apex; dorsal valve with pointed preapical process, bearing short recurrent microtrichia at tip, and rounded apex; external valve oblong and rounded, with long setae, especially on distal margin.

*Measurements* (females from Mt Kaindi). BL: 4.0-4.5 mm; FW: 4.0 mm; HW: 3.3-3.5 mm; F: 1.14 mm; T: 1.38-1.52 mm; t1: 310-350 $\mu$m; t2: 80-90 $\mu$m; t3: 100-120 $\mu$m; f1: 1.46-1.52 x 0.08 mm; f2: 0.32-0.41 mm; IO/D: 4.3. – Range of FW for all females known: 4.0-4.3 mm. Range of IO/D for all females known: 3.8-4.4.

### ***Novopsocus stenopterus*** (Thornton & Smithers) Figs 1B, 3C, 3D

*Zelandopsocus stenopterus* Thornton & Smithers, 1977: 443.
*Austropsocus stenopterus* (Thornton & Smithers). – Thornton, 1981: 439.
*Novopsocus stenopterus*. – Thornton, 1984: 380 (in part).

MATERIAL EXAMINED: AMS, holotype ♀, PNG, Central Province, Woitape, above 2000m, 28.10.1963, leg. D. K. McAlpine (in alcohol, with wings, hind legs, antennae and terminalia mounted on three slides). – MHNG: 1 ♂, PNG, Morobe Province, Mt Kaindi, 1400m, 26.4.1993, leg. Ph. Cuénoud (in poor condition, abdomen lost; assigned to species and sex on the base of head width, 0.93 mm, and IO/D ratio, 3.1). – MHNG: 1 ♂ 1 ♀, ibidem, 6.6.1993, leg. Ph. Cuénoud (1 slide with male terminalia, PC93.6.6.1, and 1 slide with female terminalia, PC93.6.6.2). – MHNG: 1 ♂, ibidem, 10.6.1993, leg. Ph. Cuénoud. – MHNG: 1 ♀, ibidem, 24.6.1993, leg. Ph. Cuénoud.

DESCRIPTION OF MALE: *Colouration*. Head dark brown, frons medially somewhat lighter, compound eye black, maxillary palp light brown. Antenna light brown at base, becoming dark brown from the middle of first flagellar segment towards apex. Thorax dark brown. Coxae dark brown at base, light brown otherwise. Trochanters, femora and tibiae light brown, first tarsal segment light brown (front- and middle legs) or very pale buff (hind legs). Second and third tarsal segments dark brown. Abdomen light brown with very little, darker, hypodermal colouration. Terminalia medium brown. Forewing brown, light at base and with a hyaline area from base of pterostigma to the Rs + M junction, and lighter zones also in the marginal cells at the wing apex and around the nodulus. Hindwing light brown, paler at base.

*Morphology*. Vertex sharp. Maxillary palp with a subglobular apical segment. Antenna similar to that of female, but with the first flagellar segment slightly thickened, but not flattened. Dorsal surface of head almost flat. Claw without a preapical tooth. Forewing narrow; veins bearing two rows of setae, CuP bare; Rs and M meeting in a point. Hindwing with bare veins, margin setose. Epiproct simple, with some short setae at apex and a subapical transversal row of 4 long setae. Trichobothrial field of paraproct with 22-23 trichobothria. Hypandrium (Fig. 3C) with a weakly prominent, apically rounded median lobe, lacking the lateral prongs found in the two other species (this character also checked and confirmed under the microscope in the male that was not dissected). Phallosome (Fig. 3D) with complex endophallic sclerites (somewhat deformed by slide mounting on Fig. 3D).

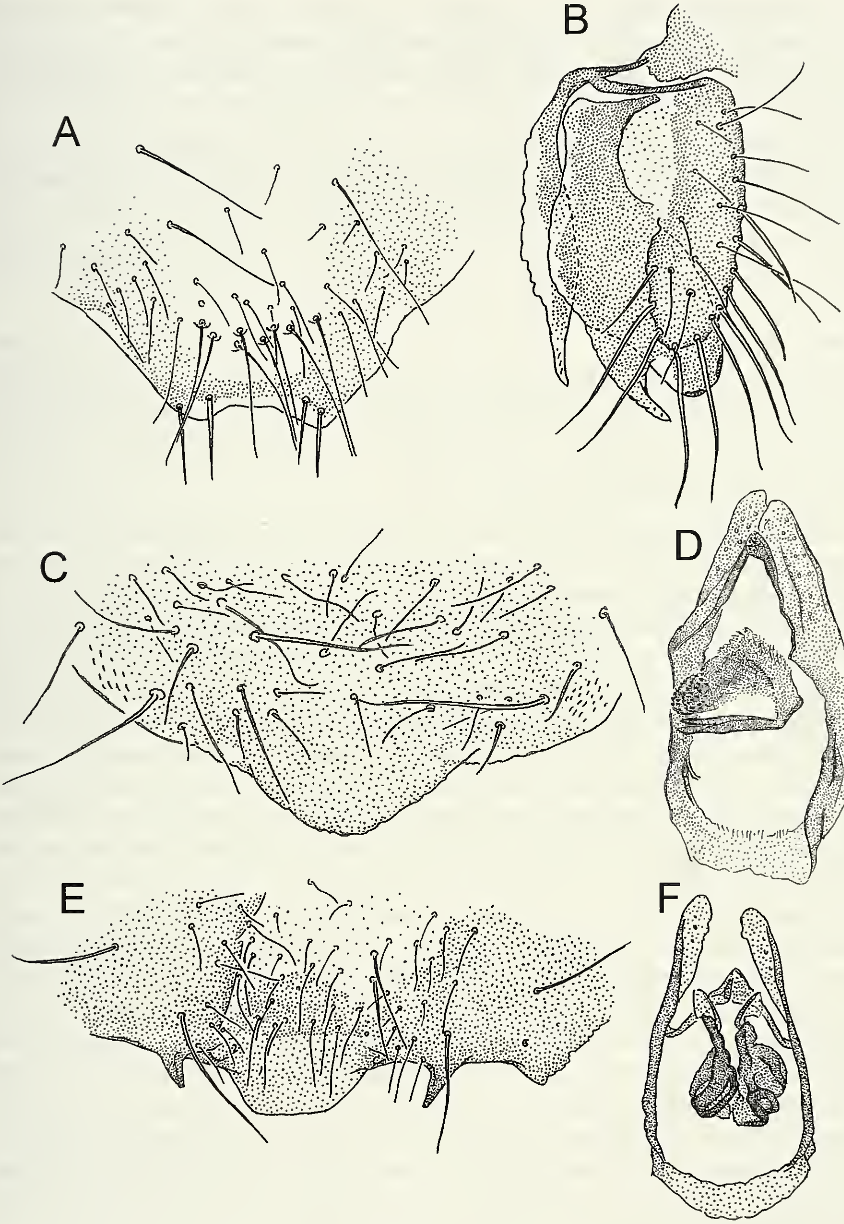

FIG. 3

*Novopsocus magnus* sp. n., female from Mt Kaindi: Subgenital plate (A) and gonapophyses (B). *N. stenopterus* (Thornton & Smithers), male: Hypandrium (C) and phallosome (D). *N. caeciliae* sp. n., male: Hypandrium (E) and phallosome (F).

*Measurements* (male from Mt Kaindi, 10.6.1993). BL: 3.0 mm; FW: 3.8 mm; HW: 3.2 mm; fF: 0.68 x 0.21 mm; F: 0.92 mm; T: 1.26 mm; t1: 300 $\mu$m; t2: 60 $\mu$m; t3: 90 $\mu$m; f1: 1.61 x 0.1 mm; f2: 0.49 mm; IO/D: 2.7. – Additional measurements (specimen PC93.6.6.1). BL: 3.2 mm; FW: 3.8 mm; f1: 1.65 x 0.1 mm; IO/D: 3.1.

DESCRIPTION OF FEMALE: See Thornton & Smithers (1977). Fore-wing length: 3.5-3.7 mm (the holotype's forewing length is 3.74 mm, not 3.30 mm as mentioned in the original description). First segment of antennal flagellum cylindrical, not thickened. Subgenital plate with two or three marginal setae on each apical lobe (female PC93.6.6.2 with three setae on one side and two on the other). IO/D: 3.4-3.6.

### ***Novopsocus caeciliae*** sp. n. Figs 1C, 3E, 3F

MATERIAL EXAMINED: MHNG, holotype ♂, PNG, Madang Province, near Baitabag, 40m, 21.9.1993, leg. Ph. Cuénoud (1 slide with terminalia, PC93.3.21.1, remaining parts in alcohol).

ETYMOLOGY: This species is named after the late Cécile Chappuis, dear friend of the author, who left us all too early.

DESCRIPTION OF MALE: *Colouration*. Head dark brown, compound eye black, maxillary palp light brown. Antenna medium brown, base of first flagellar segment light brown. Thorax dark brown. Coxae and trochanters light brown. Fore leg: femur, tibia and first tarsal segment light brown, second and third tarsal segments dark brown. Middle leg: femur dark brown, very pale buff at its base, tibia and first tarsal segment light brown, second and third tarsal segments dark brown. Hind leg: femur dark brown, its basal half very pale buff, tibia light brown, first tarsal segment very pale buff, second and third tarsal segments dark brown. Abdomen light brown ventrally, with uniform dark hypodermal colouration dorsally. Terminalia dark brown. Forewing brown, light in the basal 40%, with a hyaline area from the pterostigma to the Rs + M junction and lighter zones around the nodulus and in the marginal cells between the pterostigma and vein M1. Hindwing pale at base, light brown in distal half.

*Morphology*. Vertex sharp. Maxillary palp with a short, subglobular fourth segment. Antenna with first flagellar segment somewhat flattened but only weakly thickened. Head dorsally slightly convex. Claw without a preapical tooth. Forewing narrow; veins bearing two rows of setae, CuP bare; Rs and M meeting in a point. Hindwing with bare veins and short marginal setae. Epiproct with short setae, trichobothrial field of paraproct with 18-20 trichobothria. Hypandrium (Fig. 3E) with a broad truncate median lobe and two pointed lateral prongs, similar to *N. magnus* (see Thornton, 1984: Fig. 5). Phallosome (Fig. 3F) with complex endophallic sclerites.

*Measurements*. BL: 2.44 mm; FW: 2.7 mm; HW: 2.3 mm; fF: 0.55 x 0.16 mm; F: 0.77 mm; T: 1.00 mm; t1: 250 $\mu$m; t2: 40 $\mu$m; t3: 60 $\mu$m; f1: 1.06 x 0.07 mm; f2: 0.37 mm; IO/D: 2.7.

### KEY TO THE SPECIES OF *NOVOPSOCUS*

1 Male: first flagellar segment of the antenna strongly broadened and flattened (Fig. 1A). Female: large, forewing length ≥ 4 mm, head width > 1.2 mm, compound eyes relatively small (IO/D ≥ 3.8) . . . . . *N. magnus* sp. n.

- Male: first flagellar segment of the antenna only weakly thickened, not flattened or only slightly flattened (Fig. 1B & C). Female: forewing length < 3.8 mm, head width ≤1.0 mm, IO/D < 3.7 . . . . . . . . . . . . . . . . . . . . . 2

2 Forewing length ≥ 3.5 mm. Male: posterior margin of hypandrium with a single median lobe (Fig. 3C) . . . . . . . . *N. stenopterus* (Thornton & Smithers)

- Forewing length ≥ 2.7 mm. Male: posterior margin of hypandrium with a median lobe and two pointed lateral prongs (Fig. 3E) . . . . . *N. caeciliae* sp. n.

## GENERAL DISCUSSION

The present study allows a re-evaluation of Thornton's (1984) phylogenetic analysis of *Austropsocus*, *Zelandopsocus* and *Novopsocus*. This analysis concluded that *Novopsocus* is embedded in the genus *Austropsocus*, being a sister to the New Guinean endemic *A. perforatus* Thornton & Smithers (a situation that questions whether *Novopsocus* should be kept separate from *Austropsocus*, the latter being, in this case, a paraphyletic group). The present study shows that three of the seven autapomorphies mentioned by Thornton (1984) for *Novopsocus* are not valid for the genus. These are: the sexually dimorphic antenna (well-developed only in *N. magnus*), the presence of more than 5 apical setae on the subgenital plate (numbers vary from 4 to 6), and the 3-lobed hypandrium (not true for *N. stenopterus*, the type species). If the latter character is considered a synapomorphy of *N. magnus* and *N. caeciliae*, *N. stenopterus* would be the basal species. The sexually dimorphic antenna would be an autapomorphy of *N. magnus* (however, a tendency to flattening of the first flagellar segment can already be observed in *N. caeciliae*), and its role (possibly in male-male competition) remains to be elucidated. The remaining autapomorphies mentioned by Thornton (1984) are supported by the present study: epiproct with dorsal setose flap; wings long, narrow, straplike; head capsule flattened, vertex sharp-edged; hypandrium median lobe simple. It seems therefore that *Novopsocus*, with its number of species increased from one to three, is monophyletic.

A similar situation was studied by Yoshizawa *et al.* (2005) in the Psocidae genera *Podopterocus* and *Dinopsocus*. They were defined by characters which later were found to be sexually dimorphic or of variable presence in closely related species (i. e. enlarged and flattened hind tibia and thickened first antennal flagellomere). The types of these genera were finally shown to be male and female of the same species. However, contrary to *Novopsocus*, it was not possible to define the genus *Podopterocus* (=*Dinopsocus*) by at least one convincing autapomorphy. The females of some of the sexually dimorphic species lack both of the above mentioned characters and correspond to the females of the closely related genus *Sigmatoneura*, and the two genera were synonymized thereafter (Yoshizawa *et al.,* 2005).

In the case of *Novopsocus* there is little argument against its monophyly but the question whether its position lies within another genus (for example *Austropsocus*, see above) is beyond the scope of the present paper.

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## REFERENCES

LIENHARD, C. 1998. Psocoptères euro-méditerranéens. *Faune de France* 83: XX + 517 pp.

THORNTON, I. W. B. 1981. The systematics, phylogeny and biogeography of the psocopteran family Philotarsidae. *Systematic Entomology* 6: 413-452.

THORNTON, I. W. B. 1984. An unusual psocopteran from New Guinea and its relationships witin the Philotarsidae. *International Journal of Entomology* 26(4): 378-385.

THORNTON, I. W. B. & SMITHERS, C. N. 1977. Philotarsidae (Psocoptera) of New Guinea. *Pacific Insects* 17(4): 419-450.

YOSHIZAWA, K. 2005. Morphology of Psocomorpha (Psocodea: 'Psocoptera'). *Insecta Matsumurana, New Series* 62: 1-44.

YOSHIZAWA, K., LIENHARD, C. & IDRIS, A. B. 2005. On the systematic position of *Podopterocus* Banks and *Dinopsocus* Banks, with a revised diagnosis of the genus *Sigmatoneura* Enderlein (Psocodea: 'Psocoptera': Psocidae). *Revue suisse de Zoologie* 112(4): 831-848.

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# Nine new species of earthworms (Oligochaeta: Megascolecidae) of the Banaue Rice Terraces, Philippines

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**Nine new species of earthworms (Oligochaeta: Megascolecidae) of the Banaue Rice Terraces, Philippines.** - Earthworm specimens collected from the Philippines from Banaue, Ifugao Province belong to 9 new species of pheretimoid earthworms. Two new species of *Pheretima* as characterized by Sims and Easton (1972) were found, including *Pheretima banauensis* sp. n., and *Pheretima cabigati* sp. n. They have spermathecae in VII-VIII and VI-IX, respectively. Four new species of *Pithemera* are *Pithemera duhuani* sp. n., *Pithemera fragumae* sp. n. and *Pithemera ifugaoensis* sp. n. of the *Pi. bicincta* group, having spermathecae in segments V-IX, and *Pithemera triangulata* with three pairs of spermathecae in segment V-VII. Three new species of *Polypheretima* are *Polypheretima fruticosa* sp. n., *Polypheretima perlucidula* sp. n., and *Polypheretima bannaworensis* sp. n. with paired spermathecae in VI, VI-VII, and VI-IX, respectively. Descriptions of the new species are provided.

**Keywords:** Earthworms - *Pheretima* - *Pithemera* - *Polypheretima* - Megascolecidae - Oligochaeta - Philippines - taxonomy.

## INTRODUCTION

The earthworm fauna of the forest and agricultural ecosystems in the municipality of Banaue, Ifugao Province, Philippines is dominated by the *Pheretima*-complex group of genera (Megascolecidae). The genera *Pheretima*, *Pithemera*, *Pleionogaster*, and *Polypheretima* are the most abundant and diverse in the natural forests of this region in the Central Cordillera of Luzon Island, Philippines. *Pheretima* has an intestinal caecum originating in segment XXVII, while *Pithemera* has an intestinal caecum originating in segment XXII, and *Polypheretima* is acaecate. *Pheretima* has male pores within copulatory pouches and nephridia on the spermathecal ducts, but *Pithemera* and the known Philippine *Polypheretima* do not have these features. Also *Pheretima* species generally have some dorsal pigment, but *Pithemera* are usually lighter, and *Polypheretima* are mostly unpigmented. So far, *Pithemera* and *Polypheretima* are generally smaller than *Pheretima*.

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The early reports of earthworm fauna from Banaue rice terraces (Barley & Kleinig, 1964; Barrion & Litsinger, 1997; Joshi *et al.*, 2000) showed that there are 4 species belonging to four genera, *Polypheretima elongata* (Perrier, 1872), *Pontoscolex corethrurus* (Müller, 1856), *Pithemera bicincta* (Perrier, 1875) and *Amynthas corticis* (Kinberg, 1867). They also listed *Pheretima* sp., *Polypheretima* sp., two species of *Pleionogaster* and a large unidentified athecal large earthworm belonging to either *Pheretima* or *Metaphire*. The 4 known species are invasives widespread around the world. This paper provides descriptions of 9 species: 2 of *Pheretima*, 4 of *Pithemera* and 3 of *Polypheretima*. Materials were collected from 16-18 March 2001, in rice terrace regions and soils and litter layers of the nearby forests in the Banaue municipality.

Holotypes and paratypes are deposited in the National Museum of the Philippines Annelid collection (NMA). Paratypes are deposited in the Museum of Natural History of Geneva (MNHG), Korean National Institute of Biological Resources (NIBR).

## DESCRIPTIONS

### FAMILY MEGASCOLECIDAE ROSA, 1891

### Genus ***Pheretima*** Kinberg, 1867

### ***Pheretima banauensis*** sp. n. Figs 1A-B

MATERIAL: Holotype, clitellate (NMA 4176), Philippines, Ifugao province, Banaue (16° 54.86'N, 121° 03.54'E), 1900 m, soil and litter layers, 17 March 2001, Y. Hong & A. Castillo colls. – 2 paratypes, 1 clitellate (NMA 4187), 1 clitellate (MHNG 49295), same data as for holotype. – Other material: 1 clitellate, Banaue (16° 55.39'N, 121° 04.38'E), 1280 m, soil and litter layers, 17 March 2001, Y. Hong & A. Castillo colls.

ETYMOLOGY: The species is named for its type locality.

DIAGNOSIS: Two pairs of spermathecal pores in 6/7, 7/8, 0.21 circumference apart; 0.5 mm openings of copulatory bursae surrounded by 1.5 mm diameter unpigmented epidermis.

DESCRIPTION: Brown dorsal pigment, segmental equators unpigmented. Dimensions 96-124 mm by 3.7-4.0 mm at segment X, 3.8-4.2 mm at XXX, 3.4-3.7 mm at clitellum, segments 86-97. Body cylindrical in cross-section. Setae regularly distributed around segmental equators, numbering 27 at VII, 26 at XX; 7 between male pores; setal formula AA:AB:YZ:ZZ = 3:2:3.5:7 at XIII. Prostomium epilobic with tongue open. Clitellum annular XIV- XVI, setae invisible externally. Genital markings lacking.

First dorsal pore 12/13. Two pairs of spermathecal pores in 6/7, 7/8, lateral, 0.21 circumference apart ventrally. Female pore single in XVI, in 0.5 mm oval. Secondary male pores 0.5 mm diameter paired in XVIII, 0.21 circumference apart ventrally, surrounded by 1.5 mm diameter unpigmented epidermis; distance between male pores 2.5 mm.

Septa 5/6-7/8 thin, 8/9, 9/10 absent, 10/11-13/14 thin. Gizzard large in VIII-X with large longitudinal blood vessels, intestine begins in XVI, small paired lymph glands from XXVII along dorsal vessel; intestinal caeca simple, originating in XXVII,

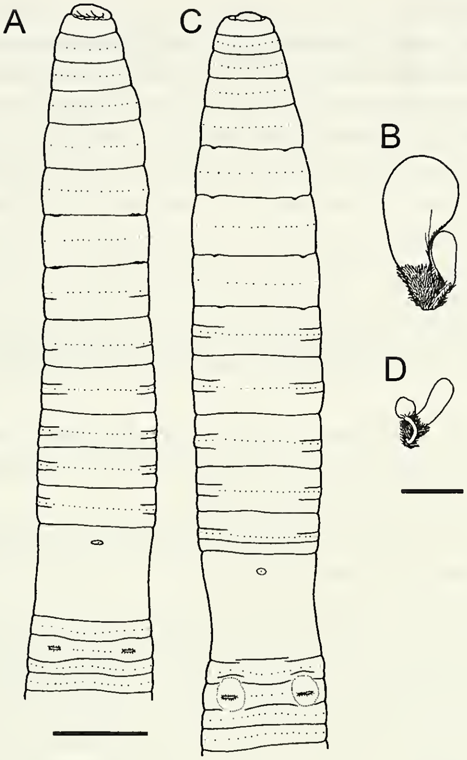

FIG. 1
*Pheretima banauensis* sp. n. (A) Ventral view. (B) Spermathecae and diverticulum. *Pheretima cabigati* sp. n. (C) Ventral view. (D) Spermathecae and diverticulum. Scale bars = 2.5 mm (A, C), 2 mm (B, D).

and extending anteriorly to XXIV or XXIII, each consisting of a finger-shaped sac; typhlosole low simple fold from XXVII; 28 longitudinal blood vessels in intestinal wall. Hearts X-XIII esophageal; IX, left side only, lateral.

Ovaries and funnels in XIII. Paired spermatheca in VII, VIII with nephridia on spermathecal ducts; spermatheca with circular to broad ovate-shaped ampulla, duct stout, short; diverticula bean-shaped, stalk 1/3 covered with nephridia, stalk shorter than ampulla. Male sexual system holandric, testes and funnels in paired sacs in X, XI. Seminal vesicles two pairs in XI, XII. Prostates in XVIII, one small lobe, curved around copulatory pouches, with duct entering center of the copulatory pouches; no stalked glands; penis with slit along medial surface, copulatory pouch opening flanked by anterior and posterior circular pads.

REMARKS: *Pheretima banauensis* sp. n. keys to the *pura*-group in Sims and Easton (1972), which is composed of three species, *P. philippina* (Rosa, 1891), *P. pura* (Rosa, 1898), and *P. tosariana* Cognetti, 1913. *P. philippina*, with three thecal segments, is wrongly placed in this species group, and should be in the *dubia*-group. The species is similar to *P. pura*, but differs from it in being shorter, having fewer setae per segment, and more closely spaced male pores. Also the species has hearts in X-XIII, but *P. pura* has hearts in XI-XIII. Compared to *P. tosariana*, *Pheretima banauensis* sp. n. is more slender, has more segments, fewer setae per segment, a stouter and shorter spermathecal duct, and lacks a side pocket of the spermathecal duct leading to the diverticulum as seen in *P. tosariana*. *P. tosariana* was collected at 2000 m elevation in the Tenger Mountains of eastern Java, Indonesia (Cognetti, 1913).

***Pheretima cabigati*** sp. n. Figs 1C-D

MATERIAL: Holotype, clitellate (NMA 4177), Philippines, Ifugao province, Banaue (16° 58.59'N, 121° 02.89'E), 1600-1665 m, soil and litter layers, 16 March 2001, Y. Hong & A. Castillo colls.

ETYMOLOGY: The species is named after Jimmy Cabigat, a Philippine Department of Agriculture official from Banaue and our host and guide while we were collecting earthworm specimens near Banaue.

DIAGNOSIS: Four pairs of spermathecal pores in 5/6-8/9, 0.22 circumference apart; 0.5 mm openings of copulatory bursae.

DESCRIPTION: Dark brownish dorsal pigment, segmental equators unpigmented. Dimensions 98 mm by 3.7 mm at segment X, 4.0 mm at XXX, 3.4 mm at clitellum, segments 89; body cylindrical in cross-section. Setae regularly distributed around segmental equators, numbering 26 at VII, 33 at XX; 6 between male pores; setal formula AA:AB:YZ:ZZ = 1.5:1:5:7 at XIII. Prostomium epilobic with tongue open. Clitellum annular XIV-XVI; setae invisible externally. Genital markings lacking.

First dorsal pore 12/13. Four pairs of spermathecal pores in 5/6/7/8/9, 0.3 circumference apart ventrally; distance between spermathecal pores 3.4 mm. Female pore single in XIV, on 0.4 mm oval; 0.5 mm openings of copulatory bursae paired in XVIII, 0.22 circumference apart ventrally; distance between male pores 2.4 mm.

Septa 5/6-7/8 thin, 8/9 absent or vestigial, 9/10 absent, 10/11-13/14 thin. Gizzard in VIII-X, intestine begins in XVI, small paired lymph glands from XXX along dorsal vessel; intestinal caeca simple, originating in XXVII, and extending anteriorly about to XXIII, each consisting of a finger-shaped sac, directed ventrally; typhlosole simple fold about 1/4 lumen diameter from XXVII; 26-28 longitudinal vessels in intestinal wall. Hearts X-XIII esophageal; IX, lateral, VIII, VII lateral reduced.

Ovaries and funnels in XIII. Spermathecae in VI-IX, with nephridia on spermathecal ducts and diverticulum stalks; spermatheca with small elongate oval to strawberry-shaped ampulla; diverticula spherical to blunt egg-shaped, shorter than ampulla. Male sexual system holandric, testes and funnels in paired sacs in X, XI. Seminal vesicles two pairs in XI, XII, vas deferens slightly muscular. Prostates in XVIII, occuping in XVI-XIX, duct thick, glands two lobes, with duct entering center of ovate copulatory pouches; no stalked glands. Copulatory pouches openings flanked by anterior and posterior circular cup-shaped pads, penis conical with medial slit pore extending to tip.

REMARKS: *Pheretima cabigati* sp. n. keys to the *darnleiensis*-group in Sims and Easton (1972). The *darnleiensis* group is composed of fifteen species, all of which were synonymized by Sims and Easton (1972) under *P. darnleiensis*. *Pheretima cabigati* sp. n. differs from *P. darnleiensis* in having fewer setae per post-clitellar segment, intestinal origin16 not 15, and in having dark brown dorsal pigment and unpigmented setal lines.

**Pithemera duhuani** sp. n. Figs 2A-B

MATERIAL: Holotype, clitellate (NMA 4178), Philippines, Ifugao province, Banaue (16° 58.59'N, 121° 02.89'E), 1600-1665 m, soil and litter layers, 16 March 2001, Y. Hong & A. Castillo colls. – Other material: same data as for holotype, 1 clitellate and 1 aclitellate specimens.

ETYMOLOGY: The species is named after Andres Duhuan, whose farm is its type locality.

DIAGNOSIS: Five pairs of spermathecal pores in 4/5-8/9. Genital papillae 0.3 mm raised circles, widely paired in XVII with sessile glands.

DESCRIPTION: Brown dorsal pigment, clitellum with pink color. Dimensions 53-59 mm by 2.5-2.7 mm at segment X, 2.4-2.5 mm at XXX, 2.0-2.3 mm at clitellum, segments 87-90. Body cylindrical in cross-section. Setae regularly distributed around segmental equators, numbering 40 at VII, 39 at XX; 6-7 between male pores; setal formula AA:AB:YZ:ZZ = 3:1.5:2:4 at XIII. Prostomium epilobic with tongue open. Clitellum annular XIV-1/2XVI; setae visible externally. Genital papillae 0.3 mm raised circles, widely paired in XVII, XIX (right side only) or XVIII only.

First dorsal pore 4/5. Five pairs of spermathecal pores in 4/5-8/9, very small, inconspicuous, 0.14-0.15 circumference apart ventrally; distance between spermathecal pores pores 1.2 mm. Female pores paired in XIV, in small circular area. Male pores superficial, slightly protuberant white spot on center of 0.4 mm round porophore in lateral margin of ventrum in XVIII, some furrows around porophores, 0.32-0.37 circumference apart ventrally; distance between male pores 2.3 mm.

Septa 5/6-7/8 thin, 8/9 absent, 9/10-13/14 thin. Gizzard usual in VIII-IX, intestine begins in XV; intestinal caeca simple, originating in XXII, and extending anteriorly about to XXI (or XXII), each consisting of a small finger-shaped sac; typhlosole simple fold about 1/6 lumen diameter from XXII. Hearts X-XII esophageal; IX lateral.

Ovaries and funnels in XIII. Spermatheca in V-IX; no nephridia on spermathecal ducts; spermatheca with small ampulla, duct medium thickness, shorter than ampulla; diverticulum egg-shaped, shorter than ampulla. Male sexual system holandric, testes and funnels in single large sacs in X, XI. Seminal vesicles two pairs in XI, XII. Prostates in XVI-XIX without copulatory pouches, ectal half of duct muscular, spindle-shaped. Sessile genital marking glands paired in XVII and right side XIX.

REMARKS: *Pithemera duhuani* sp. n. keys to the *bicincta*-group in Sims and Easton (1972), which is composed of two species, *Pi. bicincta* (Perrier, 1875) and *Pi. violacea* (Beddard, 1895) with spermathecal pores in 4/5-8/9. However, others have stated that *Pi. violacea* is a junior synonym of *Pi. bicincta* (Michaelsen, 1910; Ohfuchi, 1957; Shen & Tsai, 2002). James *et al.* (2004) recorded 2 species of *Pithemera* from

Mt. Arayat, Luzon Island, *Pi. rotunda* and *Pi. philippinensis*. These two species also key to the *bicincta* group. The spermathecae are not greatly different between *Pithemera duhuani* sp. n. and *Pi. bicincta*, but the size, numbers, and location of genital papillae are different in *Pi. bicincta* and *Pithemera lanyuensis* Shen & Tsai, 2002. *Pithemera duhuani* sp. n. has raised circles widely paired in XVII and XIX, but *Pi. bicincta* has a pair of pads covering segments XVIII to XIX, and *Pi. lanyuensis* has round paired genital papillae. The present new species has fewer setae than most of its group members.

### ***Pithemera fragumae*** sp. n. Figs 2C-D

MATERIAL: Holotype, clitellate (NMA 4179), Philippines, Ifugao province, Banaue (16° 54.97'N, 126° 03.60'E), 1070 m, soil and litter layers, 16 March 2001, Y. Hong & A. Castillo colls. – 3 paratypes: 1 clitellate (NMA 4188), 1 clitellate (MHNG 49296), 1 clitellate (NIBR). Same data as for holotype. – Other material: same data as for holotype, 11 clitellate specimens.

ETYMOLOGY: The epithet *fragumae*, Latin for strawberry, refers to the conspicuous spermathecal ampulla in this species.

DIAGNOSIS: Five pairs of spermathecal pores in 4/5-8/9. Genital papillae, circular, paired in XVII and pre and postsetal next to male pores in XVIII within male porophore.

DESCRIPTION: Worm unpigmented. Dimensions 53-101 mm by 2.8 mm at segment X, 2.7 mm at XXX, 2.3 mm at clitellum, segments 122-129. Body cylindrical in cross-section. Setae regularly distributed around segmental equators, numbering 66 at VII, 69 at XX; 10-15 between male pores; setal formula AA:AB:YZ:ZZ = 2:1:1:2 at XIII. Prostomium epilobic with tongue open. Clitellum annular XIV-1/2XVI; setae invisible externally. Genital papillae, circular, paired in XVII, and pre and postsetal next to male pores in XVIII within male porophore.

First dorsal pore 12/13. Five pairs of spermathecal pores in 4/5-8/9, inconspicuous, 0.17 circumference apart ventrally; distance between spermathecal pores 1.5 mm. Female pores paired in XIV, on 0.5 mm oval. Male pores at lateral margin of ventrum, 0.24 circumference apart ventrally; distance between male pores 1.8 mm.

Septa 5/6-6/7 thin, 7/8 thick, 8/9, 9/10 absent, 10/11-13/14 thick. Gizzard in VIII-X, intestine begins in XV; intestinal caeca simple, originating in XXII, each consisting of a small triangle-shaped sac; typhlosole simple fold about 1/3 lumen diameter from XXII. Hearts XI-XII esophageal, IX lateral.

Ovaries and funnels in XIII. Spermathecae in V-IX; no nephridia on spermathecal ducts; spermatheca with small strawberry-shaped ampulla, duct short; diverticulum sausage-shaped, shorter than ampulla. Male sexual system holandric, testes and funnels in dorsally joined sacs in X, XI. Seminal vesicles two pairs in XI, XII. Prostates in XVI-XIX without copulatory pouches, 6-7 small lobes, duct long, slender with short ectal muscular portion.

REMARKS: *Pithemera fragumae* sp. n. also keys to the *bicincta*-group. The new species without septum 9/10 is thereby unique among known *bicincta* group species. *Pithemera fragumae* sp. n. is similar to *Pi. rotunda* James and Hong, 2004, with respect to spermatheca and diverticulum shape, but easily is distinguished by the genital papillae. *Pithemera fragumae* sp. n. has circular paired genital papillae in XVII, and paired pre- and postsetal genital papillae next to the male pores within the male porophore on XVIII, but *Pi. rotunda* has three circular papillae in each of segments XVIII to XXII. *Pithemera fragumae* sp. n. has hearts in XI-XII, but *Pi. rotunda* has in X-XII. *Pi. rotunda* also has fewer setae in VII, XX, and between male pores, than *Pithemera fragumae* sp. n.

### ***Pithemera ifugaoensis*** sp. n. Figs 2E-F

MATERIAL: Holotype, clitellate (NMA 4180), Philippines, Ifugao province, Banaue (16° 54.97'N, 126° 03.60'E), 1070 m, soil and litter layers, 16 March 2001, Y. Hong & A. Castillo colls. – 1 paratype, 1 clitellate (NMA 4189), same data as for holotype. – Other material: same data as for holotype, 1 clitellate, 5 semiclitellate specimens.

ETYMOLOGY: The species is named for its type locality.

DIAGNOSIS: Five pairs of spermathecal pores in 4/5-8/9. Genital markings, paired 0.4 mm raised circles on 19/20, 0.7 mm circles paired in XX with sessile genital marking glands.

DESCRIPTION: Light brown dorsal and ventral pigment. Dimensions 38-65 mm by 3.0-4.7 mm at segment X, 3.3-5.0 mm at XXX, 2.8-4.5 mm at clitellum, segments 59-101. Body cylindrical in cross-section. Setae regularly distributed around segmental equators, numbering 41 at VII, 44 at XX; 8-10 between male pores; setal formula AA:AB:YZ:ZZ = 2:1.5:1:1.5 at XIII. Prostomium epilobic with tongue open. Clitellum annular XIV-XVI; setae visible externally. Genital markings paired 0.4 mm raised circles on 19/20, 0.7 mm circles paired in XX, medio-ventral.

First dorsal pore 12/13. Five pairs of spermathecal pores in 4/5-8/9, on small, conspicuous protuberances, 0.14-0.21 circumference apart ventrally; distance between spermathecal pores 2.0 mm. Female pores paired in XIV, on 0.4 mm circle. Male pores slightly protuberant white spots at center of 0.5 mm round porophores, lateral in XVIII, 0.15-0.24 circumference apart ventrally; distance between male pores 2.1 mm.

Septa 5/6-7/8 thin, 8/9 absent, 9/10-13/14 thin. Gizzard in VIII-IX, intestine begins in XV; intestinal caeca simple, originating in XXII, and extending anteriorly about to XXI (or XXII), each consisting of a small finger-shaped sac; typhlosole simple fold about 1/6 lumen diameter from XXII. Hearts X-XII esophageal; IX lateral.

Ovaries and funnels in XIII. Spermatheca in V-IX; no nephridia on spermathecal ducts; spermatheca with pointed ovate-shaped ampulla, duct thick, non muscular, shorter than ampulla; diverticulum slender, small seed-shaped pouch, as long as ampulla. Male sexual system holandric, testes and funnels in large sac in each of X, XI. Seminal vesicles two pairs in XI, XII. Prostates two main lobes without copulatory pouches, each divided into 4-7 lobes in XVI- XIX, ectal half of duct thick, muscular, spindle-shaped; ental half of duct thin. Genital marking glands diffuse, sessile, paired in XIX, XX.

REMARKS: This species also keys to the *bicincta*-group, but can be distinguished by its genital markings, genital pore spacings, and genital marking glands. *Pithemera ifugaoensis* sp. n. appears to be related to *Pi. lanyuensis* with round male pore region and genital papillae. *Pithemera ifugaoensis* sp. n. has genital papillae as paired raised circles on 19/20, and larger circles paired in XX, closer to the mid-ventral line, but *Pi. lanyuensis* has paired presetal genital papillae in XX. The spermathecal pores of *Pithemera ifugaoensis* sp. n. are 0.14-0.21 circumference apart, but those of *Pi. lanyuensis* are 0.25-0.33 circumference apart. *Pithemera ifugaoensis* sp. n. also is diagnosed by the diffuse sessile genital marking glands in XIX, XX, but *Pi. lanyuensis* has solid pad-like genital marking glands in XX.

### ***Pithemera triangulata*** sp. n. Figs 2G-H

MATERIAL: Holotype, clitellate (NMA 4181), Philippines, Ifugao province, Banaue (16° 54.86'N, 121° 03.54'E), 1900 m, soil and litter layers, 17 March 2001, Y. Hong & A. Castillo colls. – 3 paratypes, 1 clitellate (NMA 4190), 1 clitellate (MHNG 49297), 1 clitellate (NIBR), same data as for holotype. – Other material: Banaue (16° 58.59'N, 121° 02.89'E), 1600-1665 m, soil and litter layers, 5 clitellate, 2 semiclitellate, 17 March 2001, Y. Hong & A. Castillo colls. – Same data as for holotype, 5 clitellate specimens.

ETYMOLOGY: The species is named *triangulata*, referring to the shape of the intestinal caecum.

DIAGNOSIS: Three pairs of spermathecal pores in 4/5-6/7. Male pores near inner edges of 0.8 mm oval pads extending to 17/18 and 18/19 within thickened white area. Genital papillae lacking.

DESCRIPTION: Light brown dorsal pigment. Dimensions 47-76 mm by 2.5 mm at segment X, 2.7 mm at XXX, 2.5 mm at clitellum, segments 86-99. Body cylindrical in cross-section. Setae regularly distributed around segmental equators, numbering 41 at VII, 44 at XX; 1-3 between male pores; setal formula AA:AB:YZ:ZZ = 2:1:1.5:4 at XIII. Prostomium epilobic with tongue open. Clitellum annular XIV-1/2XVI; XVI setae visible externally. Genital markings lacking.

First dorsal pore 12/13. Three pairs of spermathecal pores in 4/5-6/7, inconspicuous, 0.06 circumference apart ventrally; distance between male pores 0.5 mm. Female pores paired in XIV, in 0.4 mm circle. Male pores near inner edges of 0.8 mm oval pads extending to 17/18 and 18/19 within thickened white area, 0.1 circumference apart ventrally; distance between male pores 0.8 mm.

Septa 5/6-7/8 thin, 8/9 absent, 9/10 thin, 10/11-13/14 thin. Gizzard in VIII-IX, intestine begins in XV, lymph glands along dorsal vessel from about XX; intestinal caeca simple, originating in XXII, and extending antero-ventrally, each consisting of a small triangle-shaped sac; typhlosole simple fold about 1/4 lumen diameter from XXII. Hearts X-XII esophageal; VII-IX lateral; hearts X, XI within testes sacs.

Ovaries and funnels in XIII. Spermathecae in V-VII; no nephridia on spermathecal ducts; spermatheca with large ampulla, duct medium thick, not muscular, as long as ampulla; diverticulum chamber digitate, slender, as long as spermathecal duct, stalks very short. Male sexual system holandric, testes and funnels in paired large sacs in X, XI. Seminal vesicles two pairs in XI, XII. Prostates 3-4 lobes in XVIII without copulatory pouches, ectal half of duct muscular, fusiform, ental half of duct thin; diffuse glandular patches on body wall 17/18-18/19.

REMARKS: In Sims and Easton (1972) *Pithemera triangulata* sp. n. keys to the *bicincta*-group, because species with first spermathecal pores in 4/5 are assigned to the

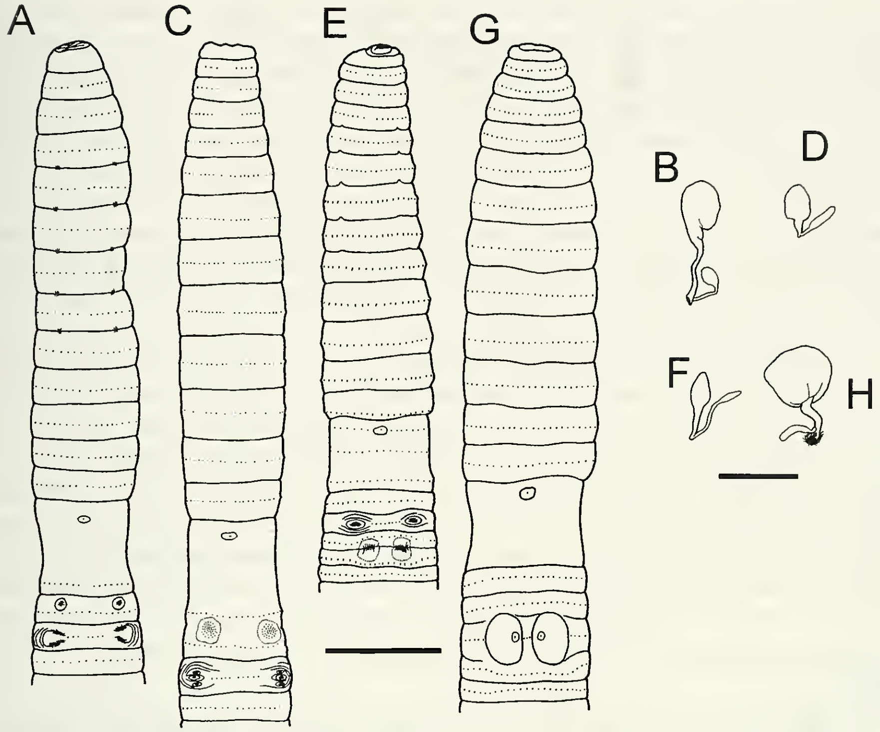

FIG. 2

*Pithemera duhuani* sp. n. (A) Ventral view. (B) Spermathecae and diverticulum. *Pithemera fragumae* sp. n. (C) Ventral view. (D) Spermathecae and diverticulum. *Pithemera ifugaoensis* sp. n. (E) ventral view. (F) Spermathecae and diverticulum. *Pithemera triangulata* sp. n. (G) Ventral view. (H) Spermathecae and diverticulum. Scale bars = 2.5 mm (A, C, E, G), 2 mm (B, D, F, H).

*bicincta* group regardless of the number of spermathecae. This species has three pairs of spermathecal pores in 4/5-6/7. *Pithemera triangulata* sp. n. differs from other *Pithemera* in having the ampulla as long as the duct, and the duct as long as the diverticulum, 3 pairs of spermathecae, and no genital papillae. It has a male porophore like the pads on discs found in some mainland Asian *Amynthas* species.

### ***Polypheretima fruticosa*** sp. n. Figs 3A-B

MATERIAL: Holotype, clitellate (NMA 4182), Philippines, Ifugao province, Banaue (16° 56.98'N, 121° 03.41'E), 1400 m, soil and litter layers, 18 March 2001, Y. Hong & A. Castillo colls. – 3 paratypes, 1 clitellate (NMA 4191), 1 clitellate (MHNG 49298), 1 clitellate (NIBR), same data as for holotype. – Other material: same data as for holotype, 5 clitellate specimens.

ETYMOLOGY: The name *fruticosa* is Latin for bushy, here referring to the shape of the seminal vesicles.

DIAGNOSIS: One pair of spermathecal pores in 5/6. Small, round genital papillae paired in XVIII or XIX on lateral margin.

DESCRIPTION: Brown dorsal pigment. Dimensions 39-61 mm by 2.3 mm at segment X, 2.0 mm at XXX, 2.0 mm at clitellum, segments 105-107. Body cylindrical in cross-section. Setae regularly distributed around segmental equators, numbering 44 at VII, 41 at XX; 9 between male pores; setal formula AA:AB = 1.5:1.0 at YZ:ZZ = no gap at XIII. Prostomium epilobic with tongue open. Clitellum annular XIV-XVI. Genital papillae paired in XVIII or XIX on lateral margin, small, round, dark.

First dorsal pore 11/12. One pair of spermathecal pores in 5/6 at lateral margin, inconspicuous, 0.25 circumference apart ventrally; distance between spermathecal pores 1.8 mm. Female pore single in XIV, in 0.4 mm circle. Male pores in XVIII on 0.5 mm round porophores in lateral margin, slightly protuberant, 0.27 circumference apart ventrally; distance between male pores 1.7 mm.

Septa 5/6-7/8 thick, 8/9 absent, 9/10 thin, 10/11 thick, 11/12-13/14 thin. Gizzard in VIII-IX, intestine begins in XV; intestinal caeca absent; typhlosole large fold about 1/2 lumen diameter from about XX. Hearts X-XII esophageal; IX lateral.

Ovaries and funnels in XIII. Spermathecae in VI; no nephridia on spermathecal ducts; spermatheca with small ampulla, duct shorter than ampulla, not muscular; diverticulum slender, longer than ampulla. Male sexual system holandric, testes and funnels in large sac in X, XI; sacs not including hearts. Seminal vesicles two pairs in XI, XII, those of XII consist of solid ventral, bushy dorsal sections. Prostates in XVIII-XXII without copulatory pouches, duct gradually thickened ectally, becoming muscular; vas deferens join prostatic duct about 1/3 of the duct from gland to body wall.

REMARKS: The present species appears to be closely related to *Po. voeltzkowi* (Michaelsen, 1907), but is separated by the genital papillae. *Polypheretima voeltzkowi* has simple, paired, postsetal papillae on XVII, and pre- and postsetal papillae medial to male pores on XVIII. However, *Polypheretima fruticosa* sp. n. has only one pair of genital papillae on XVIII or XIX, and they are of a different shape. Also the species is similar to *Po. fida* (Michaelsen, 1913), but differs by the lower number of spermathecal pores: *Po. fida* has two or three intersegmental spermathecal pores in 4/5, 5/6, or 4/5-6/7. *Polypheretima fruticosa* sp. n. only has one pair of intersegmental spermathecal pores in 5/6. Easton (1979) distinguished different groups of *Polypheretima* species by the location of spermathecal pores, intrasegmental or intersegmental. The spermathecal pores of *Po. fida* and *Polypheretima fruticosa* sp. n. are intersegmental, whereas those of *Po. voeltzkowi* are intrasegmental.

### ***Polypheretima perlucidula*** sp. n. Figs 3C-D

MATERIAL: Holotype, clitellate (NMA 4183), Philippines, Ifugao province, Banaue (16° 56.98'N, 121° 03.41'E), 1400 m, soil and litter layers, 18 March 2001, Y. Hong & A. Castillo colls. – 3 paratypes, 1 clitellate (NMA 4192), 1 clitellate (MHNG 49299), 1 clitellate (NIBR), same data as for holotype. – Other material, same data as for holotype, 10 clitellate, 7 aclitellate specimens.

ETYMOLOGY: The epithet *perlucidula* is Latin for transparent, referring to the transparent spermathecal diverticula.

DIAGNOSIS: Two pairs of spermathecal pores in 5/6, 6/7. Genital markings lacking.

Description: Worm unpigmented. Dimensions 38-56 mm by 1.5 mm at segment X, 1.3 mm at XXX, 1.5 mm at clitellum, segments 117-131. Body cylindrical in cross-section. Setae regularly distributed around segmental equators, numbering 50 at VII, 23 at XX; 12 between male pores; setal formula AA:AB:YZ:ZZ = 1.5:1:1:1.5 at XIII. Prostomium epilobic with tongue open. Clitellum annular XIV-XVI. Genital markings absent.

First dorsal pore 12/13. Two pairs of spermathecal pores in 5/6, 6/7, at lateral margin, inconspicuous, 0.28 circumference apart ventrally; distance between spermathecal pores 1.3 mm. Female pore single in XIV, on 0.2 mm circular area. Male pores on 0.3 mm round porophores at lateral margins in XVIII, slightly protuberant, 0.32 circumference apart ventrally; distance between male pores 1.3 mm.

Septa 5/6-7/8 thick, 8/9, 9/10-13/14 thin. Gizzard in VIII, intestine begins in XV; intestinal caeca absent; typhlosole large fold almost equal to lumen diameter from about XXII. Hearts X-XII esophageal; IX lateral.

Ovaries and funnels in XIII. Spermathecae in VI, VII; no nephridia on spermathecal ducts; spermatheca with very small ampulla, duct thick, longer than ampulla, not muscular; diverticulum club-shaped, shorter than ampulla, transparent, without visible contents. Male sexual system holandric, testes and funnels in X, XI, within dorsally joined sacs. Seminal vesicles two pairs in XI, XII, reduced. Prostates in XVII-XX without copulatory pouches, duct thick, muscular, cylindrical.

Remarks: *Polypheretima perlucidula* sp. n. keys to the *bifaria*-species group in Easton (1979). Among them, the new species is similar to *Polypheretima sempolensis* (Easton, 1979) with spermathecal pores in furrows 5/6 and 6/7. *Po. sempolensis* has genital markings in XVII and XIX, but the present species has no post-clitellar genital markings. The genital markings of *Po. sempolensis* are large, encroaching on the setal lines and the intersegmental lines. The new species spermathecal pores are 0.28 circumference apart, but those of *Po. sempolensis* are 0.33 body circumference apart. *Polypheretima perlucidula* sp. n. has fewer setae than *Po. sempolensis* (50 vs. 60-66 on VII, 23 vs. 44-48 on XX), and *Po. sempolensis* (100-107 segments) has fewer segments than *Polypheretima perlucidula* sp. n.

### *Polypheretima bannaworensis* sp. n. Figs 3E-F

Material: Holotype, clitellate (NMA 4185), Philippines, Ifugao province, Banaue (16° 54.86'N, 121° 03.54'E), 1900 m, soil and litter layers, 17 March 2001, Y. Hong & A. Castillo colls. – 3 paratypes: 1 clitellate (NMA 4193), 1 clitellate (MHNG 49300), 1 clitellate (NIBR), same data as for holotype. – 7 clitellate specimens.

Etymology: The species is named for its type locality. Bannawor is the original name for Banaue in the language of the local people.

Diagnosis: Four pairs of spermathecal pores in 5/6-8/9, male pores on 0.5 mm round porophores in lateral XVIII, surrounded by circular furrows.

Description: Brownish dorsal pigment. Dimensions 51-74 mm by 2.7-3.7 mm at segment X, 3.1-3.3 mm at XXX, 2.6-3.2mm at clitellum, segments 67-95. Body cylindrical in cross-section. Setae regularly distributed around segmental equators, numbering 39 at VII, 46 at XX; 6-7 between male pores; setal formula AA:AB:YZ:ZZ

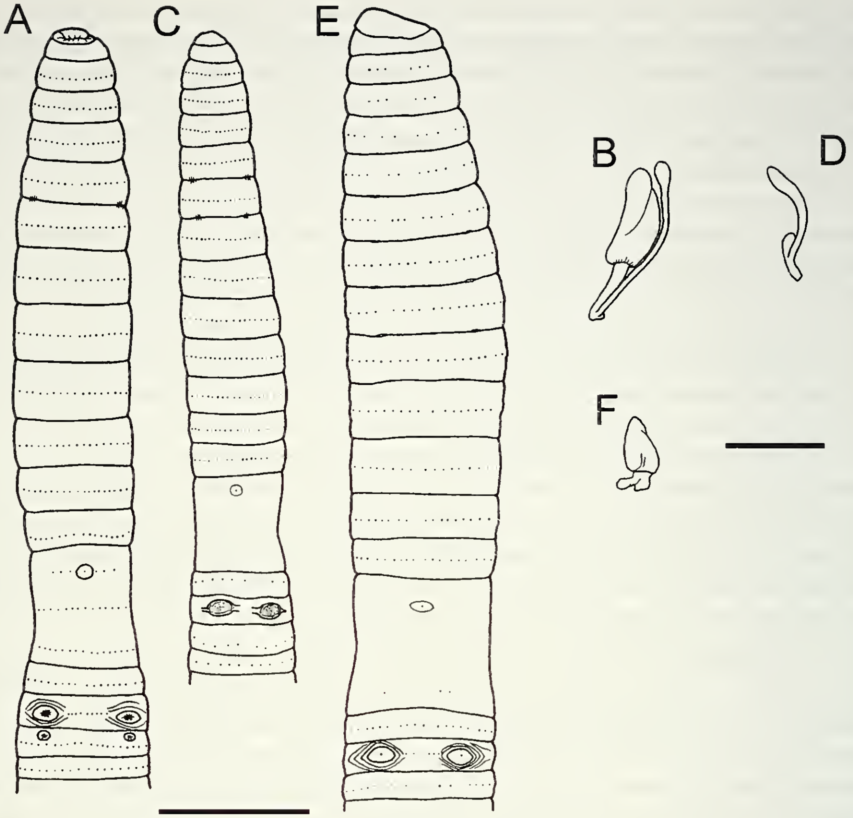

FIG. 3

*Polypheretima fruticosa* sp. n. (A) Ventral view. (B) Spermathecae and diverticulum. *Polypheretima perlucidula* sp. n. (C) Ventral view. (D) Spermathecae and diverticulum. *Polypheretima bannaworensis* sp. n. (E) Ventral view. (F) Spermathecae and diverticulum. Scale bars = 2.5 mm (A, C, E), 2 mm (B, D, F).

= 2:2:2:3 at XIII. Prostomium epilobic with tongue open. Clitellum annular XIV-XVI; setae in XVI visible externally.

First dorsal pore 11/12. Four pairs of spermathecal pores in 5/6-8/9, 0.22-0.25 circumference apart ventrally; distance between spermathecal pores 2.4 mm. Female pore single in XIV, on 0.3 mm oval. Male pores white spots on 0.5 mm round porophores in lateral XVIII, surrounded by circular furrows, slightly protuberant, 0.20-0.24 circumference apart ventrally; distance between spermathecal pores 2.0 mm. Genital markings lacking.

Septa 5/6-8/9 thick, 9/10-13/14 thin. Gizzard in VIII, intestine begins in XV, small lymph glands with dorsal vessel; intestinal caeca absent; typhlosole very low from about XXII. Hearts X-XII esophageal; IX lateral.

Ovaries and funnels in XIII. Spermathecae in VI-IX; no nephridia on spermathecal ducts; spermatheca with small strawberry-shaped ampulla, duct thick, shorter than ampulla; ovate diverticulum short, as long as duct. Male sexual system holandric, testes and funnels in large sac in X, XI. Seminal vesicles two pairs in XI, XII. Prostates in XVI- XX without copulatory pouches, duct thin, short.

REMARKS: The species shares the spermathecal pores in 5/6-8/9, and large male porophores with *Po. bifaria* (Michaelsen, 1923) and *Po. monticola* (Beddard, 1912). Michaelsen recorded two subspecies of *bifaria*, one with single and the other with paired genital markings (Michaelsen, 1938; Easton, 1979). *Po. bifaria* has numerous spermathecal pores in paired batteries in furrows 5/6/7/8 and usually in 8/9, and 1-3 spermathecae in paired batteries VI-VIII and usually in IX. It has paired pre or postsetal genital markings on V-VIII, and occasionally IX pre- and postsetal on XVIII, presetal on XVII and XIX, and occasionally XX (Easton, 1979), but the present species has no genital markings at all and more importantly is bithecal rather than polythecal. The new species spermathecal pores are 0.20-0.24 circumference apart, but those of *Po. bifaria* are 0.30 circumference apart. The new species is longer than *Po. bifaria* (length 27-49 mm), but has fewer segments than *Po. bifaria* (99-110 segments). The *Po. bifaria* species were collected from New Guinea. The new species has the same spermathecal locations as *Po. monticola*, which differs by having large circular or oval, presetal, paired genital markings on IX, XVII, and XIX-XX (Easton, 1979). The *Po. monticola* specimens were recorded from Mt. Pulag, Luzon, Philippines, which is south of Banuae in the same mountain range.

## ACKNOWLEDGEMENTS

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## REFERENCES

BAIRD, W. 1869. Description of a new species of earthworm (*Megascolex diffringens*) found in north Wales. *Proceedings of the Zoological Society of London* 1869: 40-43.

BARLEY, K. P. & KLEINIG, C. R. 1964. The occupation of newly irrigated lands by earthworms. *Australasian Journal of Science* 23: 1-7.

BARRION, A. T. & LITSINGER, J. A. 1997. *Dichogaster* nr. *curgensis* Michaelsen (Annelida: Octochaetidae): *An earthworm pest of terraced rice in the Philippine Cordilleras, Crop Protection* 16(1): 89-93.

BEDDARD, F. E. 1895. A monograph of the order Oligochaeta. *Oxford: Clarendon Press*, i-xii + 769 pp.

BEDDARD, F. E. 1912. The Oligochaeta terricolae of the Philippines part I. The genus *Pheretima*. *Philippines Journal of Science. Manila, ser.* D 7: 179-203.

COGNETTI DE MARTIIS, L. 1913. Oligochetes (de Ceram et de Waigeu). *Bijdragen tot de Dierkunde* 19: 37-41.

COGNETTI DE MARTIIS, L. 1922. Descrizione di tre nuovi megascolecini. *Bollettino dei Musei di Zoologia et Anatomia comparata della Reale Universita di Torino* 37(744): 1-6.

EASTON, E. G. 1979. Acaecate earthworms of the *Pheretima* group (Megascolecidae: Oligochaeta): *Archipheretima*, *Metapheretima*, *Planapheretima*, *Pleionogaster* and *Polypheretima*. *Bulletin of the British Museum of Natural History* (*Zoology*) 35(1): 1-126.

JAMES, S. W. 2004. New species of *Amynthas, Pheretima, Pleionogaster* (Oligochaeta: Megascolecidae) of the Mt. Kitanglad Range, Mindanao Island, Philippines. *Raffles Bulletin of Zoology, Singapore* 52(2): 289-313.

JAMES, S. W., HONG, Y. & KIM, T. H. 2004. New earthworms of *Pheretima* and *Pithemera* (Oligochaeta: Megascolecidae) from Mt. Arayat, Luzon Island, Philippines. *Revue suisse de Zoologie* 111(1): 3-10.

JOSHI, R. C., MATCHOC, O. R. O., CABIGAT, J. C. & JAMES, S. W. 2000. Survey of earthworms in the Ifugao rice terraces, Philippines. *Journal of Environmental Science and Management* 2(2): 1-12.

MICHAELSEN, W. 1891. Oligochäten des naturhistorischen Museums in Hamburg. *Jahrbuch der Hamburgischen Wissenschaftlichen Anstalten, Hamburg* 8(2): 1-42.

MICHAELSEN, W. 1896. Oligochäten Kükenthal – Ergebnisse einer zool. Forschungsreise in den Molukken und in Borneo. *Abhandlungen herausgegeben von der Senckenbergischen Naturforschenden Gesellschaft, Frankfurt* 23: 192-243.

MICHAELSEN, W. 1907. Oligochäten von Madagaskar, den Comoren und anderen Inseln des westlichen Indischen Ozeans. *Reise in Ostafrika in den Jahren 1903-1905. Wissenschaftliche Ergebnisse / ausgeführt von Alfred Voeltzkow.* Bd. 2, Heft 2: 41-50.

MICHAELSEN, W. 1910. Die Oligochäten Fauna der Vorderindisch-Ceylonischen Region. Abhandlungen aus dem Gebiete der. *Naturwissenschaften herausgegeben vom Naturwissenschaftlichen Verein in Hamburg* 19: 1-108.

MICHAELSEN, W. 1913. Die Oligochäten von Neu-Caledonien und den benachbarten Inselgruppen. *Nova Caledonia, Weisbaden* 1: 173-280.

MICHAELSEN, W. 1923. Oligochäten von Holländisch-Neuguinea. *Nova Guinae Contributions to Zoology, Leiden, s'Gravenhage* 14: 18-27.

MICHAELSEN, W. 1938. Einige interssante Pheretimen von Holländisch-Neuguinea. *Zoologischer Anzeiger, Leipzig* 121: 161-181.

OHFUCHI, S. 1957. On a collection of the terrestrial Oligochaeta obtained from the various localities in Riu-kiu Islands, together with the consideration of their geographical distribution (Part II). *Journal of Agricultural Science, Tokyo* 3: 243-261.

PERRIER, E. 1872. Recherches pour servir à l'histoire des Lombricins terrestres. *Nouvelles Archives du Muséum d'Histoire Naturelle, Paris* 8: 5-198.

PERRIER, E. 1875. Sur les vers de terre des iles Philippines et de la Cochinchine. *Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences, Paris* 81: 1043-1046.

ROSA, D. 1891. Die exotischen Terricolen des k.k.naturhistorischen Hofmuseums. *Annalen des K. K. Naturhistorischen Hofmuseums, Wien* 6: 379-406.

ROSA, D. 1898. On some new earthworms in the British Museum. *The Annals and Magazine of Natural History, including Zoology, Botany and Geology, London*, ser. 7 2: 276-290.

SHEN, H. P. & TSAI, C. F. 2002. A new earthworm of the genus *Pithemera* (Oligochaeta: Megascolecidae) from the Lanyu Island (Botel Tobago). *Journal of the National Taiwan Museum* 55(2): 1-7.

SIMS, R. W. & EASTON, E. G. 1972. A numerical revision of the earthworm genus *Pheretima* auct. (Megascolecidae: Oligochaeta) with the recognition of new genera and an appendix on the earthworms collected by the Royal Society North Borneo Expedition. *The Biological Journal of the Linnean Society, London* 4: 169-268.

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# New species of *Pholcus* and *Spermophora* (Pholcidae, Araneae) from Iran and Afghanistan, with notes on mating mechanisms

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**New species of *Pholcus* and *Spermophora* (Pholcidae, Araneae) from Iran and Afghanistan, with notes on mating mechanisms.** - The anchoring devices employed by some Pholcinae during mating are explained. 15 *Pholcus* and 3 *Spermophora* species are currently known from Iran and Afghanistan. These include the following new species: *Pholcus afghanus* sp. n., *P. arsacius* sp. n., *P. caspius* sp. n., *P. cophenius* sp. n., *P. djelalabad* sp. n., *P. elymaeus* sp. n., *P. hystaspus* sp. n., *P. kandahar* sp. n., *P. parthicus* sp. n. and *P. velitchkovskyi* Kulczynski. Iranian *Spermophora* are *S. senoculata* Dugès, *S. senoculatoides* sp. n. and *S. persica* sp. n.

**Keywords**: Arachnida - Pholcinae - taxonomy.

## INTRODUCTION

Following the description of new *Pholcus* species from Iran (Senglet, 1974), additional material has become available during two collecting trips to Iran in 1974 and 1975. This is here described together with four new *Pholcus* species from Afghanistan and two new *Spermophora* from Iran. Part of this material (illustrated in Figs 1-56) was already studied in the seventies, but remained unpublished.

## MATERIAL AND METHODS

Except the type specimen of *Pholcus velitchkovskyi*, all spider material was collected by myself. Measurements are in millimetres. The dorsal length of the prosoma does not include the clypeus. Vulvae were examined on an excavated microscopic slide, in Canada balsam or in lactic acid. Holotypes and paratypes are deposited in the Natural History Museum of Geneva; the other material remains in my collection.

## TAXONOMY AND FAUNISTIC DATA

### Genus *Pholcus* Walckenaer, 1805

### *Pholcus velitchkovskyi* Kulczynski, 1913 — Figs 1-9

*Pholcus velitchkovskyi* Kulczynski, 1913: 17, pl. 1, figs 1-2, 5 (description of ♂ and ♀).

Material examined: Holotype, ♂, RUSSIA, Walouyki district, (no locality given), (Instytut Zoologii, Polska Akademia Nauk (Kulczynski coll.), Warsaw). – 2 ♂, 2 ♀, IRAN,

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Caspian Sea, Mazanderan, Near Dasht, 37°19'N 56°04'E, 27/7/1974. – 10 ♀, IRAN, East of Tang-e-Rah, 37°20'N 56°01'E, 16/7/1975. All non-type specimens were collected from small shelters in loose stones heap.

DESCRIPTION: Prosoma marking a dark median dorsal band running over entire carapace (including clypeus and eye tubercle), indistinctly developed between eye tubercle and fovea. Opisthosoma elongated. Male (from near Dasht): Total length 4.15. Prosoma 1.00 long, 1.14 wide. Eye sizes and interdistances: AME 0.07, PME 0.11; PME-PME 0.14, PME-ALE 0.01. Ocular group 0.50 wide. Chelicera bearing a small, retrolaterally directed basal tooth close to the retrolateral-basal apophysis and a prolateral-apical apophysis with two gripping teeth. Pedipalp (Figs 1-5): Trochanter apophysis short; longitudinal groove on procursus elbow; prolateral-apical margin of procursus extended into a lobe. Bulbal apophyses (Figs 6-7): Width of the short uncus corresponding to 2/3 of its length. Appendix undivided, its base wide apart from base of uncus and embolus, its superior part widely expanded, tapering and retrolaterally directed.

Female (from near Dasht): Total length 4.50. Prosoma 1.04 long, 1.04 wide. Eye sizes and interdistances: AME 0.07, PME 0.11; PME-PME 0.20, PME-ALE 0.01. Ocular group 0.53 wide. Genital plate triangular, with a short, ventrally directed tubercle apophysis. Vulva (Figs 8-9): Two poorly sclerotized anterior folds; superior one not reaching centre of ventral wall, inferior one closer to opening of uterus internus, both merging on the sides. Dorsal sclerite narrow. Pore-plates oblique, slightly elongated; posterior margins of anchoring pockets twisted.

REMARKS: The male pedipalp shows that *P. velitchkovskyi* is closely related to *P. opilionoides*. Kulczynski's type material was examined and compared with the new material in the seventies; the type specimen is noticeably smaller.

### ***Pholcus alticeps*** Spassky, 1932

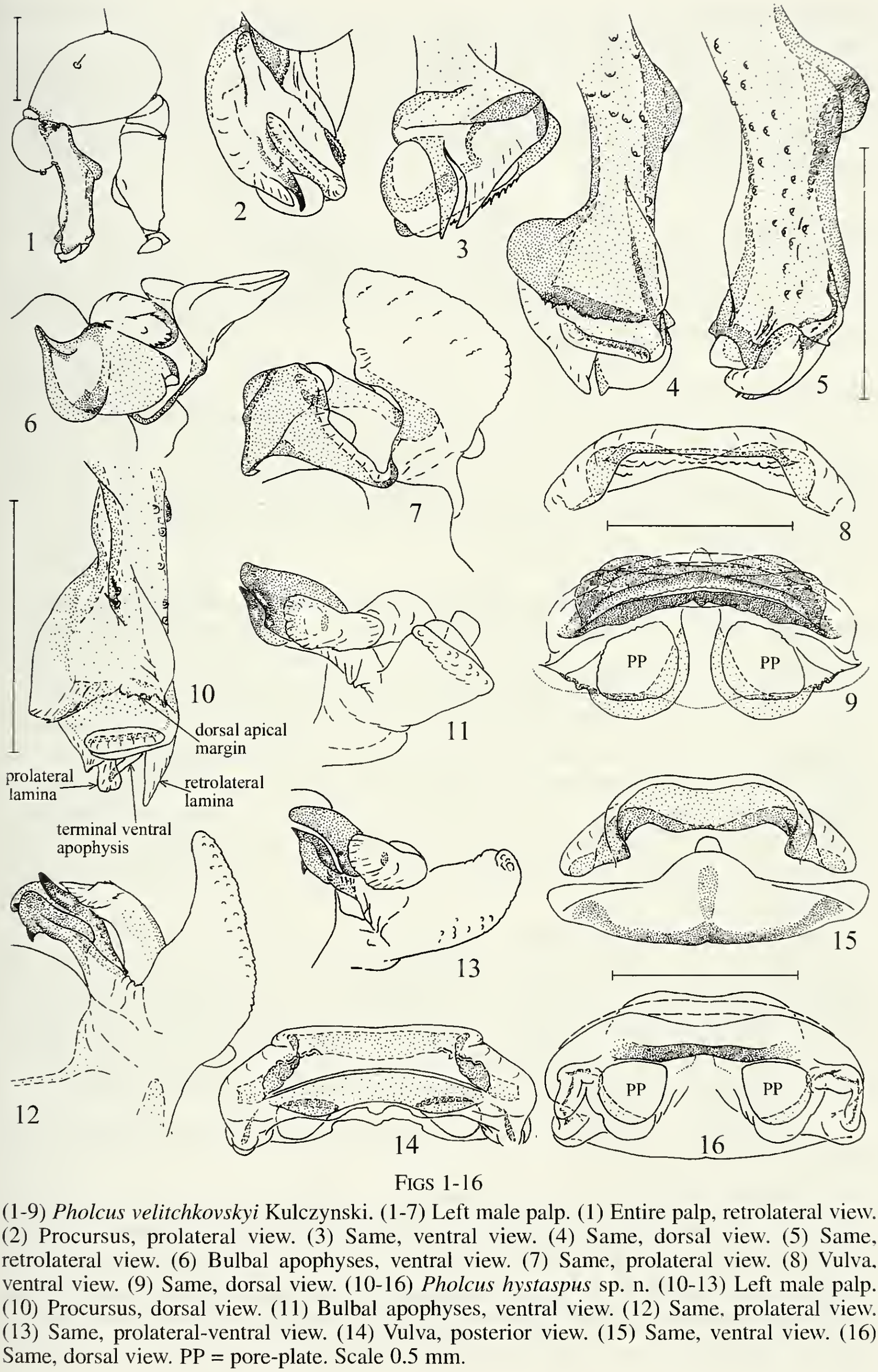
*Pholcus alticeps* Spassky, 1932: 972, figs 1-6 (description of ♂ and ♀). – Senglet, 1974: 804, figs 9-14, 35.

MATERIAL EXAMINED: 4 ♂, 5 ♀, IRAN, Caspian Sea, Mazanderan, Tang-e-Rah, 37°23'N 55°50'E, 13/7/1974. – 1 ♂, 1 ♀, IRAN, above Tchalus, 36°33'N 51°23'E, 4/8/1974. – 15 ♂, 15 ♀, IRAN, Baladeh, 2200 m, 36°13'N 51°49'E, 7/7/1975. – 9 ♂, 5 ♀, IRAN, West of Kiyasar, 36°16'N 53°25'E, 10/7/1975. – 1 ♀, IRAN, Behshahr, 36°41'N 53°54'E, 13/7/1975. – 1 ♂, 2 ♀, IRAN, Khorasan, North of Qoutchan, 37°12'N 58°29'E, 15/7/1974. All specimens were collected in forests and underneath shaded stones.

### ***Pholcus medicus***-group

Characterized by a procursus with a short dorsal apical margin (Figs 10, 31), leaving entirely visible in dorsal view a membranous transversal apical slit, a retrolateral and a prolateral membranous lamina and a variable slender terminal ventral apophysis on its ventral margin. Bulbal appendix bifid (Figs 11-13, 29). In closely related species the vulva provides characters for species discrimination.

Species included: *P. medicus* Senglet, *P. armeniacus* Senglet, *P. hyrcanus* Senglet, *P. persicus* Senglet, *P. hystaspus* sp. n. and *P. elymaeus* sp. n.



FIGS 1-16

(1-9) *Pholcus velitchkovskyi* Kulczynski. (1-7) Left male palp. (1) Entire palp, retrolateral view. (2) Procursus, prolateral view. (3) Same, ventral view. (4) Same, dorsal view. (5) Same, retrolateral view. (6) Bulbal apophyses, ventral view. (7) Same, prolateral view. (8) Vulva, ventral view. (9) Same, dorsal view. (10-16) *Pholcus hystaspus* sp. n. (10-13) Left male palp. (10) Procursus, dorsal view. (11) Bulbal apophyses, ventral view. (12) Same, prolateral view. (13) Same, prolateral-ventral view. (14) Vulva, posterior view. (15) Same, ventral view. (16) Same, dorsal view. PP = pore-plate. Scale 0.5 mm.

**Pholcus medicus** Senglet, 1974 Figs 47-48

*Pholcus medicus* Senglet, 1974: 808, figs 23-28, 39-40 (description of ♂ and ♀).

MATERIAL EXAMINED: 7 ♂, 3 ♀, IRAN, Eastern Azerbaidjan: Small cave near Miyaneh, 37°21'N 47°49'E, 11/8/1974. - 8 ♂, 7 ♀, same locality as previous, 7/6/1975. – 5 ♂, 4 ♀, IRAN, Caspian Sea, Mazanderan, Shelter cave, Baladeh, 2200 m, 36°13'N 51°49'E, 7/7/1975. – 12 ♂, 10 ♀, IRAN, shelter cave, west of Râzan, 1500 m, 36°12'N 52°08'E, 8/7/1975. All specimens were collected in small caves.

**Pholcus armeniacus** Senglet, 1974

*Pholcus armeniacus* Senglet, 1974: 810, figs 29-34, 37 (description of ♂ and ♀).

MATERIAL EXAMINED: 7 ♂, 2 ♀, IRAN, Western Azerbaidjan: Maku, 39°08'N 44°30'E, 13/8/1974. – 2 ♂, 1 ♀, IRAN, Qareh Zia-ed-Din, 38°56'N 45°03'E, 28/5/1975. All specimens were collected in small caves.

**Pholcus hystaspus** sp. n. Figs 10-16

MATERIAL EXAMINED: Holotype ♂, IRAN, Caspian Sea, Mazanderan, East of Tang-e-Rah, 37°20'N 56°01'E, 16/7/1975. – Paratypes, 8 ♂, 11 ♀, same locality as holotype. – 2 ♀, IRAN, Caspian Sea, Mazanderan, above Tang-e-Rah (under rocks), 37°25'N 55°45'E, 28/7/1974. – Paratypes, 2 ♂, 2 ♀, IRAN, above Dasht, 1600 m, 37°23'N 56°13'E, 17/7/1975. All specimens were collected under larges stones and rocks, some occurring together with *P. velitchkovskyi*, but separated in microhabitats. The latter species lives in stony debris at the foot of the rocks.

DESCRIPTION: Prosoma marking: A dark dorsal median band ragged in anterior half. Opisthosoma elongated. Male (paratype from east of Tang-e-Rah): Total length 5.66. Prosoma 1.56 long, 1.63 wide. Eye sizes and interdistances: AME 0.07, PME 0.14; PME-PME 0.43, PME-ALE 0.03. Ocular group 0.87 wide. Chelicera bearing a strong basal anterior bump, a conical retrolateral-basal and a prolateral-apical apophysis with two gripping teeth. Pedipalp: Length of trochanter apophysis almost equal to width of femur; femur with a strong bump in its basal third. Procursus see Fig. 10. Bulbal apophyses (Figs 11-13): Elongated uncus with a large basal protrusion. Appendix bifid; in apical view retrolateral branch prolaterally enlarged and prolateral branch retrolaterally flexed; in prolateral view lower tooth of prolateral branch strongly diverging from apical one.

Female (paratype from east of Tang-e-Rah): Total length 5.35. Prosoma 1.50 long, 1.40 wide. Eye sizes and interdistances: AME 0.07, PME 0.13; PME-PME 0.30, PME-ALE 0.02. Ocular group 0.67 wide. Genital plate (Fig. 15) triangular, shorter than wide, with a short straight anterior tubercle apophysis; semi-circular sides of central part of ventral sclerite often visible. Vulva (Figs 14-16): High median part of ventral sclerite with semi-circular margins on both sides; dorsal sclerite narrow.

ETYMOLOGY: The species name, an adjective, is derived from Hystaspe, the name of the father of Darius.

REMARKS: According to the shape of the procursus this species is close to *P. medicus*, but the appendix (anchoring sclerite) is clearly distinct. In apical view the retrolateral branch is prolaterally enlarged, versus not prolaterally enlarged in *P. medicus*; in prolateral view the ventral tooth is diverging from the apical point, versus not diverging; in the female the genital plate has a short straight anterior tubercle apophysis, versus longer and bent ventrally; the semi-circular sides of the

FIGS 17-32

(17-24) *Pholcus caspius* sp. n., left male palp. (17) Entire palp, retrolateral view. (18) Procursus, ventral view. (19) Same, prolateral view. (20) Same, dorsal view. (21) Same, retrolateral view. (22) Bulbal apophyses, dorsal view. (23) Same, prolateral view. (24) Same, ventral-retrolateral view. (25-32) *Pholcus elymaeus* sp. n., male. (25) Ocular group, dorsal view. (26) Same, anterior view. (27-32) Left male palp. (27) Entire palp, retrolateral view. (28) Bulbal apophyses, prolateral view. (29) Same, dorsal view. (30) Procursus, prolateral view. (31) Same, dorsal view. (32) Same, retrolateral view. Scale 0.5 mm.

median part of the ventral sclerite (Fig. 15) are often seen trough the cuticle, whereas in *P. medicus* (Figs 47-48) both sides of the ventral sclerite can be seen.

### ***Pholcus elymaeus*** sp. n. Figs 25-32, 51-52

MATERIAL EXAMINED: Holotype ♂, IRAN, Kordestan, Near Kermanshah, 34°24'N 47°10'E, 30/6/1974. – Paratypes, 1 ♂, 3 ♀ (1 ♂, 1 ♀ rehydrated); same locality as holotype. All specimens were collected in a small cave.

DESCRIPTION: Prosoma marking dark dorsal bilobate pattern diverging into four more or less ragged narrow branches. Opisthosoma elongated.

Male (holotype): Total length 4.40. Prosoma 1.40 long, 1.40 wide. Eye sizes and interdistances: AME 0.08, PME 0.14; PME-PME 0.51, PME-ALE 0.025. Ocular group 0.92 wide. Chelicera bearing an anterior-basal retrolaterally directed blunt hook, a conical retrolateral-basal and a prolateral-apical apophysis with two gripping teeth. Pedipalp (Figs 27, 30-32): Trochanter apophysis medium-sized; femur with a strong bump in its basal third; procursus with a partially sclerotized prolateral lamina and a strong acute terminal apophysis. Bulbal apophyses (Figs 28-29): Uncus with a large basal protrusion. Appendix bifid; its retrolateral branch truncated, with the prolateral margin terminating in an acute point, a diverging tooth underneath; its prolateral branch divided into two tapering ribbons.

Female: Total length 5.80. Prosoma 1.55 long, 1.70 wide. Eye sizes and interdistances: AME 0.10, PME 0.14; PME-PME 0.30, PME-ALE 0.02. Ocular group 0.70 wide. Genital plate (Fig. 52) triangular, with short anterior tubercle apophysis; median arch and lateral margins of ventral vulval sclerite often visible through the cuticle. Vulva (Fig. 51): Narrow dorsal sclerite with two dorsal bumps.

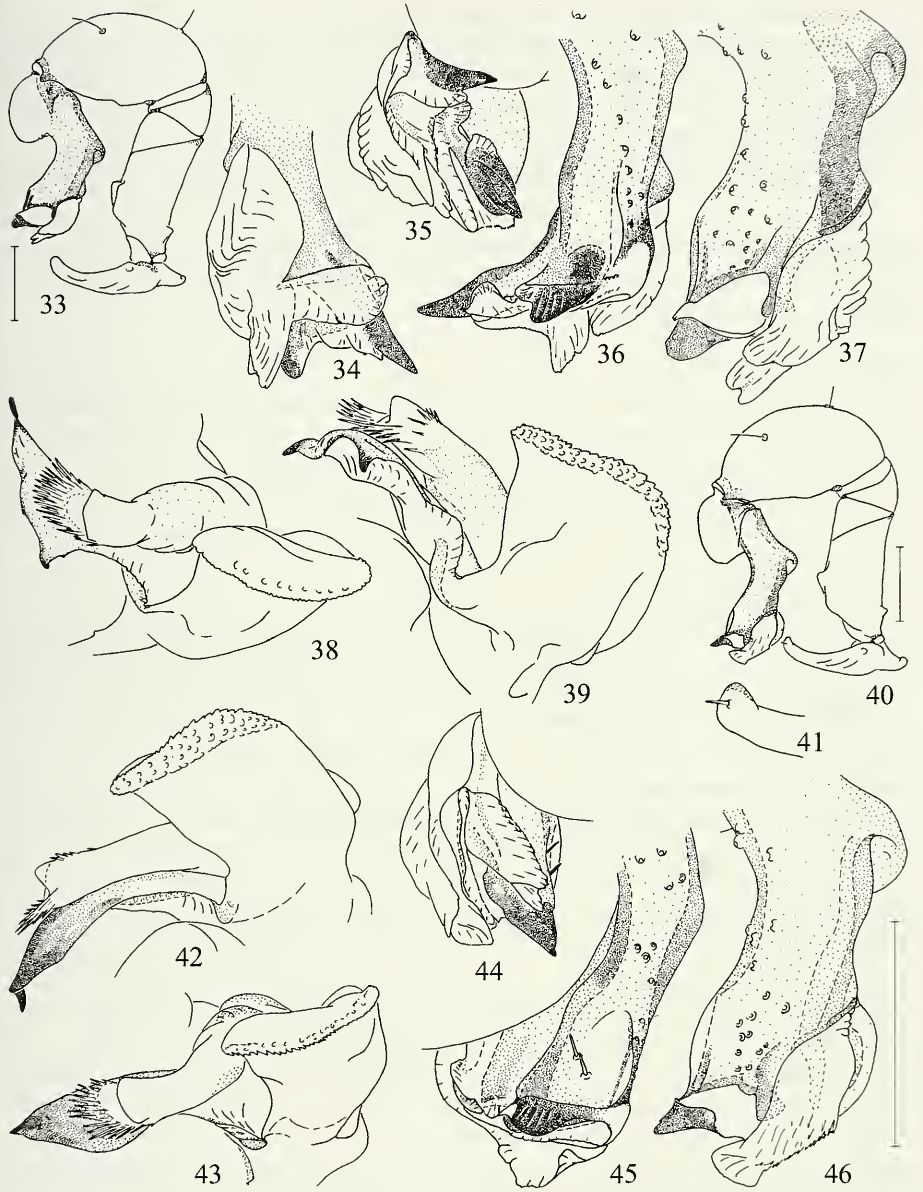
ETYMOLOGY: The species name, an adjective, is derived from Elymais, an antique region of Iran.

### ***Pholcus caspius*** sp. n. Figs 17-24, 49-50

MATERIAL EXAMINED: Holotype ♂, IRAN, Caspian Sea, Mazanderan, Delasm, 36°26'N 51°52'E, 4/8/1974. – Paratypes, 12 ♂, 10 ♀, same locality as holotype. – 3 ♂, 3 ♀, IRAN, above Tchalus, under stones in shaded grove, 36°33'N 51°23'E, 4/8/1974. All specimens were collected under rocks and overhangs.

DESCRIPTION: Prosoma marking dark dorsal band narrow in front, posteriorly widening to more than half of prosoma width. Opisthosoma elongated.

Male (paratype from Delasm): Total length 5.15. Prosoma 1.40 long, 1.60 wide. Eye sizes and interdistances: AME 0. 09, PME 0.13; PME-PME 0.47, PME-ALE 0.02. Ocular group 0.86 wide, widened and flattened, with AME at same level as ALE. Chelicera bearing a strong basal anterior bump, a conical retrolateral basal and a prolateral-apical apophysis with two gripping teeth. Pedipalp (Figs 17-24): Trochanter apophysis short; femur with a strong bump in its basal third; dorsal apical margin of procursus extended into a strong apophysis; ventral-apical apophysis acute, slightly flexed. Bulbal apophyses (Figs 22-24): Elongated arched uncus with a large basal protrusion. Appendix bifid; retrolateral branch elongated, sinuous, with a small tooth under its prolateral margin; shorter prolateral branch with a strong conical tooth underneath.



FIGS 33-46

(33-39) *Pholcus parthicus* sp. n., left male palp. (33) Entire palp, retrolateral view. (34) Procursus, prolateral-apical view. (35) Same, prolateral view. (36) Same, dorsal view. (37) Same, retrolateral view. (38) Bulbal apophyses, ventral view. (39) Same, prolateral view. (40-46) *Pholcus arsacius* sp. n., left male palp. (40) Entire palp, retrolateral view. (41) Tip of trochanter apophysis. (42) Bulbal apophyses, prolateral view. (43) Same, dorsal view. (44) Procursus, prolateral view. (45) Same, dorsal view. (46) Same, retrolateral view. Scale 0.5 mm.

Female (from Delasm): Total length 5.60. Prosoma 1.50 long, 1.42 wide. Eye sizes and interdistances: AME 0.08, PME 0.15; PME-PME 0.28, PME-ALE 0.02. Ocular group 0.67 wide. Genital plate (Fig. 50) triangular, with short anterior tubercle apophysis; lateral anterior tips of dorsal sclerites visible. Vulva (Fig. 49): Large dorsal sclerite elevated into two lateral humps.

ETYMOLOGY: The species name, an adjective, is derived from the Caspian Sea.

REMARKS: This species does not belong to any species group, but it is close to the *P. medicus*-group by the bifid bulbal appendix. It differs from that group by the dorsal margin of the procursus being elongated into an apophysis, and by the elevated dorsal vulval sclerite.

### *Pholcus nenjukovi*-group

Characterized by male procursus bent for more than 100° at ventral elbow, appendix undivided, short uncus without proper basal protrusion. Female genital plate with sclerotized lateral ridges and elevated dorsal vulval sclerite.

Species included: *P. nenjukovi* Spassky, *P. parthicus* sp. n., *P. arsacius* sp. n. and *P. afghanus* sp. n. It is probable that also some Chinese species belong to this group.

### ***Pholcus parthicus*** sp. n. Figs 33-39, 53-54

MATERIAL EXAMINED: Holotype ♂, IRAN, Khorasan, North-west of Esfarayen, 1200 m, 37°12'N 57°27'E, 20/7/1975. – Paratypes, 2 ♂, 4 ♀, same locality as holotype. – Paratypes, 3 ♂, 8 ♀, IRAN, west of Shirvan, 37°27'N 57°43'E, 19/8/1975. – Paratypes, 1 ♂, 5 ♀, IRAN, Bodjnourd, 37°29'N 57°26'E, 26/7/1974. – 2 ♂, 4 ♀, IRAN, Bodjnourd, 37°29'N 57°26'E, 20/8/1975. All specimens were collected in caves.

DESCRIPTION: Dorsal marking of prosoma bilobate, with a ragged posterior margin. Opisthosoma elongated.

Male (paratype from Bodjnourd): Total length 6.00. Prosoma 1.60 long, 1.80 wide. Eye sizes and interdistances: AME 0.10, PME 0.15; PME-PME 0.30, PME-ALE 0.02. Ocular group 0.75 wide. Chelicera bearing a small retrolaterally directed basal apophysis, a large retrolateral-basal apophysis with its tip retrolaterally directed, and a prolateral-apical apophysis with three gripping teeth. Pedipalp (Figs 33-37): Trochanter apophysis elongated, its tip strongly flexed retrolaterally. Procursus bent by 130° at its ventral elbow; dorsal apical margin of procursus extended into a strong striated apophysis and prolateral-apical margin extended into a long and narrow tooth bent around the bulbus; guiding groove along apical ventral part of procursus beginning at an almost hemispheric cupule at elbow level. Bulbal apophyses (Figs 38-39): Superior margin of elevated squared uncus bordered with numerous teeth; the usual basal protrusion being replaced by a wide expansion of uncus base. Bulbal appendix triangular in apical view, tapering to its tip; its prolateral margin sinuous, with a tooth at the angle.

Female (from Bodjnourd): Total length 6.40. Prosoma 1.80 long, 1.85 wide. Eye sizes and interdistances: AME 0.09, PME 0.15; PME-PME 0.23, PME-ALE 0.02. Ocular group 0.65 wide. Genital plate (Fig. 54) triangular, with strong sinuous lateral ridges and a long tubercle apophysis. Vulva (Fig. 53): Dorsal sclerite elevated into a bilobate anterior arch; small pore-plates in anterior position; dorsal anchoring pockets in a median position.

ETYMOLOGY: The species name, an adjective, is derived from the Parthian kingdom.

***Pholcus arsacius*** sp. n. Figs 40-46, 55-56

MATERIAL EXAMINED: Holotype ♂, IRAN, Khorasan, Road to Amirabad, 1100 m, shelter cave, 36°47'N 59°54'E, 23/7/1974. – Paratypes, 6 ♂, 8 ♀, same locality as holotype. – Paratypes, 2 ♂, IRAN, Zavi, 36°52'N 59°53'E, 22/7/1974. All specimens were collected in caves.

DESCRIPTION: Dorsal marking of prosoma bilobate, with a ragged posterior margin. Opisthosoma elongated.

Male (paratype from Amirabad): Total length 6.30. Prosoma 1.90 long, 1.90 wide. Eye sizes and interdistances: AME 0.10, PME 0.15; PME-PME 0.28, PME-ALE 0.02. Ocular group 0.78 wide. Chelicera bearing a strong basal anterior bump terminating in a retrolaterally-directed rounded apophysis, a large retrolateral basal apophysis and a prolateral-apical apophysis with three gripping teeth. Pedipalp (Figs 40-46): Trochanter apophysis elongated, with the tip strongly flexed retrolaterally. Procursus bent by 130° at its ventral elbow; dorsal apical margin of procursus extended into a strong striated apophysis; guiding groove along apical ventral part of procursus beginning at an almost hemispheric cupule at elbow level. Bulbal apophyses (Figs 42-43): Superior margin of elevated squared uncus bordered by numerous teeth; the usual basal protrusion being replaced by an expansion of uncus base. Bulbal appendix spindle-shaped, retrolateral margin forming a tooth near the tip.

Female (from Amirabad): Total length 5.60. Prosoma 1.46 long, 1.50 wide. Eye sizes and interdistances: AME 0.08, PME 0.15; PME-PME 0.20, PME-ALE 0.02. Ocular group 0.67 wide. Genital plate (Fig. 56) short and wide, with strongly sclerotized sinuous lateral ridges. Long tubercle apophysis originating behind genital plate at about 2/3 of its length. Vulva (Fig. 55): Dorsal sclerite elevated into two sclerotized anterior arches; ventral sclerite narrow. Small, widely separated pore-plates in an anterior position.

ETYMOLOGY: The species name, an adjective, is derived from Arsace, the name of the first Parthian king.

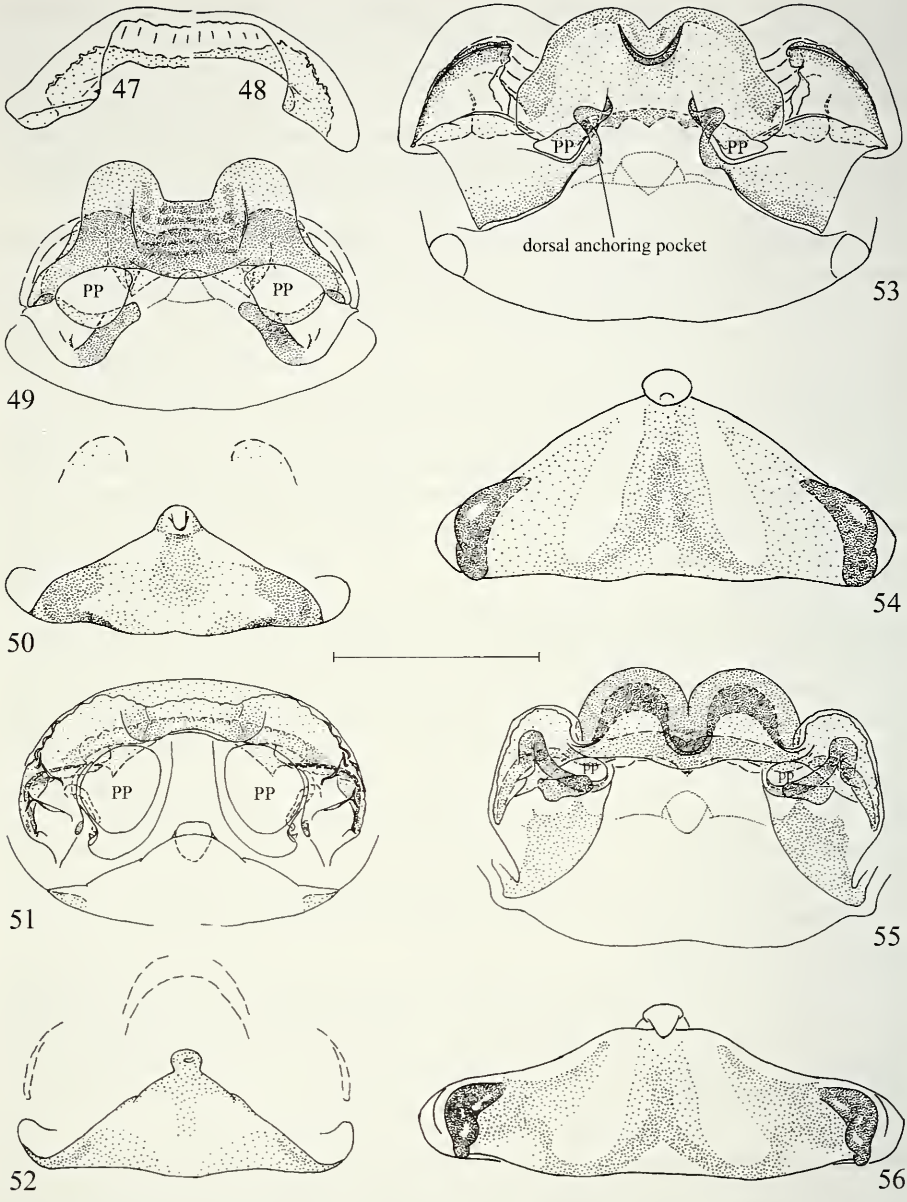
REMARKS: This species is close to *P. nenjukovi* (Spassky, 1936). Unfortunately I was not able to study that species, which was collected 1000 km away from the *P. arsacius* sp. n. localities. The genital plate is triangular in *P. nenjukovi* but short and wide in the new species.

***Pholcus afghanus*** sp. n. Figs 66-74

MATERIAL EXAMINED: Holotype ♂, AFGHANISTAN, Kabul, Kabul, in a hotel, 34°31'N 69°29'E, 3/8/1975. – Paratypes, 2 ♂, 7 ♀, same locality as holotype. – Paratypes, 3 ♂, 3 ♀, north of Charikar, 35°10'N 69°14'E, 10/8/1975. – Paratypes, 1 ♂, 6 ♀. Golbag, 34°26'N 69°07'E, 11/8/1975. All specimens were collected in small caves and in a building.

DESCRIPTION: Prosoma marking a dorsal bilobate pattern. Opisthosoma elongated.

Male (paratype from Kabul): Total length 5.33. Prosoma 1.40 long, 1.54 wide. Eye sizes and interdistances: AME 0.07, PME 0.14; PME-PME 0.27, PME-ALE 0.025.



Figs 47-56

(47-48) *Pholcus medicus* Senglet. (47) Ventral vulval sclerite, female from Miyaneh. (48) Same, female from Soltanieh. (49-50) *Pholcus caspius* sp. n. (49) Vulva, dorsal view. (50) Genital plate. (51-52) *Pholcus elymaeus* sp. n. (51) Vulva, dorsal view. (52) Genital plate. (53-54) *Pholcus parthicus* sp. n. (53) Vulva, dorsal view. (54) Genital plate. (55-56) *Pholcus arsacius* sp. n. (55) Vulva, dorsal view. (56) Genital plate. PP = pore-plate. Scale 0.5 mm.

Ocular group 0.68 wide. Chelicera bearing a pointed anterior basal knob (0.1 mm wide), a large retrolateral basal apophysis and a prolateral-apical apophysis with three gripping teeth. Pedipalp (Fig. 68): Trochanter apophysis long and slender; cylindrical femur bearing a low ventral basal ridge. Strong procursus (Figs 69-72) bent by 110° at its ventral elbow, the latter bearing a longitudinal groove; apical sclerite masked by membranous parts in retrolateral view, but clearly visible in dorsal, prolateral and apical views; in prolateral-apical view (Fig. 72) a large membranous area reaching the ventral groove of procursus; ventral groove extending to elbow; a small pit present on bulbal side. Bulbal apophyses (Figs 73-74): Uncus length about twice its width; basal protrusion reduced to slightly elevated basal margin. Undivided wide appendix terminating in a pointed tip.

Female (from Kabul): Total length 5.20. Prosoma 1.34 long, 1.46 wide. Eye sizes and interdistances: AME 0.07, PME 0.14; PME-PME 0.23, PME-ALE 0.02. Ocular group 0.60 wide. Genital plate (Fig. 66) characterized by strongly sclerotized sinuous lateral ridges. Long flexed anterior tubercle apophysis with a more or less folded membranous base. Vulva: Dorsal sclerite (Fig. 67) highly developed into two anterior membranous lobes; pore-plates small; ventral sclerite as in Fig. 66.

ETYMOLOGY: The species name, an adjective, is taken from the country where these spiders occur.

***Pholcus cophenius*** sp. n. Figs 57- 65

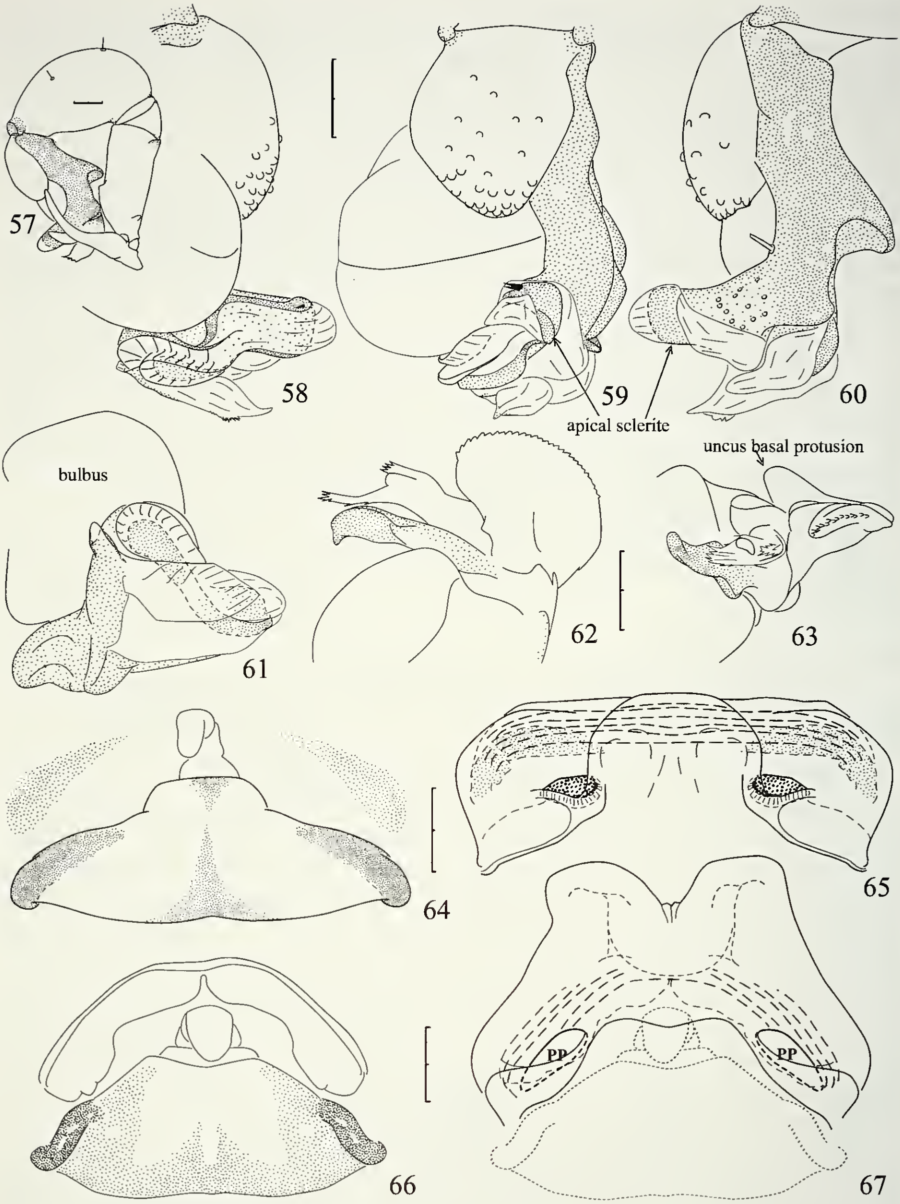
MATERIAL EXAMINED: Holotype ♂, AFGHANISTAN, East of Kabul (34°34'N 69°29'E), 4/8/1975. – Paratypes, 1 ♂, 2 ♀, same locality as holotype. All specimens were collected under large stones.

DESCRIPTION: Prosoma marking a dorsal bilobate pattern.

Male (paratype): Total length 4.80. Prosoma: 1.53 long, 1.60 wide. Eye sizes and interdistances: AME 0.08, PME 0.14; PME-PME 0.27, PME-ALE 0.02. Ocular group 0.67 wide. Chelicera bearing a small anterior basal knob (0.05 mm wide), a large retrolateral-basal apophysis with an inflated base, and a prolateral-apical apophysis with three gripping teeth. Pedipalp (Fig. 57): Trochanter apophysis long; femur cylindrical. Procursus (Figs 58-61) bent by 100° past the level of its ventral elbow; in dorsal view two tiny acute jointed processes visible on prolateral side of apical sclerite; apical sclerite large, extended to prolateral ventral side. Oblique guiding groove along apical ventral part of procursus beginning at a large concave prolateral expansion at elbow level. Bulbal apophyses (Figs 62-63): Width of uncus about 2/3 its length, bearing a large retrolateral basal protrusion. Appendix undivided.

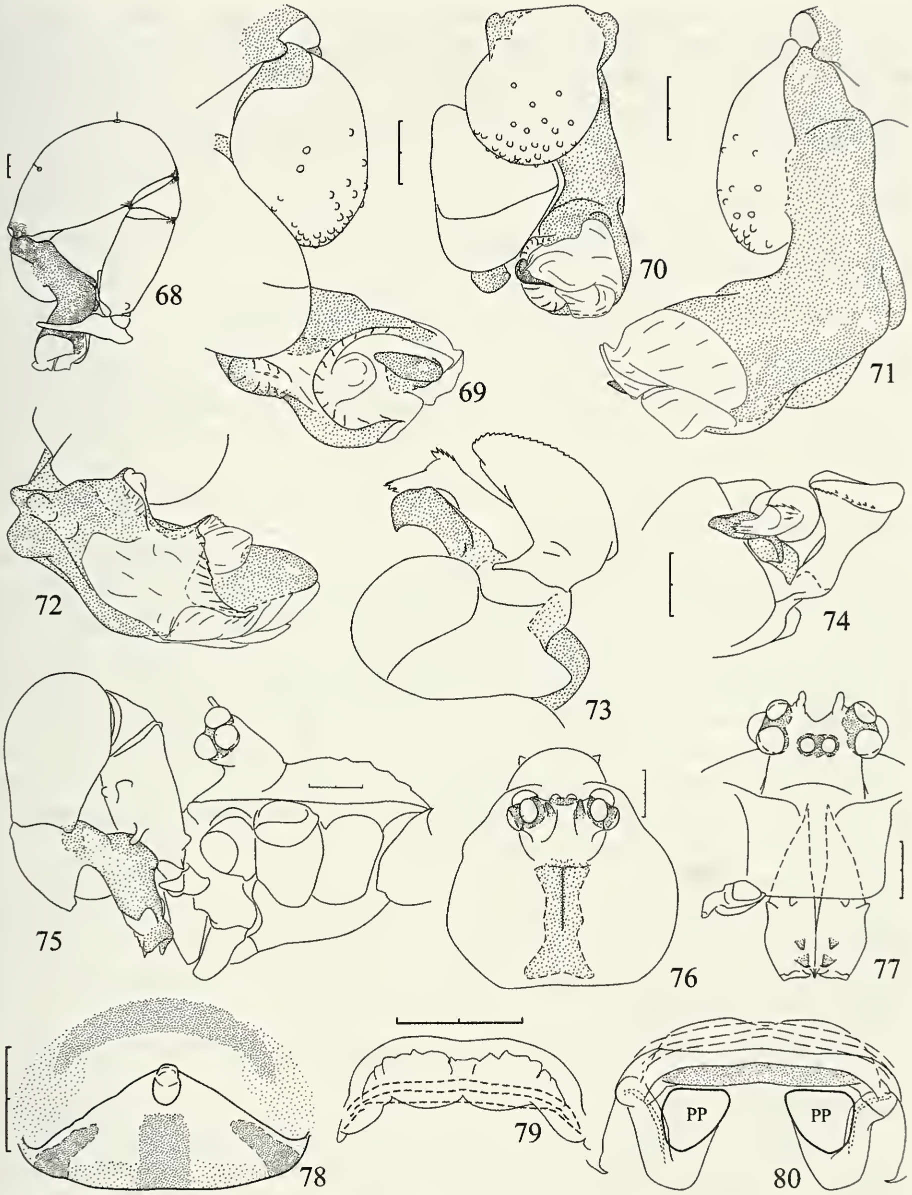
Female: Total length 5.50. Prosoma: 1.40 long, 1.50 wide. Eye sizes and interdistances: AME 0.07, PME 0.14; PME-PME 0.20, PME-ALE 0.02. Ocular group 0.54 wide. Short genital plate (Fig. 64) characterized by flat sclerotized lateral areas. Base of long flexed anterior tubercle apophysis covered by median expansion of genital plate. Vulva (Fig. 65): Dorsal wall developed into a membranous median anterior lobe. Ventral sclerite sclerotized at both extremities. Pore-plates small, oblique, their dorsal margins on sides of anterior lobe.

ETYMOLOGY: The species name, an adjective, is derived from Cophen, the ancient name of the river Kabul.



FIGS 57-67

(57-65) *Pholcus cophenius* sp. n. (57-63) Left male palp. (57) Entire palp, retrolateral view. (58) Procursus, prolateral view. (59) Same, dorsal view. (60) Same, retrolateral view. (61) Same, apical view. (62) Bulbal apophyses, prolateral view. (63) Same, ventral view. (64) Genital plate. (65) Vulva, dorsal view. (66-67) *Pholcus afghanus* sp. n. (66) Genital plate with ventral vulval sclerite. (67) Vulva, dorsal view. PP = pore-plate. Scale 0.2 mm.



FIGS 68-80

(68-74) *Pholcus afghanus* sp. n., left male palp. (68) Entire palp, retrolateral view. (69) Procursus, prolateral view. (70) Same, dorsal view. (71) Same, retrolateral view. (72) Same, prolateral-apical view. (73) Bulbal apophyses, prolateral view. (74) Same, ventral view. (75-80) *Pholcus kandahar* sp. n. (75) Male prosoma, left view. (76) Same, dorsal view. (77) Same, anterior view. (78) Genital plate. (79) Vulva, ventral view. (80) Same, dorsal view. PP = pore-plate. Scale 0.2 mm.

Remarks: This species does not belong to any species group, but it is close to the *P. nenjukovi*-group judging from the similar angle of the apical part of the procursus, and the undivided bulbal appendix. *P. cophenius* sp. n. differs from that group by the structure of its procursus tip, by a large basal protrusion on the uncus, and by the absence of sclerotized lateral ridges on the female genital plate.

### *Pholcus kandahar*-group

Characterized in the male by the presence of cephalic horns and an additional median cheliceral apophysis.

Species included: *P. kandahar* sp. n. and *P. djelalabad* sp. n.

### ***Pholcus kandahar*** sp. n. Figs 75-87

Material examined: Holotype ♂, AFGHANISTAN, West of Kandahar, 31°37'N 65°36'E, 31/7/1975. – Paratypes, 5 ♂, 4 ♀, same locality as holotype. All specimens were collected from a stone wall.

Description: Prosoma marking (Fig. 76) narrow median dorsal band widened at both ends. Opisthosoma elongated.

Male (paratype): Total length 3.40. Prosoma 0.96 long, 1.02 wide. Eye sizes and interdistances: AME 0.045, PME 0.093; PME-PME 0.21, PME-ALE 0.01. Ocular group 0.44 wide. Eye tubercle (Figs 75-77) carrying horns. Chelicera (Figs 86-87) with an additional median apophysis situated closer to the prolateral-apical apophysis (with two gripping teeth) than to the basal anterior blunt hook. Pedipalp (Figs 75, 81-85): Femur (Fig. 75) bearing a strong ventral bump and a finger-like apophysis; trochanter apophysis shorter than mid-width of femur. Procursus: Tip of large apical sclerite (Figs 83-85) strongly flattened into a thin ribbon (in *P. djelalabad* sp. n. with a cone-shaped tip); long prolateral ventral lamina (PVL) visible in retrolateral view. Bulbal apophyses (Figs 81-82): Width of appendix about a third of its length in apical view; long retrolateral expansion almost reaching tip of appendix head.

Female: Total length 4.30. Prosoma 1.00 long, 1.15 wide. Eye sizes and interdistances: AME 0.04, PME 0.10; PME-PME 0.30, PME-ALE 0.01. Ocular group 0.41 wide. Genital plate triangular (Fig. 78), with flexed tubercle apophysis. Vulva (Figs 79-80): Ventral sclerite simple; dorsal sclerite narrow.

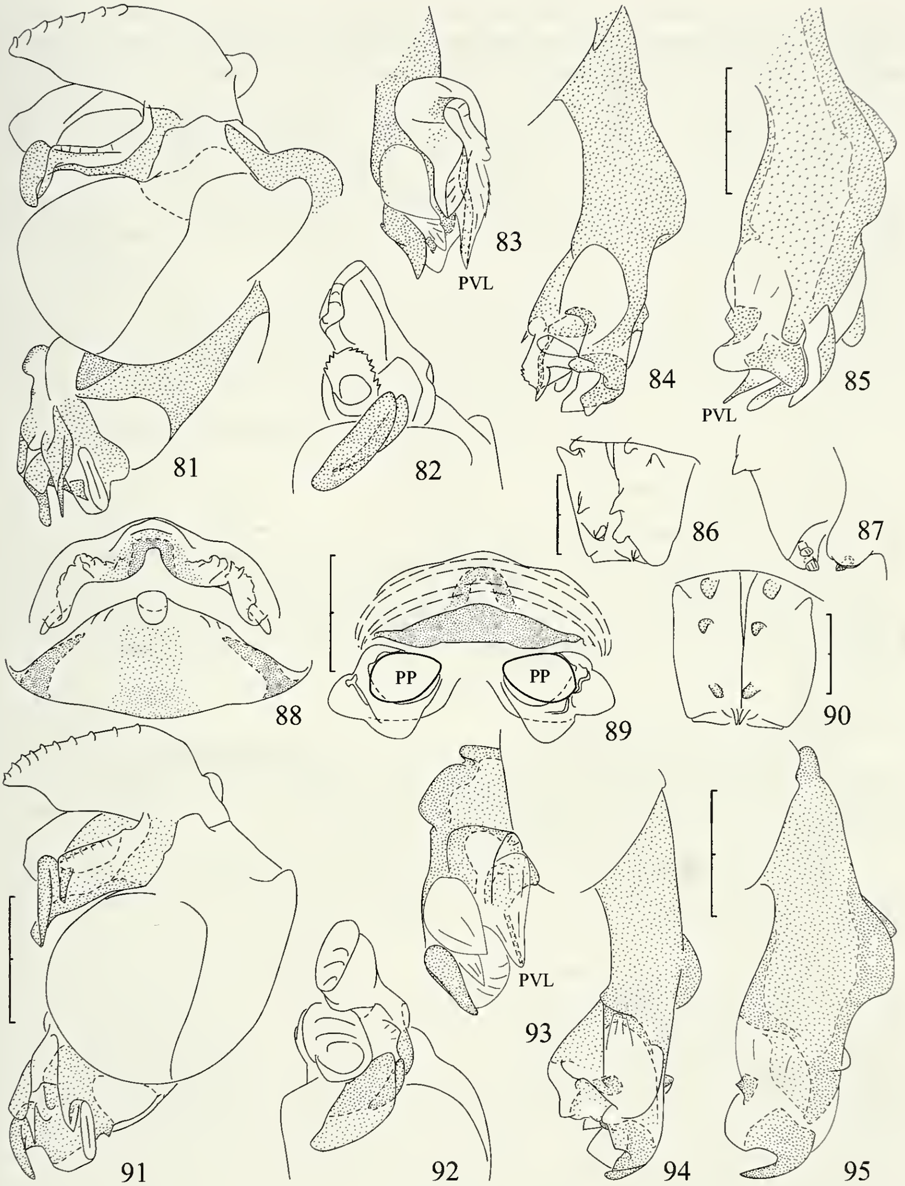
Etymology: The species name, a noun in apposition, refers to the type locality.

### ***Pholcus djelalabad*** sp. n. Figs 88-95

Material examined: Holotype ♂, AFGHANISTAN, Kabul, North-east of Djelalabad, 34°30'N 70°33'E, 8/8/1975, (1 pedipalp in microvial, legs absent except for left III and right IV). – Paratype, 1 ♀ (vulva in microvial), same locality as holotype. All specimens were collected under stones.

Description: Prosoma marking: Narrow median dorsal band slightly dilated in posterior part. Opisthosoma elongated.

Male (holotype): Total length 4.15. Prosoma 1.14 long, 1.17 wide. Eye sizes and interdistances: AME 0.057, PME 0.128; PME-PME 0.24, PME-ALE 0.01. Ocular group 0.58 wide. Eye tubercle bearing longer horns than in *P. kandahar* (see Fig. 77); base of elevated ocular group occupying 60% of ocular group width. Chelicera



Figs 81-95

(81-87) *Pholcus kandahar* sp. n., left male palp. (81) Procursus and bulbus, prolateral view. (82) Bulbal apophyses, ventral view. (83) Procursus, ventral view. (84) Same, dorsal view. (85) Same, retrolateral view. (86) Chelicerae. (87) Same, apical apophyses. (88-95) *Pholcus djelalabad* sp. n. (88) Female genital plate and vulval ventral sclerite. (89) Vulva, dorsal view. (90) Male chelicerae, retrolateral-anterior view. (91-95) Left male palp. (91) Procursus and bulbus, prolateral view. (92) Bulbal apophyses, ventral view. (93) Procursus, ventral view. (94) Same, dorsal view. (95) Same, retrolateral view. PP = pore-plate. PVL = prolateral ventral lamina. Scales 0.2 mm.

(Fig. 90) with an additional horizontally flattened median apophysis situated closer to anterior basal blunt hook than to prolateral-apical apophysis (with two gripping teeth). Pedipalp (Figs 91, 93-95): Femur like in *P. kandahar* sp. n. (see Fig. 75), carrying a strong ventral bump and a finger-like apophysis; trochanter apophysis shorter than mid-width of femur. Procursus: Large apical sclerite (Figs 94-95) terminating in a cone (tip flattened in *P. kandahar* sp. n., Figs 84-85); short prolateral ventral lamina (PVL) not visible in retrolateral view. Bulbal apophyses (Figs 91-92): Width of appendix larger than half its length in apical view; short retrolateral expansion reaching middle of appendix head.

Female: Total length 4.20. Prosoma 1.16 long, 1.17 wide. Eye sizes and interdistances: AME 0.05, PME 0.128; PME-PME 0.17, PME-ALE 0.01. Ocular group 0.5 wide. Genital plate triangular (Fig. 88), with flexed tubercle apophysis. Vulva (Figs 88-89): Ventral sclerite with a sclerotized median arch; dorsal sclerite narrow.

ETYMOLOGY: The species name, a noun in apposition, refers to the type locality.

## Genus *Spermophora* Hentz, 1841

### *Spermophora senoculata* (Dugès, 1836)

*Pholcus senoculatus* Dugès, 1836: 160. For a complete synonymy see Platnick, 2008.

MATERIAL EXAMINED: 3 ♂, 3 ♀, IRAN, Western Azerbaidjan, Qareh Zia-ed-Din, 38°56'N 45°03'E, 28/5/1975. – 18 ♂, 50 ♀, IRAN, Caspian Sea, Mazanderan, East of Tang-e-Rah, 37°20'N 56°01'E, 16/7/1975. This holarctic species is present in the less arid northern part of Iran. All specimens were collected from the vegetation.

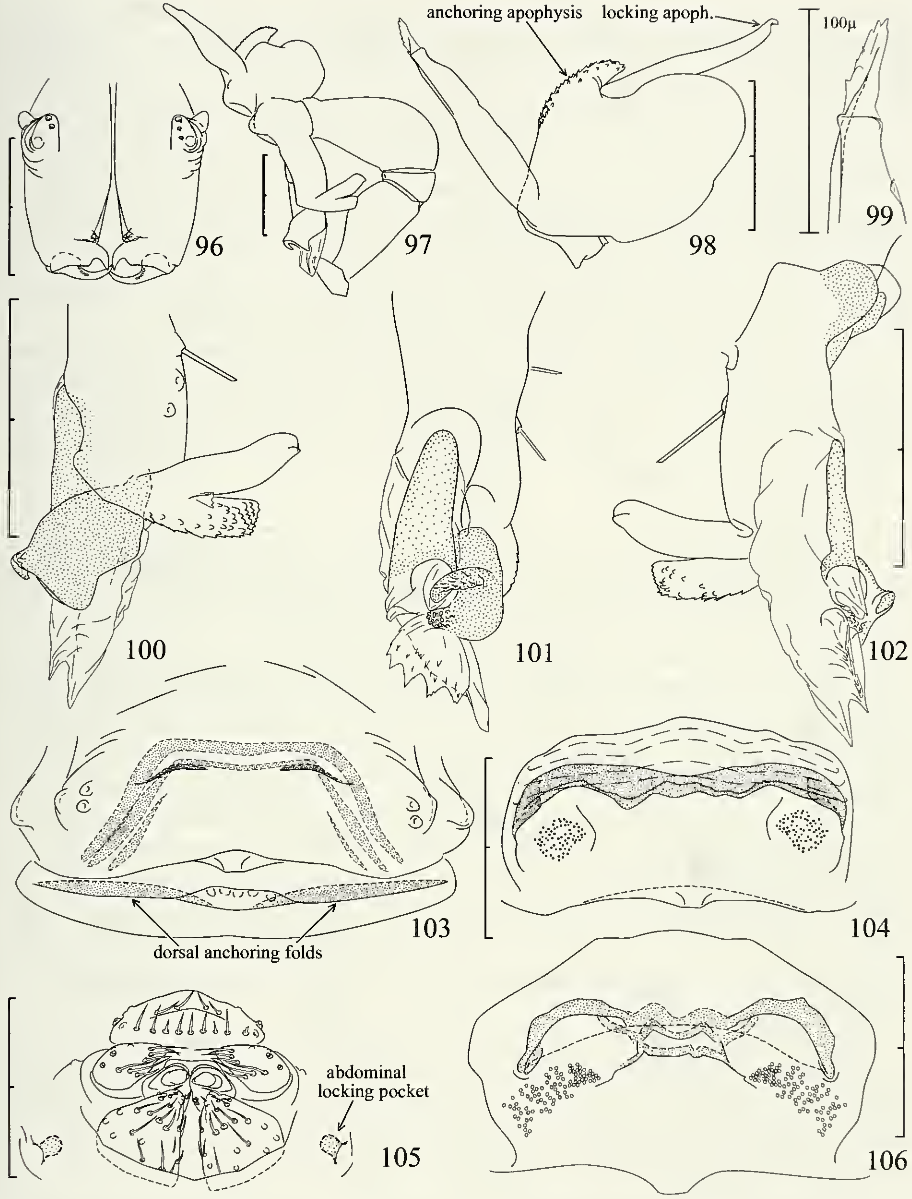
### *Spermophora senoculatoides* sp. n. Figs 96-105

MATERIAL EXAMINED: Holotype ♂, IRAN, Kordestan, south-east of Berendjan, 34°33'N 47°02'E, 12/9/1975. – Paratypes, 2 ♂, same locality as holotype (last moult 1-10/11/1975). – Paratype, 1 ♀, IRAN, Near Kermanshah, 34°24'N 47°10'E, 30/6/1974, (vulva on microscopic slide PHO 50). All specimens were collected under stones in caves.

DESCRIPTION: Colouration of whole spider pale, prosoma with a faint dark marking in posterior half. Eyes in two compact triads (each of them 0.09 wide), separated by 0.17.

Male (holotype): Prosoma 0.68 long, 0.74 wide. Chelicera with prolateral-apical (with two gripping teeth) and retrolateral-basal apophyses; a short and flat inconspicuous ridge (Fig. 96) present in front and just under the retrolateral-basal apophysis; during copulation ridges in contact with slits on the female genital plate (holding against the traction caused by the apical apophyses on the soft knob). Pedipalp (Fig. 97): Trochanter apophysis short; bulbus in a dorsal position. Procursus (Figs 100-102) bearing a retrolateral, ventrally-directed apophysis divided in two branches, the shorter apical one toothed, with a membrane at junction of both branches; apical sclerite blunt, rooted under retrolateral apophysis, wide and oblique, carrying a protruding transverse dorsal appendix. Bulbal apophyses (Fig. 98): An elongated toothed apophysis and a long straight apophysis terminating in a small hook. Embolus on one side with an elongated membranous extension reinforced at its base with a longitudinal ridge extended along the embolus (Fig. 99).

Female: Genital plate (Fig. 103) bearing two transverse shallow slits with posterior opening; posterior membranous knob protruding more or less distinctly from



FIGS 96-106
(96-105) *Spermophora senoculatoides* sp. n. (96) Male chelicerae. (97-102) Left male palp. (97) Entire palp, retrolateral view. (98) Bulbus, prolateral view. (99) Tip of embolus. (100) Procursus, retrolateral view. (101) Same, dorsal view. (102) Same, prolateral view. (103) Genital plate. (104) Vulva, dorsal view. (105) Female spinnerets, ventral view. (106) *S. senoculata*, vulva, dorsal view. Scale 0.2 mm.

margin of genital plate. Sclerotized ventral vulval folds visible through the cuticle. Vulva (Fig. 104) with compact pore-plate (widened and uneven in *S. senoculata* Fig. 106).

ETYMOLOGY: The specific name indicates a close relationship to the type species of the genus.

REMARKS: Similar to *S. senoculata*, but male with a short, flat, inconspicuous ridge close to the retrolateral basal apophysis of the chelicera (Fig. 96) instead of a flattened anteromedian apophysis (Senglet, 2001: figs 46-47). Apical sclerite of procursus blunt, with a transverse dorsal appendix instead of a simple, elongated and acute one. Female with a pair of shallow transverse slits on genital plate.

The female paratype, which is clearly distinct from females of *S. senoculata*, was found in a cave in 1974. During my visit to the same area in 1975 that cave was no longer accessible for military reasons. I collected (and reared to maturity) the male holotype and two males paratypes from a different cave nearby. I assume the specimens from both caves are conspecific.

### ***Spermophora persica*** sp. n. Figs 107-117

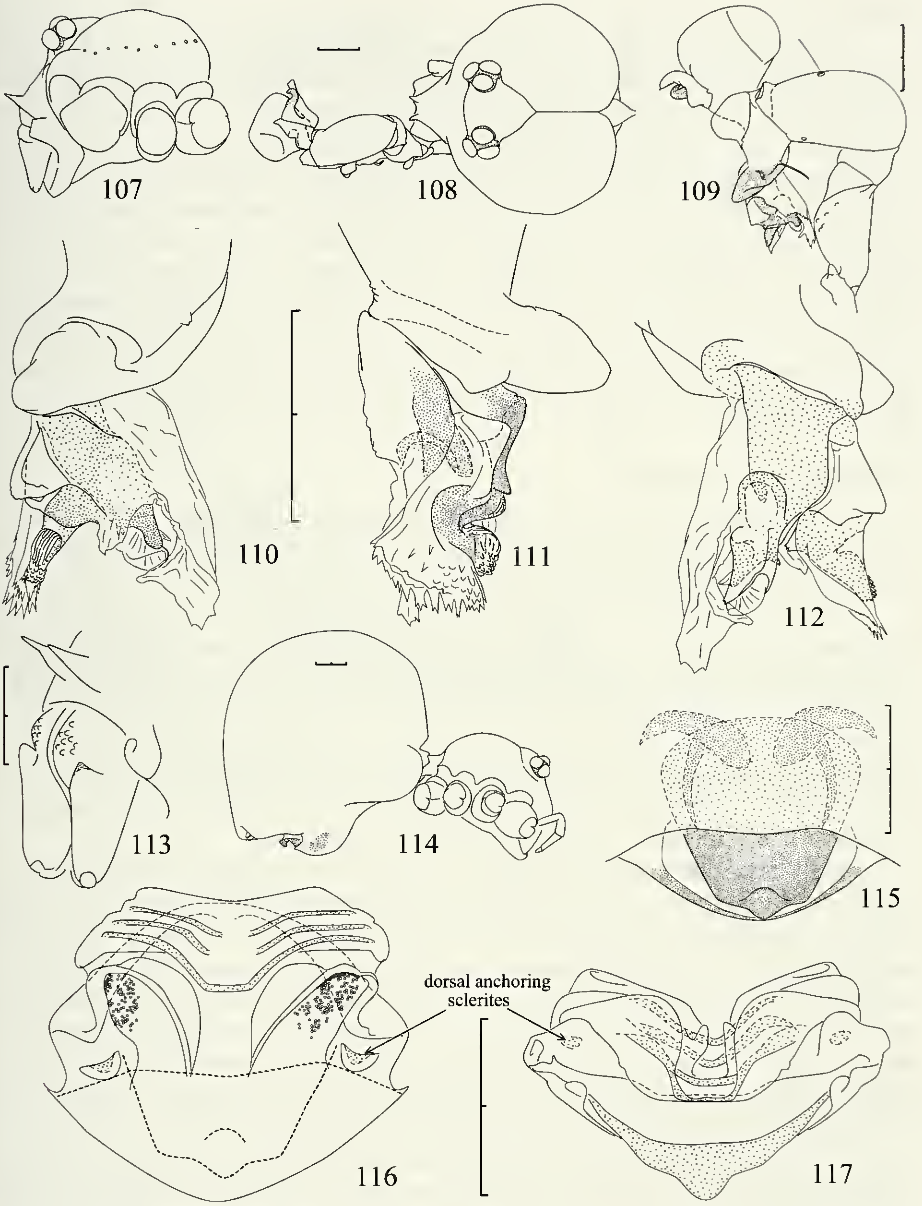
MATERIAL EXAMINED: Holotype ♂, IRAN, Kordestan, North of Kermanshah, 34°28'N 47°00'E, 18/6/1975. – Paratypes, 2 ♂, 3 ♀ (one of them with vulva destroyed), same locality as holotype. All specimens were collected under stones in a large cave.

DESCRIPTION: Male (paratype): Total length 2.60. Prosoma 0.80 long, 1.00 wide. Eye sizes and interdistances: PME 0.10; PME-PME 0.18, PME-ALE 0.02. Ocular group 0.48 wide. Leg I: 17.7 (4.75+0.35+4.35+6.3+2), femur II 3.5, femur III 2.8, femur IV 3.4. Femur I 0.2 in diameter. Legs I-IV with three tarsal claws; paired claws curved, with more than six teeth in a single row. Femur I armed with a ventral series of 15 macrotrichia, these 0.24 long, slightly longer than the diameter of the femur. Clypeus armed with a pair of horns close to its lower margin. Chelicera (Fig. 113) with a convex sector covered with granules between apophysis and clypeus, only one retrolateral-basal apophysis present. Pedipalp (Fig. 109): Trochanter apophysis short; bulbus in a dorsal position. Procursus (Figs 110-112) bearing an undivided dorsally-directed retrolateral apophysis. Bulbal apophyses (Figs 108-109): Apophysis and embolus short and hooked.

Female: Total length 2.66. Prosoma 0.80 long, 0.10 wide. Eye sizes and interdistances: PME 0.08; PME-PME 0.15, PME-ALE 0.15. Ocular group 0.43 wide. Pedipalp with a straight toothless claw. Genital plate (Figs 114-115) characterized by a large shield-like hooked ventral sclerite protruding from the lips. Dorsal vulval wall with sclerotized sinuous anterior folds (Figs 116-117).

ETYMOLOGY: The species name, an adjective, is derived from the ancient name of Iran.

REMARKS: This species is clearly not a *Spermophora* sensu stricto (see Huber, 2005: 62). I cannot attribute this peculiar species to any other known genus and I do not want to establish a new genus for it. Therefore I provisionally place this new species in *Spermophora* sensu lato. A description of its legs is given here to facilitate a proper classification in the future.



FIGS 107-117

(107-117) *Spermophora persica* sp. n. (107) Male prosoma, lateral view. (108) Same, dorsal view. (109-112) Left male palp. (109) Entire palp, retrolateral view. (110) Tip of procursus, retrolateral view. (111) Same, dorsal view. (112) Same, prolateral view. (113) Male chelicerae. (114) Female, lateral view. (115) Genital plate. (116) Vulva, dorsal view. (117) Same, posterior view. Scale 0.2 mm.

## HABITATS

The Iranian localities of *Pholcus* and *Spermophora* are shown in Fig. 118. *Pholcus alticeps* lives in tree hollows, between tree roots and shaded stones. The small *P. velitchkovskyi*, *P. kandahar* sp.n. and *P. djelalabad* sp. n. live in small cavities in loose stone heap or stone walls. All other species that I collected in Iran and Afghanistan are living under rock overhangs, in fissures in rocks or in caves, according to their tolerance to light. Isolated karsts seem to contain ideal biotopes that facilitate speciation in pholcid spiders. For religious reasons houses in these countries are not easily accessible, therefore synanthropic species, except *Z. afghanus sp. n.* and *P. medicus*, are not know to me. Synanthropy could explain the wide distribution of the latter species. It is possible to find two species close to each other, but then they occur in different ecological niches. For example, *P. velitchkovskyi* was found in small spaces in piles of stones and the larger *P. hystaspus* in overhangs and large cavities above them.

## MATING MECHANISMS

Mating mechanisms in Pholcidae were explained in Senglet, 2001. Based on further observations of matings, complementary notes concerning anchoring device in some Pholcinae are given in the following.

The Pholcidae have a highly dynamic mating mechanism in comparison to other spider families. A very strong and stable anchoring is needed in order to permit the procursi movements. Cheliceral anchoring seems to be the usual mean, although a clypeal one is possible in some groups. A stable anchoring of bulbal apophyses maintains the emboli on the pore-plates, the procursi are slowly pushed to the back of the vulva and rapidly retracted alternately throughout the mating process (Uhl *et al.*, 1995; Huber, 2002; Senglet, 2001). Presumably it is used to transfer the sperm mass extruded on the pore plate to the bottom of the uterus externus.

Bulbal anchoring in *Spermophora* s. str. (sensu Huber, 2005): Females of these species share the presence of anchoring folds inside the dorsal lip of genital plate with additional locking pockets. Males share palpal procursi and bulbal apophyses. A toothed apophysis is clearly present in four of the oriental species (Huber, 2005 figs 57-58, 69-70, 72-73, 81-82). During copulation this anchoring device is inserted into a transverse membranous fold of the female dorsal genital lip (Huber, 2002: figs 8-9; Senglet, 2001: 50, fig. 30). This unsafe anchoring is laterally stabilized by slender locking apophyses reaching into the paired posterior locking pockets (Figs 90, 95, 97) in *S. senoculata*, and by shorter locking hooks in oriental species.

Cheliceral anchoring in *S. senoculata* and *S. senoculatoides* sp. n.: The cheliceral anchoring is achieved by the prolateral-apical apophyses grasping the soft knob-like posterior structure of the female genital region, and thus pulling open the atrium for free movement of the procursi. The sclerotized ventral vulval folds strengthen the membranous genital area. The inevitable hold to achieve this stretching relies on the median anterior cheliceral apophyses pressing on the genital area in *S. senoculata*. In *S. senoculatoides* sp. n. the ridge-like structures close to the retrolateral-basal apophyses correspond to the pair of narrow transverse pockets on the genital plate (Figs 96, 103).

FIG. 118
Known localities of *Pholcus* and *Spermophora* in Iran.

This type of stretching is also used by *Pholcus*, but in that case the knob-like structure is situated on the median anterior tip of the sclerotized genital plate. The stretching causes the plate to turn to the inside of the vulval atrium and provide backing for the unci. Counter-hold to stretching is provided by the trochanter apophyses, coupled to the chelicerae, by pressing on the anterior margin of the female genital area (Senglet, 2001, fig. 42).

Cheliceral anchoring in the nine known oriental species of *Spermophora* s. str. (sensu Huber, 2005) is done by grasping anchoring pockets on a sclerotized genital plate with the cheliceral apophyses. The locking pockets (secondary to the paired anchoring pockets), which became merged to an unpaired device, in combination with this kind of cheliceral anchoring may be a synapomorphy for this group. The same type of cheliceral anchoring is seen in *Spermophorides*.

Female membranous anchoring pockets in *Pholcus* are usually situated on the ectal side of the pore-plates (known exception *P. parthicus sp. n.*, see Fig. 53). In *Spermophora* s. str. transverse membranous folds are present on the dorsal genital lip. In *Spermophorides* sclerotized pockets occur on the dorsal genital lip.

In *Pholcus* the posterior part of the uncus is the guiding device for longitudinal and twisting movements of the procursus (Uhl *et al.*, 1995: figs 10 c-d; Senglet, 2001:

fig. 43). The corresponding counterpart is the groove of the ventral elbow of the procursus. In some groups the ventral groove may be situated beyond the elbow as far up as the apical sector of the procursus (Figs 37, 46, 60-61).

## ACKNOWLEDGEMENTS

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## REFERENCES

Dugès, A. 1836. Observations sur les aranéides. *Annales des sciences naturelles, Zoologie* (2) 6: 159-219.

Hentz, N. M. 1841. Description of an American spider, constituting a new sub-genus of the tribe Inaequiteloe of Latreille. *American Journal of Science* 41: 116-117.

Huber, B. A. 2002. Functional morphology of the genitalia in the spider *Spermophora senoculata* (Pholcidae, Araneae). *Zoologischer Anzeiger* 241: 105-116.

Huber, B. A. 2005. Revision of the genus *Spermophora* Hentz in southeast Asia and on the Pacific islands, with descriptions of three new genera (Araneae: Pholcidae). *Zoologische Mededelingen* 79: 61-114.

Kulczynski, V. 1913. Arachnoidea (pp.1-30). *In*: Velitchkovsky, V. (ed.). Faune du district de Walouyki du gouvernement de Woronège (Russie) 10. *Cracovie*.

Platnick, N. I. 2008. The world spiders catalog, version 8.5. American Museum of Natural History, online at: http://research.amnh.org/entomology/spiders/catalog.html.

Senglet, A. 1972. Note sur les *Spermophora* (Araneae: Pholcidae) méditerranéens. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft* 45: 307-319.

Senglet, A. 1974. *Pholcus* nouveaux d'Iran (Araneae: Pholcidae). *Revue suisse de Zoologie* 81: 803-812.

Senglet, A. 2001. Copulatory mechanisms in *Hoplopholcus, Stygopholcus* (revalidated), *Pholcus, Spermophora* and *Spermophorides* (Araneae, Pholcidae), with additional faunistic and taxonomic data. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft* 74: 43-67.

Spassky, S. A. 1932. Aranearum species novae, II. *Bulletin du Muséum national d'Histoire naturelle,* Paris (2) 4: 972-979.

Spassky, S. A. 1936. Araneae palaearcticae novae. *Festschrift zum 60. Geburtstag von Prof. Dr. Embrik Strand* (Riga) 1: 37-46.

Uhl, G., Huber, B. A. & Rose, W. 1995. Male pedipalp morphology and copulatory mechanism in *Pholcus phalangioides* (Fuesslin, 1775) (Araneae, Pholcidae). *Bulletin of the British Arachnological Society* 10: 1-9.

Walckenaer, C. A. 1805. Tableau des aranéides ou caractères essentiels des tribus, genres, familles et races que renferme le genre *Aranea* de Linné, avec la désignation des espèces comprises dans chacune de ces divisions. *Paris*, XII+88 pp.

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# A reassessment of the phylogeny and biogeography of *Rhabderemia* Topsent, 1890 (Rhabderemiidae, Poecilosclerida, Demospongiae)

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**A reassessment of the phylogeny and biogeography of *Rhabderemia* Topsent, 1890 (Rhabderemiidae, Poecilosclerida, Demospongiae). -** *Rhabderemia uruguaiensis* van Soest & Hooper, 1993 is redescribed from a depth of 15m at Tempano Fjord (SE Pacific, Chile). Updated phylogenetic hypotheses are offered for *Rhabderemia*, based on two alternative macroevolutionary scenarios - outgroups Desmacellidae and Raspailiidae. The biogeographies implied from these phylogenies are discussed with a focus on those results shared by both phylogenies and a previously published one, as well as on the affinities derived from two recently described new species from the SW Atlantic, *R. besnardi* Oliveira & Hajdu, 2005 and *R. itajai* Oliveira & Hajdu, 2005. Special mention is made of trans-Pacific tracks inferred here and elsewhere in the sponge phylogenetic literature. These span the following four routes: 1) Caribbean - Australia, 2) south-eastern Pacific - Tropical West Pacific, 3) south-eastern Pacific - Easter Island, 4) New Zealand - Boreal Pacific.

**Keywords:** Porifera - *Rhabderemia* - marine sponges - fjords - taxonomy - phylogeny - biogeography - SE Pacific - *Stylospira* - trans-Pacific tracks.

## INTRODUCTION

The SE Pacific bears one of the least studied sponge faunas in the world. Only about 140 species are known from the entire Chilean coast (Desqueyroux & Moyano, 1987), in spite of its 90'000 km of shoreline, stretching approximately 5000 km in a straight line (over 38 degrees of latitude), with an intricate system of islands, fjords and canals unmatched elsewhere on the planet. As part of an international effort to promote further knowledge on Chilean marine sponges, a systematic collecting plan was implemented under the auspices of Belgian, Brazilian, Chilean and Swiss institutions, which permitted visiting 18 localities since 2003 (distributed from 23 to 51°S), including 70 dives for sponge collections. Among the specimens collected several are new records of genera and/or families for the SE Pacific. The results presented here report on a new record for Chile, of *Rhabderemia (R.) uruguaiensis* van Soest & Hooper, 1993 collected at Tempano Fjord.

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In conjunction with two species recently described for the SW Atlantic, *R. besnardi* Oliveira & Hajdu, 2005 and *R. itajai* Oliveira & Hajdu, 2005, this new record povides the basis for reassessing van Soest & Hooper's (1993) proposed phylogeny and biogeography of *Rhabderemia*. An updated identification key is also provided.

## MATERIAL AND METHODS

The single specimen studied was collected by scuba and photographed in situ, as part of a collection from Tempano Fjord and vicinity (ca. 48° S, Figure 1) by Günther Försterra and Verena Häusserman, and deposited at Museu Nacional (MNRJ - Brazil) and Muséum d'histoire naturelle, Geneva (MHNG - Switzerland). Any type material derived from the study of these samples will be deposited in Chile (IZUA/UACH - Instituto de Zoologia, Universidad Austral de Chile).

Dissociated spicule slides and thick section mounts were made according to usual procedures (Hooper, 1997), boiling fragments in nitric acid, and secondly both direct cutting of specimen followed by drying under a warm lamp, as well as paraffin immersion. A Digital Scanning Microscope (DSM-940) was used to capture images of spicules at the Invertebrates Department of the Muséum d'histoire naturelle, Geneva.

The cladistic analysis performed here was undertaken with PAUP* vs. 4.0b10 (Swofford, 2002). Characters were treated as unordered or under "Dollo" parsimony, and equally weighted. The use of exact parsimony algorithms was not possible due to the large size of the datamatrix. The minimization of restricted sampling within the archipelago of trees has been achieved through replication (1000x) of heuristic searches, followed by exhaustive branch-swapping on the trees kept in PAUP's memory buffer. Ten thousand heuristic replicates were occasionally also implemented but did not produce more parsimonious results. Further cropping of sets of equally parsimonious trees was sought by subsequently-weighting characters by their RCs, a strategy repeated until size of the set of most parsimonious trees stabilized (usually 2-3 repetitions), followed by filtering for more resolved, equally-parsimonious trees.

Abbreviations used throughout the text are MHNG – Muséum d'histoire naturelle, Geneva (Switzerland), MNRJ – Museu Nacional, Universidade Federal do Rio de Janeiro (Brazil).

## RESULTS

Class Demospongiae Sollas, 1885
Order Poecilosclerida Topsent, 1928
Suborder Microcionina Hajdu, van Soest & Hooper, 1994
Family Rhabderemiidae Topsent, 1928

### Genus ***Rhabderemia*** Topsent, 1890

DIAGNOSIS: Microcionina with rhabdostyles frequently bearing an extra basal spiral twist, in one or two size categories as the only megascleres. Microscleres, if present, include spirosigmas, micro(sub)(tylo)styles, thraustosigmas, thraustoxeas and toxas. Adapted from Hooper (2002).

REMARKS: The fact that rhabdostyles are neither exclusive of *Rhabderemia*, nor of the Microcionina or the Poecilosclerida, suggests that a reevaluation of the proposed

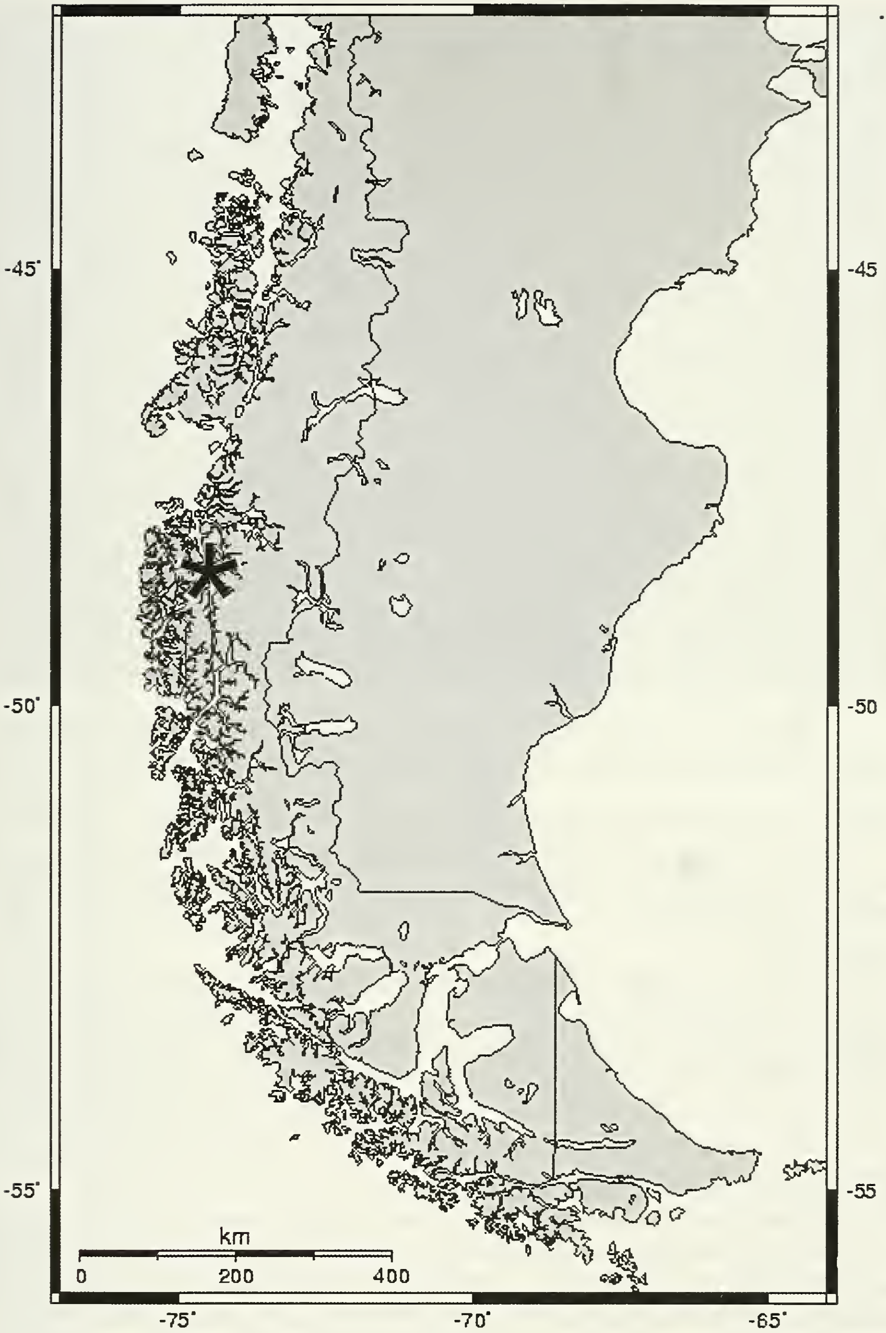

FIG. 1

Map of southern South America pointing the collecting station for *Rhabderemia uruguaiensis* van Soest & Hooper, 1993, at Fjord Tempano (Chile).

synonymy of *Stylospira* de Laubenfels, 1934 (sensu van Soest & Stentoft, 1988) is necessary. It is worthwhile noting that some *Rhabderemia* show a clear terminal twist, which is not found in raspailiids such as *Aulospongus* Norman, 1878 and *Raspailia (Raspaxilla)* (Topsent, 1913), nor in *Dragmaxia* Hallmann, 1916 (Halichondrida). For the present, van Soest & Hooper's (1993) suggestion of keeping *Stylospira* at subgeneric level, with the necessary consequence of assigning all *Rhabderemia* with microscleres to subgenus *Rhabderemia*, appears more appropriate and, accordingly, both are diagnosed below. The decision to keep both at subgeneric level considers that *Stylospira* spp. emerged as monophyletic on the phylogenetic analyses undertaken by van Soest & Hooper (1993) and here, as shown below. But, on the other hand, *Rhabderemia* s.s. may be monophyletic or paraphyletic according to the chosen outgroup, which claims for additional evidence prior to erecting both to full generic status.

Subgenus *Rhabderemia* Topsent, 1890:

*Rhabderemia* with rhabdostyles in one or two size categories as the only megascleres. These can be smooth or heavily spined. Microscleres always include spirosigmas and/or micro(sub)(tylo)styles. Additional microsclere categories may be present, viz. thraustosigmas, thraustoxeas and toxas. Type species: *Microciona pusilla* Carter, 1876 (by subsequent designation - Dendy, 1905: 180) (junior synonym of *Microciona minutula* Carter, 1876 - van Soest & Hooper, 1993: 323)

Subgenus *Stylospira* de Laubenfels, 1934:

*Rhabderemia* with a single category of entirely smooth rhabdostyles. No microscleres. Type species: *Stylospira mona* de Laubenfels, 1934: 10.

### ***Rhabderemia (Rhabderemia) uruguaiensis*** van Soest & Hooper, 1993 Figs 2, 3A-I

MATERIAL STUDIED: MNRJ 9213: Tempano Fjord (48°41'30,3"S – 74°08'9,9"W, Chilean Patagonia), 15m depth, coll. G. Försterra & V. Häusserman, 25/iii/2005. A fragment is deposited under MHNG INVE37425.

REDESCRIPTION

A single specimen has been collected. It was relatively large (over 10x10 cm), a moderately thick cushion (ca. 5 mm), and of beige color, when alive (Fig. 2). Its surface was irregular, with flat roundish projections and a system of dermal grooves which does not appear to converge to oscula. The only fragment available for study is a 3-4 mm thick crust, 34 by 27 mm in area, which kept its original color slightly after preservation. It is soft and fragile, easily torn, and bears a velvety surface, in which no openings of the aquiferous system are visible.

*Skeleton.* Ectosomal skeletal architecture unspecialized, made up of paucispicular brushes of rhabdostyles (3-8 spicules) slightly piercing the surface (up to 115 $\mu$m). Choanosomal skeletal architecture plumose to plumo-reticulate, with rhabdostyles disposed in ascending bundles echinated by the same megascleres, and terminating in the ectosomal brushes. Rhabdostyles also occur strewn at random. Microscleres abound everywhere. Very dark pigment granules (10-30 $\mu$m across) can be seen in large numbers in a moderately aggregated distribution.

FIG. 2

*Rhabderemia uruguaiensis* van Soest & Hooper, 1993. Studied specimen photographed *in situ*. Photo by G. Försterra.

*Spicules*. Megascleres, rhabdostyles (Fig. 3A-D) in a single size category, mostly smooth, but a few vestigial spines are visible on the apical third under high magnifications (Fig. 3D); rhabd mostly bent close to the base, but bending at varied distances from the center is also seen; base styloid, smooth, more frequently bearing a single regular twist, but many variations in twisting occur amongst spicules examined; 74 – *240.5* – 336 μm long and 9.6 – *12* – 16 μm thick. Microscleres, microsubtylostyles (Fig. 3E-H), acanthose/rugose, gently bent in their basal third; 26-*39.7*-51μm long; spirosigmas (Fig. 3I), acanthose, considerably contorted, frequently with a conspicuous bend on both extremities, 5-*7.9*-10 μm long.

## DISTRIBUTION AND ECOLOGY

The species was formerly known only from moderately deep waters off the SE Brazilian and Uruguayan coasts on the SW Atlantic (van Soest & Hooper 1993, Oliveira & Hajdu 2005). Its distribution is now extended to the shallow waters of the Temperate SE Pacific (Tempano Fjord, Chilean Patagonia). The species is most probably widespread in the whole Magellanic area, but given its apparent rarity, a confirmation of this supposition may still be years ahead. In support of our claim the similar Magellanic - SE Brazil distribution of *Hymenancora tenuissima* (Thiele, 1905) and *Raspailia (Raspaxilla) phakellina* (Topsent, 1913) (sensu Hajdu *et al.*, 2004) can

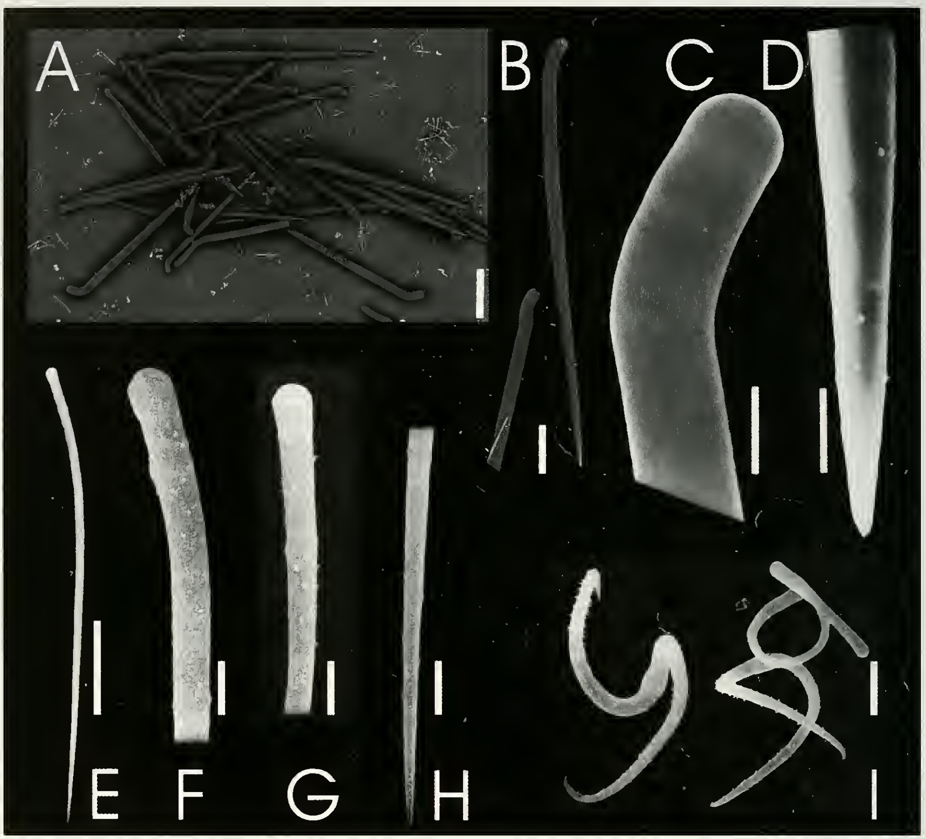

FIG. 3

*Rhabderemia uruguaiensis* van Soest & Hooper, 1993. Scanning electron micrographs of spicules. (A) Dissociated spicules with an overview of rhabdostyles and microstyles. (B-D) Rhabdostyles. (B) Whole spicule. (C) Detail of smooth rhabdose end (base). (D) Detail of slightly spined end (apex). (E-H) Microstyles. (E) Whole spicule. (F-G) Detail of slightly spined stylote end (base). (H) Detail of sharp, slightly spined end (apex). (I) Slightly centrotylote spirosigmata more heavily spined towards both ends. Scales: A, 100 $\mu$m; B, 50 $\mu$m; C-E, 10 $\mu$m; F-I, 2 $\mu$m.

be pointed out. Additional support stems from the historical link implied by the sister-species relationship found by Hajdu (1995) for *Mycale beatrizae* Hajdu & Desqueyroux-Faúndez, 1994 (SE Brazil) and *M. doellojuradoi* Burton, 1940 (NE Argentina and SW Chile).

REMARKS

The Chilean specimen matches perfectly the descriptions provided by van Soest & Hooper (1993) and Oliveira & Hajdu (2005). Noteworthy is the observation of dark microscopical pigment granules, which were not mentioned by Oliveira & Hajdu (2005), but were considered very distinctive by van Soest & Hooper (1993). A minor point of distinction appears to be the presence of microsubtylostyles in the Chilean specimen, as opposed to the microstyles found in Atlantic specimens.

### Identification key for *Rhabderemia (Rhabderemia)* (expanded from van Soest & Hooper, 1993)

1a Microscleres include toxas or toxiform "raphides" . . . . . . . . . . 2
1b Microscleres are never toxas . . . . . . . . . . 4
2a Growth form encrusting . . . . . . . . . . 3
2b Growth form elaborate, lumpy lobate or ramose . . . . . . . . . . *R. (R.) sorokinae*
3a Rhabdostyles largely smooth with only occasional spines, toxas are typical . . . . . . . . . . *R. (R.) toxigera*
3b Rhabdostyles are acanthose, toxas are only a few toxiform "raphides" . . . . . . . . . . *R. (R.) spinosa*
4a Microscleres include thraustoxeas . . . . . . . . . . 5
4b Microscleres are never thraustoxeas . . . . . . . . . . 8
5a Microstyles present . . . . . . . . . . 6
5b Microstyles absent . . . . . . . . . . *R. (R.) fascicularis*
6a Growth form elaborate, lobate-ramose . . . . . . . . . . 7
6b Growth form thinly encrusting . . . . . . . . . . *R. (R.) guernei*
7a Thraustosigmas present, microstyles up to 45 μm only . . . . *R. (R.) coralloides*
7b Thraustosigmas absent, microstyles up to 88 μm . . . . . . . . . . *R. (R.) mutans*
8a Large (>20 μm) thraustosigmas present . . . . . . . . . . 9
8b No large thraustosigmas (smaller ones, up to 15 μm occur in two species) . . . . . . . . . . 11
9a Growth form elaborate, ramose . . . . . . . . . . 10
9b Growth form thinly encrusting . . . . . . . . . . *R. (R.) intexta*
10a Microstyles present . . . . . . . . . . *R. (R.) forcipula*
10b Microstyles absent . . . . . . . . . . *R. (R.) mammillata*
11a Microstyles can be 100 μm long or more, growth form always encrusting . . 12
11b Microstyles always smaller than 70 μm long, growth form encrusting or elaborate . . . . . . . . . . 19
12a Microstyles in two size categories, spirosigmas always smaller than 12 μm . . . . . . . . . . 13
12b Microstyles in a single size category, spirosigmas are frequently larger than 12 μm . . . . . . . . . . 15
13a Rhabdostyles in two size categories seldom reaching 300 μm in length, microstyles always smaller than 150 μm long . . . . . . . . . . 14
13b Rhabdostyles in a single, albeit variable, size category reaching 400 μm in length, microstyles may be larger than 150 μm long . . . . . . *R. (R.) besnardi*
14a Rhabdostyles with a distinct spiral twist, frequently smaller than 100 μm long . . . . . . . . . . *R. (R.) africana*
14b Rhabdostyles barely curved, often almost straight, never smaller than 100 μm long . . . . . . . . . . *R. (R.) bistylifera*
15a Rhabdostyles always smaller than 400 μm long, smooth or acanthose . . . . . 16
15b Rhabdostyles can be larger than 400 μm long, always smooth . . . . . . . . . . *R. (R.) profunda*
16a Spirosigmas strongly contort, thin, finely rugose overall . . . . . . . . . . 17

16b Spirosigmas approaching C-shape, angular, relatively smooth, relatively thick .................................................... 18
17a Rhabdostyles mostly smaller than 200 $\mu$m long, spirosigmas 12-13 $\mu$m long .................................... *R. (R.) prolifera*
17b Rhabdostyles up to 350 $\mu$m long, spirosigmata 9-18 $\mu$m long . *R. (R.) minutula*
18a Rhabdostyles smaller than 180 $\mu$m long, smooth ............ *R. (R.) gallica*
18b Rhabdostyles up to 290 $\mu$m long, acanthose ............... *R. (R.) burtoni*
19a Rhabdostlyes frequently or always larger than 400 $\mu$m long, always acanthose .................................................... 20
19b Rhabdostlyes nearly always smaller than 350 $\mu$m long, smooth or acanthose .................................................... 21
20a Spirosigmas in a single size category always smaller than 10 $\mu$m long, thickly encrusting growth form ........................... *R. (R.) itajai*
20b Spirosigmas in two size categories up to 18 $\mu$m long, growth form erect ............................................. *R. (R.) acanthostyla*
21a Rhabdostyles entirely smooth ..................................... 22
21b Rhabdostyles lightly or heavily spined ............................. 23
22a Rhabdostyles up to 24 $\mu$m thick, heavily spined, dark microscopical pigment granules not recorded ...................... *R. (R.) antarctica*
22b Rhabdostyles up to 15 $\mu$m thick only, larger ones less heavily spined, smaller ones often entirely smooth, may bear abundant dark microscopical pigment granules ........................... *R. (R.) uruguaiensis*
23a Microstyles less than 2 $\mu$m thick ................................ 24
23b Microstyles 3-4 $\mu$m thick ............................ *R. (R.) stellata*
24a Spirosigmas always smaller than 10 $\mu$m long ......................... 25
24b Spirosigmas 12-15 $\mu$m long ........................... *R. (R.) indica*
25a Rhabdostyles almost straight, no spiral twist, growth form massive or thickly encrusting ................................. *R. (R.) spirophora*
25b Rhabdostyles spirally twisted, growth form massive ........ *R. (R.) topsenti*

## PHYLOGENETIC ANALYSIS

Table 1 shows the datamatrix used here to assess the phylogenetic relationships within *Rhabderemia*. It has been adapted from that developed by van Soest & Hooper (1993), to include the two recently described species, viz. *R. besnardi* and *R. itajai*, and a further outgroup, viz. the Desmacellidae (Mycalina, Poecilosclerida). The possible close relationship between Rhabderemiidae and Desmacellidae was suggested as an alternative phylogenetic hypothesis by van Soest & Hooper (1993), based in comparisons between the rugose microstyles of *Rhabderemia* and the commata of some *Biemna*. Characters and character states are listed as footnote on Table 1.

### *Notes on the character matrix*

A few changes in the character coding adopted by van Soest & Hooper (1993) were implemented as follows:

- Megascleres (character 7) has been recoded into a, styles; b, one category of rhabdostyles; c, two categories of rhabdostyles. Character 9 of van Soest & Hooper (1993) - length of megascleres has been considered non-independent to

TABLE 1: Taxon-character matrix for the cladistic analysis of *Rhabderemia*. Characters and character-states were adapted from those selected and discussed by van Soest & Hooper (1993). Changes implemented on their datamatrix are discussed in the text.

| Character<br>Taxon | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *R. (R.) acanthostyla* | a | a | b | b | a | a | b | b | a | b | c | a | a | a | a | b |
| *R. (R.) africana* | b | b | b | b | b | b | c | b | a | d | b | a | a | a | a | a |
| *R. (R.) antarctica* | a | a | a | ? | a | a | b | c | b | b | b | a | a | a | a | a |
| *R. (R.) besnardi* | b | a | a | ? | a | a | b | b | ab | d | b | a | a | a | a | a |
| *R. (R.) bistylifera* | b | a | b | b | ? | ? | c | a | a | d | b | a | a | a | a | a |
| *R. (R.) burtoni* | b | a | ? | ? | b | b | b | b | a | b | ? | a | b | a | a | a |
| *R. (R.) coralloides* | a | a | a | a | a | a | b | c | b | b | b | a | b | a | b | a |
| *R. (S.) destituta* | a | a | a | a | a | c | b | a | b | a | a | a | a | a | a | a |
| *R. (R.) fascicularis* | b | a | a | ? | a | a | b | c | b | a | b | a | a | a | b | a |
| *R. (R.) forcipula* | a | a | a | a | a | a | b | b | b | b | b | b | a | a | a | a |
| *R. (R.) gallica* | b | a | ? | ? | b | b | b | a | a | c | ? | a | b | a | a | a |
| *R. (R.) guernei* | b | a | ? | ? | a | a | b | b | a | b | b | a | a | a | b | a |
| *R. (R.) indica* | a | a | b | b | a | a | b | a | a | b | b | a | a | a | a | a |
| *R. (R.) intexta* | b | a | ? | a | a | a | b | b | a | a | b | b | a | a | a | a |
| *R. (R.) itajaí* | ab | a | a | b | a | a | c | b | b | b | b | a | a | a | a | a |
| *R. (R.) mammillata* | a | a | a | a | a | a | b | b | a | a | b | b | a | a | a | a |
| *R. (R.) minutula* | b | b | b | b | b | b | b | b | a | c | b | a | a | a | a | a |
| *R. (S.) mona* | a | a | a | ? | a | c | b | a | b | a | a | a | a | a | a | a |
| *R. (R.) mutans* | a | a | a | a | a | a | b | c | b | c | b | a | a | a | b | a |
| *R. (R.) profunda* | b | a | ? | ? | ? | ? | b | b | a | b | b | a | a | a | a | a |
| *R. (R.) prolifera* | b | b | b | b | b | b | b | b | a | c | b | a | a | a | a | a |
| *R. (R.) sorokinae* | a | a | b | a | a | a | b | b | a | b | b | a | a | b | a | a |
| *R. (R.) spinosa* | b | a | b | b | b | b | b | b | a | b | b | a | a | b | a | a |
| *R. (R.) spirophora* | a | a | b | b | a | a | b | a | a | b | b | a | a | a | a | a |
| *R. (R.) stellata* | a | a | a | a | a | a | b | a | b | b | b | a | a | a | a | a |
| *R. (R.) topsenti* | a | a | b | a | a | a | b | b | a | b | b | a | a | a | a | a |
| *R. (R.) toxigera* | b | a | b | ? | ? | ? | b | b | a | b | b | a | a | b | a | a |
| *R. (R.) uruguaiensis* | ab | a | a | ? | a | a | b | b | a | b | b | a | a | a | a | b |
| Desmacellidae | a | a | ab | ab | a | a | ab | a | ? | ab | a | a | a | b | a | ? |
| Raspailiidae | a | a | a | a | a | a | ab | a | ? | a | a | a | a | a | a | ? |

Characters and their states. 1: habit – a, elaborate; b, encrusting. 2: substrate - a, epibenthic; b, insinuating, occupying holes in the substrate. 3: consistency – a, firm; b, soft. 4: oscules – a, in stellate pattern; b, other. 5: ectosome – a, bouquet of rhabdostyles; b, single rhabdostyles. 6: choanosome – a, plumoreticulate; b, other. 7: megascleres – a, styles; b, single category of rhabdostyles; c, two categories of rhabdostyles. 8: spination of megascleres – a, smooth; b, slightly acanthose; c, heavily spined. 9: width of megascleres – a, up to 20 $\mu$m; b, up to between 20-30 $\mu$m. 10: microstyles – a, absent; b, present in one category, styloid base; c, present in one category, base slightly subtylostylote; d, present in two categories. 11: spirosigmata – a, absent; b, present. 12: large thraustosigmata – a, absent; b, present. 13: small thraustosigmata – a, absent; b, present. 14: toxas – a, absent; b, present. 15: thraustoxeas – a, absent; b, present. 16: pigment granules – a, absent; b, present.

character 7, as it actually referred to the number of categories of rhabdostyles. It has accordingly been merged here.

- *R. bistylifera* was assigned character-state 7.c here as it has two categories of rhabdostyles. In the datamatrix provided by van Soest & Hooper (l.c.), the species was coded as if possessing the plesiomorphic trait, viz. styles. This was probably a typographic error.

- *R. uruguaiensis* has been coded character-state 7.b, as we interpret the species to possess a single category of rhabdostyles (see also Oliveira & Hajdu 2005), instead of two as originally described by van Soest & Hooper (l.c.).
- Raspailiidae has been coded ambiguously for character 7 (possession of rhabdostyles) as it is yet uncertain whether the rhabdostyles present in some raspailiids are homologous or not to those in *Rhabderemia*.
- Spination of megascleres (character 8) has been recoded into a, smooth; b, slightly acanthose; c, heavily spined.
- Width of megascleres (character 9, = char. 10 of van Soest & Hooper, l.c.) has been recoded into a, up to 20 $\mu$m; b, up to between 20-30 $\mu$m. We refrained from aprioristically adding character state c for a possible reversal in character states, as suggested by van Soest & Hooper (l.c.) for *R. intexta* and *R. mammillata*.
- Microstyles (character 10) has been recoded into a, absent; b, present in one category, styloid base; c, present in one category, subtylostylote base; d, present in two categories. It results from merging van Soest & Hooper's (l.c.) characters 11, 12, 13 and 14, which we considered non-independent.
- *R. acanthostyla*, *R. gallica* and *R. mutans* were coded character-state 10.c instead of 10.b as they were described, and/or clearly illustrated to possess slightly-swollen basal terminations on their microstyles, but nevertheless, coded by van Soest & Hooper (l.c.) as if their microstyles had non-elaborate bases.
- *R. fascicularis*, *R. intexta* and *R. mammillata* were coded character-state 10.a, as we preferred not to consider aprioristically the absence of microstyles in these species as a subsequent loss.
- Outgroups were coded unknown for character 16 (presence of pigment granules).

For a comprehensive discussion on character coding for the species of *Rhabderemia* and the outgroup Raspailiidae refer to van Soest & Hooper (1993).

### *Character analysis*

If all the characters are treated as unordered under default parsimony, the size of the set of most parsimonious trees explodes, tree-buffer limit (ca. 60'000 trees) is quickly reached, preventing any more parsimonious trees being obtained. Van Soest & Hooper (1993) applied "Dollo" parsimony to megasclere length and thickness only. We have opted for coding characters 11 to 16 under "Dollo" parsimony. These are all simple "present" vs. "absent" characters, for which no biological functionality is yet known or hypothesised, which renders it much more likely that frequent parallel losses occurred, rather than the opposite, viz. parallel gains.

Two different analyses were performed, each with one of the outgroups. The analysis with Raspailiidae as the outgroup yielded on the first run 50821 trees, but only 164 after the first subsequent weighting of characters by their Rescaled Consistency Indices, 20 after the second, and 4 after the third subsequent weighting cycle, when the set of most parsimonious trees stabilized. If filtered for more resolution (polytomous trees discarded when more resolved ones exist), only two trees remained, differing by the allocation of *R. besnardi* and *R. itajai*, which can either be sister species, sisters of the clade ((*intexta*, *mammillata*) *forcipula*); or form an unresolved trichotomy with this

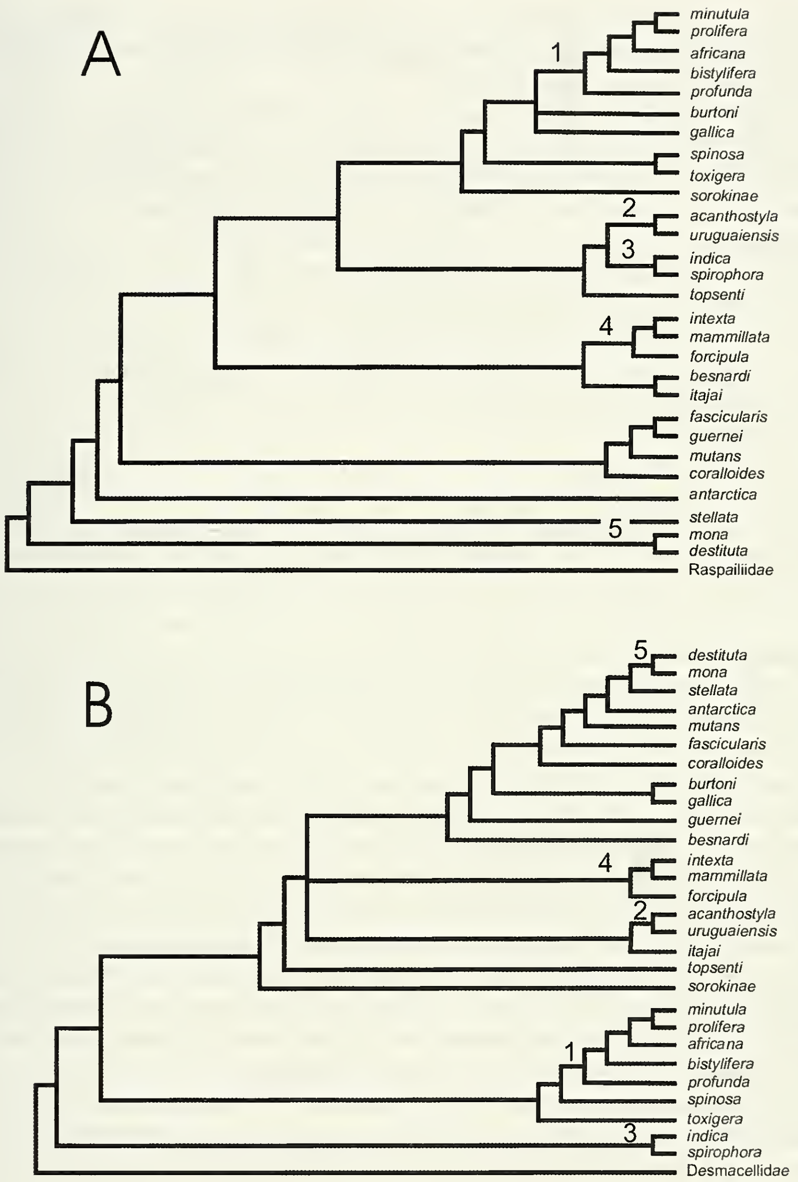

FIG. 4

Hypothetical phylogenetic relationships of the known species of *Rhabderemia*. (A) Polarized against the Raspailiidae. (B) Polarized against the Desmacellidae. Congruent clades on both are numbered 1-5 on the respective nodes. Refer to text for details on how these cladograms were obtained.

clade, and a further clade comprising 20 species. Figure 4a illustrates the first of these two alternatives, which coincides with the Nelson Consensus (sensu Page, 1989; = maximum clique, majority rule consensus with other compatible groupings of PAUP) for the four trees obtained when the set of equally parsimonious trees stabilized (CI = 0.6873, HI = 0.3127 and RI = 0.9596), and which is our preferred working hypothesis based on Raspailiidae as the outgroup.

When using Desmacellidae as the outgroup, the first run yielded only 112 trees, subsequently weighted to 12, where the set of equally parsimonious trees stabilized. If filtered for more resolution, only four trees remained, differing by the allocation of *R. profunda*, *R. fascicularis* and *R. mutans*. *R. profunda* is the sister of (((*prolifera*, *minutula*) *africana*) *bistylifera*) on two trees and forms an unresolved trichotomy with *R. besnardi* and a clade composed by another ten species. *R. fascicularis* and *R. mutans* can either be sister-species, sister to (((*destituta*, *mona*) *stellata*) *antarctica*), or *R. mutans* can be the sister to this clade, and *R. fascicularis* sister of them all. Figure 4b illustrates the preferred topology, the Nelson Consensus for the twelve trees obtained when the set of most parsimonious trees stabilized (CI = 0.5319, HI = 0.4681 and RI = 0.9286).

Important congruences are observed on both analyses. The following five clades were observed both with Raspailiidae and Desmacellidae as outgroups: *((((minutula, prolifera) africana) bistylifera) profunda)* – clade 1, *(acanthostyla, uruguaiensis)* – clade 2, *(indica, spirophora)* – clade 3, *((intexta, mammillata) forcipula)* – clade 4 and *(destituta, mona)* – clade 5. Clades 2, 3, 4 and 5 also occurred on van Soest & Hooper's (1993) analysis, and are thus considered likely robust hypotheses about phylogenetic relationships within *Rhabderemia*.

Important incongruences are more abundant though. Among these, the opposite allocation of *Rhabderemia destituta* and *mona* [= *R. (Stylospira)* spp.], *R. antarctica* and *R. stellata* is the most remarkable. Polarized against Raspailiidae these species are at a basal position on the *Rhabderemia* tree. When polarized against the Desmacellidae, they all end up at a very derived position in the cladogram. This is certainly a consequence of assuming the possibility that the microstyles of *Rhabderemia* are homologous to the commas of Desmacellidae (the family has been coded polymorphic for character 10, being thus allowed both to possess and not to possess microstyles), so that the lack of these microscleres in *R. (Stylospira)* spp. would become a derived loss higher in the tree. Such a major shift of clades in the competing postulated histories for *Rhabderemia* makes it clear that a sounder picture on the genus' whereabouts in poecilosclerid classification is needed, before the exercise of inferring its deep historical biogeography can proceed any further than essayed here.

As most of the new information discovered in this present study relates to southern South American *Rhabderemia*, these species, along with clades mentioned above as likely to be robust, form the basis for the following biogeographic analysis.

## BIOGEOGRAPHIC DISCUSSION

### *Clades shared by both phylogenetic reconstructions, and also found by van Soest & Hooper (1993)*

Figure 5 shows a world map with superimposed clades 2-5 of the *Rhabderemia* phylogenies in Fig. 4. Clade 2 comprises *R. uruguaiensis* from southern South America, and *R. acanthostyla* from India and the Indonesia area. Clade 3, *R. spirophora*, from southern Africa, and *R. indica*, also from India and the Indonesia area.

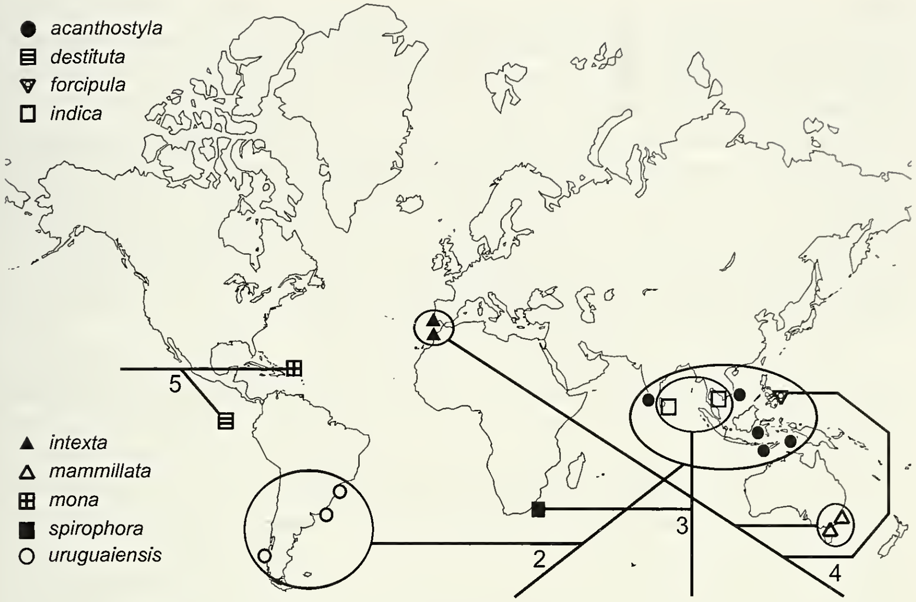

FIG. 5

World map with *Rhabderemia* clades 2-5 (Fig. 4) plotted. These clades were also obtained by van Soest & Hooper (1993). The largest ellipse plotted in the Indonesia area refers only to *R. acanthostyla*. *Rhabderemia indica* and *R. forcipula*, which also appear in the ellipse, belong to clades 3 and 4, respectively.

Clade 4 includes *R. intexta* and *R. mammillata*, respectively from the Lusitanian and south-eastern Australian areas, and their sister species, *R. forcipula*, from the Philippines. Clade 5 comprises both species of subgenus *Stylospira*, *R. (S.) mona* and *R. (S.) destituta*, respectively from the Caribbean and the Galapagos areas.

Clades 2 and 4 were listed as examples of markedly separate sister-relationships and likely consequences of widespread extinction in the history of the genus (van Soest & Hooper, 1993). The extended distribution range of *R. uruguaiensis* observed here though, turned clade 2 into another example of a Trans-Pacific track (e.g. Sluys, 1994). Formerly known only from the south-western Atlantic, the species was discovered here from the south-east Pacific (Chilean fjord area), thus slightly shortening its distance to the known distribution of its sister-species (as above). Previous approaches to demosponge biogeography found additional Trans-Pacific tracks. Hooper & Lévi (1994) found a sister-species relationship for *Ptilocaulis walpersi* (Duchassaing & Michelotti, 1864) and *P. echidnaeus* (Lamarck, 1814), a Caribbean - southern Australia relationship, which could easily date farther back than the closure of the Isthmus of Panama, thus representing another Trans-Pacific track. Hajdu (1995) found precisely the same track for the sister-pair *Mycale unguifera* Hajdu, Zea, Kielman & Peixinho, 1995 and *M. australis* (Gray, 1867). On the other hand, rather distinct routes were observed for the sister-pair *Mycale novaezelandiae* Dendy, 1924 and *M. toporoki* Koltun, 1958, respectively from New Zealand and the Boreal Pacific; as well as for *M. arenaria* Hajdu & Desqueyroux-Faúndez, 1994, *M. thielei* Hajdu & Desqueyroux-Faúndez, 1994 and *M. paschalis* Desqueyroux-Faúndez, 1990, whose clade implied the following biogeographic relationships [(south-western Atlantic, south-eastern Pacific), Easter Island]. The bridging of similarly long distances across the Pacific has been explained by several competing hypotheses, such as Expanding Earth, lost Pacifica continent and allochthonous terranes (Sluys, 1994; McCarthy, 2005), but as pointed out by van Soest & Hooper (1993), the dispersal hypothesis cannot be ruled out. Even though no concrete evidence for Trans-Pacific dispersal of sponges is available to date, a growing body of literature is demonstrating how well the rafting hypothesis fits the known distributions of several poor dispersers (e.g. pumice rafting in particular - Jokiel, 1984; Ó Foighil *et al.,* 1999; Waters & Roy, 2004; Donald *et al.,* 2005), and it is quite conceivable that sponges could rank among these.

Clade 3 shows an Indian Ocean track which, given its distinct positions in the *Rhabderemia* phylogenies obtained (Fig. 4), could be explained through the competing scenarios of vicariance and dispersal. A dispersalist hypothesis appears conceivable when Raspailiidae is used as an outgroup (Fig. 4A), because the separation of *R. indica* and *R. spirophora* appears at a more derived position in the *Rhabderemia* phylogeny, a time when the African and Indian (sub)continents were isolated for tens of millions of years already. This contrasts to van Soest & Hooper's (1993) preferred hypothesis, which albeit construed as Recent, chose a vicariant mode explanation. Which Recent vicariance it might have been was not mentioned, and none is known to us. A vicariant explanation appears more likely though, when Desmacellidae is used as an outgroup, because the position of clade 3 shifts to the basalmost location in *Rhabderemia*'s hypothetical evolutionary tree (Fig. 4B). Van Soest & Hooper (l.c.) argued that *Rhabderemia* was most likely already diverse in early Tertiary times as a consequence of Hinde & Holme's (1892) finding of *Rhabderemia*-like rhabdostyles in Late Eocene - Early Oligocene strata of New Zealand. This hypothesis assumes that widespread Recent dispersal is less likely a scenario. If these premises are indeed true, it is conceivable that clade 3 could represent the early to late Cretaceous break-up and drifting of India from the African continent.

Clade 5 stretches across the Isthmus of Panama. Van Soest & Hooper (1993) took this as sufficient evidence to infer the likelihood of a vicariance explanation for the sister pair *R. destituta* and *R. mona*, linked to the raising of the isthmus. Nevertheless, as pointed out above, the position of this clade shifts to opposite polarities (time frames) within the *Rhabderemia* phylogeny depending on the chosen outgroup. We judge that this classical vicariance explanation cannot fit such possibly distinct inferred timing for this cladogenesis. In fact, the basal position of clade 5 in van Soest & Hooper's (l.c.) cladogram, which matches our result for outgroup Raspailiidae (Fig. 4A), appears to favour more ancient than a Recent vicariance event such as the last closing of the trans-isthmian passage. This Recent vicariance scenario is more likely an explanation when Desmacellidae is used as an outgroup and clade 5 ends up at a very derived position in the *Rhabderemia* tree.

Given the likelihood that *Rhabderemia* diversified earlier than the Tertiary, *R. (Stylospira),* clade 5, must have been around significantly earlier than the nearly concomitant appearance of the recent Galapagos Islands and the raising of the Isthmus of Panama by accretion of the Chortis block (Honduras and Nicaragua) in between

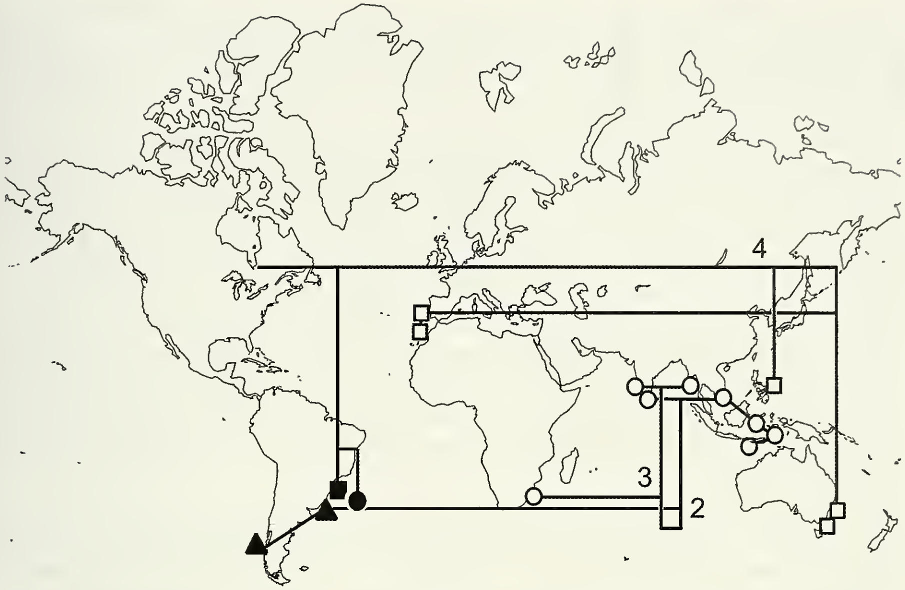

FIG. 6

World map illustrating the biogeographic affinities of *Rhabderemia besnardi* (dark square), *R. itajai* (dark circle) and *R. uruguaiensis* (dark triangles) to additional *Rhabderemia* in clades 2, 3 and 4, implied from the hypothetical phylogeny with Raspailiidae as the outgroup.

northern and southern Central America (Rosen, 1985). A scenario compatible with these events implies that *R. (Stylospira)* existed for a considerably long time, somewhere in the Tropical Eastern Pacific, from where it reached the Galapagos Islands in quite recent times via dispersal, at about the same time the clade became extinct in Tropical Eastern Coastal Pacific. Nevertheless, it is now accepted that a much older history of oceanic islands in the intersection of the Pacific, Nazca and Cocos Plates triple junction exists (Grehan, 2001), which could spread as far back as the 80-90 My of geologic hotspot activity in the area. Accordingly, clade 5 might have been around Galapagos for a rather longer time. In this way, the vicariance accounting for both species in clade 5 could have been related to other phenomena in Tropical Eastern Pacific / Caribbean geohistory, possibly in connection with the complex movements of Caribbean terranes and microplates (Rosen, 1985) and their associated volcanism.

### *Clades found for Rhabderemia besnardi and R. itajai*

Two species were included here for the first time in the postulated phylogeny of *Rhabderemia*, viz. *R. besnardi* and *R. itajai*, both known only from their type localities, in the SW Atlantic. Curiously, their postulated affinities in the phylogenetic trees (illustrated in figures 4A and 4B) are rather different. Figure 4a shows both as sister species, this sister pair being sister of the clade *((intexta, mammillata), forcipula)*. Figure 6 is a graphical representation of the clades including *R. besnardi, R. itajai* and *R. uruguaiensis*, with outgroup Raspailiidae. The implied local vicariance in the southwestern Atlantic area accounting for the sister pair *R. besnardi* and *R. itajai* is not obvious to us, possibly related to range expansions / retractions associated to varying sea levels following glacial / interglacial periods. No obvious biogeographic barrier occurs in the area, neither is known to us to have occurred. Both species were found only 200 km apart, on the outer platform or upper slope, seemingly occurring on the same water mass (Central South Atlantic Water). Nevertheless, *R. besnardi* was collected from the shallower limit of this water mass, thus suggesting a possible preference for Tropical waters. A possibly similar scenario for speciation in the south-western Atlantic has been proposed by Muricy *et al.* (2001) to explain the sister pair *Petromica ciocalyptoides* (Zea & van Soest, 1986) and *P. citrina* Muricy *et al.*, 2001 (Desmanthidae, "Lithistida"). Ecophysiological barriers could exist, explaining *P. ciocalyptoides*' apparent preference for warmer Tropical Brazilian Current waters, as found north of Rio de Janeiro State, and *P. citrina's* for slightly colder Brazilian Current waters, intermittently mixed to upwelling Central South Atlantic Waters to the south of Rio de Janeiro. This kind of reticulate evolutionary scenario was developed from inferred historical changes to connectivity derived from changing current regimes, and the opening and closing of passages, on glacial vs. inter-glacial periods (e.g. Veron, 1996).

The next cladogenetic event of concern here (CE 4) is the one responsible for the separation of *R. besnardi* plus *R. itajai* from clade 4 in figure 6. A likely vicariant explanation is not obvious, partly as a consequence of the markedly discontinuous distributions observed in the latter clade (van Soest & Hooper, 1993; and above). At least five earlier cladogenetic events are postulated for *Rhabderemia* in fig. 4A, which contribute to render an association of CE 4 with the Atlantic Deep Sea Barrier vicariance an unlikely reconstruction of the evolutionary history of these species, as this would push the genus' history too far back. The kinematics of the South Atlantic opening is still controversial (Eagles, 2007), but if CE 4 is postulated to match the onset of this biogeographic barrier, *Rhabderemia* must have been around and quite diverse in Cretaceous times already (at least six clades). At this time, a warm, narrow and shallow South Atlantic was there, and as such, the clade comprising clade 4 + *R. besnardi* and *R. itajai* would have had an open avenue for the colonization of the south-eastern Atlantic and the entire western Indian Ocean. No apparent reason, other than widespread extinction, can reasonably account for present days failure to recover descendants of CE 4 on these areas, if the time frame constructed here is correct. But, the present day moderately deep-water occurrence of both south-western Atlantic species in question, 153-380 m depth, suggests a possible preference for sub-tropical/temperate waters of their ancestors too. When did such conditions develop in the South Atlantic? A more recent jump dispersal may be the best hypothesis in the moment to account for CE 4.

Figure 7 illustrates the cladogenetic events associated with *R. besnardi* and *R. itajai's* history in the tree shown in Figure 4B, with Desmacellidae as the outgroup. The trans-pacific track spanned by *R. uruguaiensis* and *R. acanthostyla* (clade 2) has been discussed above. Differently from what has been discussed in the above paragraph, *R. itajai* has a sister species relationship to this clade (instead of to *R. besnardi* as in Fig. 4a), which is suggestive of an unusual east-west polarity for the above quoted track. As the whole clade pertains to a trichotomy, it is difficult to pursue any further discussion on deeper historical events leading to the colonization of the south-western Atlantic.

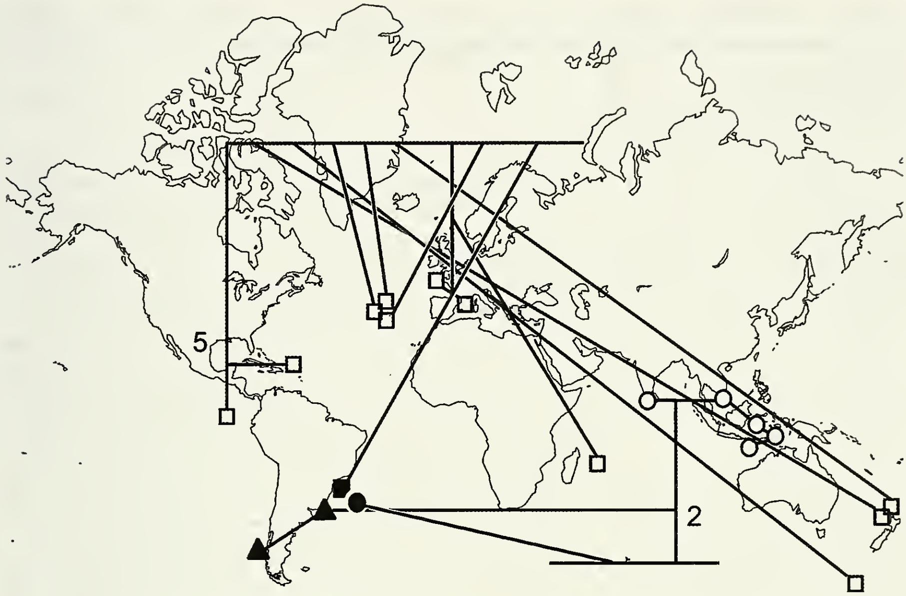

FIG. 7

World map illustrating the biogeographic affinities of *Rhabderemia besnardi* (dark square), *R. itajai* (dark circle) and *R. uruguaiensis* (dark triangles) to additional *Rhabderemia* in clades 2, 3, 4 and 5,implied from the hypothetical phylogeny with Desmacellidae as the outgroup.

*Rhabderemia besnardi*, on the other hand, is sister to another ten species in the genus, with important North Atlantic (five species) and south-western Pacific (two species) components. The occurrence of *R. burtoni* in the western Indian Ocean, and of its sister species *R. gallica* extending its known distribution in the western Mediterranean, makes a Tethyan relict hypothesis more conceivable for the entire ten species clade. The cladogenetic event splitting these two species has been equated by van Soest & Hooper (1993) to a likely consequence of the Miocene collision of the African and Asian continents, severing the Tethyan gateway. What is perhaps unusual for a Tethyan clade is a south-western Atlantic sister species, which in this case has to be seen as a Gondwanan relict, as its ancestors must have reached the south-western Atlantic from the south. The alternative scenario of this entire clade reaching the south-western Atlantic through the Equatorial Atlantic implies accepting an early connection between the northern and southern sectors of this ocean, which appears likely in recent reconstructions (e.g. Silveira & Stutzmann, 2002; Eagles, 2007), but also of possible widespread extinction of shallower species in the western margin of the South Atlantic, as well as every likely founder *Rhabderemia* species on its eastern margin.

A last point for consideration regards the highly derived position of clade 5 in Figure 4B. Opposing what has just been suggested for clade 2, the polarity of clade 5 is most likely a west-east one, as inferred from the present days distribution of its two next sister species. First, *R. stellata*, which is known from northern New Zealand.

Second, *R. antarctica*, known from the Antarctic region. These two species suggest a range extension towards the Tropical Eastern Pacific first, followed by invasion of the Caribbean area.

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## REFERENCES

DESQUEYROUX, R. & MOYANO, H. 1987. Zoogeografia de Demospongias chilenas. *Boletin de la Sociedad de Biologia de Concepción, Chile* 58: 39-66.

DONALD, K. M., KENNEDY, M. & SPENCER, H. G. 2005. The phylogeny and taxonomy of austral monodontine topshells (Mollusca: Gastropoda: Trochidae), inferred from DNA sequences. *Molecular Phylogenetics and Evolution* 37: 474-483.

EAGLES, G. 2007. New angles on South Atlantic opening. *Geophysical Journal International* 168: 353-361.

GREHAN, J. 2001. Biogeography and evolution of the Galapagos: integration of the biological and geological evidence. *Biological Journal of the Linnean Society*74: 267-287.

HAJDU, E. 1995. *Macroevolutionary Patterns Within the Demosponge Order Poecilosclerida. Phylogeny of the marine cosmopolitan genus* Mycale*, and an integrated approach to biogeography of the seas.* PhD Thesis, University of Amsterdam. Centralle Drukkerij, Amsterdam. 1-174 pp.

HAJDU, E., SANTOS, C. P., LOPES, D. A., OLIVEIRA, M. V., MOREIRA, M. C. F., CARVALHO, M. S. & KLAUTAU, M. 2004. Filo Porifera (pp: 49-56). *In*: AMARAL, A.C.Z. & ROSSI-WONGTSCHOWSKI, C.L.D.B. (org.). *Biodiversidade Bentônica da região sul-sudeste do Brasil - Plataforma Externa e Talude.* Série Documentos REVIZEE Score Sul. 216 pp.

HINDE, G. J. & HOLMES, W. M. 1891. Sponge remains in the Tertiary of New Zealand. *Linnean Journal of Zoology* 24: 177-262.

HOOPER, J. N. A. 1997. *Guide to sponge collection and identification*. Copyright, Qld. Museum, 143 p., pls 1-35.

HOOPER, J. N. A. 2002. Family Rhabderemiidae (pp. 511-513). *In:* HOOPER, J. N. A. & SOEST, R. W. M. (eds). *Systema Porifera: a guide to the classification of sponges*. Kluwer Academic/Plenum Publishers, New York, 1, i-xx + 1101 pp. + xxi-xlviii.

HOOPER, J. N. A. & LÉVI, C. 1994. Biogeography of Indo-west Pacific sponges: Microcionidae, Raspailiidae, Axinellidae (pp. 191-212). *In*: SOEST, R.W.M. van, BRAEKMAN, J.-C. & KEMPEN, Th. van (eds). *Sponges in Time and Space, Proceedings of the Fourth International Porifera Congress*. Balkema, Rotterdam. i-xviii, 1-515 pp.

JOKIEL, P. L. 1984. Long distance dispersal of reef corals by rafting. *Coral Reefs* 3: 113-116.

MCCARTHY, D. 2005. Biogeographical and geological evidence for a smaller, completely-enclosed Pacific Basin in the Late Cretaceous. *Journal of Biogeography* 32: 2161-2177.

MURICY, G., HAJDU, E., MINERVINO, J. V., MADEIRA, A. V. & PEIXINHO, S. 2001. Systematic revision of the genus *Petromica* Topsent (Demospongiae: Halichondrida), with a new species from the southwestern Atlantic. *Hydrobiologia* 443: 103-128.

O'FOIGHIL, D. O., MARSHALL, B. A., HILBISH, T. J. & PINO, M. A. 1999. Trans-Pacific range extension by rafting is inferred for the flat oyster *Ostrea chilensis. Biological Bulletin* 196: 122-126.

OLIVEIRA, M. V. & HAJDU, E. 2005. Taxonomy of *Rhabderemia* Topsent, 1890 collected from the southeastern Brazilian continental shelf and slope by Programme REVIZEE (Rhabderemiidae, Poecilosclerida, Demospongiae), with the description of two new species. *Zootaxa* 844: 1-12.

PAGE, R. D. M. 1989. Comments on component-compatibility in historical biogeography. *Cladistics* 5: 167-182.

ROSEN, D. E. 1985. Geological hierarchies and biogeographical congruence in the Caribbean. *Annals of the Missouri Botanical Garden* 72: 636-659.

SILVEIRA, G. & STUTZMANN, E. 2002. Anisotropic tomography of the Atlantic Ocean. *Physics of the Earth and Planetary Interiors* 132: 237-248.

SLUYS, R. 1994. Explanations for biogeographic tracks across the Pacific Ocean: a challenge for paleogeography and historical biogeography. *Progress in Physical Geography* 18: 42-58.

SWOFFORD, D. L. 2002. *PAUP*: Phylogenetic Analysis Using Parsimony (and Other Methods) 4.0 Beta*, CD-ROM (+ b10 upgrade). Sinauer Associates, Sunderland.

VAN SOEST, R. W. M. & HOOPER, J. N. A. 1993. Taxonomy, phylogeny, and biogeography of the marine sponge genus *Rhabderemia* Topsent, 1890 (Demospongiae, Poecilosclerida). *Scientia Marina* 57(4): 319-351.

VAN SOEST, R. W. M. & STENTOFT, N. 1988. Barbados deep-water sponges. *Studies on the Fauna of Curaçao and other Caribbean Islands* 215: 1-175.

WATERS, J. M. & ROY, M. S. 2004. Out of Africa: the slow train to Australasia. *Systematic Biology* 53, 18-24.

VERON, J. E. N. 1996. *Corals in Space and Time: the Biogeography and Evolution of the Scleractinia.* New South Wales University Press, Sidney. 321 pp.

REVUE SUISSE DE ZOOLOGIE 115 (2): 397-431; juin 2008

# Specie del genere *Pseudoplandria* Fenyes, 1921 nel Borneo (Coleoptera, Staphylinidae)*

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**The species of the genus *Pseudoplandria* Fenyes, 1921 from Borneo (Coleoptera, Staphylinidae).** - This study on the genus *Pseudoplandria* Fenyes from Borneo provides illustrations of *P. ruficollis* Cameron, the only known species from Borneo of which a lectotypus is designated. The followings 32 species are described as new: *P. globulitheca* sp. n., P. *cavicola* sp. n., *P. seditiosa* sp. n., *P. zerchei* sp. n., *P. belalongica* sp. n., *P. anomala* sp. n., *P. subtricarinata* sp. n., *P. laminaris* sp. n., *P. pseudobellicosa* sp. n., *P. liwaguensis* sp. n., *P. plicatella* sp. n., *P. subliwaguensis* sp. n., *P. subtilis* sp. n., *P. dilatatalamina* sp. n., *P. bruneicola* sp. n., *P. bellicosa* sp. n., *P. sabahensis* sp. n., *P. nobilis* sp. n., *P. altitudinis* sp. n., *P. fugax* sp. n., *P. obscura* sp. n., *P. sinusifera* sp. n., *P. subanomala* sp. n., *P. sanguinicollis* sp. n., *P. pseudosanguinicollis* sp. n., *P. superba* sp. n., *P. parasanguinicollis* sp. n., *P. distinctatheca* sp. n., *P. kinabaluicola* sp. n., *P. expansa* sp. n., *P. biperforata* sp. n. and *P. serpentina* sp. n. Habitus as well as male and female genitalia of the new species and of *P. ruficollis* Cameron are illustrated. A key to the species is provided.

**Key words:** Coleoptera - Staphylinidae - Aleocharinae - taxonomy - Borneo.

## INTRODUZIONE

Il presente lavoro ha lo scopo di esporre il risultato dell'esame delle Aleocharinae del genere *Pseudoplandria* Fenyes, 1921, raccolte nel Parco Nazionale del Monte Kinabalu e altrove nel Borneo, dal Dr. Aleš Smetana di Ottawa, dal Dr. Burckhardt e dal Dr. Ivan Löbl già del Museo di Storia Naturale di Ginevra. Alcuni esemplari sono proprietà del DEI di Müncheberg. Nel corso dell'esame del nuovo materiale si costata che le specie di questo genere nel Borneo erano assai poco note. Il gran numero di nuove specie osservate ne è la prova.

## MATERIALE E METODO

L'esame è basato prevalentemente sugli esemplari adulti raccolti generalmente nel Parco Nazionale del Monte Kinabalu dal Dr. Aleš Smetana di Ottawa durante le sue

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* 212° Contributo alla conoscenza delle Aleocharinae.

Manoscritto accettato il 21.03.2008

spedizioni nel 1987 e 1988, dalla spedizione Burckhardt & Löbl del Museo di Storia Naturale di Ginevra del 1987 e 1988.

La tassonomia delle nuove specie del Borneo presenta serie difficoltà, superate sempre grazie all'esame dei caratteri dell'organo copulatore maschile e della spermateca. Prima della pubblicazione del presente lavoro nessun esame a fini tassonomici di questi importanti organi e strutture è stato compiuto dagli autori del lontano passato. Parte della serie tipica dell'unica specie nota del Borneo, *P. ruficollis* Cameron, è stata da me esaminata e inserita nella chiave qui data per la prima volta. L'etimologia delle nuove specie è omessa quando evidente come *sabahensis* o *kinabaluensis*.

Quasi tutti gli esemplari sono stati dissezionati per le serie di pochi individui. Le strutture genitali sono state montate in balsamo del Canadà su piccoli rettangoli trasparenti di materiale plastico, infilzati sullo spillo dell'esemplare. Le strutture genitali sono state studiate usando un microscopio composto e disegnate mediante oculare a reticolo. Gli habitus sono stati disegnati con l'uso di un oculare micrometrico di un microscopio binoculare. Tutti i disegni sono dell'autore fino alla fase finale.

Il sicuro riconoscimento, da parte del lettore, dei generi e delle specie è qui affidato soprattutto alla parte illustrativa che ha linguaggio internazionale. Per questo motivo le descrizioni sono brevi, limitate a porre in evidenza ciò che non è riproducibile graficamente come il colore, la reticolazione e la granulosità. D'altronde per le specie della sottofamiglia Aleocharinae la sola descrizione anche molto accurata e lunga non dà quasi mai la certezza di un'esatta identificazione delle varie specie. È l'osservazione del disegno dell'edeago e/o della spermateca, insieme con quello dell'habitus, che aiuta molto a risolvere problemi interpretativi dati dalla sola descrizione.

Gli holotypi delle nuove specie sono depositati nel Museo di Storia Naturale di Ginevra (MHNG), nel DEI di Müncheberg (DEI) e nell'Institut Royal des Sciences Naturelles de Belgique di Bruxelles (IRSN). Paratypi sono conservati in collezione Smetana, nel Museo di Storia Naturale di Ginevra e nell'Institut Royal des Sciences Naturelles de Belgique di Bruxelles.

## ***Pseudoplandria* Fenyes, 1921**

Il genere *Pseudoplandria* Fenyes, 1921, è diffuso unicamente della regione orientale. Prima dell'inizio dei miei studi sulle Aleocharinae del Borneo, una sola specie di questo genere era nota di quest'isola: *P. ruficollis* Cameron, 1928, del Mt. Dulit. Ho esaminato due cotypi della serie tipica (BMNH, Museo di Storia Naturale di Londra).

### ***Pseudoplandia ruficollis* Cameron, 1928**

*Pseudoplandia ruficollis* Cameron, 1928: 422.

LECTOTYPUS (presente designazione): BMNH; maschio, etichettato Mt. Dulit, E 9.83, *Pseudoplandria ruficollis* Cam., Figg. 5-7.

PARALECTOTYPUS: BMNH; femmina, stessa provenienza, Fig. 8.

MATERIALE SUPPLEMENTARE: Non della serie tipica, mi è nota anche su 3 maschi del DEI così etichettati: N. Borneo, Sabah, Bunsit, Kenningan, 31.VII-2.VIII.1985, leg. K. Maruyama.

## CHIAVE DELLE SPECIE DEL GENERE *PSEUDOPLANDRIA* FENYES, 1921 NEL BORNEO

| | | |
|---|---|---|
| 1 | Sutura delle elitre evidentemente più corta della linea mediana del pronoto | 2 |
| - | Sutura delle elitre circa lunga quanto la linea mediana del pronoto o evidentemente più lunga | 8 |
| 2 | Pronoto giallo-rossiccio | 3 |
| - | Pronoto bruno o bruno-rossiccio | 5 |
| 3 | Capo e addome uniformemente giallo-rossiccio; edeago Figg. 2-3, spermateca Fig. 4. Lunghezza 2,5 mm | *P. globulitheca* sp. n. |
| - | Capo bruno e addome bicolore giallo-rossicci e bruno | 4 |
| 4 | Undicesimo antennomero uniformemente bruno-rossiccio; quinto antennomero più lungo che largo; occhi più lunghi delle tempie, in visione dorsale; addome giallo-rossiccio con una fascia bruna; edeago Figg. 6-7, spermateca Fig. 8. Lunghezza 2,4 mm | *P. ruficollis* Cameron, 1928 |
| - | Undicesimo antennomero bicolore bruno con apice giallo-rossiccio; quinto antennomero trasverso; occhi più corti delle tempie, in visione dorsale; addome bruno con pigidio giallo-rossiccio; spermateca Fig. 10. Lunghezza 4,1 mm | *P. cavicola* sp. n. |
| 5 | Corpo uniformemente rossiccio e undicesimo antennomero giallo-rossiccio; pronoto molto più stretto delle elitre; edeago Figg. 12-13. Lunghezza 2,9 mm | *P. seditiosa* sp. n. |
| - | Corpo bicolore bruno o rossiccio e nero-bruno; undicesimo antennomero bruno o bruno con apice giallo-rossiccio; pronoto poco più stretto delle elitre | 6 |
| 6 | Solco basale degli uroterghi liberi terzo e quarto senza punteggiatura; undicesimo antennomero bruno con apice giallo-rossiccio; spermateca Fig. 15. Lunghezza 2,7 mm | *P. zerchei* sp. n. |
| - | Solco basale degli uroterghi liberi terzo e quarto con punteggiatura più o meno forte; undicesimo antennomero uniformemente bruno | 7 |
| 7 | Pronoto distintamente trasverso, poco ristretto in avanti e con margini laterali rossicci; punteggiatura degli uroterghi liberi terzo e quarto superficiale; rapporto lunghezza pronoto/lunghezza sutura delle elitre pari a 1,27; edeago Figg. 17-18. Lunghezza 2,7 mm | *P. belalongica* sp. n. |
| - | Pronoto poco trasverso, molto ristretto in avanti e unicolore rossiccio; rapporto lunghezza pronoto/lunghezza sutura delle elitre pari a 1,33; spermateca fig. 19. Lunghezza 3,7 mm | *anomala* sp. n. |
| 8 | Sutura delle elitre circa lunga quanto la linea mediana del pronoto | 9 |
| - | Sutura delle elitre distintamente più lunga della linea mediana del pronoto | 25 |
| 9 | Corpo in gran parte giallo-rossiccio | 10 |
| - | Corpo prevalentemente bruno, rossiccio e bruno-rossiccio | 15 |
| 10 | Elitre del maschio con caratteri sessuali secondari evidenti, come pliche o carene | 11 |
| - | Elitre del maschio senza caratteri sessuali secondari | 12 |

11 Elitre del maschio con una plica a ciascun angolo posteriore interno, fig. 21; tutti gli uroterghi liberi con una carena mediana posteriore saliente; edeago ampiamente arcuato, Figg. 23-24; introflessione apicale del bulbo distale della spermateca presente, Fig. 22. Lunghezza 3,8 mm . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *P. subtricarinata* sp. n.

- Elitre del maschio con un rilievo saliente ricurvo e obliquo, Fig. 25; uroterghi liberi del maschio senza carene mediane; edeago quasi rettilineo al lato ventrale, Figg. 27-28; bulbo distale della spermateca senza introflessione apicale, Fig. 26. Lunghezza 3,4 mm . . . . . . . . . . . . *P. laminaris* sp. n.

12 Punti del fondo degli uroterghi liberi terzo e quarto allungati longitudinalmente; edeago profondamente arcuato al livello della «crista apicalis», Figg. 30-31. Lunghezza 3,6 mm . . . . . . . . . . . *P. pseudobellicosa* sp. n.

- Punti del fondo degli uroterghi liberi terzo e quarto non allungati; edeago mai profondamente arcuato al livello della «crista apicalis» . . . . . . . 13

13 Pronoto poco trasverso, con quattro punti disposti sui vertici di un rettangolo discale; armatura genitale interna dell'edeago composta di numerosi pezzi ben sclerificati, Figg. 33-34; spermateca Fig. 35. Lunghezza 2,6 mm . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *P. liwaguensis* sp. n.

- Pronoto molto trasverso, senza punti in rettangolo sul disco; armatura genitale interna dell'edeago ridotta; spermateca con strie interne della porzione mediana . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 14

14 Undicesimo antennomero giallo-rossiccio; corpo più tozzo, Fig. 37; quinto urotergo libero del maschio senza plica mediana; edeago, in visione ventrale, largo alla porzione distale, Figg. 38-39; introflessione apicale del bulbo distale della spermateca non raggiungente il centro dello stesso bulbo distale, Fig. 40. Lunghezza 2,3 mm . . . . . *P. plicatella* sp. n.

- Undicesimo antennomero bruno; corpo snello, Fig. 41; quinto urotergo libero del maschio con una plica mediana; edeago, in visione ventrale, stretto alla porzione distale, Figg. 42-43; introflessione apicale del bulbo distale della spermateca raggiungente il centro dello stesso bulbo distale della stessa spermateca, Fig. 44. Lunghezza 2,3 mm . . *P. subliwaguensis* sp. n.

15 Corpo uniformemente bruno, al massimo il margine posteriore degli uroterghi liberi è rossiccio . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 16

- Corpo multicolore bruno con parti rossicce, nero-brune o giallo-rossicce . . . 18

16 Edeago ampiamente e profondamente arcuato al livello della «crista apicalis», Figg. 46-47; spermateca Fig. 48. Lunghezza 3,5 mm . . . *P. subtilis* sp. n.

- Edeago non arcuato al livello della «crista apicalis» o strettamente arcuato . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 17

17 Occhi lunghi quanto le tempie, in visione dorsale, Fig. 49; undicesimo antennomero lungo quanto i quattro antennomeri precedenti riuniti; edeago senza plica ventrale, Figg. 50-51. Lunghezza 3,2 mm . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *P. dilatatalamina* sp. n.

- Occhi più lunghi delle tempie, in visione dorsale, Fig. 52; undicesimo antennomero lungo quanto i tre antennomeri precedenti riuniti; edeago con plica ventrale, Figg. 53-54; spermateca Fig. 55. Lunghezza 2,7 mm . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *P. bruneicola* sp. n.

18 Undicesimo antennomero giallo-rossiccio o giallo . . . . . . . . . . . . . . . . . . . . 19

- Undicesimo antennomero bruno o nero . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 22

19 Pigidio giallo-rossiccio . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 20

- Pigidio bruno o bruno-rossiccio . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 21

20 Elitre del maschio con una carena arcuata, Fig. 56; uroterghi liberi terzo e quarto con base densamente punteggiata, Fig. 56; armatura genitale interna dell'edeago lunghissima, Figg. 58-59; introflessione apicale del bulbo distale della spermateca assente, Fig. 57. Lunghezza 3,2 mm . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *P. bellicosa* sp. n.

- Elitre del maschio semplici Fig. 60; uroterghi liberi terzo e quarto senza punteggiatura basale; armatura genitale interna dell'edeago corta Figg. 61-62; spermateca Fig. 63. Lunghezza 3,2 mm . . . . . . . . . . *P. sabahensis* sp. n.

21 Occhi molto sviluppati e sporgenti; addome unicolore rossiccio; introflessione apicale del bulbo distale della spermateca profondissima. Lunghezza 2,8 mm . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *P. pluvialis* Pace, 1986

- Occhi poco sviluppati e non sporgenti; addome bicolore bruno-rossiccio e rossiccio; introflessione apicale del bulbo distale della spermateca debole, Fig. 67. Lunghezza 3,6 mm . . . . . . . . . . . . . . . *P. nobilis* sp. n.

22 Occhi ridotti, più corti o lunghi quanto le tempie; zampe giallo-rossicce . . . . 23

- Occhi enormi e tempie cortissime; zampe brune . . . . . . . . . . . . . . . . . . . . . . 24

23 Margine posteriore degli uroterghi liberi secondo, terzo, quarto e quinto, rossiccio; edeago profondamente ricurvo al lato ventrale, Figg. 69-70. Lunghezza 2,6 mm . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *P. altitudinis* sp. n.

- Uroterghi liberi uniformemente rossicci; edeago non ricurvo al lato ventrale, Figg. 72-73. Lunghezza 2,3 mm . . . . . . . . . . . . . . . . . . *P. fugax* sp. n.

24 Pronoto fortemente trasverso; uroterghi liberi terzo e quarto punteggiati alla base; introflessione apicale del bulbo distale della spermateca a pareti strette e senza scanalatura basale; bulbo prossimale della spermateca assai poco sviluppato. Lunghezza 2,1 mm . . . *P. borneensis* Pace, 1986

- Pronoto debolmente trasverso, Fig. 74; uroterghi liberi terzo e quarto senza punteggiatura basale; edeago Figg. 75-76; spermateca Fig. 77. Lunghezza 2,8 mm . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *P. obscura* sp. n.

25 Pronoto giallo-rossiccio . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 26

- Pronoto rossiccio, bruno, bruno-rossiccio o giallo-bruno . . . . . . . . . . . . . . . . 31

26 Addome giallo-rossiccio . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 27

- Addome bruno-rossiccio o bruno . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 29

27 Capo giallo-rossiccio; introflessione apicale del bulbo distale della spermateca profondissima, Fig. 81. Lunghezza 2,6 mm . . . . . . . *P. sinusifera* sp. n.

- Capo bruno; introflessione apicale del bulbo distale della spermateca assente, Fig. 83 . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 28

28 Elitre bicolori bruno-rossicce con base giallo-rossiccia; spermateca esile, Fig. 83. Lunghezza 3,6 mm . . . . . . . . . . . . . . . . . . . . . *P. subanomala* sp. n.

- Elitre unicolori brune; spermateca robusta, Fig. 87; edeago Figg. 84-85. Lunghezza 3,8 mm . . . . . . . . . . . . . . . . . . . . . . . . . . . . *P. sanguinicollis* sp. n.

29 Quinto urotergo libero del maschio senza tubercolo mediano, Figg. 88; edeago triangolare in visione ventrale, Figg. 89-90. Lunghezza 3,6 mm . . . . . . . . *P. pseudosanguinicollis* sp. n.

\- Quinto urotergo libero del maschio con un tubercolo mediano allungato; edeago a lati paralleli, in visione ventrale . . . . . . . . 30

30 Elitre lunghissime, Fig. 91; zampe rossicce con tarsi giallo-rossicci; edeago robusto e profondamente incavato al livello della «crista apicalis», Figg. 92-93; introflessione apicale del bulbo distale della spermateca brevissima Fig. 94. Lunghezza 4 mm . . . . . . . . *P. superba* sp. n.

\- Elitre meno lunghe, Fig. 95; zampe rossicce; edeago esile, senza profonda incavatura al livello della «crista apicalis», Figg. 96-97; introflessione apicale del bulbo distale della spermateca profonda, Fig. 98. Lunghezza 3,8 mm . . . . . . . . *P. parasanguinicollis* sp. n.

31 Corpo uniformemente bruno o bruno-rossiccio . . . . . . . . 32

\- Corpo bicolore bruno e rossiccio o giallo-bruno . . . . . . . . 33

32 Corpo bruno; pronoto meno trasverso, Fig. 99; spermateca breve, Fig. 100. Lunghezza 2,3 mm . . . . . . . . *P. distinctatheca* sp. n.

\- Corpo rossiccio; pronoto più trasverso Fig. 101; spermateca lunga Fig. 104; edeago Figg. 102-103. Lunghezza 3,9 mm . . . . . . . . *P. kinabaluicola* sp. n.

33 Pronoto giallo-bruno in contrasto con il capo e le elitre bruno-rossicce; armatura genitale interna dell'edeago forte Figg. 106-107. Lunghezza 2,0 mm . . . . . . . . *P. expansa* sp. n.

\- Pronoto bruno come il capo e le elitre; armatura genitale interna dell'edeago esile. Figg 109-110 . . . . . . . . 34

34 Angolo posteriore interno delle elitre del maschio con una plica obliqua, Fig. 108; zampe brune con tarsi gialli; edeago con due lunghe armature interne Figg. 110-111. Lunghezza 3,2 mm . . . . . . . . *P. biperforata* sp. n.

\- Angolo posteriore interno delle elitre del maschio semplice, Fig. 111; zampe giallo-rossicce; armatura genitale interna dell'edeago sinuata, Figg. 112-113. Lunghezza 3,6 mm . . . . . . . . *P. serpentina* sp. n.

## KEY TO SPECIES OF THE GENUS *PSEUDOPLANDRIA* FENYES, 1921 FROM BORNEO

1 Suture of the elytra evidently shorter than the median line of the pronotum . . 2

\- Suture of the elytra around as long as the median line of the pronotum or evidently longer . . . . . . . . 8

2 Pronotum yellow-reddish . . . . . . . . 3

\- Pronotum brown or brown-reddish . . . . . . . . 5

3 Head and abdomen uniformly yellow-reddish; aedeagus Figs 2-3, spermatheca Fig. 4. Length 2.5 mm . . . . . . . . *P. globulitheca* sp. n.

\- Head brown and abdomen bicoloured yellow-reddish and brown . . . . . . . . 4

4 Eleventh antennomere brown-reddish uniformly; fifth antennomere longer than wide: eyes longer than the temples, in dorsal view; abdomen yellow-reddish with a brown band; aedeagus Figs 6-7, spermatheca Fig. 8. Length 2.4 mm . . . . . . . . *P. ruficollis* Cameron, 1928

- Eleventh antennomere bicoloured brown with apex yellow-reddish; fifth antennomere transverse; eyes shorter than the temples, in dorsal view; abdomen brown with yellow-reddish pigidium; spermatheca Fig. 10. Length 4.1 mm . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *P. cavicola* sp. n.

5 Body uniformly reddish and eleventh antennomere yellow-reddish; pronotum narrower than the elytra; aedeagus Figs 12-13. Length 2.9 mm . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *P. seditiosa* sp. n.

- Bicoloured body brown or reddish and black-brown; eleventh antennomere brown or brown with apex yellow-reddish; pronotum a little narrower than the elytra . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 6

6 Basal sulcus of the free third and fourth urotergites without dots; eleventh antennomere brown with yellow-reddish apex; spermatheca Fig. 15. Length 2.7 mm . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *P. zerchei* sp. n.

- Basal sulcus of the free third and fourth urotergites more or less strongly dotted; eleventh antennomere uniformly brown . . . . . . . . . . . . . . . . . . . . . . . 7

7 Pronotum distinctly transverse, a little narrow in front and with lateral borders reddish; dots of the free third and fourth urotergites superficial; ratio pronotum length / length elytra suture 1.27; aedeagus Figs 17-18. Length 2.7 mm . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *P. belalongica* sp. n.

- Pronotum a little transverse, very narrow in front and reddish unicoloured; ratio pronotum length / length elytra suture 1.33; spermatheca Fig. 19. Length 3.7 mm . . . . . . . . . . . . . . . . . . . . . . . . . *P. anomala* sp. n.

8 Suture of the elytra about as long as the median line of the pronotum . . . . . . 9

- Suture of the elytra distinctly longer than the median line of the pronotum . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 25

9 Body mostly yellow-reddish . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 10

- Body predominantly brown, reddish and brown-reddish . . . . . . . . . . . . . . . . . 15

10 Elytra of the male with evident secondary sexual characters such as plicae or carinae . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 11

- Elytra of the male without secondary sexual characters . . . . . . . . . . . . . . . . 12

11 Elytra of the male with a plica at every inside posterior angle, Fig. 21; all the free uritergites with a salient posterior median carina; aedeagus broadly arched, Figs 23-24; «introflexio apicalis» of the distal bulb of the spermatheca present, Fig. 22. Length 3.8 mm . . . . . *P. subtricarinata* sp. n.

- Elytra of the male with an arched and oblique salient relief, Fig. 25; free urotergites of the male without median carina; aedeagus almost rectilinear to the ventral side, Figs 27-28; distal bulb of the spermatheca without «introflexio apicalis», Fig. 26. Length 3.4 mm . . . . . *P. laminaris* sp. n.

12 Points of the bottom of the free third and fourth uritergites lengthened longitudinally; aedeagus deeply arched to the level of the «crista apicalis», Figs 30-31. Length 3.6 mm . . . . . . . . . . . . . *P. pseudobellicosa* sp. n.

- Points of the bottom of the free third and fourth uritergites not lengthened; aedeagus never deeply arched to the level of the «crista apicalis» . . . . 13

13 Pronotum a little transverse, with four points placed on the vertexes of a discal rectangle; inside genital armour of the aedeagus composed of

numerous well sclerified pieces, Figs 33-34; spermatheca Fig. 35. Length 2.6 mm . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *P. liwaguensis* sp. n.

- Pronotum very transverse, without points in rectangle on the disk; inside genital armor of the aedeagus reduced; spermatheca with inside stripes of the median portion . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 14

14 Eleventh antennomere yellow-reddish; more squat body, Fig. 37; fifth free urotergum of the male without median plica; aedeagus, in ventral view, wide to the distal portion, Figs 38-39; «introflexio apicalis» of the distal bulb of the spermatheca that doesn't reach the center of the same distal bulb, Fig. 40. Length 2.3 mm . . . . . . . . . . . . . . . . . . *P. plicatella* sp. n.

- Eleventh antennomere brown; body slender, fig. 41; fifth free urotergum of the male with a median plica; aedeagus, in ventral view, narrow to the distal portion, Figs 42-43; «introflexio apicalis» of the distal bulb of the spermatheca that reaches the centre of the same distal bulb of the same spermatheca, Fig. 44. Length 2.3 mm . . . . . . . . . . . . . *P. subliwaguensis* sp. n.

15 Uniformly brown body, only sometimes the posterior border of the free uritergites reddish . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 16

- Multicoloured body, brown with reddish, black-brown or yellow-reddish parts . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 18

16 Aedeagus broadly and deeply arched to the level of the «crista apicalis», Figs 46-47; spermatheca Fig. 48. Length 3.5 mm . . . . . . . . . . . *P. subtilis* sp. n.

- Aedeagus non arched to the level of the «crista apicalis» or tightly arched . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 17

17 Eyes as long as the temples, in dorsal view, fig. 49; eleventh antennomere as long as the four reunited preceding antennomeres; aedeagus without ventral plica, Figs 50-51. Length 3.2 mm . . . . . *P. dilatatalamina* sp. n.

- Eyes longer than the temples, in dorsal view, Fig. 52; eleventh antennomere as long as the three reunited preceding antennomeres; aedeagus with ventral plica, Figs 53-54; spermatheca Fig. 55. Length 2.7 mm . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *P. bruneicola* sp. n.

18 Eleventh antennomere yellow-reddish or yellow . . . . . . . . . . . . . . . . . . . . . 19

- Eleventh antennomere brown or black . . . . . . . . . . . . . . . . . . . . . . . . . . . 22

19 Pigidium yellow-reddish . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 20

- Pigidium brown or brown-reddish . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 21

20 Elytra of the male with an arched carina, Fig. 56; free third and fourth urotergites with densely dotted base, Fig. 56; inside genital armour of the aedeagus long, Figs 58-59; «introflexio apicalis» of the distal bulb of the spermatheca absent, Fig. 57. Length 3.2 mm . . . . . . . . . . *P. bellicosa* sp. n.

- Elytra of the male simple, Fig. 60; free third and fourth urotergites without basal dots; inside genital armour of the aedeagus short, Figs 61-62; spermatheca Fig. 63. Length 3.2 mm . . . . . . . . . . . . *P. sabahensis* sp. n.

21 Eyes very developed and protruding; unicoloured abdomen reddish; «introflexio apicalis» of the bulb distal of the spermatheca deep. Length 2.8 mm . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *P. pluvialis* Pace, 1986

- Eyes a little developed and non-protruding; bicolor abdomen brown-reddish and reddish; «introflexio apicalis» of the distal bulb of the spermatheca weak, Fig. 67. Length 3.6 mm . . . . . . . . . . . . . . . . . . *P. nobilis* sp. n.

22 Eyes reduced shorter or as long as the temples; yellow-reddish legs . . . . . . . 23

- Eyes enormous and temples short; legs brown . . . . . . . . . . . . . . . . . . . . . . . 24

23 Posterior border of the free second, third, fourth and fifth uritergites reddish; aedeagus deeply curved to the ventral side, Figs 69-70. Length 2.6 mm . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *P. altitudinis* sp. n.

- Free urotergites uniformly reddish; aedeagus non-curved to the ventral side; Figs 72-73. Length 2.3 mm . . . . . . . . . . . . . . . . . . . . . . . . *P. fugas* sp. n.

24 Pronotum strongly transverse; free third and fourth urotergites punctured at the base; «introflexio apicalis» of the distal bulb of the spermatheca with straight walls without basal groove; proximal bulb of the spermatheca very little developed. Length 2.1 mm . . . *P. borneensis* Pace, 1986

- Pronotum a little transverse, Fig. 74; free third and fourth urotergites without basal puncture; aedeagus Figs 75-76; spermatheca Fig. 77. Length 2.8 mm . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *P. obscura* sp. n.

25 Pronotum yellow-reddish . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 26

- Pronotum reddish, brown, brown-reddish or yellow-brown . . . . . . . . . . . . . 31

26 Abdomen yellow-reddish . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 27

- Abdomen brown-reddish or brown . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 29

27 Head yellow-reddish; «introflexio apicalis» of the distal bulb of the spermatheca deep, Fig. 81. Length 2.6 mm . . . . . . . . . . . . . . . . . *P. sinusifera* sp. n.

- Head brown; «introflexio apicalis» of the distal bulb of the spermatheca absent, Fig. 83 . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 28

28 Elytra bicoloured brown-reddish with yellow-reddish base; spermatheca slender, Fig. 83. Length 3.6 mm . . . . . . . . . . . . . . . . . . . . *P. subanomala* sp. n.

- Elytra unicoloured brown; spermatheca strong, Fig. 87; aedeagus Figs 84-85. Length 3.8 mm . . . . . . . . . . . . . . . . . . . . . . . . . *P. sanguinicollis* sp. n.

29 Fifth free urotergum of the male without median tubercle, Figs 88; aedeagus triangular, in ventral view, Figs 89-90. Length 3.6 mm . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *P. pseudosanguinicollis* sp. n.

- Fifth free urotergum of the male with a lengthened median tubercle; sides aedeagus parallel, in ventral view . . . . . . . . . . . . . . . . . . . . . . . . . . 30

30 Elytra long, Fig. 91; reddish legs with yellow-reddish tarsi; aedeagus strongly and deeply hollow to the level of the «crista apicalis», Figs 92-93; «introflexio apicalis» of the distal bulb of the spermatheca brief Fig. 94. Length 4 mm . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *P. superba* sp. n.

- Elytra less long, Fig. 95; legs reddish; aedeagus slender, without deep hollow to the level of the «crista apicalis», Figs 96-97; «introflexio apicalis» of the distal bulb of the spermatheca deep, Fig. 98. Length 3.8 mm . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *P. parasanguinicollis* sp. n.

31 Body uniformly brown or reddish . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 32

- Body bicoloured brown and reddish or yellow-brown . . . . . . . . . . . . . . . . . . 33

32 Body brown; pronotum less transverse, Fig. 99; spermatheca brief, Fig. 100. Length 2.3 mm . . . . . . . . . . . . . . . . . . . . . . . . . . *P. distinctatheca* sp. n.

- Body reddish; pronotum transverse Fig. 101; spermatheca long Fig. 104; aedeagus Figs 102-103. Length 3.9 mm . . . . . . . . . . . . . *P. kinabaluicola* sp. n.

33 Pronotum yellow-brown in contrast with the brown-reddish head and the elytra; inside genital armour of the aedeagus strong, Figs 106-107. Length 2.0 mm . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *P. expansa* sp. n.

- Pronotum as brown as the head and the elytra; inside genital armour of the aedeagus slender. Figs 109-110 . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 34

34 Inner posterior angle of the elytra of the male with an oblique plica, Fig. 108; legs brown with yellow tarsus; aedeagus with two long inside armours Figs 110-111. Length 3.2 mm . . . . . . . . . . . . . . . . *P. biperforata* sp. n.

- Inner posterior angle of the elytra of the male simple, Fig. 111; legs yellow-reddish; inside genital armours of the aedeagus sinuous, Figs 112-113. Length 3.6 mm . . . . . . . . . . . . . . . . . . . . . . . . . . . *P. serpentina* sp. n.

***Pseudoplandria globulitheca*** sp. n. Figg. 1-4

HOLOTYPUS: Femmina, Borneo, Sabah, Poring Hot Springs, 500 m, 6.V.1987, leg. Burckhardt & Löbl (MHNG).

PARATYPI: 1 maschio e 1 femmina, Sabah, Poring Hot Springs, 500 m, 11.V.1987, leg. Burckhardt & Löbl. – 1 maschio, Sabah, Poring Hot Springs, 500 m, 7.V.1987, leg. Burckhardt & Löbl. – 1 femmina, Sabah, Poring Hot Springs, 500 m, 13.V.1987, leg. Burckhardt & Löbl. – 2 es., Sabah, Poring Hot Springs, 550-600 m, 9.V.1987, leg. Burckhardt & Löbl.

DESCRIZIONE: Lunghezza 2,5 mm. Corpo lucido e giallo-rossiccio con elitre bruno-rossicce; antenne bruno-rossicce con i tre antennomeri basali giallo-rossicci; zampe giallo-rossicce. Il corpo è privo di reticolazione. La punteggiatura del capo è poco distinta, quella del pronoto è fine. La granulosità delle elitre è saliente. La base degli uroterghi liberi terzo e quarto è punteggiata. Le elitre del maschio presentano una carena discale saliente e lievemente ricurva, Fig. 1. Edeago Figg. 2-3, spermateca Fig. 4.

DERIVATIO NOMINIS. Il nome delle nuova specie significa «spermateca globosa».

***Pseudoplandria cavicola*** sp. n. Figg. 9-10

HOLOTYPUS: Femmina, Sabah, Mt. Kinabalu Nat. Pk., Paka Cave, 2997 m, 5.V.1987, leg. A. Smetana (MHNG).

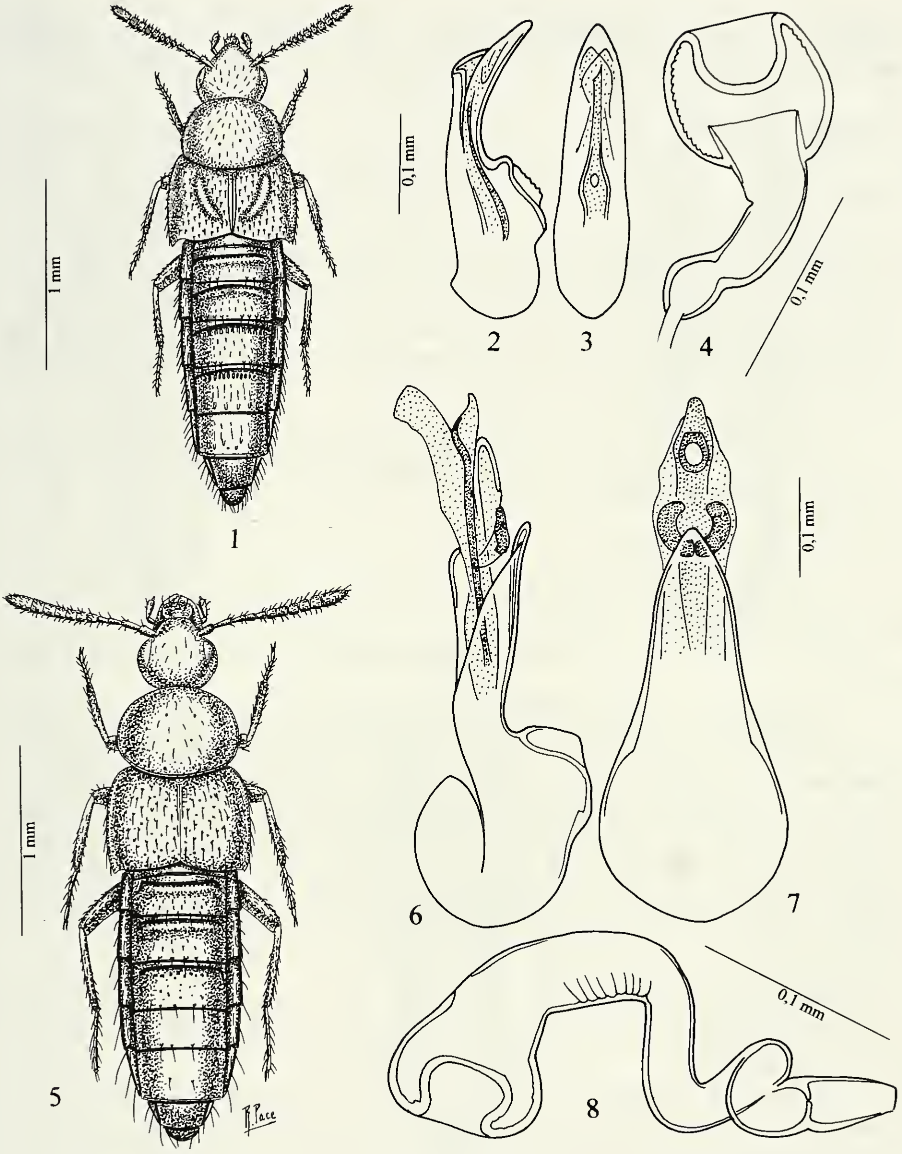
DESCRIZIONE: Lunghezza 4,1 mm. Corpo lucido e giallo-rossiccio, con capo, elitre e addome, tranne il pigidio, bruni; antenne brune con i tre antennomeri basali e l'apice dell'undicesimo giallo-rossicci; zampe giallo-rossicce. Il corpo è privo di reticolazione. La punteggiatura del capo è fine e superficiale. La granulosità del pronoto è distinta, quella delle elitre è saliente. La base degli uroterghi liberi terzo e quarto è superficialmente punteggiata. La metà posteriore del quinto urotergo libero della femmina è striata. Il pronoto mostra una larga depressione mediana posteriore. Spermateca Fig. 10.

DERIVATIO NOMINIS: Il nome delle nuova specie significa «abitatrice di caverna».

***Pseudoplandria seditiosa*** sp. n. Figg. 11-13

HOLOTYPUS: Maschio, Borneo, Sabah, Crocker Ra., 1550-1650 m, 16.V.1987, leg. Burckhardt & Löbl (MHNG).

PARATYPUS: 1 maschio, stessa provenienza.



FIGG. 1-8

Habitus, edeago in visione laterale e ventrale e spermateca. (1-4) *Pseudoplandria globulitheca* sp. n. (5-8) *Pseudoplandria ruficollis* Cameron, lectotypus maschio e paralectotypus femmina.

DESCRIZIONE: Lunghezza 2,9 mm. Corpo lucido e rossiccio; antenne bruno-rossicce con i tre antennomeri basali e l'undicesimo giallo-rossicci; zampe rossicce. Il corpo è privo di reticolazione. La punteggiatura del capo è indistinta, quella del pronoto è poco evidente e quella delle elitre è profonda. Solo il solco basale del primo urotergo libero è senza punteggiatura. Edeago Figs 12-13.

Derivatio nominis: Il nome della nuova specie indica che l'edeago è ribelle al modo di estroflessione dell'armatura genitale interna rispetto quella dell'edeago di altre specie. Come osservato nel paratypus, infatti, essa si distacca facilmente.

***Pseudoplandria zerchei*** sp. n. Figg. 14-15

Holotypus: femmina, N. Borneo, Sabah, Bunsit Keningan, 31.VII.1985, leg. K. Maruyama (DEI).

Descrizione: Lunghezza 2,7 mm. Corpo lucido e bruno con elitre nero-brune; antenne brune con i tre antennomeri basali e l'apice dell'undicesimo giallo-rossicci; zampe rossicce. Il corpo è privo di reticolazione. La granulosità del capo e del pronoto è fine, quella delle elitre è saliente. La punteggiatura dei solchi trasversi basali degli uroterghi liberi è assente. Il pronoto mostra quattro punti discali del pronoto disposti ai vertici di un quadrato. Spermateca Fig. 15.

Derivatio nominis: La nuova specie è dedicata al noto studioso di Staphylinidae Dr. Lothar Zerche del DEI di Müncheberg (Berlino) che mi ha affidato in esame questa e altre nuove specie.

***Pseudoplandria belalongica*** sp. n. Figg. 16-18

Holotypus: Maschio, Borneo, Brunei, Temburong, Kuala Belalong KBFSC, 25.II.1995, leg. Borcherding (IRSN).

Paratypus: 1 maschio, Sabah, Poring Hot Springs, 500 m, 7.V.1987, leg. Burckhardt & Löbl.

Descrizione: Lunghezza 2,7 mm. Corpo lucido e bruno-rossiccio con margine laterale e posteriore del pronoto e i due uroterghi liberi basali rossicci e con elitre brune; antenne brune con i tre antennomeri basali gialli; zampe brune con tarsi giallo-rossicci. Il corpo è privo di reticolazione. La punteggiatura del capo è superficiale e assente sulla fascia longitudinale mediana. La punteggiatura del pronoto è rada e molto superficiale, tranne alcuni punti forti distribuiti come da Fig. 16. La granulosità delle elitre è saliente. Il pronoto è molto convesso. La base degli uroterghi liberi terzo e quarto è chiaramente punteggiata. Edeago Figg. 17-18.

***Pseudoplandria anomala*** sp. n. Figg. 19-20

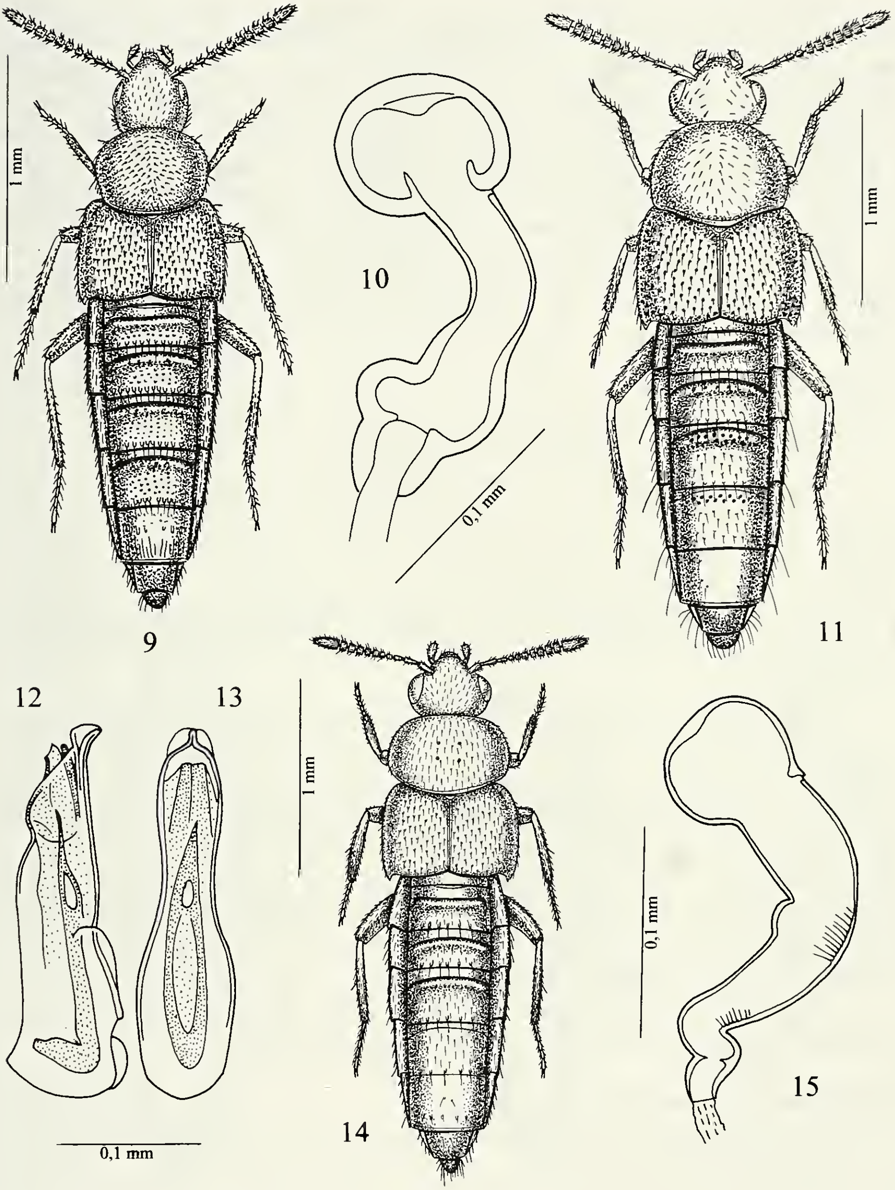
Holotypus: Femmina, Borneo, Brunei, Temburong, Kuala Belalong (West), 11.II.1995, leg. Borcherding (IRSN).

Descrizione: Lunghezza 3,7 mm. Corpo lucido e rossiccio con elitre bruno-rossicce; antenne brune con i tre antennomeri basali e la metà apicale dell'undicesimo rossicci; zampe rossicce. Il corpo è privo di reticolazione. La punteggiatura del capo e del pronoto è molto superficiale. La granulosità delle elitre è saliente. La base degli uroterghi liberi terzo e quarto è chiaramente punteggiata. Spermateca Fig. 19.

Derivatio nominis: La nuova specie presenta la forma della spermateca che devia dalla forma che comunemente si ritiene consueto di quest'organo.

***Pseudoplandria subtricarinata*** sp. n. Figg. 21-24

Holotypus: Maschio, Borneo, Sabah, Mt. Kinabalu N.P., HQ Liwagu Rv. trail, 1520 m, 11.VIII.1988, leg. A. Smetana (MHNG).



FIGG. 9-15

Habitus, spermateca e edeago in visione laterale e ventrale. (9-10) *Pseudoplandria cavicola* sp. n. (11-13) *Pseudoplandria seditiosa* sp. n. (14-15) *Pseudoplandria zerchei* sp. n.

PARATYPI: 4 es., Borneo-Sabah, Mt. Kinabalu,1500 m, 25.IV.1987, leg. Burckhardt & Löbl. – 2 maschi, Sabah, Mt. Kinabalu, 1750 m, 21.IV.1987, leg. Burckhardt & Löbl. – 1 femmina, Sabah, Mt. Kinabalu, 1550-1650 m, 24.IV.1987, leg. Burckhardt & Löbl.

Descrizione: Lunghezza 3,8 mm. Corpo lucido e giallo-rossiccio con elitre bruno-rossicce; antenne brune con i tre antennomeri basali e metà apicale dell'undicesimo gialli; zampe giallo-rossicce. Il corpo è privo di reticolazione. La punteggiatura del capo e del pronoto è molto superficiale; sul pronoto si trovano punti mediani allineati come da Fig. 21. La granulosità delle elitre è molto saliente. Solo la base dell'urotergo libero quinto è chiaramente punteggiata. Sull'angolo posteriore interno delle elitre del maschio si trova una plica obliqua. Tutti gli uroterghi liberi del maschio mostrano una carena mediana posteriore. Edeago Figg 23-24, spermateca Fig. 22.

Derivatio nominis: Il nome della nuova specie «quasi con tre carene» è in riferimento all'apparenza di tre carene addominali mediane, invece ad un'attenta osservazione sono cinque.

***Pseudoplandria laminaris*** **sp. n.** Figg. 25-28

Holotypus: Maschio, Borneo, Sabah, Mt. Kinabalu N.P., Poring Hot Springs, nr. Bat Cave, 600 m, 10.V.1987, leg. Burckhardt & Löbl (MHNG).

Paratypi: 1 maschio, Borneo, Sabah, Mt. Kinabalu N.P., HQ Silau-Silau Tr., 1550 m, 12.VIII.1988, leg. A. Smetana. – 1 maschio, Borneo, Sabah, Mt. Kinabalu Nat. Pk., HQ Silau-Silau Tr., 1540 m, 14.VIII.1988, leg. A. Smetana. – 1 maschio e 1 femmina, Borneo, Sabah, Mt. Kinabalu N. P., Poring Hot Springs, area Eastern Ridge tr., 1000 m, 28.VIII.1988, leg. A. Smetana. – 1 maschio, Sabah, Poring Hot Springs, 500 m, 8.V.1987, leg. Burckhardt & Löbl. – 1 maschio, Borneo, Sabah, Mt. Kinabalu N.P., Poring Hot Springs, 500 m, 11.V.1987, leg. Burckhardt & Löbl. – 1 maschio e 2 femmine, Borneo, Sabah, Crocker Ra., 1550-1650 m, 16.V.1987, leg. Burckhardt & Löb. – 2 maschi, Sabah, Poring Hot Springs, 500 m, 7.V.1987, leg. Burckhardt & Löbl.

Descrizione: Lunghezza 3,4 mm. Corpo lucido e giallo-rossiccio con elitre rossicce; antenne rossicce con i tre antennomeri basali e l'undicesimo giallo-rossicci; zampe giallo-rossicce. Il corpo è privo di reticolazione. La punteggiatura del capo è evidente, quella del pronoto è quasi indistinta. La granulosità delle elitre è superficiale. Sono punteggiati solo i solchi basali degli uroterghi liberi secondo, terzo e quarto. Gli uroterghi liberi terzo, quarto e quinto sono coperti di strie longitudinali. Le elitre del maschio presentano un sinuoso rilievo saliente convergente all'angolo posteriore interno. Sulla sutura delle elitre del maschio si trova una lamina posteriore saliente. Edeago Figg. 27-28, spermateca Fig. 26.

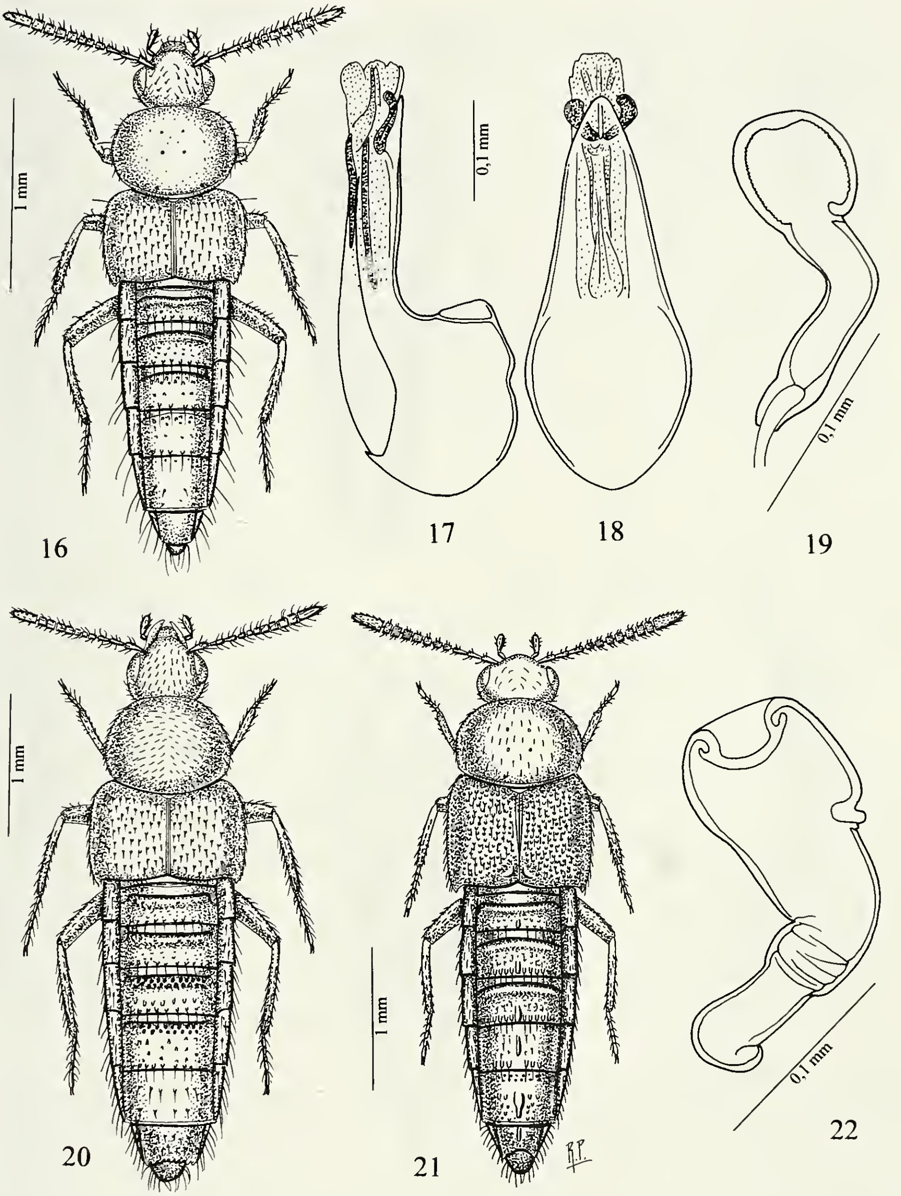
Derivatio nominis: Il nome della nuova specie significa «a forma di lamina». La lamina è quella dell'armatura genitale interna dell'edeago.

***Pseudoplandria pseudobellicosa*** **sp. n.** Figg. 29-31

Holotypus: Maschio, Sabah, Poring Hot Springs, Langanan river, 850 m, 14.V.1987, leg. Burckhardt & Löbl, (MHNG).

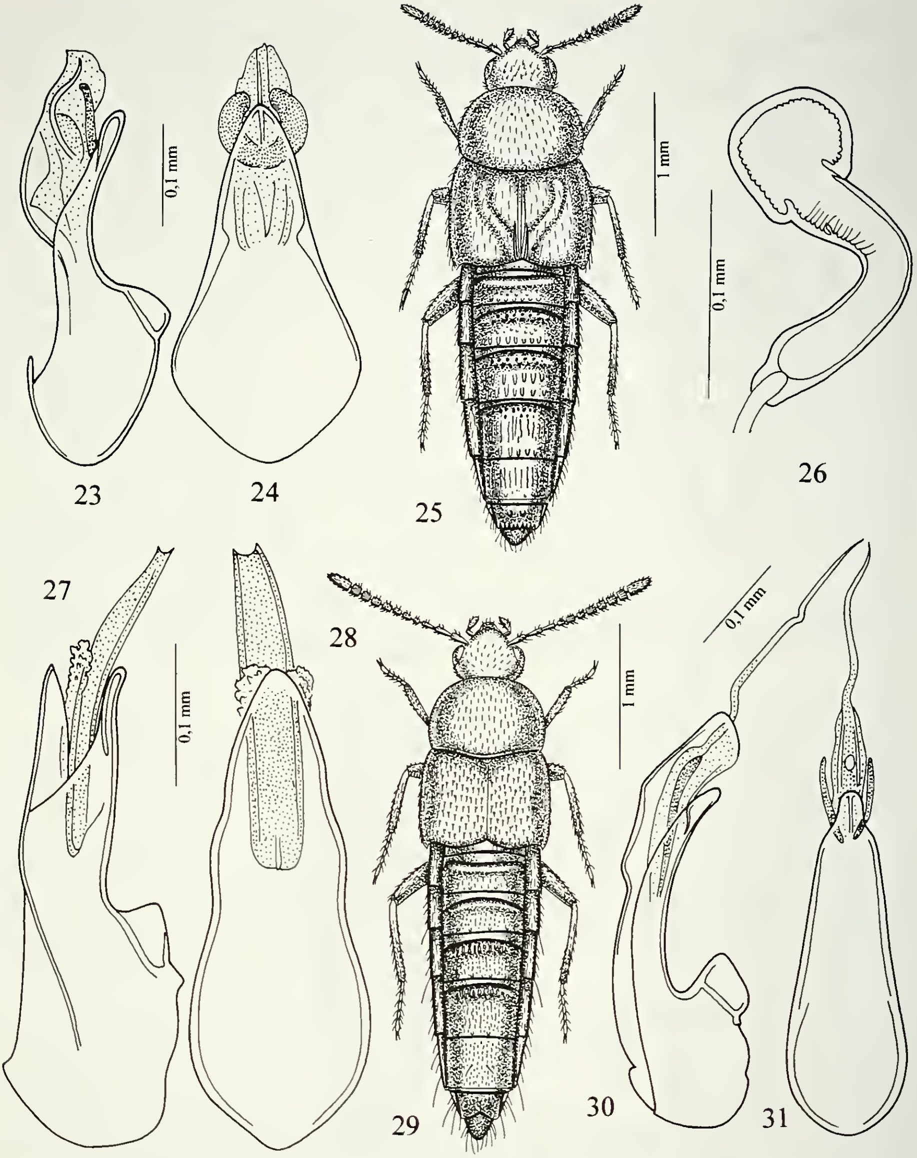
Paratypi: 1 maschio, stessa provenienza. – 1 maschio, Sabah, Poring Hot Springs, 500 m, 7.V.1987, leg. Burckhardt & Löbl.

Descrizione: Lunghezza 3,6 mm. Corpo lucido e giallo-rossiccio con elitre brune, tranne la base; antenne rossicce con i due antennomeri basali, la base del terzo e l'undicesimo giallo-rossicci; zampe giallo-rossicce con tibie rossicce. Il corpo è privo di reticolazione. La punteggiatura del capo è fine ed evidente, quella del pronoto è indistinta. La granulosità delle elitre è saliente. Nei solchi trasversi basali degli uroterghi liberi terzo e quarto la punteggiatura è longitudinale. Edeago Figg. 30-31.



FIGG. 16-22
Habitus, edeago in visione laterale e ventrale e spermateca. (16-18) *Pseudoplandria belalongica* sp. n. (19-20) *Pseudoplandria anomala* sp. n. (21-22) *Pseudoplandria subtricarinata* sp. n.

DERIVATIO NOMINIS: Il nome della nuova specie significa «falsa *bellicosa*». Il colore del corpo, infatti è simile a quello di *P. bellicosa* nuova specie descritta qui di seguito.



FIGG. 23-31

Edeago in visione laterale e ventrale, habitus, e spermateca. (23-24) *Pseudoplandria subtricarinata* sp. n. (25-28) *Pseudoplandria laminaris* sp. n. (29-31) *Pseudoplandria pseudobellicosa* sp. n.

**Pseudoplandria liwaguensis** sp. n. Figg. 32-36

HOLOTYPUS: Maschio, Borneo, Sabah, Mt. Kinabalu Nat. Pk., HQ at Liwagu Rv., 1500 m, 30.IV.1987, leg. A. Smetana (MHNG).

PARATYPI: 1 femmina, stessa provenienza. – 3 maschi e 2 femmine, Borneo, Sabah, Mt. Kinabalu N.P., summit tr. Pondok Lowii, 2300-2400 m, 28.IV.1987, leg. A. Smetana. – 1 maschio, Borneo-Sabah, Mt. Kinabalu N.P., Summit Trail, 1890 m, (data mancante), leg. A. Smetana. – 1 maschio e 1 femmina, Borneo-Sabah, Mt. Kinabalu N.P., below Layang Layang, 2590 m, 1.V.1987, leg. A. Smetana. – 1 maschio, Borneo-Sabah, Mt. Kinabalu N. P., Headquarters, 1558 m, 2.IX.1988, D.E. Bright collector. – 1 femmina, Borneo Sabah, Mt. Kinabalu Nat Pk., HQ 1560 m, 24.IV.1987, Beating foliage, leg. D.E Bright.– 1 maschio, Borneo, Sabah, Mt. Kinabalu N.P., below Layang Layang, 2600 m, 2-8.V.1987, leg. A. Smetana. – 1 maschio, Borneo, Sabah, Mt. Kinabalu N.P., below Layang Layang, 2595 m, 2.IV.1987, leg. A. Smetana. – 1 maschio e 1 femmina, Borneo, Sabah, Crocker Ra., 1550-1650 m, 16.V.1987, leg. Burckhardt & Löbl. – 3 maschi e 1 femmina, Borneo, Sabah, Mt. Kinabalu N.P., 1580 m, 27.IV.1987, leg. Burckhardt & Löbl. – 2 maschi e 1 femmina, Borneo, Sabah, Crocker Ra., 1600 m, Km 51 rte. Kinabalu-Tambunan, 18.V.1987, leg. Burckhardt & Löbl. – 2 maschi e 1 femmina, Sabah, Mt. Kinabalu, 1550-1650 m, 24.IV.1987, leg. Burckhardt & Löbl. – 3 es., Borneo, Sabah, Mt. Kinabalu N.P., HQ Liwagu Riv. trail, 1500-1550 m, 27.IV.1987, leg. A. Smetana. – 2 maschi, Borneo-Sabah, Mt. Kinabalu, 3150-3200 m, 3.V.1987, leg. Burckhardt & Löbl. – 2 maschi, Sabah, Mt. Kinabalu, 1500 m, 25.IV.1987, leg. Burckhardt & Löbl, – 1 es., Sabah, Crocker Ra., km 51 rte Kta Kinabalu- Tamburan, 1600m, 18.VII.1987, leg. Burckhardt & Löbl.

DESCRIZIONE: Lunghezza 2,6 mm. Corpo lucido e giallo-rossiccio con metà posteriore delle elitre bruna; antenne brune con i quattro antennomeri basali e metà distale dell'undicesimo gialli; zampe giallo-rossicce. Il corpo è privo di reticolazione. La punteggiatura del capo e del pronoto è molto superficiale. La granulosità delle elitre è evidente, quella dell'addome è più saliente sugli uroterghi liberi posteriori che su quelli anteriori. Nei solchi trasversi basali degli uroterghi liberi terzo e quarto la punteggiatura è poco evidente. Sul pronoto si trovano quattro punti discali in rettangolo. Edeago Figg. 33-34, spermateca di forma variabile Figg. 35-36.

### ***Pseudoplandria plicatella*** sp. n. Figg. 37-40

HOLOTYPUS: Maschio, Borneo-Sabah, Mt. Kinabalu N.P., HQ at Liwagu Rv., 1500 m, 25.IV.1987, leg. A. Smetana (MHNG).

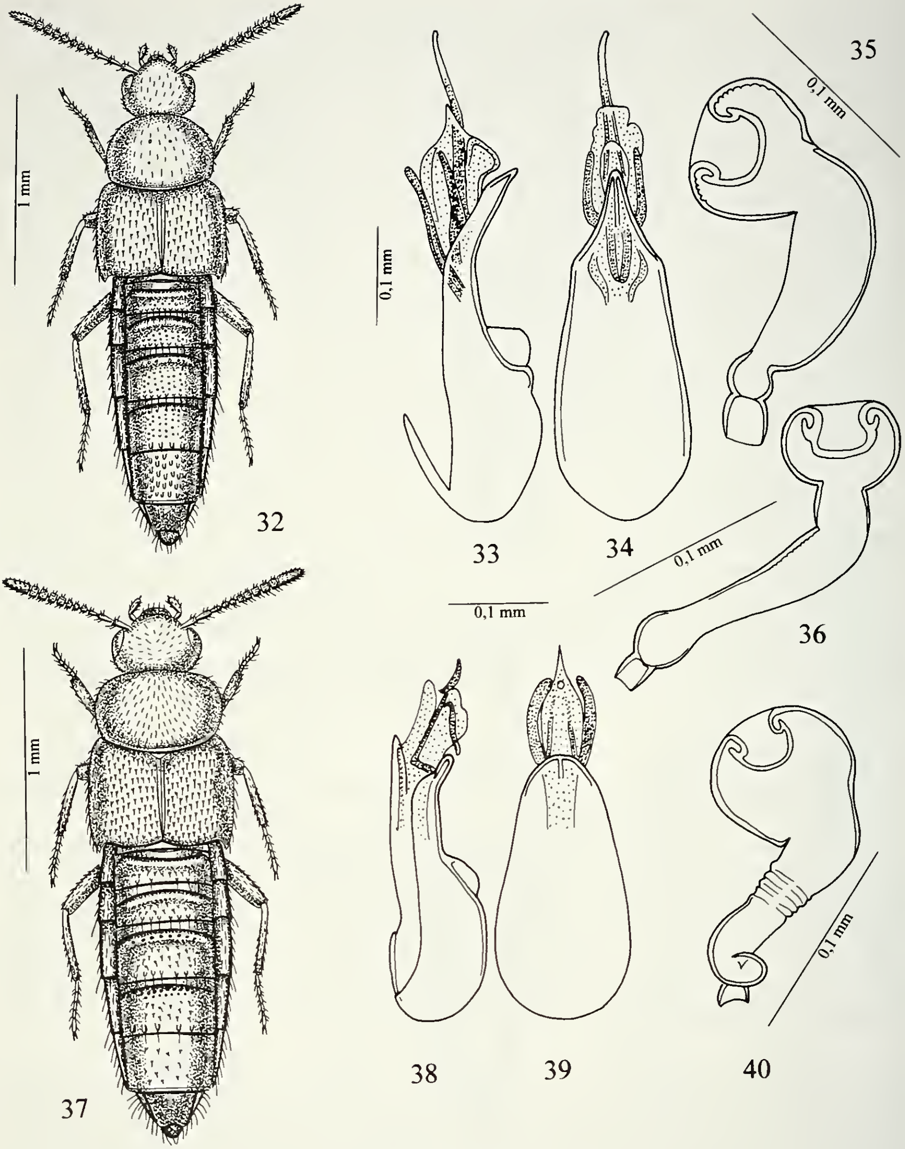
PARATYPI: 1 femmina, stessa provenienza. – 1 femmina, Sabah, Mt. Kinabalu N.P., 1550-1650 m, 24.IV.1987, leg. Burckhardt & Löbl. – 12 es., Borneo, Sabah, Mt. Kinabalu N.P., HQ Liwagu River Trail, 1520 m, 11.VIII.1988, leg. A. Smetana. – 1 es., Borneo, Sabah, Mt. Kinabalu N.P., HQ Liwagu Rv. tr., 1490 m, 10.VIII.1988, leg. A. Smetana. – 1 maschio e 1 femmina, Borneo, Sabah, Mt. Kinabalu N.P., HQ Liwagu Riv., 1490 m, 5.VIII.1988, leg. A. Smetana. – 12 es., Borneo, Sabah, Mt. Kinabalu N.P., 1580 m, 27.IV.1987, leg. Burckhardt & Löbl. – 2 es., Borneo, Sabah, Mt. Kinabalu N.P., 1550 m, 29.IV.1987, leg. Burckhardt & Löbl. – 2 femmine, Sabah, Mt. Kinabalu, 1550 m, 28.IV.1987, leg. Burckhardt & Löbl.

DESCRIZIONE: Lunghezza 2,3 mm. Corpo lucido e giallo-rossiccio con elitre brune, tranne la metà basale; antenne brune con i tre antennomeri basali e l'undicesimo giallo-rossicci; zampe giallo-rossicce. Il corpo è privo di reticolazione. La granulosità del capo e del pronoto è fine e distinta, quella delle elitre è saliente. Nei solchi trasversi basali degli uroterghi liberi terzo e quarto la punteggiatura è evidente. Edeago Figg. 38-39, spermateca Fig. 40.

DERIVATIO NOMINIS: La nuova specie prende nome dalla plica ventrale del suo edeago.

### ***Pseudoplandria subliwaguensis*** sp. n. Figg. 41-44

HOLOTYPUS: Maschio, Borneo, Sabah, Mt. Kinabalu N.P., summit trail Pondok-Ubah, 2050 m, 26.IV.1987, leg. A. Smetana (MHNG).



FIGG. 32-40

Habitus, edeago in visione laterale e ventrale e spermateca. (32-36) *Pseudoplandria liwaguensis* sp. n. (37-40) *Pseudoplandria plicatella* sp. n.

PARATYPI: 1 maschio, Sabah, Mt. Kinabalu Nat. Pk, HQ 1560-1660 m, 24.IV.1987, leg. A. Smetana. – 1 femmina, Borneo, Sabah, Mt. Kinabalu N.P., HQ Liwagu Riv. trail, 1500-1550 m, 27.IV.1987, leg. A. Smetana. – 3 femmine, Borneo, Sabah, Crocker Ra., 1550-1650 m, 16.V.1987, leg. Burckhardt & Löbl. – 1 femmina, Sabah, Mt. Kinabalu, 1750 m, 27.IV.1987, leg. Burckhardt & Löbl. – 1 femmina, Sabah, Mt. Kinabalu, 1550 m, 28.IV.1987, leg. Burckhardt & Löbl. – 1 femmina, Borneo, Sabah, Crocker Ra., 1600 m, Km 51 rte. Kinabalu-Tambunan, 18.V.1987, leg. Burckhardt & Löbl. – 1 es., Sabah, Poring Hot Springs, Langanan Falls, 900-950m, 12.V.1987, leg. Burckhardt & Löbl.

DESCRIZIONE: Lunghezza 2,3 mm. Corpo lucido e giallo-rossiccio con elitre brune tranne la base; antenne brune con i tre antennomeri basali gialli; zampe gialle. Il corpo è privo di reticolazione. La punteggiatura del capo è superficiale, quella del pronoto è evidente. La granulosità delle elitre è saliente. I solchi trasversi basali degli uroterghi liberi non sono punteggiati. Edeago Figg. 42-43, spermateca fig. 44.

### ***Pseudoplandria subtilis*** sp. n. Figg. 45-48

HOLOTYPUS: Maschio, Sabah, Mt. Kinabalu Nat. Pk, HQ 1560-1660 m, 24.IV.1987, leg. A. Smetana (MHNG).

PARATYPI: 11 es., Sabah, Mt. Kinabalu Nat. Pk, HQ at Liwagu Rv., 1500 m, 17.V.1987, leg. A. Smetana & D.E. Bright. – 9 es., Borneo, Sabah, Mt. Kinabalu N.P., Silau-Silau Trail, 1558 m, 2.IX.1988, leg. D.E. Bright. – 2 es., Borneo-Sabah, Mt. Kinabalu N. P., Headquarters, 1550 m, 3-12.VIII.1988, beating foliage, leg. D.E. Bright. – 1 femmina, Borneo, Sabah, Mt. Kinabalu Nat. Pk., 26.IV.1987, leg. A. Smetana. – 1 maschio, Borneo, Sabah, Mt. Kinabalu N.P., 1750 m, 27.IV.1987, leg. Burckhardt & Löbl.

DESCRIZIONE: Lunghezza 3,5 mm. Corpo lucido e bruno con margine posteriore degli uroterghi liberi primo, secondo e terzo bruno-rossiccio, antenne brune con i tre antennomeri basali e apice dell'undicesimo giallo-rossicci; zampe bruno-rossicce con tarsi rossicci. Il corpo è privo di reticolazione. La punteggiatura del capo è evidente. La granulosità del pronoto è fine, più evidente sulla metà anteriore che su quella posteriore. La granulosità delle elitre è saliente. Nei solchi trasversi basali degli uroterghi liberi terzo e quarto la punteggiatura è evidente. Edeago Figg. 46-47, spermateca Fig. 48.

DERIVATIO NOMINIS: Il nome di «sottile» della nuova specie deriva dalla parte distale dell'edeago che è stretta, in visione laterale.

### ***Pseudoplandria dilatatalamina*** sp. n. Figg. 49-51

HOLOTYPUS: Maschio, Borneo, Sabah, Mt. Kinabalu N.P., Poring Hot Springs, Langanan Falls, 900-950 m, 12.V.1987, leg. Burckhardt & Löbl (MHNG).

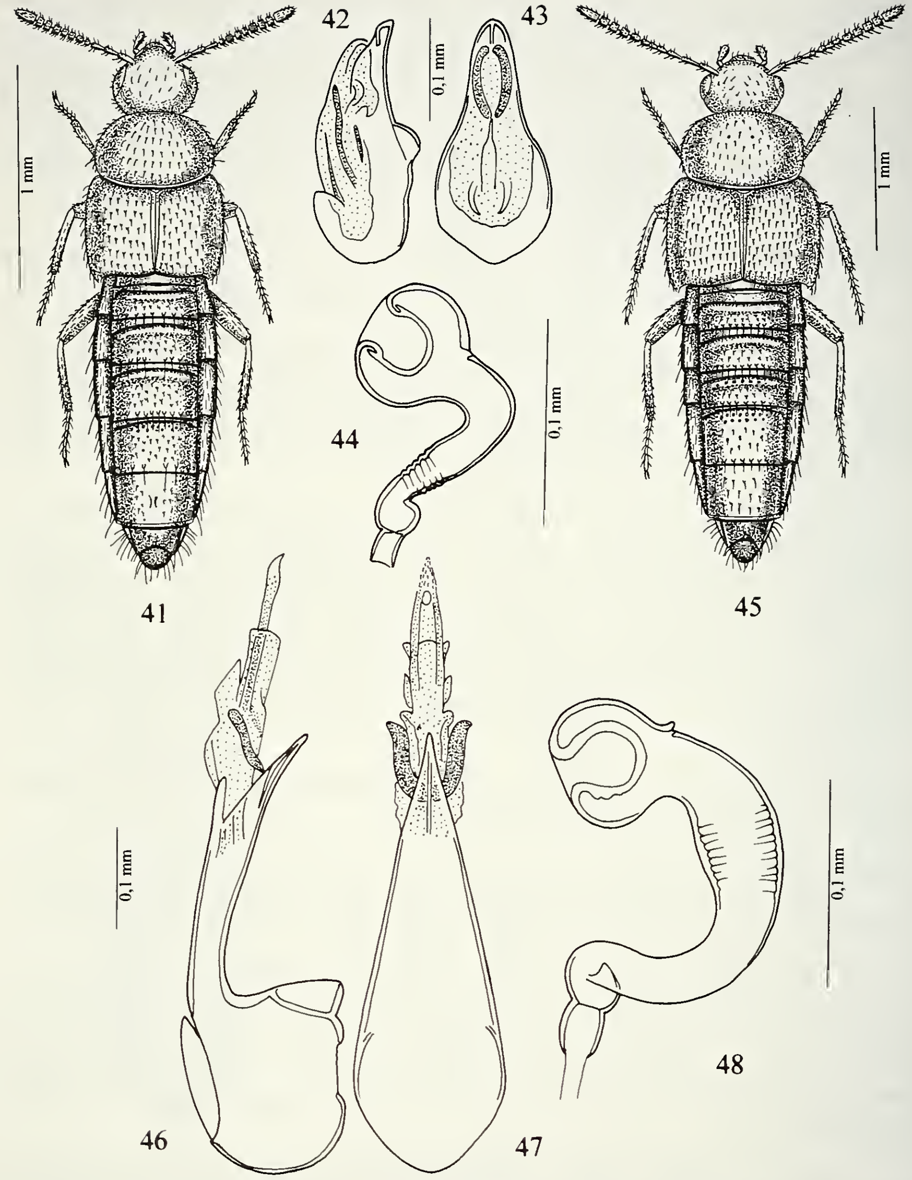
DESCRIZIONE: Lunghezza 3,2 mm. Corpo lucido e bruno; antenne brune con i quattro antennomeri basali giallo-rossicci; zampe brune con tibie e tarsi rossicci. Il corpo è privo di reticolazione. La punteggiatura del capo è fine e poco evidente. La granulosità del pronoto è poco evidente, quella delle elitre è ben visibile. Nei solchi trasversi basali degli uroterghi liberi terzo e quarto la punteggiatura è rada ed evidente. Edeago Figg. 50-51.

DERIVATIO NOMINIS: Il nome di «lamina dilatata» della nuova specie deriva dalla lamina dilatata dell'armatura genitale interna dell'edeago sporgente dall'orifizio apicale.

### ***Pseudoplandria bruneicola*** sp. n. Figg. 52-55

HOLOTYPUS: Maschio, Borneo, Brunei, Temburong, Kuala Belalong KBFSC, 27.III.1995, leg. Borcherding (IRSN).

PARATYPI: 1 maschio, stessa provenienza. – 1 femmina, Borneo, Brunei, Temburong, Kuala Belalong (West), 17.II.1995, leg. Borcherding.



FIGG. 41-48

Habitus, edeago in visione laterale e ventrale e spermateca. (41-44) *Pseudoplandria subliwaguensis* sp. n. (45-48) *Pseudoplandria subtilis* sp. n.

DESCRIZIONE: Lunghezza 2,7 mm. Corpo lucido e bruno; antenne brune con i due antennomeri basali gialli e apice dell'undicesimo giallo-rossiccio; zampe giallo-brune. Il corpo è privo di reticolazione. La punteggiatura del capo è molto superficiale, quella del pronoto non è visibile. La granulosità delle elitre è molto saliente alla base e gradualmente meno saliente all'indietro. Nei solchi trasversi basali degli uroterghi liberi terzo e quarto la punteggiatura è assente. Edeago Figg. 53-54, spermateca Fig. 55.

### ***Pseudoplandria bellicosa*** sp. n. Figg. 56-59

HOLOTYPUS: Maschio, Borneo, Sabah, Mt. Kinabalu Nat.Pk., HQ Liwagu Riv. trail, 1500-1550 m, 27.iv.1987, leg. A. Smetana (MHNG).

PARATYPI: 1 maschio, Borneo, Sabah, rte. Ranau-Kota Kinabalu, 1150 m, 24.V.1987, leg. Burckhardt & Löbl. – 2 femmine, Borneo, Sabah, Mt. Kinabalu N.P., Poring Hot Springs, 550-600 m, 9.V.1987, leg. Burckhardt & Löbl. – 1 es., Sabah, Poring Hot Springs, 500 m, 7.V.1987, leg. Burckhardt & Löbl. – 1 femmina, Borneo, Sabah, Mt. Kinabalu N.P., HQ Liwagu Rv. trail, 1500-1550 m, 27.IV.1987, leg. A. Smetana. – 1 femmina, Borneo, Sabah, Mt. Kinabalu N.P., Poring Hot Springs, nr. Bat Cave, 600 m, 10.V.1987, leg. Burckhardt & Löbl. – 1 femmina, Sabah, Mt. Kinabalu, 1550 m, 28.IV.1987, leg. Burckhardt & Löbl.

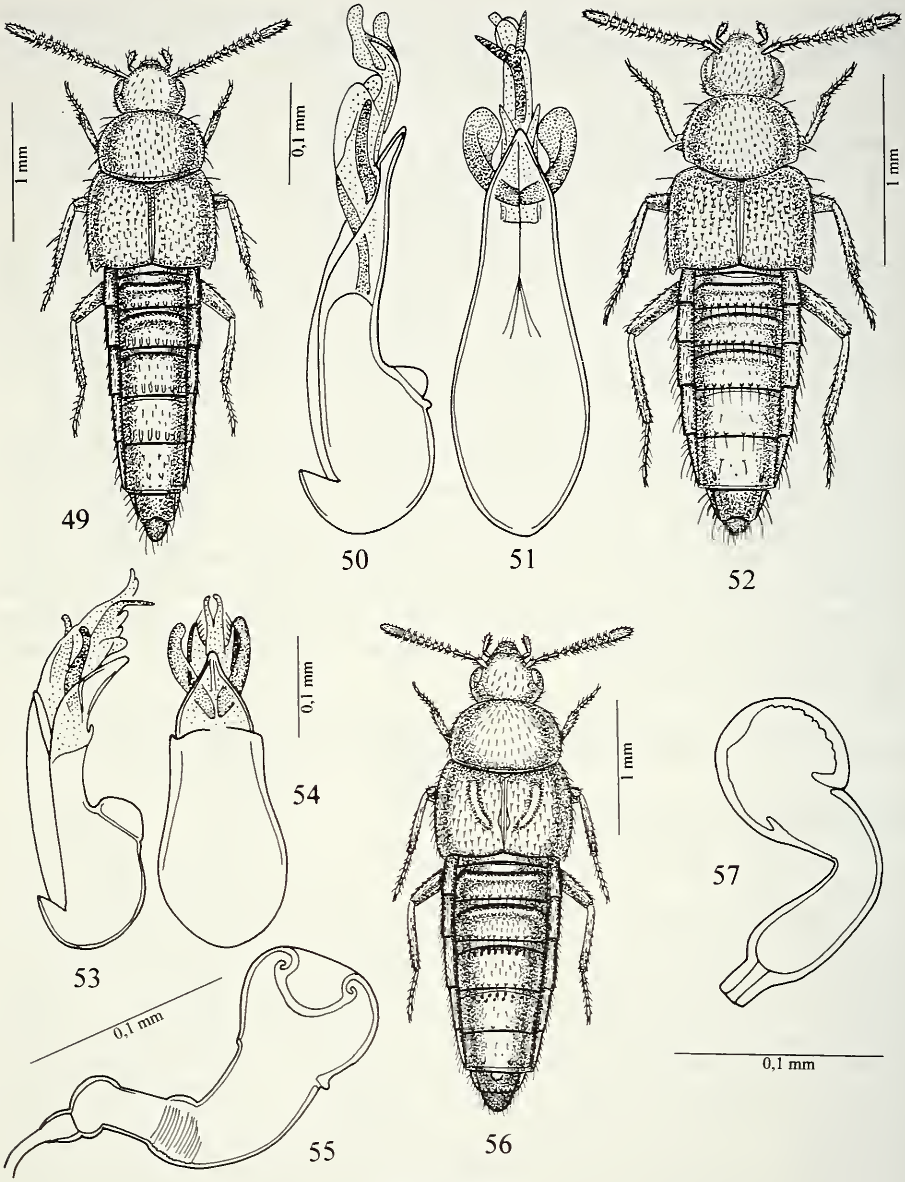
DESCRIZIONE: Lunghezza 3,2 mm. Corpo lucido e rossiccio con elitre brune, tranne gli omeri e il pigidio giallo-rossicci; antenne bruno-rossicce con i tre antennomeri basali e l'undicesimo giallo-rossicci; zampe gialle. Il corpo è privo di reticolazione. La punteggiatura del capo e del pronoto è poco evidente. La granulosità delle elitre è distinta. Nei solchi trasversi basali degli uroterghi liberi terzo e quarto la punteggiatura è evidente. Le elitre del maschio presentano una carena saliente ricurva che dalla base è diretta alla metà posteriore della sutura che mostra una lamina saliente, Fig. 56. Il sesto urotergo libero del maschio possiede un'ampia bozza mediana. Edeago Figg. 58-59, spermateca Fig. 57.

DERIVATIO NOMINIS: A motivo dell'armatura genitale interna dell'edeago molto sviluppata, la nuova specie prende nome di *bellicosa* o incline alla guerra.

### ***Pseudoplandria sabahensis*** sp. n. Figg. 60-63

HOLOTYPUS: Maschio, Sabah, K.K. Pulau Gaya, 27.X.1990, leg. G. De Rougemont (IRSN).

PARATYPI: 2 femmine, stessa provenienza. – 2 femmine, Sabah, Kinabalu N.P., 8.III.1990, G. De Rougemont. – 1 maschio e 4 femmine, Borneo, Sabah, Mt. Kinabalu N.P., HQ Silau-Silau Tr., 1550 m, 12.VIII.1988, leg. A. Smetana. – 1 femmina, Borneo, Sabah, Mt. Kinabalu N.P., HQ Liwagu Rv. trail, 1520 m, 11.VIII.1988, leg. A. Smetana . – 5 es., Borneo-Sabah, Mt. Kinabalu Nat. Pk., Silau-Silau trail, 1558 m, 2.XI.1988, leg. Bright. – 2 es., Sabah, Mt. Kinabalu Nat. Pk., HQ Silau-Silau Tr., 1540 m, 14.VIII-1.IX.1988, leg. A. Smetana. – 4 es., Borneo-Sabah, Mt. Kinabalu N. P., Headquarters, 1558 m, 3-12.VIII.1988, D.E. Bright collector. – 3 es., Borneo-Sabah, Mt. Kinabalu Nat. Pk., HQ Silau-Silau Tr., 1560 m, 30.IV.1987, leg. A. Smetana. – 4 es., Sabah, Mt. Kinabalu Nat. Pk, HQ 1560 m, beating foliage, 24.IV.1987, leg. D.E. Bright. – 2 es., Sabah, Mt. Kinabalu Nat. Pk., Poring Hot Springs, 510 m, 12.V.1987, leg. A. Smetana. – 2 femmine, Borneo, Sabah, Mt. Kinabalu N.P., Poring Hot Springs, 500 m, 6.V.1987, leg. Burckhardt & Löbl. – 1 maschio e 1 femmina, Sabah, Mt. Kinabalu, 1750 m, 21.V.1987, leg. Burckhardt & Löbl. – 1 maschio, Borneo, Sabah, Mt. Kinabalu N.P., Poring Hot Springs, Langanan Falls, 900-950 m, 12.V.1987, leg. Burckhardt & Löbl. – 1 maschio, Borneo-Sabah, Mt. Kinabalu N.P., Summit Trail, 1890 m, (data mancante), leg. A. Smetana. – 1 maschio e 3 femmine, Borneo, Sabah, Mt. Kinabalu N.P., HQ Liwagu River, 1490 m, 5.VIII.1988, leg. A. Smetana. – 1 maschio, Sabah, Poring Hot Springs, 486 m, 14.V.1987, leg. D.E. Bright.. – 4 es., Sabah, Mt. Kinabalu, 1750 m, 21.IV.1987, leg. Burckhardt & Löbl. – 1 es., Borneo-Sabah, Mt. Kinabalu,1500 m, 25.IV.1987, leg. Burckhardt & Löbl. – 2 es., Sabah, Mt. Kinabalu N.P., 1550-1650 m, 24.IV.1987, leg. Burckhardt & Löbl. – 1 es., Sabah, Kibongol V., 7 Km N. Tambunan, 700 m, 20.V.1987, leg. Burckhardt & Löbl. – 3 es., Sabah, Poring Hot Springs,

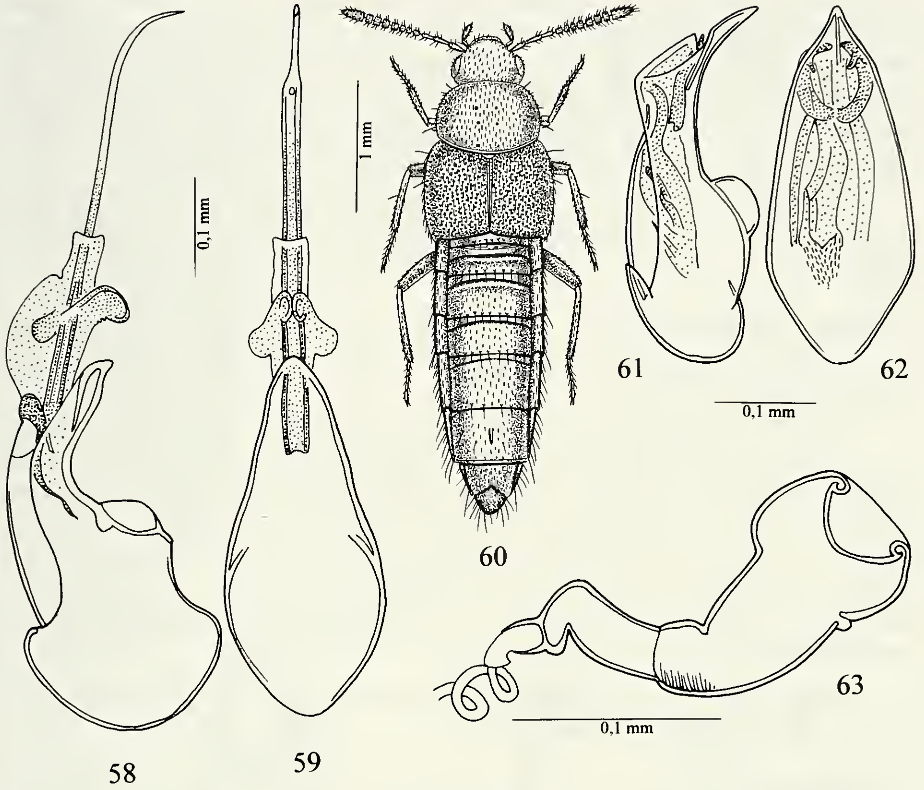


FIGG. 49-57

Habitus, edeago in visione laterale e ventrale e spermateca. (49-51) *Pseudoplandria dilatatalamina* sp. n. (52-55) *Pseudoplandria bruneicola* sp. n. (56-57) *Pseudoplandria bellicosa* sp. n.

500 m, 7.V.1987, leg. Burckhardt & Löbl. – 5 es., Sabah, Poring Hot Springs, 500 m, 8.V.1987, leg. Burckhardt & Löbl. – 1 es., Sabah, Poring Hot Springs, 500m, 13.V.1987, leg. Burckhardt & Löbl. – 1 es., Sabah, Mt. Kinabalu, 1550-1650, 24.IV.1987, leg. Burckhardt & Löbl.

DESCRIZIONE: Lunghezza 3,2 mm. Corpo lucido e bruno, con lati del pronoto e uroterghi liberi basali primo e secondo bruno-rossiccii. pigidio giallo-rossiccio;



FIGG. 58-63
Edeago in visione laterale e ventrale, habitus, e spermateca. (58-59) *Pseudoplandria bellicosa* sp. n. (60-63) *Pseudoplandria sabahensis* sp. n.

antenne brune con i tre antennomeri basali e l'undicesimo giallo-rossicci; zampe rossicce. Il corpo è privo di reticolazione. La punteggiatura del capo e del pronoto è poco distinta. La granulosità delle elitre è saliente. I solchi trasversi basali degli uroterghi liberi terzo e quarto non sono punteggiati. Il pronoto presenta alcuni punti forti allineati sulla fascia longitudinale mediana, Fig. 60. Edeago Figg. 61-62, spermateca Fig. 63.

***Pseudoplandria nobilis*** sp. n. Figg. 64-67

HOLOTYPUS: Maschio, Sabah, Kinabalu N.P., 29.X.1990, leg., G. De Rougemont (IRSN).

PARATYPI: 1 femmina, stessa provenienza. – 22 es., Borneo, Sabah, Mt. Kinabalu, 1500 m, 30.IV.1987, leg. Burckhardt & Löbl. – 20 es., Borneo, Sabah, Crocker Ra., 1550-1650 m, 16.V.1987, leg. Burckhardt & Löbl. – 1 femmina, Sabah, Kinabalu N.P., 8.III.1990, leg G. De Rougemont. – 1 femmina, Borneo, Sabah, Mt. Kinabalu Nat. Pk., HQ at Liwagu Rv., 1500 m, 4.VIII.1988, leg. A. Smetana. – 14 es., Sabah, Mt. Kinabalu 1550 m, 29.IV.1987, leg. Burckhardt & Löbl.

DESCRIZIONE: Lunghezza 3,6 mm. Corpo lucido e bruno-rossiccio con i tre quarti posteriori delle elitre bruni, tranne il margine posteriore rossiccio, margine posteriore degli uroterghi liberi e pigidio rossicci; antenne rossicce con i due antennomeri basali e l'undicesimo giallo-rossicci; zampe rossicce. Il corpo è privo di reticolazione. La punteggiatura del capo e del pronoto è finissima e quasi indistinta. La granulosità delle elitre è poco saliente. I solchi basali degli uroterghi liberi non sono punteggiati. Il pronoto presenta alcuni punti forti allineati sulla fascia longitudinale mediana, Fig. 64. Edeago Figg. 65-66, spermateca Fig. 67.

DERIVATIO NOMINIS: A motivo della grande taglia corporea, rispetto a quella di altre specie dello stesso genere, la nuova specie si presenta distinta, come rivestita di nobiltà.

### ***Pseudoplandria altitudinis*** sp. n. Figg. 68-70

HOLOTYPUS: Maschio, Borneo-Sabah, Mt. Kinabalu, 3150-3200 m, 3.V.1987, leg. Burckhardt & Löbl (MHNG).

DESCRIZIONE: Lunghezza 2,6 mm. Corpo lucido e bruno-rossiccio, con addome bruno con margine posteriore degli uroterghi liberi secondo a quinto e pigidio rossicci, urotergo libero quarto e base del quinto nero-bruni; antenne brune con i quattro antennomeri basali gialli; zampe giallo-rossicce. La reticolazione del capo e delle elitre è superficiale, quella del pronoto è molto evanescente. La punteggiatura del capo è poco visibile. La granulosità del pronoto è finissima, quella delle elitre è saliente. I solchi trasversi basale degli uroterghi liberi non sono punteggiati. Il pronoto presenta quattro punti discali evidenti, Fig. 68.

DERIVATIO NOMINIS: Il nome «dell'altitudine» deriva dal fatto che l'holotypus è stato raccolto ad alta quota altimetrica.

### ***Pseudoplandria fugax*** sp. n. Figg. 71-73

HOLOTYPUS: Maschio, Borneo, Sabah, Crocker Ra., 1600 m, Km 51 rte. Kinabalu-Tambunan, 18.V.1987, leg. Burckhardt & Löbl (MHNG).

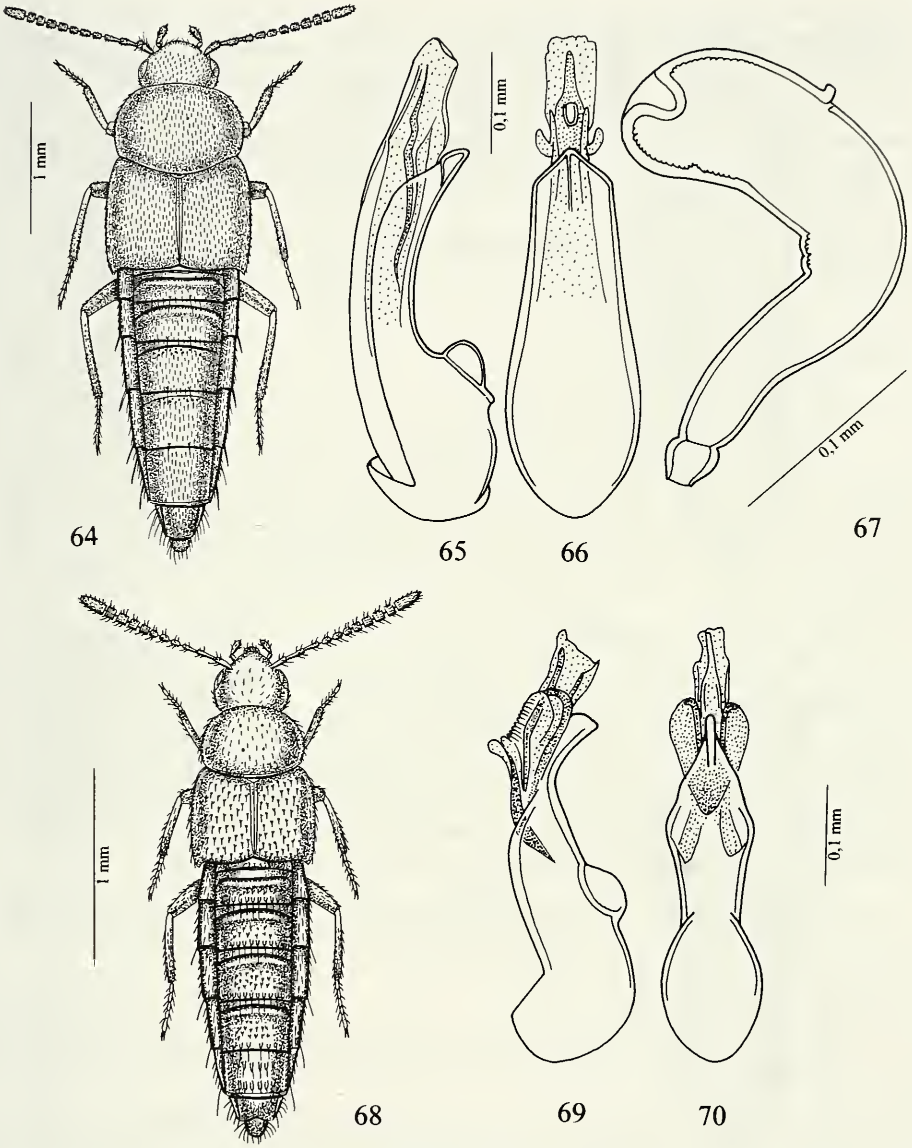
PARATYPUS: 1 maschio, Sabah, Mt. Kinabalu N.P., 1550-1650 m, 24.IV.1987, leg. Burckhardt & Löbl

DESCRIZIONE: Lunghezza 2,3 mm. Corpo lucido e rossiccio con elitre brune, tranne la base; antenne brune con i due antennomeri basali e la base del terzo giallo-rossicci; zampe giallo-rossicce. Solo il pronoto presenta una reticolazione che però è molto superficiale, sul resto del corpo manca qualsiasi tipo di reticolazione. La punteggiatura del capo e del pronoto è poco evidente. La granulosità delle elitre è ben visibile. Solo il solco trasverso basale del quarto urotergo libero mostra punteggiatura. Il quinto urotergo libero del maschio possiede un tubercolo mediano allungato. Edeago Figg. 72-73.

DERIVATIO NOMINIS: Il nome di «sfuggevole» della nuova specie deriva dal fatto che in un primo tempo avevo determinato come *P. sediziosa* questo esemplare. Ad un riesame mi sono reso conto che mi stava sfuggendo la corretta determinazione dell'esemplare.

### ***Pseudoplandria obscura*** sp. n. Figg. 74-77

HOLOTYPUS: Maschio, N Borneo-Sabah, Ranau, 2.VIII.1985, leg. K. Maruyama (DEI).



Figg. 64-70

Habitus, edeago in visione laterale e ventrale e spermateca. (64-67) *Pseudoplandria nobilis* sp. n. (68-70) *Pseudoplandria altitudinis* sp. n.

Paratypi: 1 femmina, N Borneo, Sabah, Bunsit, Keningau, 31.VII.1985, leg. K. Maruyama. – 1 maschio, Borneo, Sabah, Mt. Kinabalu N.P., Poring Hot Springs, 500 m, 10.V.1987, leg. A. Smetana. – 9 es., Sabah, Poring Hot Springs, 486 m, 14.VIII.1988, leg. D.E. Bright.

Descrizione: Lunghezza 2,8 mm. Corpo lucido e bruno con pronoto e gli uroterghi liberi primo, secondo e sesto bruno-rossicci; antenne brune con i tre antennomeri basali giallo-rossicci; zampe bruno-rossiccio con tarsi giallo-rossicci. Il corpo è privo di reticolazione. La punteggiatura del capo è superficiale, quella del pronoto è finissima ed evidente. La granulosità delle elitre è particolarmente grossolana dal disco verso la sutura. I solchi trasversi basali degli uroterghi liberi non sono punteggiati. Il pronoto presenta alcuni punti forti allineati sulla fascia longitudinale mediana, Fig. 74. Il quinto urotergo libero del maschio mostra un tubercolo mediano allungato. Edeago Figg 75-76, spermateca Fig. 77.

DERIVATIO NOMINIS: Il colore oscuro del corpo è all'origine del nome della nuova specie.

### ***Pseudoplandria sinusifera*** sp. n. Figg. 78-81

HOLOTYPUS: Maschio, Borneo, Sabah, Mt. Kinabalu Nat. Pk., HQ at Liwagu Rv., 1500 m, 4.VIII.1988, leg. A. Smetana (MHNG).

PARATYPI: 8 es., Borneo, Sabah, Mt. Kinabalu N. P., Poring Hot Springs, area Eastern Ridge tr., 850 m, 28.VIII.1988, leg. A. Smetana. – 3 es., Borneo-Sabah, Mt. Kinabalu Nat. Pk., HQ Silau-Silau Tr., 1550 m, 2.IX.1988, leg. A. Smetana. – 2 maschi e 2 femmine, Borneo, Sabah, Crocker Ra., 1270 m, Km 60 rte. Kota Kinabalu-Tambunan, 2-17.V.1987, leg. Burckhardt & Löbl. – 1 femmina, Borneo, Sabah, Mt. Kinabalu N.P., 1550m, 28.IV.1987, leg. Burckhardt & Löbl. – 1 maschio, Borneo-Sabah, Mt. Kinabalu,1500 m, 25.IV.1987, leg. Burckhardt & Löbl.

DESCRIZIONE: Lunghezza 2,6 mm. Corpo lucido e giallo-rossiccio con elitre bruno-rossicce; antenne brune con i tre antennomeri basali giallo-rossicci e metà apicale dell'undicesimo gialla; zampe giallo-rossicce. Il corpo è privo di reticolazione. La punteggiatura del capo è poco evidente, quella del pronoto è fine. La granulosità delle elitre è saliente. Sono punteggiati i solchi trasversi basali degli uroterghi liberi secondo, terzo e quarto. Il pronoto ha una profonda fossetta sinistra, probabilmente prodotta da difetto di farfallamento. Il quinto urotergo libero del maschio presenta un tubercolo mediano posteriore. Edeago Figg. 79-80, spermateca Fig. 81.

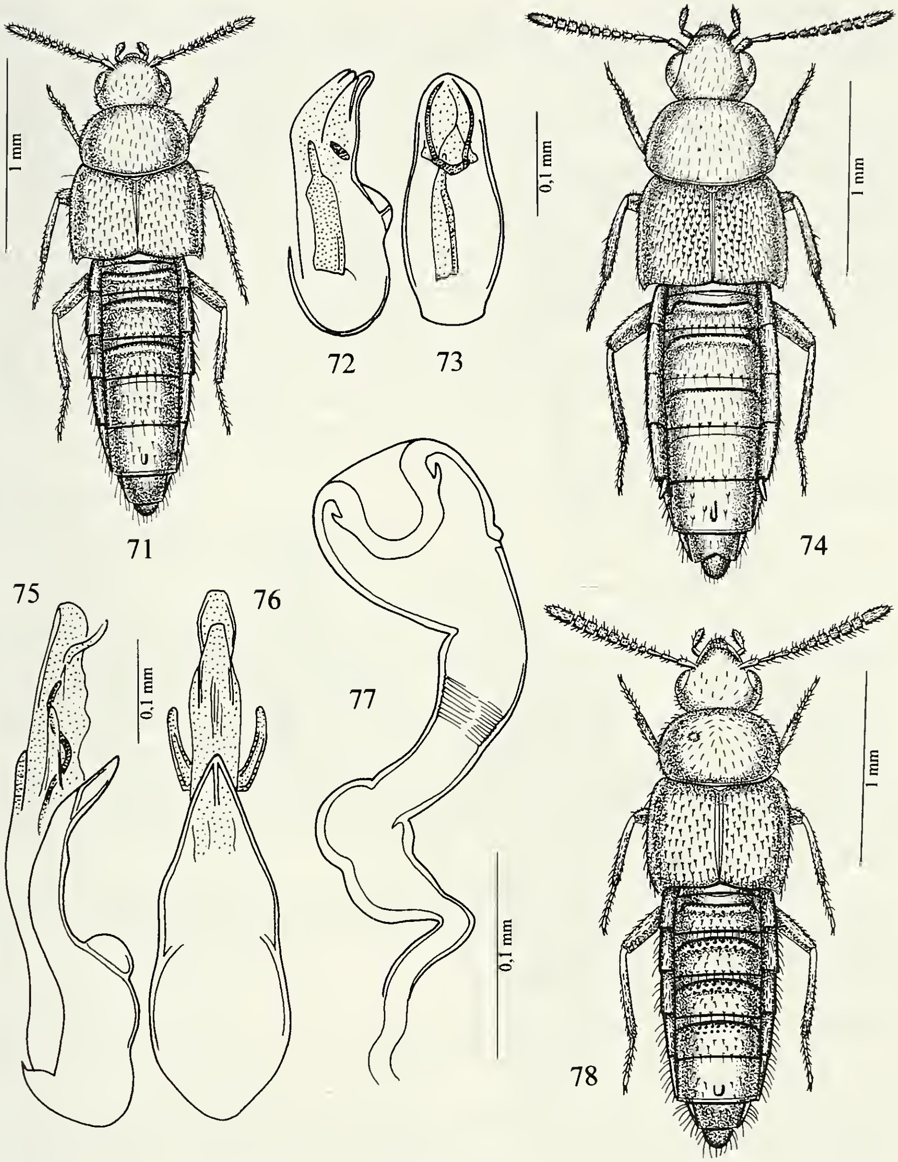
DERIVATIO NOMINIS: Il nome della nuova specie significa «portatrice di sinuosità», quella della parte apicale dell'edeago, in visione laterale.

### ***Pseudoplandria subanomala*** sp. n. Figg. 82-83

HOLOTYPUS: Femmina, Sabah, Mt. Kinabalu, 1550-1650 m, 24.IV.1987, leg. Burckhardt & Löbl (MHNG).

DESCRIZIONE: Lunghezza 3,6 mm. Corpo lucido e giallo-rossiccio, con capo e metà posteriore delle elitre bruno-rossicci; antenne brune con i due antennomeri basali e i tre quarti apicali dell'undicesimo giallo-rossicci; zampe giallo-rossicce. La reticolazione del capo e del pronoto è molto evanescente, sul resto del corpo essa è assente. La punteggiatura del capo e del pronoto è molto superficiale. La granulosità delle elitre è saliente. Sono punteggiati i solchi trasversi basali degli uroterghi liberi terzo, quarto e quinto. Il quinto urotergo libero mostra una rugosità longitudinale posteriore. Il pronoto presenta quattro punti discali, Fig. 82. Spermateca Fig. 83.

DERIVATIO NOMINIS: Il nome della nuova specie sta ad indicare, in base alla forma della spermateca, la sua stretta affinità con *P. anomala* sp. n. sopra descritta.



FIGG. 71-78

Habitus, edeago in visione laterale e ventrale e spermateca. (71-73) *Pseudoplandria fugax* sp. n. (74-77) *Pseudoplandria obscura* sp. n. (78) *Pseudoplandria sinusifera* sp. n.

***Pseudoplandria sanguinicollis*** sp. n. Figg. 84-87

HOLOTYPUS: Maschio, Borneo, Sabah, Mt. Kinabalu N.P., below Layang Layang, 2600 m, 2-8.V.1987, in Trap, leg. A. Smetana (MHNG).

PARATYPI: 6 maschi e 2 femmine, stessa provenienza. – 1 maschio, Sabah, Mt. Kinabalu, 1750 m, 27.IV.1987, leg. Burckhardt & Löbl. – 1 maschio, Borneo, Sabah, Mt. Kinabalu N. P.

below Layang Layang, 2600 m, 9-20.V. 1987, Int. Trap, leg. A. Smetana. – 1 maschio, Borneo, Sabah, Mt. Kinabalu, 2600 m, 1.V. 1987, leg. Burckhardt & Löbl. – 1 maschio e 1 femmina, Borneo, Sabah, Mt. Kinabalu, 2600 m, 2.V.1987, leg. Burckhardt & Löbl.

DESCRIZIONE: Lunghezza 3,8 mm. Corpo lucido e giallo-rossiccio, con capo ed elitre bruni; antenne brune con i tre antennomeri basali e i tre quarti apicali dell'undicesimo giallo-rossicci; zampe giallo-rossicce. La reticolazione del capo e del pronoto è molto superficiale. Assente è la reticolazione delle elitre e dell'addome. La punteggiatura del capo è molto evanescente. La granulosità del pronoto e delle elitre è evidente. La punteggiatura dei solchi trasversi basali degli uroterghi liberi è presente solo sul quarto. Il pronoto presenta un'ampia depressione posteriore. Uno spigolo superficiale attraversa obliquamente ciascuna elitra, Fig. 86. Il quinto urotergo libero del maschio presenta un tubercolo mediano. Edeago Figg. 84-85, spermateca Fig. 87.

DERIVATIO NOMINIS: Il nome della nuova specie significa «pronoto di sangue», ciò a motivo del colore giallo-rossiccio appunto del pronoto.

### ***Pseudoplandria pseudosanguinicollis*** sp. n. Figg. 88-90

HOLOTYPUS: Maschio, Borneo, Sabah, Mt. Kinabalu N.P., Layang Layang, 2610 m, 2.V.1987, leg. A. Smetana (MHNG).

PARATYPI: 3 maschi, stessa provenienza.

DESCRIZIONE: Lunghezza 3,6 mm. Corpo lucido e giallo-rossiccio con capo bruno-rossiccio ed elitre brune, margine posteriore degli uroterghi liberi giallo-rossiccio; antenne brune con i tre antennomeri basali giallo-rossicci e il quarto rossiccio; zampe rossicce. Il corpo è privo di reticolazione. La punteggiatura del capo è poco evidente. La granulosità del pronoto è fine e assai poco visibile, quella delle elitre è saliente. La punteggiatura dei solchi trasversi basali degli uroterghi liberi è assente. Il quinto urotergo libero del maschio ha la fascia longitudinale mediana libera di granulosità. Edeago Figg. 89-90.

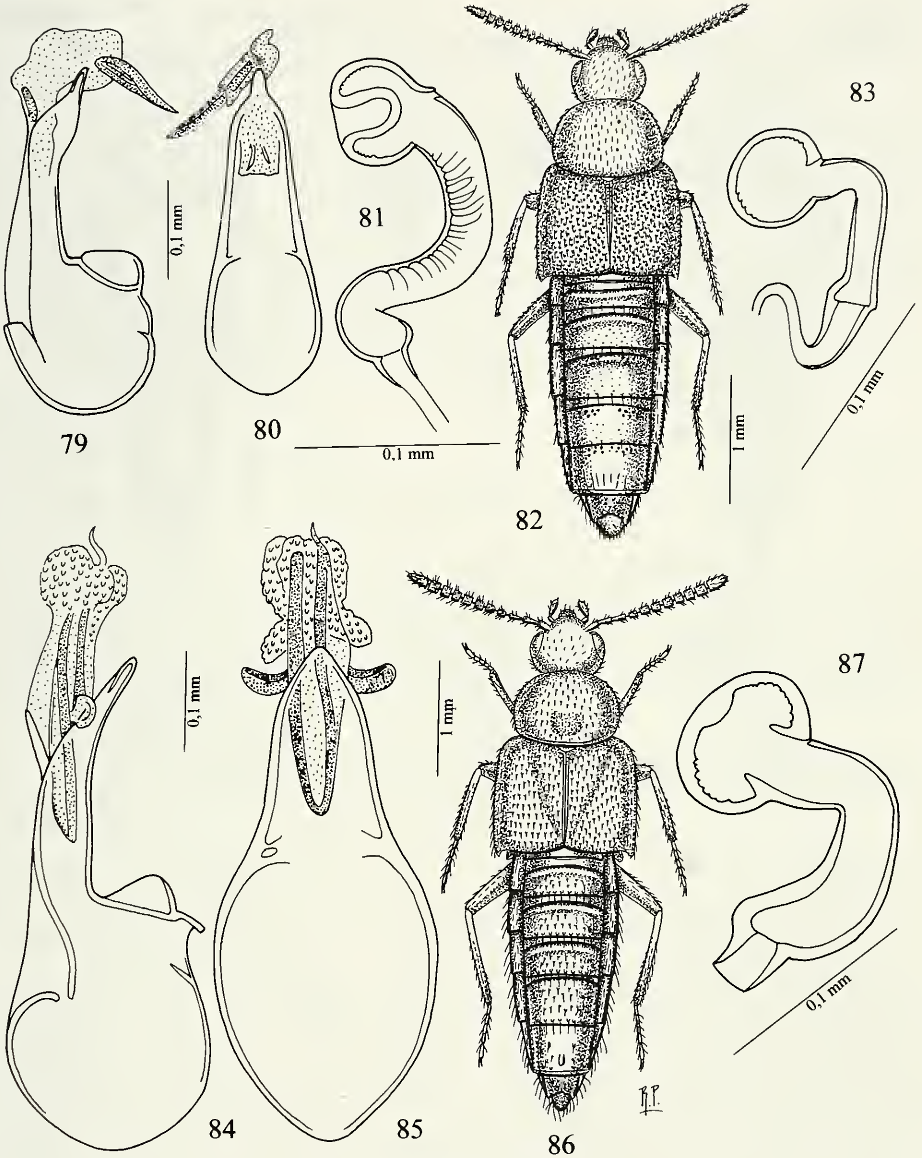
DERIVATIO NOMINIS: Il nome della nuova specie significa «falsa *sanguinicollis*», a motivo del colore del corpo molto simile a quello di *P. sanguinicollis* sp. n., ma l'edeago è differente.

### ***Pseudoplandria superba*** sp. n. Figg. 91-94

HOLOTYPUS: Maschio, Sabah, Mt. Kinabalu N.P., below Laban Rata, 3150 m, 5.V.1987, leg. A. Smetana (MHNG).

PARATYPI: 17 es., stessa provenienza. – 4 es., Sabah, Mt. Kinabalu N.P., Laban Rata, 3200-3250 m, 4.V.1987, leg. A. Smetana. – 1 es., Sabah, Mt. Kinabalu N.P., below Laba, Rata, 3150 m, 7.VIII.1988, leg. A. Smetana. – 1 femmina, Sabah, Mt. Kinabalu N.P., Laban Rata, 3200 m, 4-8.V.1987, int. Trap, leg. A. Smetana. – 4 es., Sabah, Mt. Kinabalu N.P., below Sayat-Sayat, 3700 m, 7.VIII.1988, leg. A. Smetana. – 3 es., Sabah, Mt. Kinabalu N.P., above Gunting Lagadan, 3400 m, 6.VIII.1988, leg. A. Smetana. – 1 es., Sabah, Mt. Kinabalu N.P., below Layang Layang, 2590 m, 1.V.1987, leg. A. Smetana. – 1 es., Sabah, Mt. Kinabalu N.P., Summit trail, Pondok Lowii, 2300-2400 m, 28.IV.1987, leg. A. Smetana. – 8 es., Sabah, Mt. Kinabalu, panar Laban, 3300m, 4.V.1987, leg. Burckhardt & Löbl.

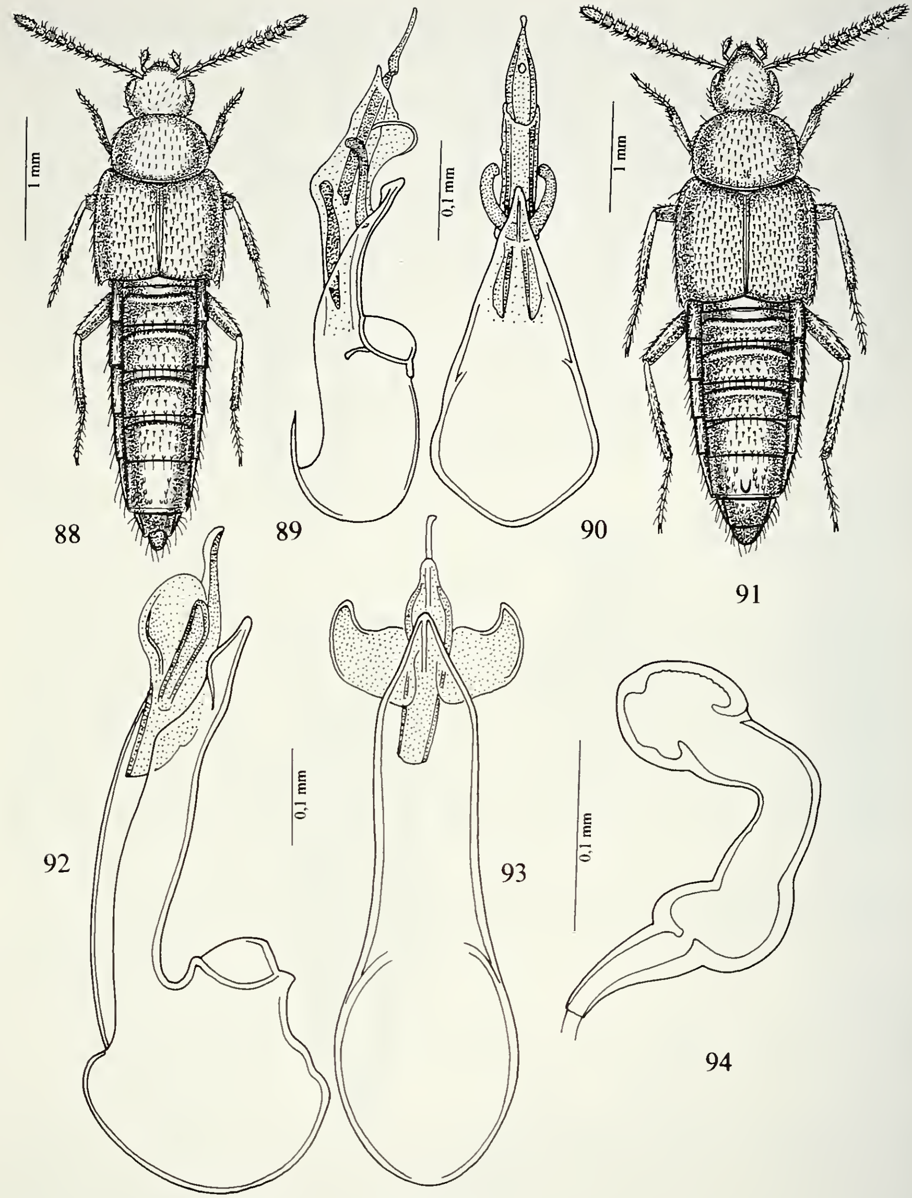
DESCRIZIONE: Lunghezza 4 mm. Corpo lucido e bruno, con pronoto giallo-rossiccio e addome bruno-rossiccio con gli uroterghi liberi terzo, quarto e base del quinto bruni; antenne brune con i tre antennomeri basali giallo-rossicci e quarto



FIGG. 79-87

Edeago in visione laterale e ventrale, spermateca e habitus. (79-81) *Pseudoplandria sinusifera* sp. n. (82-83) *Pseudoplandria subanomala* sp. n. (84-87) *Pseudoplandria sanguinicollis* sp. n.

rossiccio; zampe rossicce con tarsi giallo-rossicci. Il corpo è privo di reticolazione. La punteggiatura del capo è fine ed evidente. La granulosità del pronoto è fine e ben visibile, quella delle elitre è saliente. La punteggiatura dei solchi trasversi basali degli uroterghi liberi è assente. Il pronoto presenta una fossetta mediana posteriore. Il quinto



Figg. 88-94

Habitus, edeago in visione laterale e ventrale e spermateca. (88-90) *Pseudoplandria pseudosanguinicollis* sp. n. (91-94) *Pseudoplandria superba* sp. n.

urotergo libero del maschio mostra un tubercolo mediano posteriore. Edeago Figg. 92-93, spermateca Fig. 94.

Derivatio nominis: Il nome della nuova specie deriva dalla taglia esagerata o magnifica del corpo.

**Pseudoplandria parasanguinicollis** sp. n. Figg. 95-98

Holotypus: Maschio, Borneo, Sabah, MT. Kinabalu N.P., 2600 m, 2.V.1987, leg. A. Smetana (MHNG).

Paratypi: 2 maschi e 1 femmina, stessa provenienza.

Descrizione: Lunghezza 3,6 mm. Corpo lucido. Capo ed elitre bruni, pronoto giallo-rossiccio, addome rossiccio; antenne brune con i tre antennomeri basali e metà apicale dell'undicesimo rossicci; zampe giallo-rossicce. Il corpo è privo di reticolazione tranne che sul pronoto su cui è molto superficiale. La granulosità del capo e del pronoto è evidente, quella delle elitre è saliente. Il pronoto presenta un debole appiattimento mediano posteriore. Il quinto urotergo libero del maschio mostra granuli forti tra cui uno appiattito mediano posteriore. Edeago Figg. 96-97, spermateca Fig 98.

Derivatio nominis: Il nome della nuova specie indica la sua somiglianza corporea con *P. sanguinicollis* sp. n.

**Pseudoplandria distinctatheca** sp. n. Figg. 95-98

Holotypus: Femmina, Sabah, Mt. Kinabalu,1750 m, 27.IV.1987, leg. Burckhardt & Löbl (MHNG).

Descrizione: Lunghezza 2,3 mm. Corpo lucido e bruno; antenne brune con i quattro antennomeri basali giallo-rossicci; zampe giallo-brune con tibie anteriori e tarsi giallo-rossicci. Il corpo è privo di reticolazione tranne che sul pronoto su cui è superficiale. La punteggiatura del capo è molto evanescente. La granulosità del pronoto è evidente, quella delle elitre è saliente. La punteggiatura dei solchi trasversi basali degli uroterghi liberi è assente. Spermateca Fig. 100.

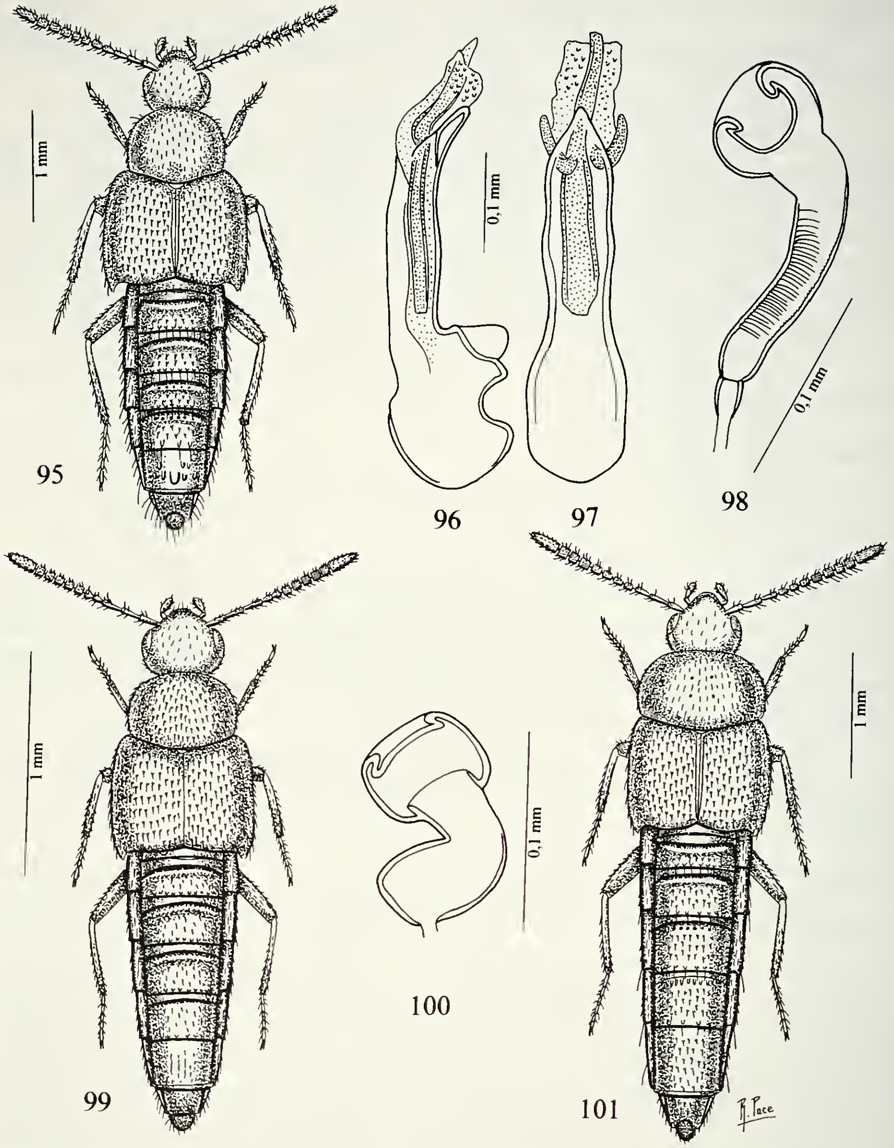
Derivatio nominis: Il nome della nuova specie significa «spermateca distinta». Essa infatti è così corta da distinguersi chiaramente da quella delle altre specie di *Pseudoplandria.*

**Pseudoplandria kinabaluicola** sp. n. Figg. 101-104

Holotypus: Maschio, Sabah, Mt. Kinabalu Nat. Pk, HQ 1560-1660 m, 24.IV.1987, leg. A. Smetana (MHNG).

Paratypi: 10 es., stessa provenienza. – 26 es., Sabah, Mt. Kinabalu Nat. Pk, HQ 1560-1660 m, 24.IV.1987, leg. Burckhardt & Löbl. – 17 es., Borneo, Sabah, Mt. Kinabalu Nat.Pk., HQ at Liwagu Rv., 1500 m, 25.IV.1987, leg. A. Smetana. – 3 es., Borneo, Sabah, Mt. Kinabalu Nat.Pk., HQ at Liwagu Rv., 1520 m, 11.VIII.1988, leg. A. Smetana. – 1 es., Borneo, Sabah, Mt. Kinabalu Nat.Pk., HQ at Liwagu Rv., 1490 m, 10.VIII.1988, leg. A. Smetana. – 1 es., Borneo, Sabah, Mt. Kinabalu Nat.Pk., HQ at Liwagu Rv., 1490 m, 3.IX.1988, leg. A. Smetana. – 1 femmina, Borneo, Sabah, Mt. Kinabalu Nat. Pk., HQ Silau-Silau Tr., 1540 m, 14.VIII.1988, leg. A. Smetana. – 2 es., Borneo, Sabah, Mt. Kinabalu Nat. Pk., HQ Silau-Silau Tr., 1550 m, 2.IX.1988, leg. A. Smetana. – 8 es., Sabah, Mt. Kinabalu, 1550 m, 23.IV.1987, leg. Burckhardt & Löbl. – 3 es., Sabah, Mt. Kinabalu, 1450-1550 m, 23.IV.1987, leg. Burckhardt & Löbl. – 5 es., Sabah, Mt. Kinabalu, 1750 m, 27.IV.1987, leg. Burckhardt & Löbl.. – 20 es., Borneo-Sabah, Mt. Kinabalu N.P., HQ at Liwagu Rv., 1500 m, 25.IV.1987, leg. Burckhardt & Löbl. – 19 es., Borneo, Sabah, Crocker Ra., 1600 m, Km 51 rte. Kinabalu-Tambunan, 18.V.1987, leg. Burckhardt & Löbl. – 4 es., Borneo, Sabah, Crocker Ra., 1600 m, Km 51 rte. Kota Kinabalu-Tambunan, 18.V.1987, leg. Burckhardt & Löbl. – 1 es., Borneo, Sabah, Crocker Ra., 1550-1650 m, 16.V.1987, leg. Burckhardt & Löbl.

Descrizione: Lunghezza 3,9 mm. Corpo lucido e rossiccio; antenne bruno-rossicce con i tre antennomeri basali e l'undicesimo giallo-rossicci; zampe rossicce con



FIGG. 95-101

Edeago in visione laterale e ventrale, spermateca e habitus. (95-98) *Pseudoplandria parasanguinicollis* sp. n. (99-100) *Pseudoplandria distinctatheca* sp. n. (101) *Pseudoplandria kinabaluicola* sp. n.

tarsi giallo-rossicci. Il corpo è privo di reticolazione. La punteggiatura del capo è molto superficiale. La granulosità del pronoto è molto superficiale, quella delle elitre è evidente. La punteggiatura è presente solo nei solchi trasversi basali degli uroterghi liberi terzo e quarto. il pronoto presenta punti isolati forti sulla fascia longitudinale mediana. Edeago Figg. 102-103, spermateca Fig. 104.

***Pseudoplandria expansa*** sp. n. Figg. 105-107

HOLOTYPUS: Maschio, Sabah, Mt. Kinabalu Nat. Pk., Paka Cave, 2997 m, 6.V.1987, leg. A. Smetana (MHNG).

DESCRIZIONE: Lunghezza 2,8 mm. Corpo lucido e bruno-rossiccio, con pronoto giallo-bruno; antenne brune con i tre antennomeri basali giallo-rossicci; zampe giallo-rossicce. La reticolazione del capo e delle elitre è molto superficiale. Sul resto del corpo è assente. La punteggiatura del capo è superficiale. La granulosità del pronoto è fine e poco evidente, quella delle elitre è saliente. La punteggiatura dei solchi trasversi basali degli uroterghi liberi è assente. Sul pronoto si trovano quattro punti discali in quadrangolo. Edeago Figg. 106-107.

DERIVATIO NOMINIS: La nuova specie prende nome dalla parte dilatata dell'apice dell'edeago, in visione laterale.

***Pseudoplandria biperforata*** sp. n. Figg. 108-110

HOLOTYPUS: Maschio, Sabah, Crocker Ra., 1200 m, Km 63 rte Kota Kinabalu-Tambunan, 19.V.1987, leg. Burckhardt & Löbl, (MHNG).

DESCRIZIONE: Lunghezza 2,8 mm. Corpo lucido e bruno con margine posteriore degli uroterghi liberi primo, secondo e terzo rossicci; antenne brune con i tre antennomeri basali e metà apicale dell'undicesimo giallo-rossicci; zampe brune con tarsi giallo-rossicci. Il corpo è privo di reticolazione. Il pronoto presenta due punti discali. Le elitre del maschio mostrano una plica all'angolo posteriore interno. La punteggiatura dei solchi trasversi basali degli uroterghi liberi è presente solo sul terzo e quarto. Il quinto urotergo libero del maschio ha un tubercolo mediano allungato.

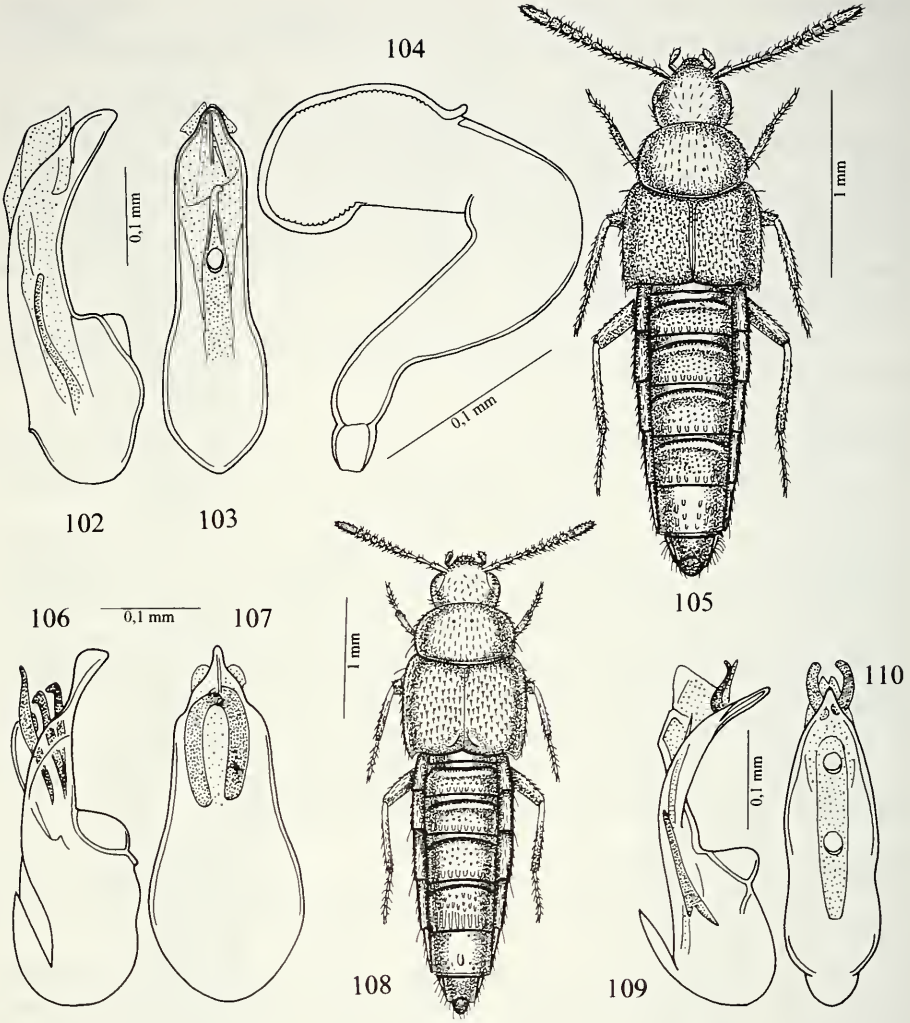
DERIVATIO NOMINIS: La nuova specie prende nome dalla presenza di due fori dell'armatura genitale interna dell'edeago, in visione ventrale.

***Pseudoplandria serpentina*** sp. n. Figg. 111-113

HOLOTYPUS: Maschio, Borneo, Sabah, Mt. Kinabalu N.P., 1580 m, 27.IV.1987, leg. Burckhardt & Löbl (MHNG).

DESCRIZIONE: Lunghezza 3,6 mm. Corpo lucido e bruno con margine posteriore degli uroterghi liberi primo, secondo e terzo rossiccio; antenne brune con i quattro antennomeri basali e la metà apicale dell'undicesimo giallo-rossicci; zampe giallo-rossicce. Il corpo è privo di reticolazione. La punteggiatura dei solchi trasversi basali degli uroterghi liberi è presente solo sul terzo e quarto. Il pronoto presenta quattro punti discali in quadrangolo. Il quinto urotergo libero del maschio ha una carena mediana esile. Edeago Figg. 112-113.

DERIVATIO NOMINIS. La nuova specie prende nome da un'armatura genitale interna dell'edeago che ha forma serpeggiante, in visione laterale.



FIGG. 102-110

Edeago in visione laterale e ventrale, spermateca e habitus. (102-104) *Pseudoplandria kinabaluicola* sp. n. (105-107) *Pseudoplandria expansa* sp. n. (108-110) *Pseudoplandria biperforata* sp. n.

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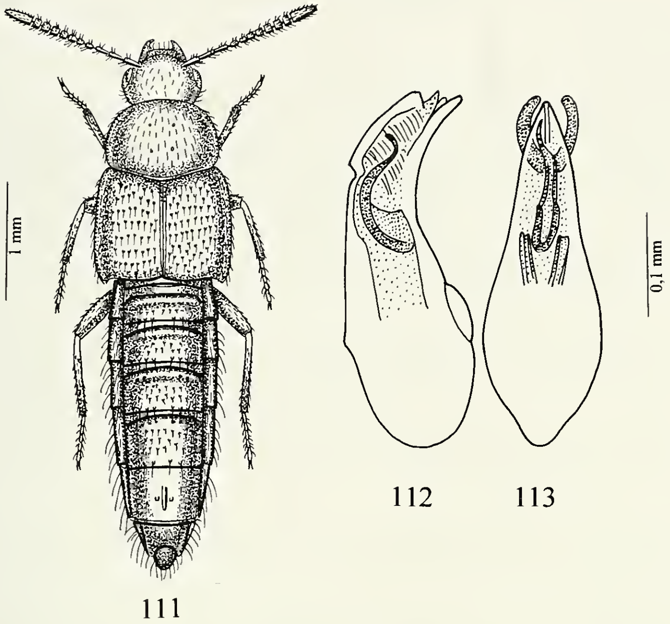

FIGG. 111-113
Habitus e edeago in visione laterale e ventrale. (111-113) *Pseudoplandria serpentina* sp. n.

## BIBLIOGRAFIA

CAMERON, M. 1928. New Species of Staphylinidae from Borneo. *Sarawak Museum Journal* 3(4)11: 413-422.

FENYES, A. 1921. New genera and species of Aleocharinae with a polytomic synopsis of the tribes. *Bulletin of the Museum of Comparative Zoology*, 65: 17-36.

PACE, R. 1986. Aleocharinae dell'Asia sudorientale raccolte da G. de Rougemont (Coleoptera, Staphylinidae) (LXXII Contributo alla conoscenza delle Aleocharinae). *Bolletino del Museo civico di Storia naturale di Verona* 23: 139-237.

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## Tome 115 — Fascicule 2

Pages

REVUE SUISSE DE ZOOLOGIE

Volume 115 — Number 2

**Indexed in** CURRENT CONTENTS, SCIENCE CITATION INDEX

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| REVISION DER PALÄARKTISCHEN ARTEN DER GATTUNG *BRACHYGLUTA* THOMSON, 1859 (COLEOPTERA, STAPHYLINIDAE) (1. Teil)<br>(*Instrumenta Biodiversitatis* VI), G. Sabella, Ch. Bückle, V. Brachat & C. Besuchet, vi + 283 p., 2004 | Fr. | 100.— |
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Volume 115 - Number 2 - 2008

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