RESEARCH ARTICLE



A revision of the genus *Muricea* Lamouroux, 1821 (Anthozoa, Octocorallia) in the eastern Pacific. Part I: Eumuricea Verrill, 1869 revisited

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Abstract

Muricea is an amphi-American genus. Verrill proposed dividing the species from the Pacific Ocean into three genera and established the genus *Eumuricea* for five eastern Pacific species with tubular calyces. *Eumuricea* is basically characterized by colonies with elongate, cylindrical calyces with truncate margins and star-like opercula, and the occurrence of unilateral spinous spindles. According to these characteristics, *Eumuricea* does not show enough difference from *Muricea* to be treated as a separate genus. Original type material of *Eumuricea* was morphologically analysed and illustrated using optical and scanning electron microscopy. We conclude that the eastern Pacific species should be placed in the genus *Muricea* and form a group characterised by tubular calyces that comprises four species at present, *M. acervata, M. hispida, M. squarrosa*, and *M. tubigera* and a dubious species *M. horrida*. Lectotypes were designated for *M. squarrosa* and *M. hispida* to establish their taxonomic status. The genus *Eumuricea* has also been misunderstood by former authors who erroneously assigned species to it. For these species we propose new combinations: *Swiftia pusilla, Astrogorgia splendens* and *A. ramosa*.

Keywords

Alcyonacea, Astrogorgia, Cnidaria, eastern Pacific, Eumuricea, Muricea, Leptogorgia, plexaurid gorgonian, soft corals, Swiftia, taxonomy

Introduction

Muricea Lamouroux, 1821 is an amphi-American genus with representatives in the western Atlantic and the eastern Pacific (Verrill 1869a, Bayer 1961). The eastern Pacific species were revised by Verrill (1869a) in his paper "Notes on Radiata", where three subdivisions for the genus were proposed (Verrill 1869: 449-450), and considered by him as more than subgeneric value – two groups for the eastern Pacific species: *Eumuricea* and *Muricea* (family Plexauridae), and a third group for the Indian Ocean: *Muricella* Verrill, 1869a (presently in the family Acanthogorgiidae).

The genus *Muricella* includes species with rather thin coenenchyme, filled with long spindles, low subconical calyces arising from between the large spindles, usually standing at right angles from the axis, and covered with much smaller and shorter spindles (Verrill 1869a). As defined by Verrill, many other species could fit in this genus. Fabricius and Alderslade (2001) gave a more precise description: *Muricella* has planar fans, often net-like, and at least two-thirds of a meter tall. The polyps are short and dome-shaped, non-retractile. The sclerites are mainly spindles and small capstan, and rods. The colonies could be brown, yellow, pink and white. The polyp colour may contrast to the coenenchyme colour. The zoogeographic distribution of this genus is not clear (Fabricius and Alderslade 2001).

The eastern Pacific *Eumuricea* and *Muricea* were separated, according to Verrill (1869a), by differences in the calyx structures. He established *Eumuricea* for species with "tubular calyces, without a prolonged lower border and not bilabiate; and *Muricea* for species with more or less prominent calyces, with a more or less prolonged lower border, and bilabiate". Hickson (1928) commented on the vaguely-defined characters used by Verrill to separate the *Muricea* groups, but did not proposed a better alternative. He pointed out, defining *Muricea* based on "bilabiate calyx" and "one-sided" spindles is inappropriate, especially because the terms were not properly explained. He said that in most of the species of *Muricea* the calyx is bent more or less upwards, a characteristic that cannot be observed in well preserved specimens, and also that the "one-sided" spindles are present in most of the species and there is a large variety of them. For these reasons Hickson (1928) considered that the only valid character to separate the groups is the tubular calyces in *Eumuricea*, but he did not refer to that as a character of generic value.

Eumuricea was proposed by Verrill (1869a) for four species in the YPM collection (during his time) from various localities along the eastern Pacific; he also transferred *Muricea horrida* Möbius, 1861 (from Perú) to *Eumuricea*. The lack of good illustrations and clear definitions has historically led authors to assign species erroneously to this genus (e.g. Riess 1929 (in Kükenthal 1919 and 1924), Nutting 1909, Thomson and Simpson 1909, Thomson (1927). Riess (1929) described *Eumuricea atlantica* from Jamaica; however, her description was not consistent with the characters proposed for *Eumuricea*. Deichmann (1936) made reference to this same species without any comment about its status. Later, Bayer (1961) clarified the status of *E. atlantica* as being a species of *Muricea*. Thomson (1927) listed two species for the eastern Atlantic *Eumuricea rugosa* and *Eumuricea rigida*; however, Deichmann (1936) doubted that

these species belonged to this genus. Grasshoff (1992) synonymised *E. rugosa* with *Leptogorgia ruberrima* (W. Koch, 1886), and Ofwegen (2014) assigned *E. rigida* to the genus *Thesea*. Three other species: *Eumuricea splendens* Thomson & Simpson, 1909, *Eumuricea ramosa* Thomson & Simpson, 1909, and *Eumuricea pusilla* Nutting 1909, were included in this genus. The taxonomic status of these species is discussed here.

Other authors revisited this genus. Kükenthal (1924) published a key and a short review of the described species of *Eumuricea*. Aurivillius (1931) commented about this genus and remarked that the species described by Thomson and Simpson (1909), and by Nutting (1909) did not belong to the genus *Eumuricea*. Bayer in his 1981 key restored several genera that had been treated as junior synonyms or as subgenera by previous authors to a valid generic status, and stated the possibility of several more that would be validated when comparative studies have been completed. Thus, the genus *Eumuricea* was retained and separated from *Muricea*.

As it has been addressed before (e.g. Breedy and Guzman 2011), the lack of welldefined characters, good specimen and sclerite illustrations, and holotype designations in the original publications have made it difficult to recognise with certainty the species of *Muricea* (as is the case in other eastern Pacific genera).

This research represents the first part of the fifth review in a series proposed to evaluate the gorgonian genera historically reported for the shallow eastern Pacific waters. The second part will treat the genus *Muricea* Lamouroux, 1821 *sensu stricto*. Previous reviews dealt with *Pacifigorgia* Bayer, 1951 (Breedy and Guzman 2002), *Leptogorgia* Milne Edwards & Haime, 1857 (Breedy and Guzman 2007) and *Eugorgia* Verrill, 1868 (Breedy et al. 2009), in the family Gorgoniidae; and *Heterogorgia* Verrill, 1868 in the family Plexauridae (Breedy and Guzman 2011).

Acronyms

MNHUK	Museum of Natural History (former BM, British Museum), London, UK									
CIEMIC	Centro de Investigación en Estructuras Microscópicas, Universidad de									
	Costa Rica									
CRBMco	Colección de referencia de Biología Marina Universidad Del Valle, Cali,									
	Colombia									
IMARPE	Instituto del Mar de Perú, Lima, Perú									
INN	NAZCA Instituto de Investigaciones Marinas, Salinas, Ecuador									
MCZ	Museum of Comparative Zoology, Harvard University, Boston, USA									
SEM	Scanning Electron Microscopy									
STRI	Smithsonian Tropical Research Institute, Panamá									
UCR	Museo de Zoología, Escuela de Biología, Universidad de Costa Rica, Costa Rica									
UNIAND	ES-BIOMMAR Universidad de Los Andes, Laboratorio de Biología									
	Molecular Marina, Bogotá, Colombia									
UPCH	Colecciones Biológicas, Universidad Peruana Cayetano Heredia, Lima, Perú									
USNM	Museum of Natural History (former United States National Museum),									

Smithsonian Institution, Washington, USA

YPM Yale Peabody Museum of Natural History, New Haven, USAZMH Zoologisches Institut und Zoologisches Museum der Universität Hamburg, Germany

Material and methods

The type specimens used in this study were analysed during visits to museums or acquired on loan from the BM, MCZ, USNM, and YPM. Comparative material was analysed from the collections deposited in CRBMco, IMARPE, INN and UPCH. In addition to specimens recently collected from the Pacific coast of Costa Rica and Panama deposited in the UCR and STRI. All reference material was collected by scuba diving down to 40 m in depth. The type material presented here from the western Atlantic and Indo-Pacific was the only one available to us at this time.

Morphological study

For microscopic study, specimens were prepared for SEM following the standard protocol described in Breedy and Guzman (2002). For optic microscopy, sclerites were mounted in water or glycerine and photographed with an Olympus LX 51 inverted microscope. Sclerites of the coenenchyme and calyces are variable in size and form; the prevailing kinds are illustrated and described. Measurements of the sclerites were obtained from pictures and directly from the microscope using an optical micrometer. Length of the sclerites was measured from one tip to the other and the width was taken from the most distant points across the sclerites, reporting the largest sizes found in the samples and also, a range of variation. The diameter of the branches, branchlets, and stems are given taking in account the calyces length, the reported measurements represent the largest sizes found in the sample and in some cases, a range of variation. The mean number of calyces by cm was taken from pictures, counting the number of calyces on one side (the one showed in the picture) of each tip branch of the colony and is reported as the mean (number of calyces by cm/ number of branches measured). The limitations found in this procedure were due to the preservation state of the specimens and the number of branches. We emphasize that this measure is just a reference number and does not represent the real number of calyces/cm around the branch of each species, but is a good character to show the tendency in a species. The calyx length given corresponds to the upper parts of the branches. The colours of the colonies and sclerites are stable, and persist after fixation. Some fading is observed in dry specimens. When possible the colours of the colony alive, preserved and dry are mentioned.

Data on geographical distribution are from our personal collections, museum catalogues, and published monographs. In some cases there is just one specimen in the collection under a species name, which automatically constitutes the holotype. When needed we designated lectotypes to establish the species identity and avoiding future confusion.

Terminology

Terminology is according to Bayer (1961) and Bayer et al. (1983). Some term modifications dealing with *Muricea* descriptions are included below.

- *branched spindle*: a spindle with some of the processes much elongated and branchlike, often crooked.
- *calyx*: cylindrical or wartlike projecting anthostele. In *Muricea*, it is mostly formed by the same type as the outer coenenchyme sclerites. They are arranged as a fringe around the border of the calyx with the sharp or spiny processes projecting outwards.
- calyx shelf-like: calyx with prolonged lower border, polyp opens upwards.
- *calyx tubular*: tube-like calyx with mostly even, truncate borders, polyp opens straight and distally.
- *club*: monoaxial sclerite enlarged at one end, the head, and tapered at the other end, the handle. According to the modification of the head they are classified in leaf, thorn, wart or torch. *Muricea*, the heads are mostly ornamented by sharp, thorn-like or spine-like processes, and the handles are warty, or of an almost smooth surface, curved or straight.
- *unilateral spinous spindles*: sclerites with asymmetrically arranged warts on the surface. Inner side with low composite warts, close together or very crowded, their processes often anastomose. Outer side with fewer cone-shaped tubercles, long projecting in some cases. Ends of the sclerites blunt, acute or both.

Notes on morphological characters

Variation is expected in the diameter of stems and branches either in preserved or dry material, due to the preservation history of specimens. Most of the type material is dry and old (more than a century). Some specimens are deteriorated. According to Hickson (1928) the drying or preservation process can affect some characteristics, especially the calyces. However, we have observed that the tendency of the calyces to be slightly raised or prominent is kept after retraction during preservation, and it is also observed in living specimens. The calyx length and spacing vary from the larger branches to the thinner, being larger and acute, and closer placed on the branchlets and shorter, blunt, and distant on the main branches. For these reasons, we record measurements of these characters from the upper part of the branches. The sclerites that compose the outer coenenchyme and the calyx are mostly large spindles of several shapes. Bayer (1961) refers to this type of spindle as unilateral spinous and it is the term that we used here for the descriptions (defined above).

The polyp sclerites are basically rods and spindles, in most of the cases it was not possible to determine the anthocodial arrangement because of the deterioration of the type material, few type specimens were found preserved in ethanol. However, we did notice that there is no collaret and points arrangements as in other plexaurids. The sclerites are mostly placed longitudinally in irregular arrangements or in some cases in points. Although some variation is expected, the colour of sclerites and colonies is remarkably constant. Some species dye the ethanol a dark purplish colour when preserved. In this genus, colours are mostly hues of brown, and the sclerites do not present much colour variation.

Taxonomy

Key to distinguish genera (modified from Bayer 1981)

1	Sclerites in form of spindles and capstans, with tubercular sculpture arranged in
	whorls, measuring less than 0.3 mm long. Anthocodial sclerites mainly flat rods
	forming weak or irregular collaret and points arrangements Leptogorgia
_	Sclerites in form of spindles highly modified, measuring more than 0.3 mm
	long. Anthocodial sclerites other than flat rods forming collaret and points or
	variation of that arrangement
2	Coenenchyme contains unilateral spinous sclerites, polyps retract into shelf-
	like or tubular calyces
_	Coenenchyme does not contain unilateral spinous sclerites, polyps retract
	into prominent or slightly raised dome-shaped polyp mounds
3	Coenenchymal sclerites mostly spindles, straight, curved, branched, heavily
	ornamented with complex tubercles, and prickles. Sclerites below the points
	may be transverse, but small and numerous, not forming distinct collaret
	Astrogorgia
_	Coenenchymal sclerites mainly capstans, radiates and spindles, thin, sharp, with
	tubercles, some modified as incomplete disks, but not heavily ornamented
	Swiftia

Class Anthozoa Ehrenberg, 1834 Subclass Octocorallia Haeckel, 1866 Order Alcyonacea Lamouroux, 1812 Family PLEXAURIDAE Gray, 1859

Genus Muricea Lamouroux, 1821

Muricea Lamouroux, (pars) 1821: 36; Blainville (pars) 1834: 509; Ehrenberg (pars) 1834: 134; Dana 1846: 673; Milne Edwards and Haime 1850: 142; Kölliker 1865: 135; Verrill 1868b: 411; Verrill 1869a: 418–419, 450; Studer 1887: 58; Wright and Studer 1889: 93; Gorzawsky 1908: 8; Nutting 1910: 9; Kükenthal 1919: 835; 1924: 141; Riess 1929: 383–384; Aurivillius 1931: 102–104; Deichmann 1936:

99; Bayer 1956: F210; 1959: 12; 1961: 179–180; 1981: 930 (in key); 1994: 23–24; Tixier-Durivault 1969–1970: 154; Harden 1979: 140; Hardee and Wicksten 1996: 127–128; Marques and Castro 1995: 162; Castro et al. 2010: 779.

Eumuricea (pars) Verrill, 1869: 449; Riess 1929: 397; Studer 1887: 58; Wright and Studer 1889: pl LVI; Nutting 1909: 718; Thomson and Simpson 1909: 258; Thomson 1927: 48–49; Kükenthal 1919: 836; 1924: 149–150; Riess 1919: 397–398; Aurivillius 1931: 50 (emended); Deichmann 1936: 104.

Eumuricea (Muricea) Bayer 1981: 930 (in key).

Type species. *Muricea spicifera* Lamouroux, 1821, by subsequent designation: Milne Edwards and Haime 1850. [*M. spicifera* was later synonymised with *Muricea muricata* (Pallas, 1766) *apud* Bayer 1961: 179–180]

Diagnosis (based on Bayer 1961, 1994; Marques and Castro 1995; Castro et al. 2010). Colonies planar or multiplanar, bushy, arborescent, laterally branched, pinnately branched, dichotomous or with long flexible branches without occasional branch anastomosis. Branches and branchlets upward bending almost parallel, and with about the same thickness all along, frequently with slightly enlarged tips. Coenenchyme moderately to very thick (compared to other plexaurids) with a circle of longitudinal canals surrounding the axis and dividing the coenenchyme into a thin inner layer or axial sheath, and a thicker outer layer. Polyps fully retractile within prominent calyces longitudinally and closely placed and at all sides of the branches. Calyces prominent, shelflike or tubular, with prickly projecting spindles, longitudinally arranged, imbricate or not. Anthocodial sclerites mainly small spindles, in weakly differentiated transverse collaret and points below the tentacles, or just with some sclerites scattered along the neck zone of the polyp. Sclerites of the outer coenenchyme mostly long, unilateral spinous spindles, often massive, sculptured on inner surface by crowded complex tubercles and on outer surface by simple spines or prickles, and in some species with a few more or less prominent coarse, prickly projections. Axial sheath composed of capstans, spindles, or oval forms. Sclerite colours white, various hues of yellow, amber, orange, purple and red. Anthocodials with lower colour hues.

Distribution. From Cape Hatteras, North Carolina to Brazil, including Bahamas, Greater and Lesser Antilles, and Caribbean islands (Bayer 1961); in the eastern Pacific from southern California to Peru. The genus occurs at depths down to 200 m, but normally found less than 100 m. *Muricea midas* Bayer, 1959 is the deepest record for the genus in the western Atlantic, 146 m (Bayer 1959); and *Muricea galapagensis* Deichmann, 1941 in the eastern Pacific, 91 m.

Remarks. Colony shape and branching patterns are variable among *Muricea* species. The shape of calyces shelf-like or tubular, and related features as being imbricate or sparse show many intermediate forms. In the tubular-calyces species group the apical branches show a closer arrangement of calyces and smaller projecting angles in respect to the branch than at the lower branches. Therefore, the strongest character that separates *Muricea* from other genera is the type of sclerites.

Muricea acervata Verrill, 1866

Figures 1-2

Muricea acervata Verrill, 1866: 327–328; Rossi 1955; Harden 1979: 142. *Muricea (Eumuricea) acervata* Verrill, 1869a: 419–421. *Eumuricea acervata* Kükenthal, 1924: 143.

Material. Holotype: YPM 1791 (figured specimen), dry, Bay of Panamá, Panamá, F.H. Bradley, 1866, no more data. Schizotype: USNM 1130758 (donated by YPM).

Description. The holotype is a 20 cm tall and 12 cm wide colony, the branching is lateral, almost in one plane (Fig. 1A) candelabrum-like. All branches are thick and rigid with almost the same diameter, 7–8 mm, from base to top. Two main branches, subdivide from a 2 cm long stem in secondary branches that remain unbranched up to the top of the colony, or subdivide up to 3 times producing branchlets of almost the same diameter. The branches are up to 20 mm apart, branch at angles of 45°–90°, and curve upwards, with blunt tips. Undivided terminal ends are up to 7 mm in diameter and 70 mm long (Fig. 1A–B). A vestige of the holdfast remains at the base of the stem. Axes are



Figure 1. *Muricea acervata* Verrill, 1866 YPM 1791. **A** Colony **B** Detail of branches **C** Sclerites, light micrograph.



Figure 2. *Muricea acervata* Verrill, 1866 YPM 1791. **A** Calycular and coenenchymal spindles **B**, **C** Axial sheath spindles and radiates **D** Anthocodial sclerites.

amber at the tips and darker at the base. Calyces are uniformly crowding the branches, close together, about 21 calyces/cm. They are up to 2.50 mm long and about the same in width, 1.8–2.0 mm. The rounded, small calyx apertures contain remains of anthocodial sclerites. The anthocodia are retracted and the eight projections of the calyces close over them. They are separated by slightly sunken grooves, which show an octoradiate star-like arrangement, that Verrill remarked as typical of this species (Verrill 1869a) (Fig. 1B). However, it is the normal condition of polyps in this genus, when retracted. The coenenchyme is thick compared with the other three species. The outer coenenchyme is composed basically by the same type of sclerites found in the calyx. They are spindles of several shapes, mostly unilateral spinous, curved, straight, with blunt or acute ends, or one acute end and the other bifurcate. They are 0.50–1.82 mm long and 0.15–0.28 mm wide (Fig. 2A), Verrill (1869a) reported spindles up to 2 mm long. They are of a light brownish to dark orange colour, some with the outer surface darker than the inner (Fig. 1C). The axial sheath is composed of pale yellow to colourless (Fig. 1C), warty elongated spindles 0.15–0.30 mm long and 0.060–0.085 mm wide (Fig. 2B), and irregular radiates, up to 0.24 mm long and 0.10 mm wide (Fig. 2C). Anthocodial sclerites are pale yellow, irregular warty rods with a spinulose end 0.25–0.30 mm long and 0.037–0.060 mm wide, and small torch-like clubs with a warty handle, measuring up to 0.28 mm long and 0.10 mm wide (Fig. 2D). The colour of the colony is brown.

Distribution. Reported only from the type locality, Bay of Panamá. This species has not been found in our recent surveys along the Pacific coast of Panamá. No data available about the depth range.

Remarks. This species was first mentioned by Verrill (1866) as *Muricea acervata* in 1869. It was transferred to the genus *Eumuricea* and properly described from just one specimen from Panamá that represents the holotype. The species is different from the others by the thicker coenenchyme, and especially the shorter calyces with a wider apical aperture that exposes the contracted polyps, which in the other species are hidden in the tubes. The dark orange colour of the calycular and coenenchymal sclerites is not present in the other species, which are of various hues of brown instead.

Muricea hispida Verrill, 1866

Figures 3–4

Muricea hispida Verrill, 1866: 328; Harden 1979: 151–152. Muricea (Eumuricea) hispida Verrill, 1869a: 422–423. Eumuricea hispida Kükenthal, 1924: 151–152; Riess 1929: 398.

Material. Lectotype (here designated): YPM 567, dry, Panamá, no depth given, F.H. Bradley, 1866. Paralectotype: YPM 1790, figured specimen in Verrill 1868, plate VII, fig 4, data as in the lectotype.

Other material. USNM 49386 (erroneously identified as *E. hispida*), dry, Punta Arenas, Isla San Lucas, Golfo de Nicoya, Costa Rica, M. Valerio, 15 January 1930. USNM 34063 (erroneously identified as this species; it is a species of *Muricea*), dry, Panamá Bay, L.C. Cash, no more data. USNM 1016582, (erroneously identified as *E. hispida*), dry, Punta Paitilla, Panamá Bay, C.D. Ridder, 14 August 1976.

Description. The lectotype is an 8.5 cm tall and 4 cm wide incomplete colony, branching is sparingly dichotomous (Fig. 3A). A short stem, 0.4 cm long, arises from a



Figure 3. *Muricea hispida* Verrill, 1866 YPM 567 **A** Colony **B** Detail of branches **C** Sclerites, light micrograph.

small remainder of the holdfast, and subdivides in two main branches deprived of coenenchyme, one of them is broken and the other subdivides in two secondary branches, 7–10 mm in diameter, that subdivide up to 4 times. All branches are almost the same diameter, with blunt, clavate tips. The branches are separated at distances of 0.6–5 cm and growing upwards at close angles of 30°–45°. Undivided terminal branches are up to 20 mm long, and 8 mm in diameter. The axes are dark brown at the base, and amber at the branchlets. The calyces are all around the branches, close together, about 14 calyces/cm. They are tubular and elongated reaching up to 3.5–4.0 mm long and up to 1.8–2.0 mm wide at the clavate tips; with projecting spines around the polyp apertures (Fig. 3B). The polyps are situated at the summit of the tubular calyces, the apertures are covered by anthocodial sclerites that represent what remained of the polyps. The coenenchyme is very thin, basically composed by the same type as the calyx sclerites. The outer coenenchyme and calycular spindles are unilateral spinous, spinulose on the outer surface and warty on the inner, 0.90–1.60 mm long and 0.14–0.20 mm wide,



Figure 4. *Muricea hispida* Verrill, 1866 YPM 567. **A**, **B** Calycular and coenenchymal spindles **C** Axial sheath spindles **D** Anthocodial sclerites.

with acute ends, or one acute and the other blunt; others have stout, complex terminal spikes, 0.57–0.83 mm long and 0.10–0.14 mm wide (Fig. 4A, B). The axial sheath is composed of warty spindles with sparse warts and/or conical tubercles with acute tips; and irregular rods branched at one end, 0.13–0.56 mm long and 0.04–0.09 mm wide (Fig. 4C). The anthocodial sclerites are complex irregular branched forms, thorn scale-like with complex warts on the surface, sparse conical spines and/or with one

spinulose end; irregular club-like spindles with warty handlers, straight or curved, and with spinulose, shaft-like heads. These sclerites are 0.26–0.70 mm long and 0.05–0.03 mm wide (Fig. 4D). All the sclerites are colourless (Fig. 3C). The colour of the colony is light brown.

Distribution. Panamá, Bahía de Caraquéz, Ecuador (Riess 1929). No data available about the depth range.

Remarks. This species was first mentioned by Verrill in1866, together with *M. acervata* with a minimal description. They both were properly described in 1869a. *Muricea hispida* was described from two specimen fragments from Panamá. *Muricea hispida* is similar to *M. squarrosa* and *M. tubigera*. These three species have long tubular calyces, similar colour and shape of the colonies. The main difference that separates them is the calyx length *M. tubigera* with the largest and *M. squarrosa* with the shortest (Table 1). The calyces in *M. hispida* are sharp and distally curved upwards with projecting spines beyond the calyx border as in *M. tubigera*, however, the latter has thinner, longer and more crowded calyces (Table 1). *Muricea tubigera* has the largest spindles, up to 2 mm long, in *M. hispida* up to 1.6 mm and in *M. squarrosa*, up to 1.3 mm (Table 1). *Muricea hispida* was misidentified in some collections, including the syntypes. For example, YPM 1636 listed as a syntype belongs to a different *Muricea species*, and other specimens, such as USNM 49386, 1016582 belong to *M. squarrosa*. We designate YPM 567as the lectotype of *M. hispida* to establish the identity of this species and avoid future misinterpretation.

Muricea horrida Möbius, 1861 (sp. dubia)

Figure 5

Muricea horrida Möbius, 1861: 11–12; Kölliker 1865: 135; Harden 1979: 152. *Muricea (Eumuricea) horrida* Verrill, 1869a: 423. *Eumuricea horrida* Kükenthal, 1924: 151.

Material. Plate 3, figs 5–8 (Möbius 1861), no material available.

Holotype figured. According to Möbius (1861) the holotype was deposited in the Hamburg Museum (ZMH); however, the material was not housed there anymore (P. Stiewe and H. Roggenbuck, ZMH, pers. comm. 2011).

Description (after Möbius 1861 and Verrill 1869a). The figured specimen is a fragment of a 20 cm tall and 22 cm wide colony with a thin, 6 cm diameter holdfast attached to a rock. The branching looks mostly dichotomous and starts close to the base (Fig. 5 [5]). The branches are closely placed and divergent, they subdivide at small angles and up to 6 times. All branches are about the same diameter with slightly tapered ends. Undivided terminal branches are short. The axes are brown at the base, and light yellow at the branchlets. The coenenchyme is granulose and brittle. The calyces are all around the branches, close together. They are mostly standing perpendicular to the branches, closer together and inclined upwards, at smaller angles, at the upper branch-



Figure 5. Muricea horrida Möbius, 1861. From plate 3, figs 5-8 (Möbius 1861).

lets (Fig. 5[6]). They are tubular and elongated, up to 1.5 mm long with truncate tips. There is not enough information about the sclerites. They are straight or curved warty spindles reaching up to 1.2 mm long. They are yellow and seem asymmetric, perhaps unilateral spinose as for the genus, but from the drawings it is difficult to tell (Fig. 5[7, 8]). The colour of the colony is light brown.

Distribution. Reported for Perú, the type locality.

Remarks. According to Kükenthal (1924, in key) *M. horrida* differs from *M. squarrosa* in having shorter coenenchymal sclerites. Möbius (1861) description and illustration **Table 1.** Comparative features of the eastern Pacific genus *Muricea* Lamouroux, 1821. Diameter of the branches is including calyces; size of the sclerites and other measurements are based on type material examined in this study. () Represents Verrill max size of sclerites. All measurements are given in mm.

Species	Colony colour	Colony shape	Length unbranched ends	Diameter of end branchlets	Coenenchyme	Calyx height	Calyx diameter	Calyx arrangement at branchlets	No. calyces/cm	Largest spindles	Axial sheath sclerites length range	Sclerite colours
M. acervata	Ь	cand	70	7	Т	2.50	2	cl	21	1.8 (2)	0.15-0.30	lb, do, py, w
M. hispida	lb	bu	20	8	t	4	1.80	cl	14	1.6 (2.6)	0.13-0.56	w, c
*M. horrida	lb	bu	-	-	-	-	1.50	s	-	1.2	-	-
M. squarrosa	lb-b	bu	40	5	mt	2.6	1.75	s	14	1.3 (1.8)	0.14-0.30	py, lb, w, c
M. tubigera	lb	cand	70	8	mt	5	0.70	cl	26	2.0 (2.28)	0.12-0.46	w, c

(*) No type material available for this study, data given from Möbius 1861.

(-) No information available

calyx arrangement: cl, close; s, sparse

coenenchyme: t, thin, T, thick, mt, moderate thick

colour: b, brown, bi, bicoloured; c, colourless, transparent; do, dark orange; lb, light brown; py, pale yellow; w, whitish.

colony shape: bu, bushy, ascending; cand, candelabrum, irregular dichotomous

show a species that is similar to *M. squarrosa* from Perú. *Muricea squarrosa* is a common species in Perú. We did not find another similar species, a possible *M. horrida*, in the UPCH octocoral collection that is very comprehensive and well documented. It is indeed possible that *M. squarrosa* is a synonymous of *M. horrida*; however, without a specimen to analyse we prefer to keep the status of *M. horrida* as dubious.

Muricea squarrosa Verrill, 1869

Figures 6-8

Muricea (Eumuricea) squarrosa Verrill, 1869a: 423–424. Eumuricea squarrosa Kükenthal, 1924: 159. Muricea squarrosa Harden, 1979: 159–160.

Material. Lectotype (here designated): YPM 1561a, dry (with sponge), Pearl Islands, Panamá, F.H. Bradley, 1866, no further data; YPM 1563 [fragment of lectotype, possible figured specimen (Verrill 1869a)]. Paralectotypes: MCZ 4975; MCZ 7017; USNM 33592 (YPM 1561); YPM 1561b-d, YPM 566, data as for the lectotype. YPM 1636 (previously identified as *E. hispida*), ethanol preserved, Pearl Islands, F.H. Bradley, 1866, no further data.

Other material. COSTA RICA: UCR 587, dry, Pitaya Beach, Guanacaste, Pacific coast, Costa Rica, 20–23 m, J. Cortés, 16 June, 1991; UCR 1742, ethanol preserved,



Figure 6. *Muricea squarrosa* Verrill, 1869a YPM 1561a. **A** Colony **B** Detail of branches **C** Sclerites, light micrograph.

Bajo Negro, Marino Ballena National Park, 25 m, O. Breedy,13 April 2008; UCR 2261, ethanol preserved, Isla Larga Oeste, Manuel Antonio National Park, 19 m, O. Breedy and H. Guzman, 6 February 2012; UCR 2262, ethanol preserved, Isla Larga, Manuel Antonio National Park, 25 m, O. Breedy and H. Guzman, 7 February 2012; UCR 2396, ethanol preserved, Marino Ballena National Park, 25 m, O. Breedy, 27 April 2002; UCR 2410; 2414, ethanol preserved, La Danta, Santa Elena Bay, 35 m, O. Breedy and Minor Lara, 10 August 2014; UCR 2418-2419, ethanol preserved, Bajo Mixta, Golfo Dulce, 21 m, O. Breedy and H. Guzman, 7 February 2009 ECUADOR: IIN 25, dry, Bajo Lunes, Reserva de Producción Faunística Marino Costera Puntilla de Santa Elena, 18 m, P. Martínez, F. Rivera, R. Nabot and O. Breedy, 21 July 2010; IIN 47, dry, Gigima, Reserva de Producción Faunística Marino Costera Puntilla de Santa Elena, 14 m, P. Martínez, F. Rivera, R. Nabot and O. Breedy, 22 July 2010. PAN-AMÁ: STRI 561, 563, 569–571, ethanol preserved, Islas Viudas, Chiriquí Gulf, Panamá, 20 m, H. Guzman, 18 April 2003; STRI 867-868, ethanol preserve, Achotines, Chiriquí Gulf, 10 m, H. Guzman, 5 May 2004; STRI 575A, ethanol preserved, Isla Saboga, 1–5 m, H. Guzman, 14 December 2001. PERÚ: UPCH-CZA 280, 284, 291, 296, 298, 302, 411, dry, Canoas de Punta Sal, Tumbes, 10-13 m, Y. Hooker, 2 July 2011; UPCH-CZA 410, Cabo Blanco, Piura, 10–13 m, Y. Hooker, 13 August 2012.

Description. The lectotype is a 14 cm tall and 12 cm wide colony, flabellate, spreading in one plane. It has a sponge attached to the main branches (Fig. 6A). The branching



Figure 7. *Muricea squarrosa* Verrill, 1869a YPM 1561a. **A** Calycular and coenenchymal spindles **B** Anthocodial sclerites **C** Axial sheath spindles.

is mostly dichotomous. A short stem, 0.4 cm long, 60 mm diameter, arises from an irregular holdfast, 23 mm in diameter, covered by a layer of coenenchyme, but deprived of calyces. The stem subdivides in two main branches that produce secondary branches



Figure 8. *Muricea squarrosa* Verrill, 1869a. *In situ* colonies, **A–C** Canoas de Punta Sal, Tumbes, Perú. Photograph by Yuri Hooker **D** Reserva de Producción Faunística Marino Costera Puntilla de Santa Elena, Ecuador. Photograph by Fernando Rivera.

subdividing up to 3 times. All branches are about the same in diameter, 40-80 mm (including calyces), with tapered ends. The branches are separated at distances of 0.5-6cm and spread at small angles and bend upwards in a curve. The branchlets are situated almost perpendicular to the main branch. Undivided terminal branches are up to 40 mm long. The axes are brown at the base, and lighter at the branchlets. The calyces are all around the branches, close together, about 14 calyces/cm. They are mostly directed perpendicular to the branches, but also incline upwards at small angles (Fig. 6B). They are tubular and elongated, up to 2.6 mm long and up to 1.75 mm wide with clavate tips, between the larger calyces there are a number of smaller ones (Fig. 6B). The remains of the polyps are at the summit of the tubular calyces, the apertures are covered by anthocodial sclerites. The coenenchyme has a few layers of sclerites and is basically composed of the same types as the calyx spindles. They are straight or with a slight curvature. They are mostly acute, but can have one end blunt or lobed. They are unilateral spinous with the inner side with complex warts, crowded together so much that their processes anastomose, while on the outer side there are less and sparse spines. Some calycular spindles are club-like with warty elongated handles, straight or curved, and various types of head arrangement, from few conical spines to sharp and long spines crowding the upper part or along the outer side of the sclerite; they have stout terminal spikes (Fig. 7A). The spindles reach up to 1.3 mm long and 0.23 mm wide (Fig. 7A), Verrill (1869a) reported spindles

up to 1.8 mm long. They are of a dull yellow to a light brownish colour. The axial sheath is composed of whitish and colourless, tuberculate spindles, 0.14–0.30 mm long and 0.03–0.075 mm wide (Fig. 7C) and irregular forms with- the same range of size, and immature forms 0.06–0.07 mm long and 0.015–0.02 mm wide. The anthocodial sclerites are of a pale yellow colour to colourless, mostly club-like as described for the calycular spindles, but shorter (Fig. 7B). The colour of the colony light brown.

Variability. The other material examined is very consistent with the lectotype, variation is basically in the number of branches and size of the colonies. The largest colony measured was a specimen from Perú reaching 35 cm tall and 30 cm wide (Fig. 8C, *in situ*). The colony branching is abundant in some colonies (Fig. 8C, D). The colour of the colonies when alive is reddish brown (Fig. 8A–D). This colour fades in dry or ethanol preserved colonies. Fresh collected colonies turn the alcohol into a dark brownish colour. The polyps are pale yellow to whitish (Fig. 8A–D).

Distribution. Panamá: Gulf of Chiriquí, Pearl Islands, 10–20 m. Costa Rica: Nicoya Gulf, Santa Elena Peninsula, Marino Ballena National Park, Golfo Dulce, from 25–40 m. Colombia: Málaga Bay (Prahl et al. 1986, specimens in CRBMco). Ecuador: Puntilla de Santa Elena, Salinas 18–20 m. Perú: Cabo Blanco, Canoas de Punta Sal, 10– 13 m deep. Nicaragua: La Flor, Hueco de Diego, South Pacific, 2–5 m. The species has a wide bathymetric range from 2 m to 40 m, the deepest range being found in Costa Rica.

Remarks. This species was described by Verrill (1869a) with specimens from Pearl Islands without a holotype designation and appropriate illustrations. We designate YPM 1561a as the lectotype of *M. squarrosa* to establish the identity of this species and avoid future misinterpretation.

The main difference to separate this species from *M. hispida* and *M. tubigera* is that the calyces are shorter and more distantly placed. Other differences were discussed above (under *M. hispida*).

Muricea tubigera Verrill, 1869

Figures 9-10

Muricea (Eumuricea) tubigera Verrill, 1869a: 421–422. *Eumuricea tubigera* Kükenthal, 1924: 150.

Material. Holotype: YPM 807, dry, figured specimen, Pearl Islands, Panamá, low tide, F.H. Bradley, 1866.

Description. The holotype is a 17 cm tall and 10 cm wide stout and rigid colony, branching mostly dichotomous (Fig. 9A). A short stem, 1 cm in diameter, 1.5 cm long, arises from an oval 3 cm diameter holdfast, and subdivides in two main branches, 0.8–1.2 mm diameter, that fork producing secondary branches that subdivide up to 3 times. All branches are almost the same diameter with blunt, clavate tips. The branches are at distances of 2–7 cm apart and stick upwards at small angles of 30°–35°. Undivided terminal branches are up to 70 mm long, and 7–8 mm in diameter. The axes are dark brown. The calyces are uniformly crowding the branches, close together, about 26 calyces/cm. They



Figure 9. *Muricea tubigera* Verrill, 1869a YPM 807. **A** Colony **B** Detail of branches **C** Sclerites, light micrograph.

are tubular, slender and elongated, up to 5 mm long and up to 0.75 mm wide, with clavate summits. The borders of the calyces are surrounded by long, slender and sharp spindles that project from the surface giving a prickly appearance to the branches (Fig. 9B). What remains of the polyps is at the summit of the elevated calyces, the apertures are covered by anthocodial sclerites and some calyx sclerites. The coenenchyme is of a few layers of sclerites, basically of the same types as the calyx spindles. They are mostly unilateral spinous spindles, large, slender, with sharp, blunt or bifurcated ends, some are spinulose on the outer surface and tuberculate on the inner, measuring 0.80–2.0 mm long and 0.07–0.30 mm wide (Fig. 10A). The calyx wall is mostly formed by warty, slender rods with one end acute and the other with long complex spines These sclerites are 0.435–0.76 mm long and 0.50–0.65 mm wide, they can have conic spines on the outer side of the sclerite and sparse warts on the inner side (Fig. 10 B). Verrill (1869a) reported a maximum size of 2.34 mm



Figure 10. *Muricea tubigera* Verrill, 1869a YPM 807. **A**, **B** Calycular and coenenchymal spindles **C**, **D** Axial sheath spindles.

long. The axial sheath is composed of warty spindles (Fig. 10C) and tuberculate radiates, 0.12–0.46 mm long and 0.1–0.4 mm wide (Fig. 10D). All sclerites are whitish to colourless (Fig. 9C). The colour of the colony is light brown.

Distribution. Reported only from the type locality, Pearl Islands, Panamá. This species has not been found in our recent surveys along the Pacific coast of Panamá.

Remarks. Verrill (1869a) described this species with one specimen that constitutes the holotype. The very long and slender calyces of this species, the sharper spindles and the thickness of the branches separate this species from the others (Table 1).

Genus Swiftia Duchassaing & Michelotti, 1864

Figure 12

Synonymy in Breedy et al. (2015)

Diagnosis. Colonies branching mostly in one plane, fan-like, dichotomous, pinnatelike, or unbranched. Branches mostly free or with some anastomosing. Polyp mounds conical, prominent, or slightly raised, scattered or crowded, usually biserial and with two opposed polyp mounds at the tip of the branches. Coenenchyme usually thin. Coenenchymal sclerites mainly capstans, radiates and spindles. Thin, sharp and elongated spindles concentrated in the polyp mounds. Anthocodiae with points arrangements of bar-like rods straight or curved, frequently long. Collaret absent or of a few bar-like rods. Axis horny and flexible. Colour of the colonies red, orange, pink, or white.

Type species. Gorgonia exserta Ellis & Solander, 1786, by monotypy.

Swiftia pusilla (Nutting, 1909), comb. n.

Figure 11

Eumuricea pusilla Nutting, 1909: 718–719; Kükenthal 1924: 152.

Material. Holotype. USNM 25430, ethanol/dry preserved, Point Loma, San Diego, California, Albatross R/V, California Coast Expedition, 166–177 m, 15 May 1904.

Description (after Nutting 1909: 718). The holotype was a small, roughly flabellate colony, 37 mm long, branching in an irregular manner. The main stem gives off four alternate branches at irregular intervals, the two longest being 13 mm apart. The calyces are low rounded domes, about 1 mm long and 2 mm wide, separated about 2.5 mm from summit to summit. The polyps are completely retracted. "The calycular walls are covered with very hispid spicules (sclerites), which have their edges somewhat overlapping and are, in general, disposed transversely rather than otherwise". Nutting reports the presence of a collaret and tentacles armed with sharp spindle-shaped sclerites longitudinally arranged, but *in chevron* at the base of the tentacles. Other type of sclerites are asymmetrical spindles with irregular sharp edges and processes, various types of clubs, scales, stars and double stars. The colour of the colony is whitish to gray.

Distribution. Reported for the type locality Point Loma, California.

Remarks. What remain from the holotype are small pieces of branches: two fragments, 16 mm and 12 mm long, the former with 9 polyps, the latter with 5 (pers.



Figure 11. *Swiftia pusilla* (Nutting, 1909). **A** Fragment of the holotype **B** SEM sclerites. Photographs by S. Cairns (USNM).

Species	Original author	Author *	Actual status	Proposed status	Distribution	Depth (m)
E. atlantica	Riess, 1929	Bayer 1961	<i>Muricea</i> Lamouroux		Tortugas, Kingston, Jamaica, Caribbean sea	18
E. pusilla	Nutting, 1909	herein	Eumuricea	<i>Swiftia</i> Duchassaing & Michelotti, 1864	Point Loma, California, Pacific Ocean	176
E. ramosa	Thomson & Simpson, 1909	herein	Eumuricea	<i>Astrogorgia</i> Verrill, 1868	Andaman sea, Indian Ocean	83–494
E. rigida	Thomson, 1927	Ofwegen, L.P. van 2014	Thesea		Along Monaco, Western Atlantic	1732
E. rugosa	Thomson, 1927	Grasshoff, 1992	Leptogorgia ruberrima		Iles Cap Vert, Western Atlantic	91
E. splendens	Thomson & Simpson, 1909	herein	Eumuricea	<i>Astrogorgia</i> Verrill, 1868	Marble Rock, Mergui Archipelago, Andaman sea, Indian Ocean	not given

Table 2. Proposed genera for species misplaced in the genus *Eumuricea* Verrill, 1869.

(*) Author who transferred the original species to another genera or our new proposed genera for the species.

comm. S. Cairns) (Fig. 11A). Nutting's illustrations (1909, PL. LXXXVIII) show some fragments of a thin colony. The sclerites are almost disintegrated, SEMs obtained by S. Cairns (USNM) show spindles as the prevailing type of sclerites (Fig. 11B). It is not possible to confirm the other types of sclerites described by Nutting (1909) and his description is fairly general. However, the characteristics that we could analyse of the species fit with the genus *Swiftia*. For this reason, we herein propose the genus *Swiftia* as a more accurate alternative for the species (Table 2).

Genus Astrogorgia Verrill, 1868

Astrogorgia Verrill, 1868b: 414; Verrill 1870: 77–78; Bayer 1981: 931 (in key); Grasshoff 1999: 38; 2000: 67; Fabricius and Alderslade 2001: 210–213; Hermanlimianto and Ofwegen 2006: 103.

Muricella Kükenthal, 1924: 169.

Acanthomuricea Fabricius & Alderslade, 2001: 212.

Type species. *Astrogorgia sinensis* Verrill, 1868b by monotypy.

Diagnosis [based on Grasshoff (2000), Fabricius and Alderslade (2001), Hermanlimianto and Ofwegen (2006)]. Colonies growing in one plane as open fans, with irregular lateral branching, never net-like. Polyps retractile into raised calyces, arranged in rows or all around the branches. Coenenchymal sclerites mostly spindles, straight, curved, branched, heavily ornamented with complex tubercles, and prickles; and smaller spindles and some capstans in the inner-coenenchyme. Anthocodiae with numerous flattened sclerites around the tentacle bases and up the tentacles in numerous oblique rows. Collaret does not occur. Colour of the colonies, various hues of red, orange, yellow, whitish or yellowish brown.

Astrogorgia splendens (Thomson & Simpson, 1909), comb. n. Figures 12–13

Eumuricea splendens Thomson & Simpson, 1909: 258-259.

Material. Holotype: BM 1933.05.03.094, ethanol preserved, Marble Rock, Mergui Archipelago, Myanmar, Andaman Sea. No more data available.

Description [see also Thomson and Simpson (1909)]. The holotype is a 9.5 cm tall and 6 cm wide colony. Several stems arise from a spreading holdfast but only one branch ramifies in two secondary branches, the others are broken close to the base (Fig. 13A, B) that is partially covered by a sponge. The branching is lateral and irregular, predominantly in one plane. Secondary branches subdivide up to 7 times upwards at small angles. Free end branches reach up to 3.5 cm long. The axis is



Figure 12. *Astrogorgia splendens* (Thomson & Simpson, 1909), BM 1933.05.03.094. **A** Colony **B** Detail of branches **C** Sclerites, light micrograph.



Figure 13. Astrogorgia splendens (Thomson & Simpson, 1909), BM 1933.05.03.094. SEM sclerites.

horny and of a light brown colour. The polyps are prominent and distributed longitudinally in two rows at the base of the main branches, but more irregularly and crowded at the upper parts. The calyces are prominent up to 2 mm in diameter and up to 1.5 mm high (Fig 12B). The anthocodial sclerites are arranged in collaret and points, "en chevron" at the base of the tentacles. The anthocodiae are completely retractile and show an octoradiate star-like arrangement. The coenenchyme and calyces are composed of whitish and reddish sclerites (Fig. 12C). They are mostly warty spindles, straight, curved, and branched, mostly with acute ends, and ornamented with complex tubercles and prickles. These spindles measure 0.21–1.0 mm long and 0.046–0.16 wide (Fig. 13). The anthocodials are warty rods, 0.15–0.20 mm long and 0.03–0.06 mm wide (Fig. 12C). The colour of the colony is pale pink with reddish calyces.

Distribution. From the type locality, Marbel Rock, Mergui Archipelago, Andaman Sea, Indian Ocean. No data available about the depth range.

Remarks. The two species described in *Eumuricea* by Thomson and Simpson (1909) appear in the BM catalogue as species of the genus *Muricella, ramosa* and *splendens*. However, Fabricius and Alderslade (2001), and Grasshoff (1999) refer to the genus *Muricella* as being planar large fans, often net-like, and large, with thick coenenchyme.

Eumuricea splendens sensu Thomson & Simpson (1909) is a small specimen 9.5 cm in height, and *E. ramosa* is supposedly a large specimen, both with thin coenenchyme, and without net-like colonies. The description and sizes of the sclerites given by the above authors for the genus *Muricella* do not fit these two species. Furthermore, Thomson and Simpson's (1909) holotype of *E. splendens* does not agree with the characteristics of *Eumuricea*. Although Thomson and Simpson (1909), acknowledge some resemblance with *E. acervata*, the holotype does not have tubular calyces and does not show the characteristic unilateral spinous spindles of *Eumuricea*. The dominant types of sclerites are acute warty spindles and variations. Therefore, we propose to transfer this species to the genus *Astrogorgia*.

Astrogorgia ramosa (Thomson & Simpson, 1909), comb. n.

Eumuricea ramosa Thomson & Simpson, 1909: 260-261.

Material. None available.

Description [based on Thomson and Simpson (1909)]. Thomson and Simpson (1909) described a colony 23 cm tall and 30 cm wide. The branching is irregular, predominantly in one plane. The main stem is sinuous, about 8 mm in diameter arising from a conical holdfast. The branches are tapered at the ends, and the twigs are of almost the same thickness throughout, some are clavate. The axis is horny, composed of thin sheets of gorgonian. The coenenchyme is moderately thin. It is composed of colourless sclerites irregularly arranged at the lower part of the branches and more longitudinally placed at the twigs. The polyps are distributed all around the branches closer at the upper branches and more separated at the lower parts. The anthocodiae are completely retractile into slightly elevated cones, 1 mm in height and 1 mm in diameter at the base. The anthocodial sclerites are arranged in eight distinct groups "en chevron" at the base of the tentacles with projecting teeth around the oral aperture. The coenenchymal sclerites are spindles, straight, curved or S-shaped, with acute or blunt ends, with the surface covered by warts, they measure 0.4-1.5 mm long and 0.075-0.17 wide. The anthocodiae are club-shaped, with warty heads and smooth handles, 0.3-0.6 mm long and 0.05-0.1 mm wide. The colour of the colony is a grevish white.

Distribution. From the type locality, Andaman sea, Indian Ocean, 83–494 m in depth.

Remarks. We only have a few drawings of sclerites of this species from Thomson and Simpson (1909: Plate VIII. Fig. 15). The type material was not available for analysis, however, the sclerite drawings, the depth range and the geographic distribution of this species is not consistent with the genus *Eumuricea*. Considering that the Thomson and Simpson's (1909) description and illustrations of this species and *E. splendens* closely agree; we also propose, with some caution, to transfer *E. ramosa* to the genus *Astrogorgia* (Table 2).

Family Gorgoniidae Lamouroux, 1812

Leptogorgia ruberrima (W. Koch, 1886)

Figure 14

Gorgonia ruberrima W. Koch, 1886: 14–18.
Eumuricea rugosa Thomson 1927: 48.
Leptogorgia monodi Stiasny 1937: 309.
Leptogorgia ruberrima Stiasny, 1940: 361; Grasshoff 1988: 111; 1992: 72 (synonymy according to Grasshoff 1992).

Material. Holotype: BM 1933.03.13.024, fragment, ethanol preserved, Campagne 1901, Stn. 1203: 15°54' N, 22°54'45"E, Iles du Cap Vert, 91 m, 18 August 1901.

Description (see also Thomson 1927). The holotype is a bright red fragment, 3 cm long and 3 cm wide (Fig. 14A). Thompson (1927) described a 15.5 cm tall colony. The branches are 2 mm in diameter. The axis is amber. The calyces are cones projecting up to 0.75 mm high and about 1 mm in diameter. They are placed all



Figure 14. *Leptogorgia ruberrima* (W. Koch, 1886), BM 1933-03-13-024. **A** Fragment of the holotype **B** Sclerites, light micrograph **C** SEM sclerites.

around the branches about 1 mm apart. The coenenchymal sclerites are red and basically warty spindles with acute ends, straight or curved, 0.2 mm–0.32 mm long and 0.065 mm–0.087 mm wide, and radiates 0.10–0.20 mm long and 0.04 mm–0.045 mm wide (Fig. 14B–C). Anthocodial sclerites are flat orange rods in an irregular point and collaret formation. They are 0.050 mm–0.15 mm long, with lobed or smooth borders (Fig. 14B). The sizes of sclerites given by Thomson (1927) are smaller than the ones we analysed in the holotype fragment. The colour of the colony is bright red.

Distribution. Reported from the scientific campaigns of Prince Albert 1st de Monaco in 1901, Station 1203, along Iles du Cap Vert, 15°54' N, 22°54'45"E, Western Atlantic.

Remarks. Thomson (1927) described two species of *Eumuricea*, *E. rigida* and *E. rugosa*but neither of these fit in the genus *Eumuricea*. The former was transferred to *Thesea* (Table 2) by Ofwegen (2014), and the latter does not show the characteristic spheroid plate-like sclerites of *Thesea* in the outer coenenchyme. The coenenchyme of *E. rugosa* is composed of acute, elongated spindles instead. We confirm the finding of Grasshoff (1992) that this is nothing other than *Leptogorgia ruberrina* (W. Koch, 1886).

Conclusions

Firstly, we conclude that Verrill's genus *Eumuricea* was misinterpreted by former authors who erroneously assigned this genus to a diverse group of species. Secondly, that *Eumuricea* corresponds to a group of *Muricea* with tubular calyces as Verrill proposed, but because all other characteristics are found in *Muricea*, we do not consider the shape of the calyx as a sole character to separate this genus, since there are at least three more types of calyx structure within Muricea. And thirdly, the Muricea group with tubular calyces comprises four valid species M. acervata, M. hispida, M. squarrosa and M. tubigera, and a dubious one, M. horrid, reported for the eastern Pacific. It is intriguing that Muricea squarrosa is the only species in the genus that recently has been collected at various localities along the eastern Pacific. Although extensive surveys have been conducted along the Pacific coast of Panama and Peru (main type localities), the other species have not been found. Presently, we do not have data to support the idea of local extinction of species, but it is very likely that changing oceanographic conditions could have affected octocoral diversity. Perhaps more survey effort along the eastern Pacific would give further information about this genus. Presently, we recommend taking into account the status of the species of *Eumuricea* for biodiversity records and assessments.

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RESEARCH ARTICLE



Checklist of recent brachiopod species collected during the Terrasses and Exbodi cruises in the New Caledonian region, SW Pacific

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Abstract

Twenty species belonging to 16 genera, i.e. *Neoancistrocrania, Novocrania, Basiliola, Basiliolella, Ebiscothyris, Stenosarina, Kanakythyris, Xenobrochus, Terebratulina, Eucalathis, Fallax, Frenulina, Septicollarina, Campages, Annuloplatidia*, and *Thecidellina* have been identified in the material collected during the Terrasses and Exbodi cruises in the New Caledonian region, SW Pacific. The species *Basiliolella grayi* (Woodward, 1855) and *Fallax neocaledonensis* Laurin, 1997 are the most common in the studied collection, while *Eucalathis murrayi* (Davidson, 1878) is reported for the first time from the New Caledonian region.

Keywords

Brachiopoda, biodiversity, New Caledonia, South-West Pacific

Introduction

The New Caledonia Exclusive Economic Zone, comprising the area from Vanuatu to Chesterfield Islands, is one of the most intensively investigated regions in the Indo-West Pacific Province; more than 40 oceanographic expeditions have been organized by French institutions within the programme Tropical Deep-Sea Benthos (formerly



Figure 1. Location map of the brachiopod-bearing stations of the Terrasses and Exbodi expeditions. **I** DW 3032 **2** DW 3039–3042; **3** CP 3047 **4** CP 3051 **5** DW 3056 **6** DW 3059–3060 **7** DW 3062–3063, CP 3065–3068, DW 3069, CP 3070 **8** DW 3072, DW 3075–3077 **9** DW 3078–3079, DW 3082–3083 **I0** DW 3086, DW 3089–3090, CP 3091 **I1** DW 3093–3094, CP 3834 **I2** DW 3100, DW 3102, CP 3104, DW 3106–3110 **I3** DW 3120–3124, DW 3129 **I4** DW 3784–3785, CP 3786, DW 3787, CP 3788–3789, CP 3791–3793 **I5** DW 3798 **I6** CP 3842–3844, DW 3845 **I7** DW 3846, CP 3848–3849 **I8** CP 3851–3852, DW 3896, CP 3898, DW 3900 **I9** DW 3862–3863 **20** CP 3871, DW 3872 **21** DW 3880, CP 38882–3885, DW 3887, DW 3889, DW 3895 **22** DW 3902–3903, DW 3913, DW 3916–3918 **23** DW 3905–3907, CP 3911 **24** DW 3922–3925, CP 3927, DW 3928, DW 3930, DW 3932–3933, DW 3949–3940.

Musorstom; see also Bouchet et al. 2008). Brachiopods collected in this region have been described in many publications (e.g. d'Hondt 1987; Laurin 1992, 1997; Bitner 2007a, 2009, 2010, 2011; Bitner et al. 2008; Bitner and Cohen 2015).

This paper deals with brachiopods collected during two cruises, Terrasses and Exbodi, organized by the Muséum national d'Histoire naturelle, Paris and by the Institut de la Recherche pour le Développement, Nouméa, New Caledonia on R.V. "*Alis*" (Fig. 1). The cruise Terrasses (http://expeditions.mnhn.fr/campaign/terrasses) was carried out from 15 to 31 October 2008, south of New Caledonia, whereas the cruise Exbodi (http://expeditions.mnhn.fr/campaign/exbodi) to the Loyalty Ridge, east of New Caledonia was carried out from 2 to 28 September 2011. Samples were collected using a Warén dredge (DW) or a trawl (CP, CC). The brachiopods were found in 46 of 99 Terrasses stations, and in 56 of 161 Exbodi stations. See the Appendix for details of the stations and species distributions. The collections are stored in the Muséum national d'Histoire naturelle, Paris under catalogue numbers IB-2013-171 to IB-2013-271, IB-2013-516 to IB-2013-552, and IB-2013-585 to IB-2013-616.

Results

The brachiopod fauna recognized in the Terrasses and Exbodi cruises consists of 20 species belonging to 16 genera in 11 families (Craniidae, Basiliolidae, Terebratulidae, Dyscoliidae, Cancellothyrididae, Chlidonophoridae, Aulacothyropsidae, Frenulinidae, Dallinidae, Platidiidae, Thecidellinidae), four orders (Craniida, Rhynchonellida, Terebratulida, Thecideida), and two subphyla (Craniiformea, Rhynchonelliformea).

Family Craniidae Menke, 1828

Neoancistrocrania norfolki Laurin, 1992

Fig. 2A–B

This species, represented only by young individuals, was found only in two Exbodi stations at depths of 388–520 m. *N. norfolki* differs from other craniids by its massive ventral valve and internally by two erect divergent processes on the dorsal valve (Laurin 1997; Bitner 2009). Originally described from the Norfolk Ridge (Laurin 1992), it seems to be restricted to the Western Pacific (Cohen et al. 2014).

Novocrania sp.

The second craniid brachiopod is very rare and too poorly preserved to permit identification to species level. It was found in two stations (600–802 m). Morpho-species identification of *Novocrania* is uncertain and previous specimens from the region of New Caledonia have been described as *N. reevei* Lee & Brunton, 1986 (see Bitner 2010). In the opinion of Robinson and Lee (2011) this is a synonym of *N. japonica* (Adams, 1863).

Family Basiliolidae Cooper, 1959

Basiliola beecheri (Dall, 1895) Fig. 2G–H

This is one of three rhynchonellide species recognized in the studied material. *B. beecheri* is relatively common, found in 10 samples, with a depth range of 400–990 m



Figure 2. A–B *Neoancistrocrania norfolki* Laurin, 1992, dorsal and lateral views of complete specimen (IB-2013–600), SEM, cruise Exbodi, stn DW 3925, 388 m **C–D** *Basiliola lucida* (Gould, 1862), dorsal and anterior views of complete specimen (IB-2013–542), cruise Exbodi, stn DW 3900, 366–357 m **E–F** *Basiliolella grayi* (Woodward, 1855), dorsal and anterior views of complete specimen (IB-2013–188), cruise Terrasses, stn DW 3062, 300–320 m **G–H** *Basiliola beecheri* (Dall, 1895), dorsal and anterior views of complete specimen (IB-2013–215), cruise Terrasses, stn DW 3083, 470–570 m.

and was already reported from the New Caledonian region (Laurin 1997; Zezina 2005; Bitner 2009). It also occurs in the Hawaii and Fiji regions (Dall 1895; Bitner 2006b, 2008).

Basiliola lucida (Gould, 1862)

Fig. 2C–D

This species, already noted from New Caledonia (Laurin 1997; Bitner 2009), is rare, being found in 5 stations. Its depth range in the studied area is 300–510 m. Originally described from off Japan (Hatai 1940), *B. lucida* also occurs in the Fiji region (Bitner 2008).

Basiliolella grayi (Woodward, 1855)

Fig. 2E-F

This is one of the most common species (nearly 500 specimens). It was found in 13 Terrasses stations and 12 Exbodi stations (see Appendix), with a depth range of
150-584 m. *Basiliolella grayi* is restricted to the SW Pacific (Laurin 1997; Logan 2007; Bitner 2009).

Family Terebratulidae Gray, 1840

Ebiscothyris bellonensis Bitner & Cohen, 2015

Fig. 3E–J

This species, recently described from the Coral Sea by Bitner and Cohen (2015), is common only in the material collected during the Exbodi cruise. Its depth range is very great, from 70 to 1180 m. Externally, *E. bellonensis* is very similar to *Abyssothyris wyvillei* (Davidson, 1878), but it differs internally in the character of the loop; in *A. wyvillei* the loop has a narrow, anteriorly convex transverse band (see Cooper 1983; Bitner 2006b, 2008), while in *E. bellonensis* the transverse band is broad and medially folded. Molecular analysis confirms this separation (Bitner and Cohen 2015).

Stenosarina crosnieri (Cooper, 1983)

Fig. 3O–P

This short-looped terebratulide is a relatively common species in the investigated material, being already recorded from New Caledonia (Laurin 1997; Bitner 2009). About 50 specimens were found in 17 stations, with a depth range of 340–951 m. *S. crosnieri* was originally described from the south-western Indian Ocean (Cooper 1983).

Stenosarina globosa Laurin, 1997

Fig. 3K–L

The second *Stenosarina* species in the studied material is much rarer, being found in only five samples (386–570 m). *Stenosarina globosa* is smaller than *S. crosnieri* and characterized by a strongly convex shell. So far known only from the New Caledonia area (Laurin 1997), this species can be considered as endemic to this region.

Kanakythyris pachyrhynchos Laurin, 1997

Fig. 3M-N

This species is very characteristic with its thick shell, strongly incurved beak and very small foramen. It is relatively rare, being found in six samples (150–510 m). It is known only from the New Caledonian region (Laurin 1997; Bitner 2009) and can be regarded as endemic to this area.

Family Dyscoliidae Fischer & Oehlert, 1890

Xenobrochus africanus (Cooper, 1973)

Fig. 3A-B

A single specimen of this species was found in one Terrasses station at 150–180 m but it was earlier recorded from New Caledonia (Laurin 1997; Bitner 2010). *X. africanus* was originally described from South Africa (Cooper 1973).

Xenobrochus indianensis (Cooper, 1973)

Fig. 3C-D

This second species of *Xenobrochus* is also very rare, found in one Exbodi station at a depth of 388 m. Laurin (1997) already noted this species from New Caledonia. It was originally described from South Africa (Cooper 1973). *Xenobrochus indianensis* can be distinguished from *X. africanus* by a more convex shell, incurved beak with a partly concealed symphytium, and internally by the presence of a distinct cardinal process (Cooper 1973, 1983; Laurin 1997).

Family Cancellothyrididae Thomson, 1926

Terebratulina pacifica Yabe & Hatai, 1934 Fig. 4D

This is a relatively common species, found in 12 stations (180–790 m). Its presence in the studied area was already noted (Laurin 1997; Bitner 2009), and it is common off Japan (Hatai 1940). This wide distribution suggests that a careful molecular analysis of a wide range of Pacific Ocean samples might lead to the recognition of multiple forms that have not been distinguished morphologically (e.g. Lüter and Cohen 2002).

Family Chlidonophoridae Muir-Wood, 1959

Eucalathis murrayi (Davidson, 1878)

Fig. 4A–C

This species is very rare and was found in only two Exbodi stations (388–802 m). Although known from the nearby New Zealand region (MacFarlan et al. 2009), this is the first report of *E. murrayi* from the vicinity of New Caledonia. Originally described from off the Kermadec Islands (Davidson 1880) it has a wide distribution in the south-western Pacific (Bitner 2006a) and is known from the western Indian Ocean (Zezina 1987).



Figure 3. A–B Xenobrochus africanus (Cooper, 1973), dorsal view of complete specimen (IB-2013–236), and enlargement of the posterior part to show details of the beak, SEM, cruise Terrasses, stn DW 3109, 150–180 m C–D Xenobrochus indianensis (Cooper, 1973), dorsal view of complete specimen (IB-2013–602), and enlargement of the umbonal part to show details of the beak, SEM, cruise Exbodi, stn DW 3925, 388 m E–J Ebiscothyris bellonensis Bitner & Cohen, 2015, cruise Exbodi, E–G dorsal and anterior views of complete specimens (IB-2013–262), stn CP 3844, 815–970 m H–I interior and tilted (I) views of dorsal valve (IB-2013–262), SEM, stn CP 3844 J interior of dorsal valve (IB-2013–254), SEM, stn CP 3791, 750–863 m K–L Stenosarina globosa Laurin, 1997, dorsal and lateral views of complete specimen (IB-2013–227), cruise Terrasses, stn DW 3102, 410–430 m M–N Kanakythyris pachyrhynchos Laurin, 1997, dorsal and lateral views of complete specimen (IB-2013–251), cruise Terrasses, stn DW 3107, 380–440 m O–P Stenosarina crosnieri (Cooper, 1983), dorsal and lateral views of complete specimen (IB-2013–175), cruise Terrasses, stn DW 3041, 800–840 m.



Figure 4. A-C Eucalathis murrayi (Davidson, 1878), cruise Exbodi, SEM A-B dorsal view of complete specimen (IB-2013–601), and enlargement (B) of posterior part to show details of the beak, stn DW 3925, 388m C dorsal view of complete specimen (IB-2013–588), stn CP 3911, 680–802 m D Terebratulina pacifica Yabe & Hatai, 1934, dorsal view of complete specimen (IB-2013–214), cruise Terrasses, stn DW 3082, 290 m E Campages mariae (Adams, 1860), dorsal view of complete specimen (IB-2013–259), cruise Exbodi, stn CP 3834, 27–258 m F-G Frenulina sanguinolenta (Gmelin, 1791)
F interior of dorsal valve (IB-2013–525), SEM, cruise Exbodi, stn 3872, 159–756 m G dorsal view of complete specimen (IB-2013–192), cruise Terrasses, stn DW 3063, 430–480 m H–I Septicollarina zezinae Bitner, 2009, cruise Terrasses, stn DW 3040, 750–780 m (IB-2013–173) H dorsal view of complete specimen I exterior of ventral valve, visible randomly distributed, small pustules J-K Fallax neocaledonensis Laurin, 1997, dorsal and anterior views of complete specimen (IB-2013–210), cruise Terrasses, stn DW 3077, 420–540 m.

So far the only representative of the family Chlidonophoridae reported from New Caledonia has been *Eucalathis rugosa* Cooper, 1973 (see Laurin 1997; Bitner 2009, 2010), which is characterized by strong ornamentation of single, coarse ribs, while in *E. murrayi* ribs are numerous, finer, and bifurcating. DNA sequences of these species have not yet been compared (B.L. Cohen, pers. communication).

Family Aulacothyropsidae Dagys, 1972

Fallax neocaledonensis Laurin, 1997

Fig. 4J–K

This long-looped brachiopod is one of the most common (more than 250 specimens) and was identified in 20 stations (260–840 m). *F. neocaledonensis* was originally described from New Caledonia by Laurin (1997; see also Bitner 2009) and was also recognized in material from Fiji (Bitner 2006b, 2008).

Septicollarina zezinae Bitner, 2009

Fig. 4H–I

This rare species was found in one station of each cruise (680–802 m). Originally described from the Norfolk Ridge (Bitner 2009) it was also identified around Fiji and French Polynesia (Bitner 2008, 2014).

Family Frenulinidae Hatai, 1938

Frenulina sanguinolenta (Gmelin, 1791) Fig. 4F–G

This easily recognizable species was found in 20 stations but was abundant only in the Exbodi material where it appears to have a very wide bathymetric range (110 to 1100 m). However this range probably is the result of the wide depth-range of the DW3932 dredge haul (500 to 1100 m), the specimens of this generally shallow-water form probably having been collected only in the shallower water.

Frenulina sanguinolenta is one of the most widely distributed species of living brachiopods, known from Japan, Australia, New Caledonia, Fiji, French Polynesia and Hawaii (Hatai 1940; Emig 1987; Saito 1996; Laurin 1997; Bitner 2006a, 2006b, 2007a, 2008, 2009, 2010, 2014). Recently this species has also been identified in the western Indian Ocean (Bitner and Logan in press).

Family Dallinidae Beecher, 1893

Campages mariae (Adams, 1860) Fig. 4E

In the studied material this species was found in 16 stations in the material of both cruises at depths of 180–790 m. Originally described from off Japan (Hatai 1940), *C. mariae* occurs in the Western Pacific (Logan 2007; Bitner 2009, 2010).

Family Platidiidae Thomson, 1927

Annuloplatidia richeri Bitner, 2009

Fig. 5F–J

This species was originally described from the Norfolk Ridge where it was very common (see Bitner 2009). Here, *A. richeri* is rare, found in one Terrasses station and two Exbodi stations (622–802 m). It is characterized by numerous, transversely elongate pustules that cover the ventral valve (Fig. 5H–J). *A. richeri* can be treated as endemic to the New Caledonian region as it has not yet been recognized in other areas.

Annuloplatidia curiosa Bitner, 2014

Fig. 5K-L

This species is very rare, found in only one Exbodi station at depths of 400–520 m. It was already reported from New Caledonia by Laurin (1997), but was wrongly assigned by him to *Megerlia echinata* (Fischer & Œhlert, 1890) (see discussion in Bitner 2014: 256). It has a very wide distribution, being known from New Zealand, Wallis and Futuna Islands, and French Polynesia (Bitner 2007b, 2008, 2014).

Family Thecidellinidae Elliott, 1953

Thecidellina maxilla (Hedley, 1899) Fig. 5A–E

This is the only thecideide brachiopod in the investigated material. This species was found in 10 Exbodi stations with a very wide depth range (159 to 1100 m) but as noted before (see *Frenulina sanguinolenta* above) this may be an artefact. Already noted from New Caledonian waters (Laurin 1997; Bitner 2007a, 2009, 2010), *Thecidellina maxilla* is widely distributed in the SW Pacifc, from New Zealand to French Polynesia (Lee and Robinson 2003; Bitner 2007b, 2008, 2014; Logan 2007; MacFarlan et al. 2009).

Summary

The brachiopods collected south of New Caledonia during the Terrasses cruise are represented by 15 species belonging to 13 genera. In the material from the Loyalty Ridge collected during the Exbodi cruise 19 species belonging to 16 genera have been identified. Fourteen species, i.e. *Novocrania* sp., *Basiliola beecheri*, *B. lucida*, *Basiliolella grayi*, *Ebiscothyris bellonensis*, *Stenosarina crosnieri*, *S. globosa*, *Kanakythyris pachyrhynchos*, *Terebratulina pacifica*, *Fallax neocaledonensis*, *Septicollarina zezinae*, *Frenulina sanguinolenta*,



Figure 5. A–E *Thecidellina maxilla* (Hedley, 1899), cruise Exbodi, stn DW 3905, 300 m, (IB-2013–549) **A–B** dorsal view of complete specimen and enlargement of the posterior part to show flat pseudodeltidium (planodeltidium) **C–E** inner, posterior (**D**) and oblique (**E**) views of dorsal valve to show bridge, median lobe of cardinal process and median septum **F–J** *Annuloplatidia richeri* Bitner, 2009 **F–G** dorsal view of complete specimen (IB-2013–616), and enlargement of the umbonal part, cruise Terrasses, stn DW 3040, 750–780 m **H–I** ventral view of complete specimen (IB-2013–592), and enlargement of shell surface to show nodes, cruise Exbodi, stn DW 3913, 622 m **J** dorsal view of complete specimen (IB-2013–590), cruise Exbodi, stn DW 3911, 680–802 m **K–L** *Annuloplatidia curiosa* Bitner, 2014, ventral and dorsal views of complete specimen (IB-2013–522), cruise Exbodi, stn DW 3862, 400–520 m. All SEM.

Annuloplatidia richeri and Campages mariae are common to both collections. One species, Xenobrochus africanus, found in the Terrasses collection was not recognized in the Exbodi material, whereas Neoancistrocrania norfolki, Xenobrochus indianensis, Eucalathis murrayi, Annuloplatidia curiosa, and Thecidellina maxilla were found in the Exbodi cruise but not in the Terrasses cruise. Eucalathis murrayi was reported for the first time from the New Caledonian region. Most species recognized here have a wide geographical distribution, being known either in the Western Pacific or in the Indo-West Pacific Province. Only four species, *E. bellonensis, S. globosa, K. pachyrhynchos*, and *A. richeri* can be treated as endemic to the New Caledonian region.

With the new record of *E. murrayi* from New Caledonia, the total number of species recognized in this region is now 45 (d'Hondt 1987; Laurin 1997; Bitner 2007a, 2009, 2010, 2011, 2014; Bitner et al. 2008; Bitner and Cohen 2015), of which 8 are in common with New Zealand (compare Bitner 2010, 2014, and this study). The New Caledonian brachiopod fauna shows the greatest affinity with that from Fiji, sharing 11 of 22 species (Bitner 2006b, 2008).

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Appendix

Station	Location	Species				
	Terrasses					
	Loyalt	y Ridge				
DW 3032	22°41'S, 168°58'E	760–820 m	Basiliola beecheri			
DW 3039	23°57'S, 169°44'E	600–680 m	Novocrania sp.			
DW 3040	23°58'S, 169°43'E	750–780 m	Septicollarina zezinae Annuloplatidia richeri			
DW 3041	23°59'S, 169°44'E	800–840 m	Basiliola beecheri Stenosarina crosnieri Fallax neocaledonensis			
DW 3042	23°56'S, 169°43'E	920–990 m	Basiliola beecheri			
CP 3047	23°35'S, 169°37'E	266–267 m	Basiliolella grayi Stenosarina crosnieri Fallax neocaledonensis			
	Norfol	k Ridge				
CP 3051	23°48'S, 168°17'E	410–530 m	Stenosarina crosnieri Fallax neocaledonensis Campages mariae			
DW 3056	23°42'S, 168°01'E	250–330 m	Basiliolella grayi			
DW 3059	23°40'S, 167°44'E	440–450 m	Campages mariae			
DW 3060	23°39'S, 167°44'E	440–450 m	Campages mariae			
DW 3062	23°22'S, 168°02'E	300–320 m	Basiliolella grayi Frenulina sanguinolenta			
DW 3063	23°23'S, 168°00.4'E	430–480 m	Terebratulina pacifica Fallax neocaledonensis Frenulina sanguinolenta			
CP 3065	23°21'S, 168°00'E	480–550 m	Fallax neocaledonensis			
CP 3066	CP 3066 23°18'S, 167°59'E 650–790 m		Stenosarina crosnieri Fallax neocaledonensis			
CP 3067	23°17'S, 167°58'E	800 m	Stenosarina crosnieri			
CP 3068	CP 3068 23°16'S, 167°57'E 790 m <i>Een Fal</i> u <i>CP 3068 23°16'S</i> , 167°57'E 790 m <i>Ten</i> <i>Falu</i> <i>C</i>		Basiliola beecheri Stenosarina crosnieri Terebratulina pacifica Fallax neocaledonensis Campages mariae			
DW 3069	DW 3069 23°18'S, 168°05'E 300–320 m Stenosarina Campages		Basiliola lucida Stenosarina crosnieri Campages mariae			
CP 3070	23°18'S, 168°05'E	300–320 m	Stenosarina crosnieri			
DW 3072	23°19'S, 168°16'E	180–220 m	Terebratulina pacifica			
DW 3075	23°17'S, 168°14'E	270 m	Basiliolella grayi			
DW 3076	23°14'S, 168°13'E	390–570 m	Stenosarina globosa			
DW 3077 23°15'S, 168°14'E		420–540 m	Stenosarina crosnieri Fallax neocaledonensis			

List of brachiopod-bearing stations and species per station.

Station	Location	Depth	Species
	SW Te	errasses	
DW 3078	22°29'S, 167°30'E	180–210 m	Basiliolella grayi Campages mariae
DW 3079	22°28'S, 167°29'E	300–420 m	Basiliolella gravi
DW 3082	22°29'S, 167°23'E	290 m	Terebratulina pacifica
DW 3083	22°27'S, 167°25'E	470–570 m	Basiliola beecheri Terebratulina pacifica Fallax neocaledonensis
DW 3086	22°15'S, 167°13'E	400 m	Ebiscothyris bellonensis
DW 3089	22°17'S, 167°12'E	390–410 m	Stenosarina globosa
DW 3090	22°16'S, 167°08'E	260 m	Basiliolella grayi Campages mariae
CP 3091	22°17'S, 167°09'E	260–270 m	Fallax neocaledonensis
DW 3093	22°06'S, 167°03'E	190–200 m	Basiliolella grayi
DW 3094	22°04'S, 167°03'E	250–300 m	Basiliolella grayi
	Norfol	k Ridge	
DW 3100	DW 3100 22°59'S, 168°23'E		Basiliolella grayi Terebratulina pacifica
DW 3102	22°59'S, 168°23'E	410–430 m	Stenosarina globosa
CP 3104	CP 3104 22°58'S, 168°21'E		Kanakythyris pachyrhynchos
DW 3106	W 3106 23°02'S, 168°21'E		Basiliolella grayi Campages mariae
DW 3107	W 3107 23°01'S, 168°23'E		Kanakythyris pachyrhynchos Fallax neocaledonensis
DW 3108	23°01'S, 168°239'E	370–440 m	Kanakythyris pachyrhynchos
DW 3109	23°01'S, 168°18'E	150–180 m	Basiliolella grayi Kanakythyris pachyrhynchos Xenobrochus africanus
DW 3110	23°02'S, 168°16'E	270–310 m	Basiliolella grayi
	Pine	Island	
DW 3120	DW 3120 22°44'S, 167°15'E		Fallax neocaledonensis
DW 3121	DW 3121 22°45'S, 167°13'E		Fallax neocaledonensis
DW 3122	22°47'S, 167°12'E	390–410 m	Fallax neocaledonensis
DW 3123	22°53'S, 16°13'E	420–450 m	Fallax neocaledonensis
DW 3124	22°54'S, 167°15'E	460 m	Fallax neocaledonensis
DW 3129	22°42'S, 167°15'E	110–130 m	Frenulina sanguinolenta

Exbodi New Caledonia				
DW 3785	22°15'S, 167°10'E	386–387 m	Stenosarina globosa	
CP 3786	22°15'S, 167°13'E	406–442 m	Stenosarina globosa	
DW 3787	22°13'S, 167°06'E	223–249 m	Basiliolella grayi Campages mariae	

Station	Location	Depth	Species	
CP 3788	22°13'S, 167°07'E	264–273 m	Basiliolella grayi Campages mariae	
CP 3789	22°11'S, 167°07'E	335–350 m	Basiliolella grayi Campages mariae	
CP 3791	22°15'S, 167°19'E	750–863 m	Ebiscothyris bellonensis	
CP 3792	22°18'S, 167°22'E	850–876 m	Ebiscothyris bellonensis	
CP 3793	22°16'S, 167°23'E	951–1180 m	Ebiscothyris bellonensis	
DW 3798	21°32'S, 166°21'E	478–480 m	Basiliola beecheri	
CP 3834	22°06'S, 167°04'E	257–258 m	Basiliolella grayi Campages mariae	
CP 3842	22°23'S, 167°22'E	756–769 m	Ebiscothyris bellonensis	
CP 3843	22°22'S, 22°22'S	776–800 m	Ebiscothyris bellonensis	
CP 3844	22°20'S, 167°22'E	815–970 m	Ebiscothyris bellonensis	
DW 3845	22°30'S, 167°09'E	70–72 m	Ebiscothyris bellonensis	
DW 3846	22°04'S, 168°38'E	396 m	Basiliolella grayi	
CP 3848	22°03'S, 168°42'E	430–440 m	Kanakythyris pachyrhynchos	
CP 3849	22°03'S, 168°41'E	360–560 m	Fallax neocaledonensis	
CP 3851	CP 3851 22°19'S, 168°45'E 471–510 m		Basiliola lucida Stenosarina crosnieri Kanakythyris pachyrhynchos Terebratulina pacifica Fallax neocaledonensis Campages mariae	
CP 3852	CP 3852 22°17'S, 168°43'E		Stenosarina crosnieri Fallax neocaledonensis Campages mariae	
DW 3862	22°20'S, 169°01'E	400–520 m	Neoancistrocrania norfolki Basiliola beecheri Annuloplatidia curiosa	
DW 3863	22°21'S, 168°59'E	540–660 m	Frenulina sanguinolenta	
CP 3871	22°53'S, 169°25'E	580–780 m	Basiliola beecheri	
DW 3872	22°54'S, 169°27'E	159–756 m	Frenulina sanguinolenta Thecidellina maxilla	
DW 3880	DW 3880 22°22'S, 171°39'E 350 m Basiliolella Terebratulina		Basiliolella grayi Terebratulina pacifica	
CP 3882	22°21'S, 171°40'E	288 - 361 m	Basiliolella grayi	
CP 3883 22°21'S, 171°39'E		433–516 m	Basiliolella grayi	
CP 3884	CP 3884 22°22'S, 171°38'E		Basiliolella grayi Terebratulina pacifica	
CP 3885	22°23'S, 171°39'E 558–584		Basiliolella grayi Terebratulina pacifica	
DW 3887	22°22'S, 171°42'E 257–298 m Basilio		Basiliolella grayi	
DW 3889	22°25'S, 171°41'E	354 m	Basiliolella grayi	
DW 3895	22°25'S, 171°40'E	380 m	Stenosarina crosnieri	
DW 3896 22°19'S, 168°41'E		340–343 m	Basiliola lucida Terebratulina pacifica	

Station	Location	Depth	Species	
CP 3898 22°18'S, 168°42'E		340-346 m	Basiliola lucida	
		910 910 m	Stenosarina crosnieri	
DW 3900	22°17'S, 168°41'E		Basiliola lucida	
		355–357 m	Stenosarina crosnieri	
			Campages mariae	
DW 3902	19°53'S, 165°49'E	410 m	Frenulina sanguinolenta	
DW 3903	19°52'S, 165°50'E	580 m	Frenulina sanguinolenta Thecidellina maxilla	
DW 3905	19°50'S, 165°34'E	300 m	Frenulina sanguinolenta Thecidellina maxilla	
DW 3906	19°50'S, 165°33'E	490–580 m	Terebratulina pacifica Frenulina sanguinolenta Thecidellina maxilla	
DW 3907	19°50'S, 165°33'E	608–671 m	Thecidellina maxilla	
CP 3911	19°50'S, 165°33'E	680–802 m	Novocrania sp. Basiliola beecheri Eucalathis murrayi Septicollarina zezinae Annuloplatidia richeri	
DW 3913	19°45'S, 165°45'E	i5'S, 165°45'E 622 m Basiliola beech Annuloplatidia r		
DW 3916	19°52'S, 165°55'E	749–922 m	Ebiscothyris bellonensis	
DW 3917	19°52'S, 165°55'E 753–951 n		Stenosarina crosnieri	
DW 3918	19°52'S, 165°55'E 748–922 m		Stenosarina crosnieri	
DW 3922	18°33'S, 164°21'E	525–560 m	Frenulina sanguinolenta	
DW 3923	DW 3923 18°33'S, 164°20'E 580–703 m <i>Frenuli</i> <i>Theci</i>		Frenulina sanguinolenta Thecidellina maxilla	
DW 3924	18°35'S, 164°23'E	730 m	Frenulina sanguinolenta	
DW 3925	18°35'S, 164°19'E	388 m	Meoancistrocrania norfolki Eucalathis murrayi M Xenobrochus indianensis Frenulina sanguinolenta Thecidellina maxilla	
CP 3927	CP 3927 18°36'S, 164°20'E 381 m Frenulina sang Campages		Frenulina sanguinolenta Campages mariae	
DW 3928	DW 3928 18°38'S, 164°20'E 362–402 m <i>Frenulina s</i> <i>Thecidelli</i>		Frenulina sanguinolenta Thecidellina maxilla	
DW 3930	3930 18°37'S, 164°26'E 448–464 m Frenulina san		Frenulina sanguinolenta	
DW 3932	DW 3932 18°32'S, 164°21'E 500–1100 m Frent The		Frenulina sanguinolenta Thecidellina maxilla	
DW 3933	18°32'S, 164°22'E	474 m	Frenulina sanguinolenta Thecidellina maxilla	
DW 3939	18°36'S, 164°24'E	489–860 m	Frenulina sanguinolenta	
DW 3940	18°36'S, 164°24'E	380–430 m	Frenulina sanguinolenta	

RESEARCH ARTICLE



Distribution of pelagic squids Abraliopsis Joubin, 1896 (Enoploteuthidae) and Pterygioteuthis P. Fischer, 1896 (Pyroteuthidae) (Cephalopoda, Decapodiformes, Oegopsida) in the Mexican Pacific

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Abstract

The oegopsid squids *Abraliopsis* and *Pterygioteuthis* are abundant and diverse genera with taxonomic and distributional problems. Identification and distribution of species in the Mexican Pacific has been somewhat controversial. Here are provided a large series of new records for *Abraliopsis affinis*, *A. falco*, *Pterygioteuthis gemmata*, *P. giardi* and *P. hoylei* from the Gulf of California and off the SW coast of Mexico. All five species were collected in the central or the southern Gulf of California, or in both. *Abraliopsis affinis falco* was much less represented in the samples (14 specimens) but it was found in 10 localities, four of which correspond to the central-southern Gulf of California (north to 27°44'53"N) and six to SW Mexico (south to 16°49'18"N). In the case of *Pterygioteuthis gemmata*, only two records (three specimens) were obtained, both in the SW Gulf of California, while *P. giardi* (nine specimens) records were all from the central Gulf of California (27°44'53" to 25°39'59"N). In the case of *P. hoylei* (nine specimens), material was obtained in six localities, also in a restricted latitudinal range (24°23'48" to 25°56'56"N).

Keywords

Mexican Pacific, squids, Abraliopsis, Pterygioteuthis, distribution, TALUD cruises

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Introduction

Cephalopoda is a major group of marine mollusks with almost 1000 species worldwide (Roper et al. 1995). An important component of the natural communities, they are active predators mostly on invertebrates (e.g., mollusks, crustaceans) and fishes. They are also used as prey for many medium to large size marine species (e.g., fish, marine mammals, sea birds) and therefore occupy an important position in the marine food web (Boyle and Rodhouse 2005). They also represent a significant portion of the worldwide catch of marine products, either by the fishing fleets or by fisherman in coastal, shallow water (Jereb et al. 2014).

Cephalopods are essentially divided into two natural groups: the pelagic forms that permanently swim into the water column (i.e., squids, nautilus or cuttlefishes) and the benthic species, that live on or close to the bottom (i.e., octopuses) (Strugnell et al. 2005). Our knowledge on distribution, ecology and biology of small pelagic squids, their larvae, paralarvae and juvenile phases are very limited, particularly in tropical oceans (Vidal et al. 2010; Alejo-Plata et al. 2013). Pelagic cephalopods are fast-moving animals and are able to detect the approach of sampling gears either by vision or detection of vibrations (Boyle and Boletzky 1996). They are therefore very effective at avoiding nets (Lansdell and Young 2007). The use of large sampling gear like the RTM8 deployed off the Brazilian coast (Vidal et al. 2010) has proved very effective at capturing small cephalopods, thus increasing the potential for their study.

Within the pelagic forms there is a general agreement to recognize two groups: 1) the Myopsida squids, which contains mainly the loliginids species, and 2) the Oegopsida, a more diverse and rich group characterized by the presence of an ocular membrane (Jereb and Roper 2010). At present, the Oegopsida is composed by 24 families and contains very large and very small species, some living in very deep water. It also contains some commercial species. The "Enoploteuthidae" is a group forming a clade of closely-related families, all of which are of small size (< 5 cm), live in the mesopelagic zone, and possess a large amount of photophores along their entire body (Young et al. 2012).

According to Young et al. (1998) 12 species of *Abraliopsis* Joubin, 1896 (type species: *A. pfefferi* Joubin, 1896) are known worlwide, while Roper and Jereb (2010) included only 11 species of *Abrialopsis* in their list. According to Bouchet and Gofas (2014) the genus *Abraliopsis* contains 12 species. Bouchet and Gofas (2014), however, indicated that the status of several species is somewhat imprecise. According to Young and Tsuchiya (2014) there are approximately twenty species of *Abraliopsis* worldwide, of which ten are undescribed. These authors presented a tentative list of taxonomic features that allows the separation in four genera of *A. braliopsis*, but they indicated that further study is in need before a final decision is taken in dividing the genus. Only three species of *Abraliopsis* have been reported in the eastern Pacific: *A. affinis* (Pfeffer, 1912) *A. falco* Young, 1972, and *A. felis* McGowan & Okutani, 1968 (Young et al. 1998; Roper and Jereb 2010). *Abraliopsis affinis* occurs in the tropical waters of the eastern Pacific Ocean, and is known from Chile, Colombia, Costa Rica, Ecuador, El Salvador, Guatemala, Honduras, Mexico, Nicaragua, Panama and Peru. *Abraliopsis*

falco has been reported from off the Baja California Peninsula (type locality and only area where it has been found so far) (Young et al. 1998; Abitia Cardenas et al. 2011). The third species, *A. felis*, is found off the west coast of North America, from about 27° to 43°N (Young et al. 1998). Species are separated by the number, size, and position of photophores, and by the number, size and distribution of the hooks and suckers on the tentacles (Sweeney et al. 1992).

The genus *Pterygioteuthis* P. Fischer, 1896 (type species *P. giardi*, P. Fischer, 1896) contains another group of small pelagic squids with a worldwide distribution. Young et al. (1998) considered three species within the genus Pterygioteuthis: P. giardi, P. gemmata Chun, 1908, and P. microlampas Berry, 1913. They further indicated that two subspecies of *P. giardi* have been recognized: the nominal subspecies, occurring in the Atlantic (Diekman et al. 2002) and the Indo-West Pacific, and P. g. holyei Pfeffer, 1912 from the tropical eastern Pacific. The eastern Pacific subspecies was elevated to genus based on a detailed morphological study (Lindgren 2010). A detailed study of the distribution of *P. hoylei* in the Gulf of California (including paralarvae and adults) was provided by De Silva-Dávila et al. (2013). Lindgren (2010) also analyzed the distribution of other species of Pterygioteuthis in the west central and eastern Pacific, noting that only P. gemmata (Indo-West Pacific, eastern Pacific and Atlantic) and P. hoylei (eastern Pacific and Equatorial Countercurrent to about 125°W) are present in the eastern Pacific. Members of this genus are most commonly collected in mid water surveys, specially the paralarvae, while adult specimens are usually not very abundant in the samples (Bowerl et al. 1999).

Together with fishes, stomatopods and benthopelagic shrimps, species of Abraliopsis (e.g., A. pacifica Tsuchiya & Okutani, 1990) are an important component of the micronecton near seamounts (Drazen et al. 2011). Juveniles and adults of small squids are also important prey items for many species of pelagic fishes and some marine mammals (Fiscus et al. 1989). Specimens of Abraliopsis affinis have been found to be part of the diet of the Peruvian hake (Merluccius gavi peruanus Ginsburg, 1954) (Blaskovic 2011), of the striped marlin Kajikia audax (Philippi, 1887) from off Cabo San Lucas (Abitia Cardenas et al. 2011), and of sharks in the Ecuadorian and Mexican Pacific (Galván-Magaña et al. 2013). Abraliopsis sp. was found in stomach content of the Indo-Pacific sailfish, Istiophorus platypterus (Shaw, 1792) (Varghese et al. 2013). Other records include specimens of Abraliopsis falco Young, 1972 and Abraliopsis spp. found as part of the diet of the yellowfin tuna Thunnus albacares (Bonnaterre, 1788) in the eastern tropical Pacific (Olson et al. 2014). Abraliopsis lineata (Goodrich, 1896) is part of the diet of the common dolphinfish, Coryphaena hippurus Linnaeus, 1758, in the eastern Arabian Sea (Varghese et al. 2013). Enoploteuthidae constituted over 25% of estimated biomass of squids consumed by a specimen of the pygmy sperm whale Kogia breviceps (de Blainville, 1838), stranded on a beach in Tasmania (Beasley et al. 2013). Although not fully identified, Abraliopsis gilchristi Robson, 1924 and Enoploteuthis galaxias Berry, 1918 were probably the two species of Enoploteuthidae found in the stomach content of this whale. Specimens of Abraliopsis have also been found as an important item in the diet of the shrimp Aristaeomorpha foliacea (Risso, 1827) in the

Mediterranean Sea, with *Abraliopsis pfefferi* (Robson, 1924) representing the dominant species of cephalopods in the diet (Markaida and Sosa-Nishizaki 2003). *Pterygioteuthis* species are also consumed by many marine animals, including a large variety of fish (Ménard et al. 2013), other cephalopods like *Dosidicus gigas* (D'Orbigny, 1835) (Camarillo-Coop et al. 2013), sea-birds like the shearwater *Puffinus newelli* Henshaw, 1900 (Ainley et al. 2014), and fur seal (*Arctocephalus townsendi* Merriam, 1897) (Gallo-Reynoso and Esperón-Rodríguez 2013).

There have been several studies on the occurrence of paralarvae and small juveniles of cephalopods. They are known to be related to primary production in upwelling areas (Vidal et al. 2010) and their abundance is related with temperature, especially in areas that experience fast and significant temperature changes (Vecchione 1999). Some of these recent studies deal with the eastern Pacific. Okutani and Mcgowan (1969) and Watson and Manion (2011) reported on paralarvae from the California Current, including species of Abraliopsis and Pterygioteuthis. Granados-Amores et al. (2010) studied the paralarvae of cephalopods collected off the west coast of the Baja California Peninsula. Their samples included 10 families and 17 species (plus some unidentified species). The Enoploteuthidae included at least three species of unidentified Abraliopsis and Abraliopsis felis, while the Pyroteuthidae included two unidentified species of Pterygioteuthis. Alejo-Plata et al. (2013) recorded cephalopods paralarvae and juveniles in the Gulf of Tehuantepec, noting that six families representing eight genera and at least 13 species were present in the samples. Enoploteuthidae represented 15.9% of specimens and comprise of three unidentified species of Abraliopsis and unidentifed material. A very complete study of distribution and abundance of *Pterygioteuthis hoylei* was performed by De Silva-Dávila et al. (2013) in the Gulf of California. Based on 241 plankton samples, they were able to identify most paralarvae using COI barcode information available in the Gen Bank. Their distribution data indicated that *P. hoylei* occurs from the southern Gulf of California up to ca 20°30'N.

During an intensive survey of the deep-water fauna inhabiting below the Oxygen Minimum Zone (OMZ), the TALUD project, specimens of small squids were collected in different sampling gear off the coast of western Mexico. This material belongs to the genera *Pterygioteuthis* and *Abraliopsis* and is reported herein.

Material and methods

The material on which this study is based was collected by the R/V "El Puma" of the Universidad Nacional Autónoma de México (UNAM), between 1991 and 2014. Specimens of pelagic squids were captured during sampling operations in the Gulf of California (a total of eight cruises: TALUD III, September 1991; TALUD IV, August 2000; TALUD VII, June 2001; TALUD VIII, April 2005; TALUD IX, November 2005; TALUD X, February 2007; TALUD XIII, January 2009) and off the SW coast of Mexico, from Jalisco to Guerrero (TALUD XII, March-April 2008). During these cruises, a total of 113 localities, from 216 to 2300 m depth, were sampled for benthic species.

Positional coordinates for each sampling station were obtained using a GPS navigation system. Depth was measured with an EdoWestern analogic recorder (TALUD III-VIII) or a digital recorder (TALUD IX-XIII). All the specimens were presumably captured during the ascent of a modified Agassiz dredge (2.5 m width, 1 m high) and a standard benthic sledge (2.35 m width, 0.9 m high) equipped with a modified shrimp net (ca. 5.5 cm stretched mesh size) with a ca. 2.0 cm (3/4") internal lining net. In these cases, the depth range at which the gear was operated is provided but does not indicate the depth of capture because the specimens could have been captured between surface and maximum trawling depth at each locality. In two ocasions, sample were obtained with a micronecton net or a mid water Issacs-Kidd trawl. The material collected during this survey is deposited in the Regional Collection of Marine Invertebrates (EMU), at UNAM in Mazatlán, Mexico. The size (mantle length) was measured to the nearest 0.1 mm. Abbreviations are: St., sampling station; ML, mantel length; AD, Agassiz dredge; BS, benthic sledge. Systematic sequence used herein is according to Young et al (2012).

Results

Five species of small squids were collected during sampling operations. A total of 86 specimens were obtained: *Abraliopsis affinis*, 46; *A. falco*, 18; *Pterygioteuthis gemmata*, 3; *P. giardi*, 9; and *P. hoylei*, 10.

Systematic section

Cephalopoda Class Coleoidea Superorder Decapodiformes Order Oegopsida Family Enoploteuthidae Pfeffer, 1900 *Abraliopsis* Joubin, 1896

Abraliopsis affinis (Pfeffer, 1912)

Material examined. TALUD III. St. 3B (22°36'36"N; 106°35'54"W), Aug 17, 1991, 1 org. (ML 26.5 mm), Issac Kidds mid-water trawl, 275 m (total depth, 940–950 m) (EMU-10591); St. 14A (24°38'48"N; 108°26'54"W), Aug 19, 1991, 24 orgs. (ML 22.3–34.7 mm), AD operated at 1016–1020 m (EMU-10592). TALUD IV. St. 4 (21°59'N; 106°35'W), Aug 23, 2000, 15 orgs. (ML 20.1–32.1 mm), AD operated at 1200–1290 m (EMU-10593); St. 13 (23°17'30"N; 107°29'51"W), Aug 24, 2000, 1 org. (ML 18.9 mm), BS operated at 860 m (EMU-10597). TALUD VII. St. 12 (23°18'18"N; 107°26'48"W), Jun 6, 2001, 2 orgs. (ML 25.2–27.8 mm), AD operated at 1040–1120 m (EMU-10595); St. 18 (24°14'30"N; 108°16'24"W), Jun 7, 2001, 2

orgs. (ML 27.8–32.1 mm), AD operated at 1040–1120 m (EMU-10596). TALUD VIII. St 21 (26°2'18"N; 110°37'6"W), Apr 19, 2005, 1 org. (ML 22.4 mm), AD operated at 1380 m (EMU 10598).

Abraliopsis falco Young, 1972

Material examined. TALUD IV. St. 25 (24°53'12"N; 108°59'24"W), Aug 26, 2000, 2 orgs. (ML 25.0 mm), AD operated at 778-800 m (EMU-10594). TALUD V, St. 3 (21°59'14"N; 106°28'30"W), Dec 13, 2000, 1 org. (ML 23.5 mm), BS operated at 730 m (EMU-10599). TALUD VII, St. 26 (24°25'24"N; 109°05'21"W), Jun 8, 2001, 1 org. (ML 32.2 mm), BS operated at 1180-1260 m (EMU-10600). TALUD X. St. 14 (27°44'53"N; 111°39'54"W). Feb 11, 2007, 1 org. (ML 24.2 mm), BS operated at 843-905 m (EMU-10601). TALUD XII. St. 2 (16°49'18"N; 100°30'52"W), Mar 28, 2008, 1 org. (ML 21.3 mm), BS operated at 990-1088 m (EMU-10602); St 3 (16°54'35"N; 100°44'10"W), Mar 28, 2008, 2 orgs. (ML 27.1-27.6 mm), BS operated at 1380-1456 m (EMU-10603); St. 10 (17°11'03"N; 101°28'05"W), Mar 28, 2008, 1 org. (ML 32.6 mm), BS operated at 1180-1299 m (EMU-10604); St. 29 (19°19'37"N; 105°26'20"W), Apr 2, 2008, 1 org. (ML 25.4 mm), BS operated at 1609--1643 m (EMU-10605); St. 30 (19°22'05"N; 105°16'18"W), Mar 28, 2008, 4 orgs. (ML 27.8--29.3 mm), BS operated at 1350--1380 m (EMU-10606); St. 30B (19°30'37"N; 105°19'16"W), Mar 26, 2008, 3 orgs. (ML 25.7–30.3 mm), BS operated at 865–1045 m (EMU-10607). TALUD XIII. St. B (26°19'54"N; 110°29'12"W), Jan 13, 2009, 1 org. (ML 30.8 mm), Agassiz dredge, 1295–1330 m (EMU-10608).

Family Pyroteuthidae Pfeffer, 1912 *Pterygioteuthis* P. Fischer, 1896

Pterygioteuthis gemmata Chun, 1908

Material examined. TALUD VIII. St 15 (25°21'27"N; 110°18'18"W), April 18, 2005, 2 orgs. (ML 12–16 mm), BS operated at 2100 m (EMU-10609); St. 21 (26°02'18"N, 110°37'06"W), April 19, 2005, 1 org. (ML 13 mm), BS operated at 1380 m (EMU-1598).

Pterygioteuthis giardi P. Fischer, 1896

Material examined. TALUD IV. St. 35 (25°39'59"N; 110°11'17"W). Aug 27, 2000, 1 org. (ML 20.6 mm), BS operated at 2000–2100 m (EMU-10615). TALUD VIII. St. 18 (25°50'N; 110°34'W), Feb 12, 2005, 3 orgs. (ML 15.5–17.7 mm), micronecton net, 690 m (total depth 1300 m) (EMU-10616). TALUD IX. St. 22 (26°3'42"N;

110°20'36"W), Nov 14, 2005, 1 org. (ML 19.4 mm), BS operated at 2214–2309 m (EMU-10617). TALUD X. St. 14 (27°44'53"N; 111°36'58"W), 3 orgs. (ML 17.8–19.1 mm), BS operated at 905–943 m (EMU-10618). TALUD XIII, St. 36 (26°07'12"N 110°30'53"W), Jan 15, 2009, 1 org. (ML 18.6 mm), AD operated at 2300–2360 m (EMU-10619).

Pterygioteuthis hoylei Pfeffer, 1912

Material examined. TALUD VIII. St. 15 (25°23'06"N; 110°18'24"W), Abr 18, 2005, 2 orgs. (ML 12.1–12.2 mm), BS operated at 2100 m (EMU-10609); St. 20 (25°56'56"N; 110°43'W), Abr 19, 2005, 2 orgs. (ML 16.2–18.0 mm), BS operated at 1140–1150 m (EMU-10610). TALUD IX. St. 8 (25°07'28"N; 109°49'48"W), Nov 12, 2005, 1 org. (ML 17.6 mm), BS operated at 1657 m (EMU-10611); St.15 (25°21'27"N; 110°18'18"W), Nov 13, 2005, 2 orgs. (ML 19.2 mm), BS operated at 1985–2290 m (EMU-10612); St. 16 (24°23'48"N; 110°36'42"W), Nov 13, 2005, 1 org. (ML 16.4 mm), BS operated at 997–1021 m (EMU-10613); St. 20B (25°58'7"N; 110°40'4"W), Nov 14, 2005, 2 orgs. (ML 17.4–19.6 mm), BS operated at 1229–1343 m (EMU-10614).

Distribution

All five species examined herein were collected in the central or the southern Gulf of California, or in both (Fig. 1). *Abraliopsis affinis* was found in seven samples with a total of 48 specimens, from 21°59' to 24°53'12"N. *Abraliopsis falco* was much less represented in the samples (14 specimens) but it was found in 10 localities, four of which correspond to the central-southern Gulf of California (north to 27°44'53"N) and six to SW Mexico (south to 16°49'18"N), thus covering a much wider latitudinal range than the other three species (Fig. 1). *Pterygioteuthis gemmata* (3 specimens) was collected in two stations located in the SW Gulf of California (Fig. 1). In the case of *Pterygioteuthis giardi* (9 specimens), records are only from the central Gulf of California (27°44'53" to 25°39'59"N) and, in the case of *P. hoylei* (9 specimens), material was obtained in six localities, also in a restricted latitudinal range (24°23'48" to 25°56'56"N) (Fig. 1).

Discussion

In this study the material was collected either during the ascending process of large gear used for sampling the benthos or with a micronecton net and a mid-water trawl (two samples only). Although the benthic samplers were not designed to catch small pelagic squids, a rather large series of specimens was collected over the study period. In spite of this, the two oegopsid species were very common in the samples obtained



Figure 1. Distribution of specimens of *Abraliopsis affinis* (Pfeffer, 1912), *A. falco* Young, 1972, *Pterygio-teuthis gemmata* Chun, 1908; *P. giardi*, P. Fischer, 1896, and *P. hoylei* Pfeffer, 1912 collected during the TALUD cruises off the Pacific coast of Mexico.

during the TALUD survey (*Abraliopsis affinis*, 46; *A. falco*, 18). The pyrotheutids were much less abundant in the samples (*Pterygioteuthis gemmata*, 3; *P. giardi*, 9; *P. hoylei*, 10). However, it was decided not to evaluate density of species collected in each sample due to the fact that many specimens were probably able to avoid the nets.

Two species of *Abraliopsis* were collected during the TALUD survey: *A. affinis* and *A. falco. Abraliopsis felis* has been reported from the NE Pacific, between 27° and 43°N (Young et al. 1998), but was not found during our survey. *Abraliopsis falco* type material was collected by the "*Velero IV*" from off the Baja California Peninsula, and it has not been reported from outside this area so far (Young et al. 1998). Our records indicate that this species has a wider distribution range than

previously thought. More samples are needed, however, to define its exact distribution range. It was not found in the Gulf of Tehuantepec by Alejo-Plata et al. (2014), who only reported A. affinis from that area. During the present survey A. falco was collected in the southern Gulf of California (northernmost limit set at 27°44'53"N, 111°39'54"W) and extends its distribution south to 16°49'18"N (Fig. 1). Although it also appears to be endemic to the eastern Pacific, A. affinis had a much wider distribution range, from Ecuador (02°34'N) to Mexico (14°46'N) (Young et al. 1998). Our records indicate that it extends much further north, entering the Gulf of California where its northernmost distribution limit is set at 26°2'18"N, 110°37'6"W. Young (1972) indicated that the presence of A. falco is strongly correlated with high salinity water masses, and the Gulf of California water is highly saline (≥ 35 ppm) (Alvarez-Borrego 2010). Species of Abraliopsis are reported as diurnal migrants, spending most of the day between 300 and 600 m (Roper and Young 1975). Most of our samples, however, were made in water deeper that 600 m, thus crossing the entire depth interval where these species are supposed to occur and much more (maximum depth reached by the gear, 2300 m).

Lindgren (2010) reviewed the status of the species of *Pterygioteuthis* occurring in the eastern and eastern-central Pacific, noting that *P. giardi hoylei* (sensu Young et al. 1998) *P. giardi, P. gemmata*, and *P. microlampas* occur roughly between the Equator (ca. 5°S) and 32°N. Based on morphological analysis, Lindgren (2010) upgraded *P. giardi hoylei* to full-species rank. The two species were distinguished based on several characters, including the size and numbers of hooks on arm I, the presence or absence of suckers on male arm III, the extension of chromatophores on tentacle stalk, the presence or absence of rows of chromatophores on aboral tentacle club, and on numbers and position of chromatophores on funnel and tentacles. Lindgren (2010) defined a restricted distribution of *P. giardi* in the eastern-central Pacific (not closer to the continent than 140°W), but emphasized that further sampling in the area might demonstrate that it extends further to the east, and would therefore share a large distribution range with *P. hoylei*. In the case of *P. gemmata*, morphologically indistinguishable populations occur in the Atlantic (type locality in the South Atlantic), the Indo-Pacific and the eastern Pacific (Lindgren 2010).

Our records show that *P. gemmata*, *P. hoylei* and *P. giardi* all occur in the southern Gulf of California. The bathymetric distribution and the southern distribution limit of *P. gemmata* are unclear. Lindgren (2010) reported the presence of this species from off California, USA, and off Baja California (27°26'N to 32°55'N), in Pacific Mexico. Our records appears to be the first available for the Gulf of California, and would represent the current southernmost distribution limit of the species in the eastern Pacific. *Pterygioteuthis hoylei* is restricted to the Gulf of California, the coastal area of Central America and to an offshore area extending from the Galapagos Islands to ca. 145°W, roughly matching the extension of the Oxygen Minimum Zone (OMZ) occurring in that area (Lindgren 2010). However, there are no near-shore records of this species between the mouth of the Gulf of California and Nicaragua. De Silva-Dávila et al.

(2013) processed pelagic samples from the entire Gulf of California, but found P. hoylei only in the central and southern portions of the Gulf, with a strong affinity for the area south of ca. 28°N. In our study, P. hoylei was not collected north of ca. 26°N. Our sampling effort from off the west coast of Mexico (roughly from 16°49 to 19°30'N, in 27 stations) was negative and not a single specimen of *Pterygioteuthis* was collected there. Lindgren (2010) referred to the possibility that *P. hoylei* might take advantage of the boundary effect of the OMZ, a very strong and characteristic feature of this area in the eastern Pacific Ocean (Díaz and Rosenberg 1995; Helly and Levin 2004; Serrano 2012), finding abundant food items like large zooplanktonic organisms. Distribution maps of P. hoylei in the Gulf of California presented by Lindgren (2010) and De Silva-Dávila et al. (2013) somehow matches the area of strong upwellings, while its distribution off Central America corresponds to the area of influence of the Costa Rica Dome, a highly productive zone that is also a favorite destination for marine mammals (Rosales-Nanduca et al. 2011). The OMZ core along the SW coast of Mexico is very ample, on the average covering a depth range of >700 m (Hendrickx and Serrano 2010). In shallow water, the well oxygenated fringe in this area is very narrow (<50 m) (Hendrickx and Serrano 2010), hence small squids like Abraliopsis and Pterygioteuthis probably occur below the OMZ core. There is no evidence of these species being able to migrate throughout the OMZ which features a severely hypoxic-anoxic (<0.2 ml/l O₂) central core between ca. 50–100 m and 1000 m (Hendrickx and Serrano 2010). In the western Atlantic *P. hoylei* lives between 400 to 500 m and probably migrates to 200 m depth during the night (Lu and Roper 1979). In California it has been reported between 300 and 600 m (Roper and Young 1975).

Although almost 50 samples of benthic organisms were obtained from off the west coast of the Baja California Peninsula between June 2012 and June 2014, with the benthic sledge operating at similar depth as those reported herein (see material examined), not a single specimen of pelagic squid was found. There is no clear explanation for this. Lindgren (2010) reported the presence of *Pterygioteuthis gemmata* off the Baja California Peninsula roughly north of 28°N. *Pterygioteuthis gemmata* tends to show low densities and a more northern distribution (Lindgren 2010) than the other species. Our specimens are juveniles, but their photophores pattern and other anatomical features fit well with *P. gemmata* (Lindgren, 2011). The distribution area for the other species in the genus does not include the California Current area (Lindgren 2010). *Abraliopsis affinis* has been reported from 20°N to 30°S, including off Mexico, while *A. falco* has been collected between 35°N (southern California) and 20°S, also including Mexico in its distribution range (Jerep and Roper 2010).

As for many marine taxa with wide distribution, identification and congruence of the morphological characters need to be reinforce using molecular markers; unfortunately oegopsids do not show high representativity in molecular analysis (Allcock et al. 2014).

Additional sampling using more appropriate gear that can be hauled at speed of at least 5–6 knots (e.g., large size mid-water trawl) would probably be more adequate and certainly provide larger series of specimens of these elusive organisms.

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RESEARCH ARTICLE



Contribution to the knowledge of Galumnoidea (Acari, Oribatida) of Cuba

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Abstract

An annotated checklist of identified oribatid mites of the superfamily Galumnoidea collected from Cuba, including ten species from four genera and two families, is provided. *Galumna flabellifera* Hammer, 1958, *Pergalumna bifissurata* Hammer, 1972, *P. bryani* (Jacot, 1934), *P. decorata* Balogh & Mahunka, 1977 and *Galumnopsis secunda* Sellnick, 1923 are recorded for the first time in the Cuban fauna. A new species of *Pergalumna, P. cubaensis* **sp. n.**, is described; it is morphologically similar to *P. decorata* Balogh & Mahunka, 1977, but differs from the latter by the larger body size, heavily granulated prodorsum and well-developed interlamellar setae. The adult of *Allogalumna cubana* Balogh & Mahunka, 1979 is redescribed.

Keywords

Oribatid mites, Galumnoidea, new species, systematics, morphology, supplementary description, new record, Cuba

Introduction

At present, oribatid mites of the superfamily of Galumnoidea (Acari, Oribatida) are poorly known in the Cuban fauna (Balogh and Mahunka 1979; Jeleva et al. 1984; Palacios-Vargas and Socarrás 1993; Socarrás and Palacios-Vargas 1999). During taxonomic identification of material collected from Cuba, ten galumnoid species were found, including one new for science. The main goal of the paper is to describe this species under the name *Pergalumna cubaensis* sp. n. The genus *Pergalumna* is a large genus with more than 140 species having a cosmopolitan distribution (Subías 2004, updated 2015). The updated generic diagnosis and identification key to known species in the Neotropical region were presented by Ermilov et al. (2013, 2014b).

Additionally, data are presented on the specific localities, with notes on new records, overall known distributions of registered taxa, and a supplementary description of *Allogalumna cubana* Balogh & Mahunka, 1979, which was described briefly and incompletely by Balogh and Mahunka (1979) from Cuba.

Material and methods

These results are based on collections from three localities in Cuba (unknown date and collector, mites were previously deposited in the Museum of Zoology of Tyumen State University, Russia):

- Cuba 1: Parque Nacional Alejandro de Humboldt, 20°30'N, 74°40'W, leaf litter in forest.
- Cuba 2. Cuba, Valle de Viñales National Park, 22°40'56.8"N, 83°42'57.5"W, Ancon, leaf litter in forest.
- Cuba 3: Cayo Santa Maria, 22°66'21"N, 78°96'88"W, leaf litter in forest.

Specimens were mounted in lactic acid on temporary cavity slides for measurement and illustration. The body length was measured in lateral view, from the tip of the rostrum to the posterior edge of the ventral plate. Notogastral width refers to the maximum width in dorsal aspect. Lengths of body setae were measured in lateral aspect. All body measurements are presented in micrometers. Formulas for leg setation are given in parentheses according to the sequence trochanter–femur–genu–tibia–tarsus (famulus included). Formulas for leg solenidia are given in square brackets according to the sequence genu–tibia–tarsus. General terminology used in this paper follows that of Grandjean (summarized by Norton and Behan-Pelletier 2009). Drawings were made with a camera lucida using a Carl Zeiss transmission light microscope "Axioskop-2 Plus".

Systematics

Pergalumna cubaensis sp. n.

http://zoobank.org/76C9BD7F-380A-43C5-8783-B4ADB318CF20 Figs 1–11

Diagnosis. Body size: 962–1029 × 763–780. Prodorsum, epimeral region and antero-lateral parts of pteromorphs heavily granulated. Notogaster, anogenital region, pteromorphs and genital and anal plates striate. Rostral, lamellar, interlamellar and

bothridial setae setiform, slightly barbed. Anterior notogastral margin well-developed. Three pairs of porose areas (*Aa*, *A2*, *A3*) rounded. Median pore and postanal porose area absent.

Description. *Measurements.* Body length: 1012 (holotype: female), 962, 1029 (two paratypes: female and male); notogaster width: 763 (holotype), 763, 780 (two paratypes).

Integument. Body color black-brownish. Prodorsum, epimeral region and anterolateral parts of pteromorphs heavily granulated; granules rounded or slightly elongated, their diameter or length up to 6. Notogaster, anogenital region, pteromorphs and genital and anal plates striate.

Prodorsum. Rostrum broadly rounded. Lamellar (L) and sublamellar (S) lines distinct, parallel, curving backwards. Rostral (ro, 77–86) and lamellar (le, 53–65) setae thin, slightly barbed, directed antero-medially. Interlamellar setae (in, 86–90) setae setiform, indistinctly barbed, directed medially. Bothridial setae (bs, 110–123) setiform, slightly barbed, directed postero-laterad. Exobothridial setae and their alveoli absent. Porose areas Ad absent.

Notogaster. Anterior notogastral margin well developed. Dorsophragmata (D) of medium size, elongated longitudinally. Notogastral setae represented by ten pairs of alveoli. Three pairs of porose areas (Aa, A2, A3) rounded, similar in diameter (20-24), with clear borders. Areas Aa located between setal alveoli la and lm, equal distanced from them. Median pore absent in male and females. All lyrifissures (ia, im, ip, ih, ips) distinct, im and opisthonotal gland openings (gla) located antero-laterally to A2.

Gnathosoma. Morphology of subcapitulum, palps and chelicerae typical for *Pergalumna* (Engelbrecht 1972; Ermilov and Anichkin 2011; Ermilov et al. 2014a). Subcapitulum size: $200-205 \times 196-200$. Subcapitular setae setiform, slightly barbed, *a* (36–41) longer than *m* (28–32) and *h* (24–28); *a* thickest, *h* thinnest. Two pairs of adoral setae (or_1 , or_2 , 24–28) setiform, barbed. Palp length: 176. Axillary sacculi (*sac*) distinct. Chelicera length: 303. Cheliceral setae setiform, barbed, *cha* (106) longer than *chb* (61).

Epimeral and lateral podosomal regions. Anterior tectum of epimere I smooth. Setal formula: 1-0-2-3. Setae thin, slightly barbed, *1b*, *3b*, *3c* and *4c* (41–49) longer than *4a* and *4b* (24–28) Pedotecta II trapezoid in ventral view. Discidia sharply triangular. Circumpedal carinae (*cp*) reaching insertions of *3b*.

Anogenital region. Six pairs of genital $(g_1, g_2, 36-45; g_3-g_6, 20-28)$, one pair of aggenital (ag, 20-28), two pairs of anal $(an_1, an_2, 20-28)$ and three pairs of adanal $(ad_1-ad_3, 20-28)$ setae thin, indistinctly barbed. Genital plates with two genital setae on anterior edge. Adanal lyrifissures (iad) located diagonally to anal plates. Distance ad_1-ad_2 shorter than ad_2-ad_3 . Setae ad_3 inserted laterally to *iad*. Postanal porose area absent.

Legs. Morphology of leg segments, setae and solenidia typical for *Pergalumna* (see Engelbrecht 1972; Ermilov and Anichkin 2011; Ermilov et al. 2014a). Tridactylous, claws smooth. Formulas of leg setation and solenidia: I (1–4–3–4–20) [1–2–2], II (1–4–3–4–15) [1–1–2], III (1–2–1–3–15) [1–1–0], IV (1–2–2–3–12) [0–1–0]; homology



Figures 1–2. *Pergalumna cubaensis* sp. n., adult: **I** dorsal view (striae and granules are shown partially) **2** anterior part of body, lateral view (gnathosoma and leg I not illustrated, striae and granules are shown partially). Scale bar 200 μm.



Figures 3–4. *Pergalumna cubaensis* sp. n., adult: **3** ventral view (gnathosoma and legs not illustrated, striae and granules are shown partially) **4** posterior view. Scale bar 200 μ m.



Figures 5–11. *Pergalumna cubaensis* sp. n., adult: **5** rostrum, frontal view (granules are shown partially) **6** interlamellar seta and part of sejugal region **7** bothridial seta **8** subcapitulum (in dissected specimen), ventral view **9** right genital plate and part of epimeral and aggenital regions (granules are shown partially) **10** right anal plate and part of adanal region **11** tibia of leg IV, left, antiaxial view. Scale bars 100 μ m (**5**, **6**, **8–11**), 50 μ m (**7**).

Leg	Tr	Fe	Ge	Ti	Ta
Ι	v'	d, (l), bv"	(<i>l</i>), <i>v</i> ', σ	$(l), (v), \varphi_1, \varphi_2$	$(ft), (tc), (it), (p), (u), (a), s, (pv), v', (pl), l'', \varepsilon, \omega_1, \omega_2$
II	v'	d, (l), bv"	(<i>l</i>), <i>v</i> ', σ	(<i>l</i>), (<i>v</i>), φ	$(ft), (tc), (it), (p), (u), (a), s, (pv), \omega_1, \omega_2$
III	v'	d, ev'	<i>l</i> ', σ	<i>l</i> ', (<i>v</i>), φ	(ft), (tc), (it), (p), (u), (a), s, (pv)
IV	v'	d, ev'	d, l'	<i>l</i> ', (<i>v</i>), φ	ft", (tc), (p), (u), (a), s, (pv)

Table 1. Leg setation and solenidia of adult *Pergalumna cubaensis* sp. n. (same data for *Allogalumna cubana*Balogh & Mahunka, 1979).

Note: Roman letters refer to normal setae, Greek letters to solenidia (except ε = famulus). Single prime (') marks setae on the anterior and double prime (') setae on the posterior side of a given leg segment. Parentheses refer to a pair of setae. Tr – trochanter, Fe – femur, Ge – genu, Ti – Tibia, Ta – tarsus.

of setae and solenidia indicated in Table 1. Solenidion ϕ of tibiae IV inserted dorsally at about 2/3 length of segment.

Material examined. Locality Cuba 1: holotype (female) and two paratypes (female and male).

Type deposition. The holotype is deposited in the collection of the Senckenberg Museum, Görlitz, Germany; two paratypes are in the collection of the Tyumen State University Museum of Zoology, Tyumen, Russia.

Etymology. The specific name cubaensis refers to the country of origin, Cuba.

Remarks. Pergalumna cubaensis sp. n. is morphologically most similar to *P. decorata* Balogh & Mahunka, 1977 from the Neotropical region (see Balogh and Mahunka 1977) in having a rounded rostrum, a striate notogaster, an anterior margin of notogaster, three pairs of rounded porose areas on the notogaster, and setiform bothridial setae. However, the new species differs from the latter by the larger body size $(962-1029 \times 763-780 \ vs. 637-653 \times 469-494 \ in P. decorata)$, a heavily granulated prodorsum (*vs.* striate in *P. decorata*), and the interlamellar setae being of medium size (*vs.* minute in *P. decorata*).

Allogalumna cubana Balogh & Mahunka, 1979

Figs 12-23

Supplementary description. *Measurements.* Body length: 332–348 (12 specimens: six females and six males); notogaster width: 232–249 (12 specimens). Without sexual dimorphism.

Integument. Body color brown to light brown. Body surface punctate (visible under high magnification, ×1000).

Prodorsum. Rostrum broadly rounded. Sublamellar lines distinct, curving backwards. Rostral (12–16) and lamellar (6–8) setae thin, smooth, directed antero-medially. Interlamellar setae minute (2). Bothridial setae (65–73) with elongated, unilaterally dilated and sparsely ciliated head, directed postero-laterad. Exobothridial setae and their



Figures 12–13. *Allogalumna cubana* Balogh & Mahunka, 1979, adult: **12** dorsal view (microfoveolae are shown partially) **13** anterior part of body, lateral view (gnathosoma and leg I not illustrated). Scale bar 100 μ m.


Figures 14–15. *Allogalumna cubana* Balogh & Mahunka, 1979, adult: **14** ventral view (gnathosoma and legs not illustrated) **15** posterior view. Scale bar 100 μm.



Figures 16–23. *Allogalumna cubana* Balogh & Mahunka, 1979, adult: **16** rostrum, frontal view **17** interlamellar seta and part of sejugal region **18** bothridial seta **19** left setal alveolus *c* and porose area *Aa* with additional areas **20** subcapitulum (in dissected specimen), ventral view (microfoveolae are shown partially) **21** right genital plate and part of epimeral and aggenital regions (microfoveolae are shown partially) **22** left anal plate and part of adanal region (microfoveolae are shown partially) **23** tibia of leg IV, left, antiaxial view. Scale bars 20 μm.

alveoli absent. Porose areas Ad oval, transversally oriented (8 × 4), usually visible only in dissected specimens.

Notogaster. Anterior notogastral margin not developed. Dorsophragmata of medium size, elongated longitudinally. Notogastral setae represented by 10 pairs of alveoli. Four pairs of porose areas without clear borders: Aa oval, slightly transversally oriented (32–41 × 20), but it seems round in dorsal view; A1 rounded (12–16); A2 (16–20 × 10–12) and A3 (16–24 × 12–16) oval. Areas Aa located antero-medially to la. Often small additional porose parts (Aad; one to three represented by five to nine heavily pores) present nearly of Aa, but they visible only high magnification (Fig. 19). Median pore absent in males and females. All lyrifissures distinct, *im* located between lm and A1. Opisthonotal gland openings located laterally to A1.

Gnathosoma. Morphology of subcapitulum, palps and chelicerae similar to Pergalumna cubaensis sp. n. Subcapitulum size: $86-90 \times 82-86$. Subcapitular setae setiform, slightly barbed, a (14–16) longer than m (10–12) and h (8); a thickest, h thinnest. Two pairs of adoral setae (8) setiform, barbed. Palp length: 69. Axillary sacculi distinct. Chelicera length: 127. Cheliceral setae setiform, barbed, cha (32) longer than chb (20).

Epimeral and lateral podosomal regions. Anterior tectum of epimere I smooth. Setal formula: 1-0-1-2. Setae thin, smooth, *1a*, *3b* and *4a* (10) longer than *4b* (6) Pedotecta II rectangular, rounded distally in ventral view. Discidia sharply triangular. Circumpedal carinae clearly not reaching insertions of *3b*.

Anogenital region. Six pairs of genital $(g_1, g_2, 10; g_3-g_6, 6)$, one pair of aggenital (4), two pairs of anal (4) and three pairs of adanal (4) setae thin, smooth. Genital plates with two genital setae on anterior edge. Adanal lyrifissures located parallel to anal plates. Distance ad_1-ad_2 shorter than ad_2-ad_3 . Setae ad_3 inserted laterally to *iad*. Postanal porose area oval, transversally oriented (12–16 × 6–10).

Legs. Morphology of leg segments, setae and solenidia, formulas of leg setation and solenidia similar to *Pergalumna cubaensis* sp. n. (Table 1), but solenidion φ of tibiae IV inserted dorsally at about 1/3 length of segment, directed backwards in basal part.

Material examined. Locality Cuba 2: 12 specimens (six females and six males).

Remarks. The Cuban specimens of *A. cubana* from Balogh and Mahunka's description (1979) and our specimens are identical morphologically. Hence, based on these data, the main characters of *A. cubana* are: small body size ($328-348 \times 232-251$); body surface indistinctly punctate; rostrum rounded; rostral setae longer than lamellar setae, all thin, smooth; interlamellar setae minute; bothridial setae with elongated, unilaterally dilated and sparsely ciliated head; anterior notogastral margin not developed; four pairs of oval/rounded porose areas, *Aa* slightly transversally oriented; median pore absent; epimeral and anogenital setae thin, smooth; setae *ad*₃ inserted laterally to *iad*; postanal porose area present; tridactylous.

Records

- *Galumna angularis* Jeleva, Scull & Cruz, 1984 (see Jeleva et al. 1984; Mahunka 1985; Pérez-Íñigo and Baggio 1994). Distribution: Neotropical region. **Material examined.** Locality Cuba 1: 11 specimens.
- Galumna flabellifera Hammer, 1958 (see Hammer 1958; Aoki 1964, 1982; Mahunka 1978). Distribution: Pantropical and Subtropical regions. New record in Cuba.
 Material examined. Locality Cuba 2: 16 specimens.
- *Galumna* sp. Species is morphologically similar to *Galumna lunaris* Jeleva, Scull & Cruz, 1984 (see Jeleva et al. 1984).

Material examined. Locality Cuba 3: 4 specimens.

Remarks. Jeleva et al. (1984) unclearly described *G. lunaris* from Cuba, therefore we could not identify our species without studying of the type material.

Pergalumna bifissurata Hammer, 1972 (see Hammer 1972; Ermilov et al. 2014). Distribution: Polynesia and Neotropical region. New record in Cuba.
 Material examined. Locality Cuba 1: 22 specimens.

Pergalumna bryani (Jacot, 1934) (see Jacot 1934; Hammer 1973). Distribution: Pacific Islands and Neotropical region. New record in Cuba.
 Material examined. Locality Cuba 2: 5 specimens.

Pergalumna decorata Balogh & Mahunka, 1977 (see Balogh and Mahunka 1977). Distribution: Neotropical region. New record in Cuba.

Material examined. Locality Cuba 1: 7 specimens.

Pergalumna sp. Species is morphologically similar to *Galumna brasiliensis* Sellnick, 1923 (see Sellnick 1923).

Material examined. Locality Cuba 1: 22 specimens; Locality Cuba 2: 18 specimens; Locality Cuba 3: 6 specimens.

Remarks. Sellnick (1923) briefly described several species of *Galumna* (including *G. brasiliensis*) from Brazil. To date, *G. brasiliensis* has not been redescribed in detail. Lamellar seta appear to be inserted medially to the lamellar line according to figure 27 in Sellnick (1923); therefore there is a probability, that *G. brasiliensis* is a representative of *Pergalumna*. Hence, the systematic position of *G. brasiliensis* should be investigated further.

Galumnellidae

Galumnopsis secunda Sellnick, 1923 (see Sellnick 1923). Distribution: Neotropical region. New record in Cuba.

Material examined. Locality Cuba 2: 5 specimens.

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RESEARCH ARTICLE



A new highly specialized cave harvestman from Brazil and the first blind species of the genus: *landumoema smeagol* sp. n. (Arachnida, Opiliones, Gonyleptidae)

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Abstract

A new species of troglobitic harvestman, *Iandumoema smeagol* **sp. n.**, is described from Toca do Geraldo, Monjolos municipality, Minas Gerais state, Brazil. *Iandumoema smeagol* **sp. n.** is distinguished from the other two species of the genus by four exclusive characteristics – dorsal scutum areas with conspicuous tubercles, enlarged retrolateral spiniform tubercle on the distal third of femur IV, eyes absent and the penial ventral process slender and of approximately the same length of the stylus. The species is the most highly modified in the genus and its distribution is restricted only to caves in that particular area of Minas Gerais state. The type locality is not inside a legally protected area, and there are anthropogenic impacts in its surroundings. Therefore, *Iandumoema smeagol* **sp. n.** is vulnerable and it must be considered in future conservation projects.

Keywords

Endemism, troglobitic, limestone, Espinhaço Supergroup, Minas Gerais state

Introduction

The subterranean or hypogean fauna is ecologically categorized according to the degree of the populations' dependence and specialization to that environment, as proposed by Schiner (1854) and modified by Racovitza (1907) (*apud* Barr and Holsinger 1985, Trajano 2012): trogloxenes, organisms which are regularly found in caves, but that periodically return to the surface to feed and often to reproduce; troglophiles, organisms that can complete their life-cycle in either environment; and troglobites, organisms restricted exclusively to caves. Troglobites have evolved isolated in a peculiar selective regime, distinct from their ancestrals': total absence of light, a tendency to environmental stability, lack of primary production and low energy intake (Culver and Pipan 2009). In order to survive and effectively colonize the hypogean realm, subterranean species must reproduce, defend their territories and find food and mates in this environment, regardless of vision (Gibert and Deharveng 2001). Several specializations related to the life in subterranean environment have been reported in literature – the autapomorphies, called troglomorphisms (Christiansen 2012).

In caves, harvestmen are found near to or in association with organic matter deposits or spots, under blocks and rocks, on the walls, and on the ceiling, exhibiting solitary or gregarious behavior (Reddell 2012). To date, eight species of troglobitic harvestmen have been described in Brazil, belonging to the families Gonyleptidae Sundevall, 1833 (seven species; one Pachylospeleinae and six from Pachylinae subfamily) and Escadabiidae Kury and Pérez 2003 (one species), in addition to several troglophile and trogloxene representatives (Trajano and Bichuette 2009, Willemart and Taques 2013). At least six other undescribed species has been reported as restricted to subterranean environments (Hara and Pinto-da-Rocha 2008, Willemart and Taques 2013).

The gonyleptid genus *Iandumoema* Pinto-da-Rocha 1996, comprises two strictly subterranean species (troglobitic) up to now: *I. uai* Pinto-da-Rocha 1996 and *I. seti-mapocu* Hara and Pinto-da-Rocha 2008. The genus belongs to the polyphyletic Pach-ylinae (Pinto-da-Rocha et al. 2014) and its distribution is restricted to northern Minas Gerais state (eastern Brazil): *I. setimapocu* is endemic to only one cave (Lapa do Zu cave, municipality of Coração de Jesus) (Hara and Pinto-da-Rocha 2008) and *I. uai* is restricted to two caves (Gruta Olhos d'Água and Lapa do Cipó caves, municipality of Itacarambi) (Pinto-da-Rocha 1996, Monte et al. in press).

A new cave species of *Iandumoema* is herein described, being the second troglobitic harvestman with no eyes for Brazil (the first being the Gonyleptidae *Giupponia chagasi* Perez and Kury 2002, from Serra do Ramalho karst area, Bahia state, northeastern Brazil). This record corroborates the hypothesis of an exclusively troglobitic genus.

Study area

Iandumoema smeagol sp. n. is recorded from two caves from Monjolos region, Minas Gerais State, Brazil. This region is located in the central east part of the southern portion of the São Francisco Craton, Velhas river basin, with a mean altitude of approximately 600 meters, inserted in the Sete Lagoas Formation, Bambuí Group, which has a relief typical of karst carbonate regions (Stávale 2012, Guimarães 2012) (Figure 1a). Monjolos region is characterized by evident karst relief, marked by large limestone cliffs, karrens, dolines, sinks, and resurgences, representing the exokarst (Figure 1b), and subterranean watercourses, diverse speleothems and caves, representing the endokarst (Guimarães 2012). According to the Köppen-Geiger climatic classification, the region has a tropical climate with a dry season (Kottek et al. 2006) type Aw (Sá Junior et al. 2012), with mean annual temperatures ranging between 20 and 21 °C. The vegetation is dominated by plants of the 'cerrado' *sensu strictu*, cerrado fields, and seasonal forests (Guimarães 2012). However, the vegetation surrounding the cave is under anthropogenic actions, such as pasture and agricultural activities.



Figure I. a map of the study area at Monjolos municipality, Minas Gerais state, Brazil **b** Karst relief of Monjolos regions **c** entrance of Toca do Geraldo cave, a limestone cave of Bambuí Geomorphological Unit.

Toca do Geraldo is a limestone cave which extends approximately 1.5 km, with one entrance in a crack (Figure 1c) and another in the ceiling and a subterranean stream, which extends at least 400 meters. The harvestmen were found on the wet walls and sometimes in the silt substrate, next to the drainage, always in the aphotic zone. This cave has guano piles and litter as main food source for other cave arthropods such as crickets, cockroaches, mites, etc. Because the perennial drainage, the humidity is high (higher than 70%), even during the dry season. Lapa do Santo Antonio is also a limestone cave *ca.* 4.6 km far from Toca do Geraldo and also possess a subterranean stream; however, is an impacted cave due uncontrolled visitation. This cave has *ca.* of 300 m of extension.

Methods

The type material were collected, fixed in 70% ethanol and examined under a stereomicroscope. Live specimens were collected to observe the coloration *in vivo*. We took photographs and length measurements using a Leica stereomicroscope (M205C). Methods and terminology follow Acosta et al. (2007). The pattern of the macrosetae of the penis follows Kury and Villarreal (2015). Coloration is based on specimens immersed in ethanol and living specimens. Abbreviations used in Table 2 are: Tr = trochanter; Fe = femur; Pt = patella; Ti = tibia; Mt = metatarsus; Ta = tarsus. All measurements are in millimeters. The types are deposited in the Museu de Zoologia, Universidade de São Paulo, São Paulo (MZUSP) and Laboratório de Estudos Subterrâneos, Universidade Federal de São Carlos, São Carlos (LES/UFSCAR).

In the natural habitat, through *ad libitum* method (Altmann 1974), the behavior and spatial distribution were observed. On four occasions, the minimal abundance through visual census method (Krebs 1999) was recorded, covering an extension of 300 m. Measurements of temperature and air humidity were recorded through a thermo-hygrometer.

Results

Key for the male of Iandumoema

1	Apophysis of coxa IV directed obliquely backwards (parallel to body main
	axis)2
_	Apophysis of coxa IV directed laterally (perpendicular to body main axis) I. unit
2	Dorsal scutum areas with conspicuous tubercles (paramedian pair higher than
	wide), retrolateral trochanter IV with larger tubercle on apex <i>I. smeagol</i> sp. n.
_	Dorsal scutum areas with low tubercle (as heigh as wide), retrolateral tro-
	chanter IV without larger tubercle on apex I. setimapocu

http://zoobank.org/AAFD82A9-FA5B-4A71-958A-1150951CB142 Figures 2–13

Type material. Male holotype, Brazil, Minas Gerais, Monjolos, Toca do Geraldo cave, S18°16'43.31", W44°06'10.96', 08.VII.2014, R. Fonseca-Ferreira, M.E. Bichuette, I. Arnone and J.E. Gallão leg. (MZUSP 67946). Paratypes: same locality of holotype, 22.II.2014, Rafael Fonseca-Ferreira and B.G.O. do Monte leg., one male (LES/UF-SCar 0006298); Brazil, Minas Gerais, Lapa do Santo Antônio cave, S18°19'07,65", W44°07'03.32', 21.II.2014, Rafael Fonseca-Ferreira and B.G.O. do Monte leg., one female (LES/UFSCar 0006299); same locality of holotype, 22.II.2014, Rafael Fonseca-Ferreira and B.G.O. do Monte leg., Since ferreira and B.G.O. do Monte leg., one female (LES/UFSCar 0006299); same locality of holotype, 22.II.2014, Rafael Fonseca-Ferreira and B.G.O. do Monte leg., Since ferreira and B.G.O. do Monte leg., Sinc



Figure 2. Drawing of Iandumoema smeagol sp. n. Male (holotype): habitus, dorsal view showing tubercles.

Etymology. The specific epithet refers to the hobbit named Smeagol, created by J.R.R. Tolkien, being the original name of Gollum – the dweller of the caves located below the Misty Mountains of Middle-earth of the Lord of the Rings book.

Diagnosis. *Iandumoema smeagol* sp. n. can be distinguished from other *Iandumoema* species by the following exclusive characteristics: dorsal scutum areas with conspicuous tubercles (paramedian pair much higher than wide), enlarged retrolateral spiniform tubercle on the distal third of femur IV, eyes absent and the penial ventral process slender and of approximately the same length as the stylus – and by the combination of the following characters: four pairs of macrosetae on penial basal group A+B (six in *I. uai*), three or four pairs of macrosetae on penial distal group C (six pairs in *I. uai*); and the apex of the penial truncus narrower than ventral plate basal width (wider in *I. uai*), and the setae of male pedipalpal tibia ectally and mesally with IiIi (ectally with IiIi and mesally with IiIi in *I. setimapocu*). A more detailed comparison of morphological and meristic features of *Iandumoema* species are provided in Table 1.

Description. Male: Dorsum (Figures 2, 3, 4): Measurements (paratype MZSP-67947): Dorsal scutum length 3.6; prosoma length 1.7; prosoma width 2.1; opisthosoma maximum width 3.1. Measurements of legs provided in Table 2. Frontal hump with five tubercles (paramedian pair largest), anterior margin of dorsal scutum with 4–5 tubercles on each side. Ocularium without eyes; with high upwardly directed spine, apex curved backwards. Each side of ocularium with 2-3 tubercles. Prosoma with 10 tubercles posterior to ocularium. Scutal area I divided, with three tubercles on each side; scutal area II with one transversal row of 6-7 tubercles; scutal areas III–IV each with seven tubercles, paramedian pair largest and pointed on all areas. Lateral margin of dorsal scutum with an external row of 21–24 tubercles from sulci I–IV and an internal one with 14–16 tubercles from sulci I–II. Posterior margin of dorsal scutum with 14 tubercles. Free tergite I with 11 tubercles; II with 12; III with 10 (three median larger). Anal operculum with an anterior row of seven tubercles and posterior part irregularly tuberculate.

Venter (Figure 5): Coxa I with one median row of five anterior tubercles and four posterior tubercles; coxa II with 11 tubercles; coxa III with seven tubercles; coxa IV and stigmatic area irregularly tuberculate. Posterior margin of stigmatic area, free sternites, and anal opercle each with one row of tubercles.

Chelicera: Segment I elongated, bulla poorly defined, with four tubercles. Fixed finger with four equally sized teeth on the edge; movable finger with five teeth.

Pedipalps (Figure 6): Slightly elongated. Coxa smooth. Trochanter with two dorsal and two ventral (ventro-mesal largest) tubercles. Femur with one ventro-basal large followed by three small tubercles. Patella smooth; tibial and tarsal spination: ectal and mesal IiIi.

Legs (Figures 7, 8, 9, Table 2): Coxa I with two stout tubercles; II with one stout anterior tubercle, one median small and one stout posterior; III with two stout tubercles, one anterior fused with the posterior tubercle of coxa II and one posterior IV with scattered tubercles and with dorso-apical, slightly sigmoid, backwards-directed apophysis, with one retrolateral apical long apophysis (4× longer than wide). Trochanter I with two dorsal, one retrolateral and three ventral tubercles; II with four dorsal, two prolateral, one retrolateral and three ventral tubercles; III smooth dorsally, with three

retrolateral and six ventral tubercles; IV dorsally smooth, with large basal prolateral submedian apophysis bearing one tubercle, and with four retrolateral (apical largest), and 12 small ventral tubercles. Femur–tibia III with small tubercles.

Femur IV straight, with two rows of irregular dorsal tubercles, two ventral rows of higher than others of same segment (twice as long as wide) tubercles on apex, one retrolateral row of irregular-sized tubercles, larger than other of same segment (third apical one largest), two enlarged dorso-apical tubercles (one prodorsal and one median). Patella IV with two ventral rows of tubercles, tuberculate on the sides, dorsally unarmed. Tibia IV with two rows of ventral tubercles of similar sizes. Basitarsus I of similar size as distitarsus. Tarsal segmentation: 6(3), 11(3), 6, 6.

Characters	<i>I. uai</i> Pinto-da- Rocha, 1996	<i>I. setimapocu</i> Hara & Pinto-da-Rocha, 2008	<i>I. smeagol</i> sp. n.	
Eyes condition	At least twice the diameter of tubercles on carapace	Same or similar size of diameter of tubercles on carapace	Absent	
Setae on male pedipalpal tibia	Ectally and mesally with IiIi	Ectally with IiiIi and mesally with IiIi	Ectally and mesally with IiIi	
Direction of dorso-apical apophysis on male coxa IV	Backwards and laterally	Obliquely backwards, close to body	Obliquely backwards, close to body	
Submedian prolateral apophysis on male trochanter IV	Absent	Present	Present	
Large tubercles on dorsal male femur apex	Two (one prolaterally, the other retrolaterally)	Three (two as in <i>I. uai</i> , plus a large median one)	Two (one prodorsal and one median)	
Number of pair of macrosetae on penial basal group (A+B)	6	4	4	
Number of pairs of macrosetae on penial distal group (C)	3	4	3–4	
Shape of penial ventral process	Short and serrate	Short and serrate	Slender and approx. same length as stylus, not serrate	
Apex of penial truncus	Wider than ventral plate basal width	Narrower than ventral plate basal width	Narrower than ventral plate basal width	

Table 1. Comparative morphological and meristic data for the three *Iandumoema* species from Brazilian caves (adapted from Hara and Pinto-da-Rocha 2008).

Table 2. *Iandumoema smeagol* sp. n., measurements (in mm) of appendages of male paratype (MZUSP 67947) and female paratype (LES/UFSCar 0006299; in parentheses).

	Tr	Fe	Pt	Ti	Mt	Ta	Total
Leg I	0.3 (0.4)	3.9 (3.0)	1.1 (0.8)	2.9 (2.1)	4.8 (3.5)	2.5 (2.1)	15.5 (11.9)
Leg II	0.5 (0.3)	8.1 (5.3)	1.5 (1.3)	6.8 (5.1)	9.2 (6.1)	6.9 (5.2)	25.7 (23.3)
Leg III	0.6 (0.3)	5.4 (3.9)	1.3 (0.8)	3.1 (2.2)	5.5 (4.1)	2.3 (1.5)	18.2 (12.8)
Leg IV	1.1 (0.5)	6.9 (5.5)	2.0 (1.5)	5.2 (3.8)	7.4 (6.1)	2.2 (2.3)	24.8 (19.7)
Pedipalp	0.6 (0.4)	2.1 (1.5)	0.9 (0.8)	1.6 (1.1)		1.1 (0.9)	6.3 (4.7)



Figure 3. Photography of Iandumoema smeagol sp. n. Male (holotype): habitus, dorsal view.



Figure 4. Iandumoema smeagol sp. n. Male (holotype): habitus, right lateral view.



Figure 5. Iandumoema smeagol sp. n. Male (holotype): habitus, ventral view.



Figure 6. Iandumoema smeagol sp. n. Male (holotype): right pedipalp, ventral view.



Figure 7. Iandumoema smeagol sp. n. Male (holotype): right trochanter IV, dorsal view.



Figure 8. Iandumoema smeagol sp. n. Male (holotype): right leg IV, dorsal view.



Figure 9. Iandumoema smeagol sp. n. Male (holotype): right leg IV, ventral view.

Penis (paratype MZSP-67947, Figures 10, 11): Ventral plate subrectangular, with distal margin straight and a slight median constriction on the sides. Macrosetae: distal group with 3-4 on each side (C1–C4), basal one (C4, absent in the right) half-length of other three distal setae (similar sized, curved apically); median pair of setae (D1) placed more internally than groups A–C; basal group in arch (lateral view), formed by A1–3 and B1 (ventralmost), similar in length. Glans sac enlarged in the middle, stylus long and thicker than ventral process shaft; ventral process of glans without serrate distal margin, slender than and as long as stylus; both stylus and ventral process with ventromedian small microsetae.

Coloration (Figures 3, 12). Ethanol: Pale yellowish carapace with tip of tarsus and dorsal tibia whitish (Figure 3). Live specimens show a carapace with lighter coloration compared to the same part in the preserved specimen (Figure 12).

Female (paratype, LES/UFSCar 0006299, Figure 13): Measurements: Dorsal scutum length 3.1; prosoma length 1.2; prosoma width 1.8; opisthosoma maximum width 2.4. Measurements of appendages are presented in Table 2. Only characteristics different from those of males are mentioned. Anterior margin of dorsal scutum with six tubercles on each side. Scutal area I with 3–5 tubercles on each side; scutal area II with eight; scutal area III with seven; scutal area IV with seven tubercles. Posterior margin of dorsal scutum with 13 tubercles. Free tergite I with 17; II with 17; III with 11 tubercles.



Figure 10. Iandumoema smeagol sp. n. Male (paratype, MZUSP 67947): distal part of penis, dorsal view.

Coxa IV with a shorter prolateral apophysis (half as long) than in male; trochanter IV with basal and median apophyses half as long or less than in male; tubercles on legs smaller than in male; femur IV with two enlarged dorso-apical tubercles.

Relationships. *Iandumoema smeagol* sp. n. seems to be close related to *I. setimapocu* based on number of macrosetae on penis, four pairs on group A+B (six in *I. uai*) and apex of truncus narrower than ventral plate basal width. The shape of male apophysis on coxa IV is similar in both species, being obliquely directed, as also the presence of a submedian prolateral apophysis on male trochanter IV. However, a cladistics analysis is necessary to reveal well-supported relationships among *Iandumoema* species.

Distribution and natural history. The occurrence of *Iandumoema smeagol* sp. n. in the limestone caves of Bambuí Group, more specifically in the boundaries of



Figure 11. Iandumoema smeagol sp. n. Male (paratype, MZUSP 67947): distal part of penis, left lateral view.

Serra do Espinhaço Plateau (Figure 1) shows that this region must be the eastern boundary distribution of the genus, the quartzite and the high altitudes of Serra do Espinhaço being the possible barriers. The results show that the genus *Iandumoema* only occurs in the northern Minas Gerais state, occupying an area of *ca.* 8,000 km², and is restricted to hypogean environments, being exclusive to caves. This distribution range corroborates those presented by Hara and Pinto-da-Rocha (2008). Most specimens were collected in the aphotic zone of Toca do Geraldo cave; and only one individual was recorded in the Lapa do Santo Antônio cave. The minimum distribution range for *Iandumoema smeagol* sp. n. (or occurrence area) is of 4.6 km². The specimen collected in the Lapa do Santo Antônio cave was on the rocky substrate, at the twilight zone and close to the entrance (less than 50 m away). In four visits



Figure 12. *Iandumoema smeagol* sp. n. Live male specimen foraging in its natural habitat, showing detail of the pale yellowish coloration.

at Toca do Geraldo, the opilionids were observed on the walls (rocky substrate) and few on the silt substrate, always close to water bodies (drainage or pools). Despite the observed guano piles (of hematophagous bats), not one individual was observed close to them. The adults show solitary habits; on one occasion, one individual was feeding in litter, apparently scavenging carcasses of invertebrates (Figure 12). In two occasions, active juveniles were observed on the walls while the adults showed a behavior comparatively more sedentary. In the four occasions, a total of 14 individuals were observed including adults and juveniles, always close to the cave stream, showing a low abundance. Apparently, the cave does not have dry galleries and/or conduits, showing high relative humidity of the air (*ca.* 80%) and temperature amplitude between 22 and 24 °C.

Troglomorphisms and conservation remarks. As a result of their faunistic singularities and high endemism, hypogean environments are considered fragile. Besides their unique faunistic composition, the singularity of cave habitats is related to the presence of relicts, many times represented by troglobitic species. Gallão and Bichuette (2015) observed this tendency in a small area (24 km²) located at Chapada Diamantina, northeastern Brazil (at least 23 troglobitic species, most of them relict ones). Troglobitic species have unique sets of autapomorphies, such as eyes



Figure 13. Iandumoema smeagol sp. n. Female (paratype, LES/UFSCar 6299): habitus, dorsal view.

and melanistic pigmentation reductions allied to other troglomorphisms, such as pedipalps elongation in opilionids and other arachnids. A possible endemism in a karst area, which is threatened, was observed for *Iandumoema smeagol* sp. n. in addition to the accentuated autapomorphies. Projects for the installation of small hydroelectric dams and limestone extraction for cement production represent potential impacts on the immediate environment (M. E. Bichuette and R. Fonseca-Ferreira, pers. obs.). Moreover, the extent of occurrence area of the species (4.6 km²) allied to the deforestation in the cave surroundings must place this species in a threatened category considering the IUCN criteria (Vulnerable, VU or Endangered, EN). Long-term studies focusing population biology and distribution of *I. smeagol* sp. n. are urgent and fundamental to establish an effective conservation policy, including the creation of protected area(s).

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RESEARCH ARTICLE



Redescription of "Nesticus" citrinus (Taczanowski, 1874) (Araneae, Araneoidea) from French Guyana

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Abstract

"*Nesticus*" *citrinus*, a species originally placed in *Theridion* is redescribed based on the syntype series composed by 7 females and a lectotype is designated. All syntypes have broken emboli in their epigynes. Taxonomic position of "*Nesticus*" *citrinus* is briefly discussed and its belonging to Nesticidae is doubted.

Keywords

Broken-off embolus, Nesticidae, spider, Theridiidae

Introduction

Theridion citrinum was described based on several females from Uassa in French Guyana. Original description is rather brief and lacks any drawings and comments on the epigyne. Ten years later Keyserling (1884) redescribed this species based on syntype specimens. He provided a detailed description, including leg measurements and figures of habitus and epigyne. Since then this species was only treated in two papers: by Petrunkevitch (1911) and Levi (1963). Petrunkevitch (1911) just mentioned this species in combination with currently valid genus name *Theridion*. Levi (1963) in his revision of the New World *Theridion*, transferred *T. citrinum* to *Nesticus*, but no arguments for this transfer were provided.

While working with collections in the Zoological Museum of the University of Turku we came upon a jar with the syntypes series of *Theridion citrinum*, that seems to have been borrowed for the revision of Nesticidae by Lehtinen and Saaristo (1980). At first glance this species looks very different from any other Nesticidae known to us, in having a whitish abdomen formed with guanine spots and lacking a comb on tarsi IV. Search of literature proved the existence of some "*Nesticus*" with white abdomen and well developed pattern in South America (Ott and Lise 2002). In addition the syntype females have a large and straight palpal claw (Fig. 3), typical for Nesticidae and lacking in Theridiidae. Examination of the epigyne reveals its unusual shape. The epigynes of three females have two thread-like arches extended over epigynal plate in the anterior part, just like it was illustrated by Keyserling (1884) and one female has one such arch. Dissection of the epigyne and its maceration showed that these arches are break-off tip of emboli.

Material and methods

Photographs were taken using an Olympus SZX16 stereomicroscope with an Olympus E-520 camera and prepared using CombineZP software at the Zoological Museum of the University of Turku. The epigynes were dissected and macerated in 20% potassium hydroxide aqueous solution and exposed for a few minutes in an alcohol/water solution of Chlorazol Black. Length of leg segments were measured from the dorsal side. All measurements are given in millimeters.

Taxonomy

"Nesticus" citrinus (Taczanowski, 1874) Figs 1–8

Theridium citrinum: Taczanowski 1874: 57 (♀). *Theridium citrinum*: Keyserling 1884: 86, pl. 4, f. 54 (♀). *Nesticus citrinus*: Levi 1963: 490 (transfer of species without argumentations).

Types. 7 ⁽²⁾ "Uassa-Guyane français, leg. K.Yeliki, det. H.T. Taczanowski" from Zoological Museum, Polish Academy of Sciences. Lectotype \mathcal{P} designated here, paralectotypes $3\mathcal{P}$ and 3 juv. Most likely one syntype was taken by Keyserling (1884) who mentioned 8 specimens. Specimens were dried out and original colouration in alcohol can not be described.

Note. Uassa was not located on current and old maps of the region.



Figures 1–8. Female of *Nesticus citrinus.* **1** habitus, lateral **2** abdomen, ventral **3** palpal tarsus and chelicera **4** epigyne with one broken embolus, ventral **5** epigyne with 2 broken emboli, ventral **6** epigyne, posterior **7** epigyne after maceration, dorsal **8** receptacle with complex tip of embolus inside, dorsal. Abbreviations: *Be* broken-off terminal part of embolus, *Co* copulatory openings, *Ct* complex tip of embolus, *Id* insemination ducts, *Re* receptacle, *Rp* round pit of epigynal plate.

Description. *Female.* Total length 3.45. Carapace length 1.6, width 1.13. According to Keyserling (1884) prosoma and appendages yellow. Tarsi of leg I–II with dark tips (Fig. 1). Abdomen covered with white guanine spots lacking only in front of spinnerets (Figs 1–2). Palpal tarsi with large almost straight pectinate claws (Fig. 3).

Leg measurements

	Femur	Patella	Tibia	Metatarsus	Tarsus	Total
Ι	2.03	0.75	1.83	2.03	0.85	7.49
II	2.35	0.80	1.75	2.03	0.88	7.81
III	1.50	0.53	1.00	1.20	0.55	4.78
IV	2.03	0.63	1.50	1.73	0.63	6.52

Epigyne as in Figs 4–8, large, extending epigastral fold, strongly swollen, wider than long, width subequal to 1/2 of abdomen width. Epigynal plate surrounded with long transparent hairs, its anterior edge more sclerotized than another parts. Epigynal plate with pair of round weakly sclerotized copulatory openings (*Co*), and two round pits (*Rp*) on lateral sides of the plate. Diameter of round pits more than 2 times larger than those of the copulatory openings. Copulatory openings lead to relatively short (about half of plate's width) insemination ducts (*Id*). Receptacles (*Re*) very large, egg-shaped.

Comments. All syntype females have one or two tips of embolus left (*Be*) in the epigyne (Figs 4–8). Shape and size of broken tip of emboli are the same in all observed specimens, which indicates that the embolus has a certain break-off point. The embolus penetrates not only into the insemination duct but also into the receptacle (Figs 7–8). The embolus tip (*Ct*), is quite complex and it is wider than rest of the broken part of the embolus.

Conformation of both the epigyne and tip of the embolus is unknown in other Nesticidae. This may indicate that "*Nesticus*" *citrinus* does not belong in *Nesticus* and most probably does not belong in the family Nesticidae as well.

Broken-off tip of embolus is known to occur in several families and superfamilies of spiders included in Araneoidea: Theridiidae and Linyphiidae (Wiehle 1967). "*Nesticus*" *citrinus* can not be placed in Linyphiidae due to lack of a median plate of the epigyne, and in having distinct copulatory ducts, lacking in Linyphiidae. It can neither be placed in any known Theridiidae genera, due to straight palpal claw. Bent palpal claw is known to occur in Hadrotarsinae, but it is rather short and not straight. In addition Hadrotarsinae have modified prosoma with very high clypeus, and habitually are very different from "*Nesticus*" *citrinus*.

Even though placement in *Nesticus* is somewhat doubtful, we believed it is better that it remains in *Nesticus* for now, until new specimens or a male is discovered, that could shed some light on a very mysterious spider.

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RESEARCH ARTICLE



A new species of *Pseudomegischus* van Achterberg from China, with a key to the species (Hymenoptera, Stephanidae)

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Abstract

The genus *Pseudomegischus* van Achterberg, 2002, is newly reported from China. A new species, *P. noti-ochinensis* **sp. n.**, is described and illustrated from southern China. A key to the species of *Pseudomegischus* is included.

Keywords

Pseudomegischus, new species, new record, southern China, Jiangxi, key

Introduction

The small genus *Pseudomegischus* van Achterberg, 2002 (Hymenoptera: Stephanidae) has an Indo-Australian distribution and contains four described species. The species were revised by van Achterberg (2002) and the nearest known locality of the genus (compared to China) is the southern Philippine island of Mindanao. Recently, one of us (TL) reared a series obviously belonging to a new species of *Pseudomegischus*. It is the first host record of a species of this genus and the first species known from the Asian continent. There are several host records of Stephanidae, mainly of the genus *Foenatopus*

Smith, 1860 (Aguiar 2004, Aguiar et al. 2010) and mainly concerning Buprestidae and Cerambycidae (Coleoptera). In China Stephanidae has been reported from Buprestidae by Chao (1964) (*Megischus ptosimae* Chao, 1964, reared from *Ptosima chinensis* Marseul, 1867 in peach trees) and Tan et al. (2015) (*Schlettererius determinatoris* Madl, 1991, reared from *Chrysobothris succedana* (Saunders) in *Larix* sp.). Van Achterberg and Yang (2004) reported ovipositing in Buprestid and Cerambycid larvae in various trees by *Megischus tridentatus* van Achterberg & Yang, 2004. The only case of biological control involving Stephanidae is the Nearctic *Schlettererius cinctipes* (Cresson, 1880) introduced to Tasmania from California for control of the introduced *Sirex noctilio* (Fabricius, 1793) (Hymenoptera: Siricidae; Taylor 1967; van Achterberg 2002).

Material and methods

The specimens studied of *Pseudomegischus* spp. belong to the collection of the Insect Museum of the General Station of Forest Pest Management, Shenyang (GSFPM), P.R. China, some paratypes are deposited in the insect collection of the Northwest University, Xi'an (NWUX), P.R. China, and the Naturalis Biodiversity Center, Leiden (RMNH), the Netherlands.

The morphological terminology follows van Achterberg (2002) and a key to the genera is present in this paper and in Hong et al. (2011). Observations and descriptions were made with an Olympus SZX11 stereomicroscope and fluorescent lamps. Photographic images were made with the Keyence VHX-5000 digital microscope and processed with Adobe Photoshop CS5.

Taxonomy

Pseudomegischus van Achterberg, 2002

Figs 1-13

Pseudomegischus van Achterberg, 2002: 169; Aguiar 2004: 73–74 (list of literature); Hong et al. 2011: 7. Type species (by original designation): *Stephanus sulcifrons* Schletterer, 1889.

Diagnosis. Temple with pale yellowish streak (Fig. 5); vertex anteriorly and stemmaticum (= ocellar area) with shallow median groove (Figs 10–11); pronotum with weak or strong transverse protuberance (Fig. 3); neck with two strong converging carinae laterally and antero-medially with triangular protuberance (Fig. 6); vein 1-M of fore wing $3.1-4.8 \times$ vein 1-SR; vein 1-SR of fore wing straight (Fig. 4); hind tibia with small round pit at top of depression; outer side of hind tibia with oblique striae or carinae (Fig. 7); hind femur with two large teeth (Fig. 7); pygidial process in both sexes present (Fig. 13); ovipositor sheath without ivory subapical band (Fig. 1).

Distribution. Indo-Australian.

Biology. Presumably ectoparasitoid of Cerambycidae and/or Siricidae.

Key to species of the genus Pseudomegischus

1 Hind basitarsus ivory or pale yellowish or light brown, distinctly contrasting with dark brown middle of hind tibia (fig. 603 in van Achterberg 2002); hind Hind basitarsus yellowish-brown to dark reddish-brown, less contrasting with blackish middle of hind tibia (Fig. 7; figs 255, 265 in van Achterberg 2002); hind tibia mainly smooth, at most with some obsolescent striae dor-First submarginal cell of fore wing ends near level of apex of pterostigma; 2 head infuscate dorsally; pale yellowish streak behind eye distinct (fig. 607 in van Achterberg 2002); vein 2-SR of fore wing about 1.2 × as long as vein r; median carina of neck distinct (fig. 609 l.c.); mesopleuron only anteromedially coarsely reticulate, remainder largely smooth; Philippines..... First submarginal cell of fore wing ends distinctly beyond level of apex of pterostigma (fig. 604 in van Achterberg 2002); head dark yellowish-brown dorsally; pale yellowish streak behind eye indistinct (fig. 600 l.c.); vein 2-SR of fore wing about $1.4 \times as$ long as vein r (fig. 604 l.c.); median carina of neck largely absent (fig. 601 l.c.); mesopleuron medially coarsely remotely punctate; Indonesia (Mysol)P. insidiator (Smith, 1863) 3 Vein 1-M of fore wing 4.8–5.4 × as long as vein 1-SR (fig. 261 in van Achterberg 2002); hind femur with distinct third medium-sized tooth behind large apical tooth (fig. 265 l.c.); hind basitarsus more or less infuscate dark reddishbrown, dark brown or largely blackish-brown, not distinctly contrasting with blackish hind tibia (fig. 265 l.c.); pale streak of temple rather differentiated (fig. 261 l.c.); length of ovipositor sheath about 2.1 × fore wing; Philippines, Malaysia (Sabah)...... P. sulcifrons (Schletterer, 1889) Vein 1-M of fore wing about 3 × as long as vein 1-SR (Fig. 4; fig. 257 in van Achterberg 2002); hind femur without distinct third medium-sized tooth behind large apical tooth, at most with undefined protuberance (Fig. 7; fig. 254 l.c.); hind basitarsus orange-brown, rather contrasting with blackish hind tibia (fig. 254 l.c., but less so in P. notiochinensis (Fig. 7) or basitarsus and tibia similarly coloured); pale streak of temple not well differentiated (fig. 252 l.c., but distinct in *P. notiochinensis*; Fig. 5); length of ovipositor sheath about 4 Head pale yellowish brown and without distinctly differentiated ivory streak of temple but dorsally and anteriorly darkened (figs 252-253 in van Achterberg 2002); propodeum medio-dorsally coarsely rugose (fig. 256 l.c.); fore wing membrane evenly brownish, but becoming paler apically (fig. 257 l.c.);

Pseudomegischus notiochinensis Tan & van Achterberg, sp. n.

http://zoobank.org/E51424F8-202F-49B6-B4EC-C8659C8E3AF8 Figures 1–13

Type material. Holotype, \bigcirc (GSFPM): "**China**: Jiangxi, Quannan, 8.v.2009, Shichang Li, [reared from branches of] *Castanopsis kawakamii* Hay.". Paratypes: $3 \bigcirc 8 \bigcirc$ (NWUX, RMNH, GSFPM): same data except collecting date 4, 10, 12 or 18.v.2009, and from *Castanopsis kawakamii* Hay. or *C. faberi* Hance.

Diagnosis. Head in dorsal view parallel-sided behind eyes (Fig. 10); posterior half of pronotum comparatively low and dorso-posteriorly finely transversely rugose (Fig. 6); first subdiscal cell of fore wing comparatively robust and 2.5–2.9 × longer than wide (Fig. 4); hind coxa with strong and sparse rugae, and without dorsal tooth (Fig. 8); first-third metasomal tergites black or dark brown (Fig. 1); first metasomal segment narrow in lateral view (Figs 1, 2); first tergite 6.0–7.6 × ($\bigcirc \bigcirc$) as long as its maximum width and irregularly coarsely transversely rugose (Figs 3, 12).

The new species runs to *P. celebensis* van Achterberg in the key in van Achterberg (2002), but differs by having the head mainly dark brown (much paler in *P. celebensis*), the propodeum regularly scrobiculate (partly rugose), the mesopleuron with large smooth interspaces between medium-sized to small punctures (with larger punctures and narrower interspaces) and the ivory streak of the temple distinct (obsolescent).

Description. Holotype, female, length of body 16.7 mm, and of fore wing 8.9 mm.

Head. Antenna with 39 segments; frons coarsely obliquely rugose; three anterior coronal teeth large and acute, both posterior ones arcuate and lamelliform, with two small lobe-shaped carinae on each side in front of both posterior ocelli; behind level of coronal area having four curved, progressively smaller carinae followed by rugose area, rugae rather coarse, posteriorly narrowly reaching occipital carina and widely smooth laterally; temple non-angulate (Fig. 10), punctulate but largely smooth and shiny.

Mesosoma. Neck short and robust, transversely rugose, neck at much lower level than middle part of pronotum (Figs 5, 6); middle part of pronotum largely smooth and without a distinct carina posteriorly; propleuron with sparse large punctures, shiny and rather densely setose; mesonotum irregularly foveolate and area between smooth;



Figures 1–3. *Pseudomegischus notiochinensis* Tan & van Achterberg, sp. n. l holotype, female, habitus lateral 2 paratype, male, habitus lateral 3 first metasomal tergite (T1) of male dorsal.

notauli and median groove distinct; scutellum with some coarse punctures medially, foveolate laterally; axillae coarsely punctate; mesopleuron distinctly convex, convex part foveolate-punctate and covered with long whitish setae, medially convex part of metapleuron rugose and with long whitish setae, anteriorly crenulate and intermediate area smooth; propodeum densely irregularly rugose (Fig. 6).

Wings. Fore wing (Fig. 4): vein 1-M $3.0 \times$ as long as vein 1-SR and curved; vein r ends slightly before level of apex of pterostigma; first subdiscal cell robust, $2.9 \times$ as long as its maximum width, vein cu-a entirely pigmented.



Figures 4–13. *Pseudomegischus notiochinensis* Tan & van Achterberg, sp. n., female, holotype. 4 wings 5 mesosoma lateral 6 mesosoma dorsal 7 hind leg lateral 8 hind coxa dorsal 9 hind tibia inner side 10 head dorsal 11 head anterior 12 first metasomal tergite dorsal 13 apical metasomal segments, showing pygidial process.
Legs. Hind coxa robust, without tubercle dorsally and with strong and sparse rugae (Figs 7, 8); hind femur widened, sparsely punctate and with whitish setae ventrally and dark brown setae dorsally, area in between punctures smooth and shiny, ventrally with 2 large acute teeth (the anterior one smaller than posterior one) and several denticles in between (Fig. 7); hind tibia $1.1 \times as$ long as hind femur, basal narrow part of hind tibia about $1.2 \times as$ long as widened part, widened part ventrally distinctly obliquely carinate (Fig. 7); hind basitarsus subparallel-sided, length of hind basitarsus $5.3 \times as$ long as wide medially and $3.6 \times as$ long as second tarsal segment (Fig. 7).

Metasoma. First tergite $6.0 \times$ as long as its maximum width (Fig. 12), $1.4 \times$ as long as second tergite, cylindrical, largely smooth except irregular rugae basally and some oblique aciculation after middle of tergite; remainder of tergites smooth and shiny; setose part of ovipositor sheath $1.1 \times$ as long as body and $2.3 \times$ as long as fore wing.

Colour. Black or blackish brown; tegula and palpi dark brown; scapus, pedicellus, malar space, mandible and patch near basal quarter of hind tibia partly brown; base of femora and of fore and middle tibiae and tarsi pale yellowish brown; remainder of fore and middle tibiae brown; veins and pterostigma largely dark brown, but base of pterostigma ivory; wing membrane slightly brownish but fore wing darkened near vein r and below parastigma; ovipositor sheath blackish apically (Fig. 1).

Male. Similar to female, but in most cases much smaller (Figs 2, 3).

Variation. Length of body of \bigcirc 15–19 mm, of \bigcirc 8–16 mm; length of fore wing of \bigcirc 8–11 mm, of \bigcirc 5–9 mm; antenna of \bigcirc with 38(1), 39(1), 42(1) or 47(1) segments, of \bigcirc with 28(2), 29(1), 31(1), 32(2) and 36(2) segments; first metasomal tergite entirely transversely striate or rugose to largely smooth and only basally rugose; hind basitarsus dark brown as hind tibia or brown and paler than hind tibia; length of ovipositor sheath 2.3–2.5 × fore wing.

Distribution. Oriental: China (Jiangxi).

Biology. Reared from stems of *Castanopsis kawakamii* Hay. and *C. faberi* Hance infested by Cerambycidae and Siricidae.

Etymology. Named after the area of origin, "notios" being Greek for "southern".

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RESEARCH ARTICLE



Revision of the West Indian *Wattius* Kaszab (Tenebrionidae, Toxicini, Eudysantina) with lectotype designations for Pascoe's South American species

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Abstract

The Wattius species occurring in the West Indies are revised for the first time. Wattius cucullatus (Pascoe), previously reported from Cuba, is diagnosed and restricted to Brazil. Wattius asperulus (Pascoe), currently a synonym of W. cucullatus, from Colombia is diagnosed and resurrected. All species found in the West Indies are endemic to the islands and form a single informal species-group. Three species are described: Wattius andersoni sp. n. from Cuba, Wattius emmabaconae sp. n. from Hispaniola (Dominican Republic), and Wattius viatorus sp. n. from Cuba and the Bahamas, and lectotypes are designated for Calymmus cucullatus Pascoe and Calymmus asperulus Pascoe. A key to the West Indian species is provided.

Resumen

Las especies de *Wattius* que ocurren en las Indias Occidentales se revisan por primera vez. *Wattius cucullatus* (Pascoe), que se había registrado de Cuba, se diagnostica y se limita a Brasil. *Wattius asperulus* (Pascoe), actualmente sinónimo de *W. cucullatus*, se diagnostica y **es restaurado**, habitando en Colombia. Todas las especies que se encuentran en las Indias Occidentales son endémicas de las islas y forman un solo grupo informal de especies. Se describen tres especies: *Wattius andersoni* **sp. n.** de Cuba, *Wattius emmabaconae* **sp. n.** de Hispaniola (República Dominicana) y *Wattius viatorus* **sp. n.** de Cuba y las Bahamas. Se designan los lectotipos para *Calymmus cucullatus* Pascoe y *Calymmus asperulus* Pascoe. Se proporciona una clave de identificación para las especies que habitan las Indias Occidentales.

Keywords

Darkling beetles, new species, lectotype designation, Cuba, Bahamas, Dominican Republic

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Introduction

The New World component of the tribe Toxicini currently contains three genera, *Diceroderes* Solier (1 species, plus 4 species in press), *Ozolais* Pascoe (11 species), and *Wattius* Kaszab (5 extant species, one fossil), all in the subtribe Eudysantina Bouchard, Lawrence, Davies and Newton. *Wattius* was proposed by Kaszab (1982) as a name for the New World species previously in *Calymmus* Pascoe to separate them from the New Caledonian *Calymmus berardi* (Montrouzier, 1860). Hence, *Wattius* is restricted to the Americas and includes all known Eudysantina species with a single pronotal horn. Of the New World genera, all *Ozolais* species lack pronotal horns, but several species (including *O. tuberculifera*) have one or two cephalic horns in the males; all *Diceroderes* have two pronotal horns; and all *Wattius* have a single pronotal horn that occurs in both sexes. The purpose of pronotal horns in the Eudysantina is still unclear. Label data indicates that most *Wattius* specimens have been collected by beating, under bark, or at UV lights. No specimens have been collected from fungus, with no adults present, in Jalisco, Mexico.

Two extant Toxicini species, Ozolais tuberculifera Champion, 1896 and W. cucullatus have so far been identified from the West Indies. Wattius cucullatus was recorded from Cuba (Spilman 1961, Peck 2005); however, all specimens were misidentified. Indeed, many specimens of Wattius from throughout the generic range have been mistakenly determined as W. cucullatus for over a century (Champion 1884, Cifuentes 2010), including the synonymization of Wattius asperulus (Pascoe, 1871) under W. cucullatus by Champion (1886). However, based on an examination of Pascoe's syntype (Figures 1-4) from the Natural History Museum - London and over 600 Wattius specimens from 13 collections, specimens attributable to the true W. cucullatus have only been identified from the Brazilian states of Santa Catarina and Rio de Janeiro (type locality). This species is so far unique in the genus for having rounded protuberances on the posterior surface of all femora in the males (Figure 4). Wattius asperulus (Pascoe, 1871), previously and incorrectly placed in synonymy with W. cucullatus, from Colombia is here resurrected based on an examination of the syntype (Figures 5-6). After studying all available material, three undescribed endemic species are now known to occur in the West Indies (Figure 7) and are described herein.

One fossil species, *Wattius reflexus* Doyen & Poinar, 1994, has been described from Dominican amber, and additional amber specimens potentially representing an undescribed species have been found (Smith and Poinar, unpublished data). There is still uncertainty regarding the age of Dominican amber (Grimaldi 1995, Grimaldi and Engel 2005), especially when the source mine is unknown, but *Wattius* was almost certainly present on Hispaniola somewhere between 40–15 million years ago (mya).

Materials and methods

A total of 56 West Indian *Wattius* specimens from 13 collections were examined for this study, along with ~635 non-West Indian specimens in the genus. Labels for new

type material described herein are given verbatim in quotes, with lines separated by a forward slash. Individual labels are indicated alphabetically from uppermost to bottommost label. Specimens used in this study were graciously loaned to the first author from the following collections.

AMNH American Museum of Natural History, New York, NY, USA. (Lee Herman) BMNH The Natural History Museum, London, United Kingdom. (Max Barclay) California Academy of Sciences, San Francisco, CA, USA. (Norm Penny) CASC **CUIC** Cornell University Insect Collection, Ithaca, NY, USA. (Jason Dombroskie) CMNC - Canadian Museum of Nature, Ottawa, Canada. (Bob Anderson) Essig Museum of Entomology, University of California, Berkeley, CA, USA. EMEC (Peter Oboyski) FMNH Field Museum of Natural History, Chicago, IL, USA. (Margaret Thayer) HNHM Hungarian Natural History Museum, Budapest, Hungary. (Otto Merkl) MNHN Muséum National d'Histoire Naturelle, Paris, France (Antoine Mantilleri) West Indian Beetle Fauna Project, Montana State University, Bozeman, WIBF MT, USA. (Michael Ivie) **OSUC** C. A. Triplehorn Insect Collection, Ohio State University, Columbus, Ohio, USA. (Charles A. Triplehorn) Snow Entomological Museum, University of Kansas, Lawrence, KS, USA. SEMC National Museum of Natural History, Smithsonian Institution, Washing-**USNM** ton, DC, USA. (Warren Steiner) **ZMHB** Museum für Naturkunde der Humboldt-Universität, Berlin, Germany (Bernd Jaeger)

ZSMC Zoologische Staatssammlung München, Munich, Germany (Martin Baehr)

Label data from all specimens was captured and additional specimen information, including images and determined GPS coordinates, is available online (tenebrioniD-Base.org) for many specimens.

Morphological parameters. Images of specimens and/or morphological characters and character states were taken using a BK Plus Imaging system (www.visionarydigital. com). Montaged images were assembled using Helicon Focus 5.3 (www.heliconsoft. com/) and backgrounds were cleaned in Adobe Photoshop CS6. Measurements were taken digitally using the ruler tool in Photoshop on images with known measurements based on the camera body, lens, and magnification used. Length was measured along the midline from the anterior margin of the pronotum, generally the tip of the pronotal horn, to the apex of the elytra. Width was measured across the widest point of the elytra. Color was determined under fiber optic illumination and from images. Setae are acuminate and defined as either simple (circular in cross section) or scale-like (thickened, flattened in cross section). Density of recurring features (primarily punctures, tubercles, and setae) and puncture size closely are as follows. Density: confluent (partially merged), dense (separated by between less than 1–2 feature diameters but not partially merging), moderate (separated by 2–4 feature diameters), sparse (separated by more than 4 feature diameters), or absent (impunctate, smooth, or glabrous). Puncture size: foveate

(rounded pits, diameter greater than 0.04 mm), moderate (diameter 0.03–0.04 mm), or fine (diameter less than 0.03 mm).

Wattius specimens are almost always encrusted in a waxy shellac-like exudate. The encrusting can be flaked off with a low gage pin, then wiped away with a camel hair brush. Cleaning specimens in soapy water and an ultrasonic cleaner also works but in some instances a waxy coating reformed upon drying.

Species recognition. The phylogenetic species concept of Wheeler and Platnick (2000) is employed to define a species as "the smallest aggregation of (sexual) populations or (asexual) lineages diagnosable by a unique combination of character states". This species concept is appropriate due to its emphasis on character transformations between species and the lack of available data beyond adult morphology and distribution. Species were erected based on the presence of autapomorphic morphological characters and/or a unique combination of homoplastic characters shared by all of the specimens assigned to a species. Recognized species should be considered as scientific hypotheses based on the available data and, as such, their validity can be tested as more information is gathered.

Results

The island species form a morphologically distinct group, the informal West Indian species-group, within the genus based on the lighter coloration of the antennal club (generally yellowish) compared to the other antennomeres, the glabrous and impunctate scutellum that is often relatively free of debris compared to the rest of the body, and the lack of depressions or other modifications on the frons.

Key to the West Indian species of Wattius Kaszab

1	Apterous, metaventrite length less than metacoxal cavity length; pronota
	horn reduced (Figs 8-9); mentum with weakly raised, indistinct medial lon
	gitudinal ridge; Cuba W. andersoni sp. n
_	Macropterous, metaventrite length greater than metacoxal cavity length; pro
	notal horn well developed (Figs 10-17); mentum with distinct medial longi
	tudinal ridge, projecting anteriorly; Cuba, Bahamas, Hispaniola
2(1)	Scutellum triangular (Fig. 10); frons with shallow fovea and sharp tubercles be
	tween apex of eye and clypeus; femora with raised smooth callosities; males lack
	ing apical tibial spine (Figs 4, 10–11); Hispaniola W. emmabaconae sp. n
_	Scutellum U-shaped to weakly pentagonal (Fig. 16); frons with deep fovea
	lacking sharp tubercles between apex of eye and clypeus; femora withou
	raised callosities; males with apical tibial spine on all legs; Cuba and Baha
	mas

Clave para las especies de Wattius Kaszab del Indias Occidentales

1	Áptero, longitud del metaventrito menor que la longitud de la cavidad meta-
	coxal; cuerno pronotal reducido (Figs 8–9); mentón con cresta longitudinal
	medial ligeramente elevada; Cub W. andersoni sp. n.
_	Macróptero, longitud del metaventrito mayor que la longitud de la cavidad
	metacoxal; cuerno pronotal bien desarrollado (Figs 10–17); mentón con cres-
	ta longitudinal medial muy elevada, proyectada hacia anterior; Cuba, Baha-
	mas, Hispaniola
2(1)	Escutelo triangular (Fig. 10); frente con fóvea superficial y tubérculos agudos
	entre el ápice del ojo y el clípeo; fémures con callosidades lisas y elevadas; bet-
	ter: tibias del macho sin espina apical (Figs 4, 10–11); Hispaniola
	W. emmabaconae sp. n.
_	Escutelo en forma de U a débilmente pentagonal (Fig. 16); frente con fóvea
	profunda, sin tubérculos agudos entre el ápice del ojo y el clípeo; fémures sin
	callosidades elevadas; todas las tibias del macho con una espina apical; Cuba
	and Bahamas

Species descriptions and diagnoses

Wattius cucullatus (Pascoe) Figures 1–4

Calymmus cucullatus Pascoe, 1871: 349 *Calymmus asperulus* Pascoe, 1871: 350; synonymized in Champion 1886: 225 *Wattius cucullatus* (Pascoe); Kaszab 1982: 50

Type material. LECTOTYPE, here designated, (male) labeled: on pink oval (a) "Rio"; (b) "Calymmus / cucullatus / Type Pasc"; (c) on white circle with orange border "Type"; (d) "Pascoe. / Coll. / 93–60."; (e) on blue paper "Tenebrionid Base / Aaron D. Smith / Catalog # 14794"; (f) on red paper, "LECTOTYPE / Calymmus / cucullatus / Pascoe / det. ADSmith 2015" (BMNH).

Note. Specimen designated as lectotype appears to be the one figured in the original publication (Pascoe 1871). No indication of the number of specimens in the original type series is given; however, it is possible that this was not the only individual.

Additional material examined. Thirteen specimens. Six labeled "BRAZIL: Sta. Catarina / Nova Teutonia / [dates from Jan. 1975, Nov. 1977, and Mar. 1977] / F. Plaumann" (CASC - 3°_{\circ} , $2^{\circ}_{\circ}_{\circ}$, EMEC - 1°_{\circ}). Five labeled "Lanca / St. Cath. Brazil / Oct. 1944" (AMNH - $1^{\circ}_{\circ}_{\circ}$, $4^{\circ}_{\circ}_{\circ}$). One female labeled "Cauna / S.Cath., Brazil / Dec. 1948" (AMNH). One female labeled "Rio Vermelho / S.Cath., Brazil / I. 1946" (AMNH).



Figures 1–4. *Wattius cucullatus* (Pascoe), Lectotype. I Dorsal habitus 2 Lateral habitus 3 Ventral habitus 4 Close-up of meso-leg.

Diagnosis. *Wattius cucullatus* can be separated from all other known members of the genus based on the following character combination: Frontoclypeal suture strongly incised, frons shallowly depressed anterior to eyes; pronotal horn strongly produced, apex weakly bifurcated in males, prosternal process deflexed behind coxae, rarely with small projecting tubercle near apex; flight wings fully developed, meso-and metacoxae separated by more than mesocoxal width; femora lacking smooth rounded callosities; outer margins of tibia flat with two indistinct rows of callosities, apical spine absent on all tibia in males, all male femora with rounded protuberance on anterior edge of basal half.

Wattius asperulus (Pascoe), new status

Figures 5–6

Calymmus asperulus Pascoe, 1871: 350

Type material. LECTOTYPE, here designated, (male) labeled: on pink oval (a) "Colombia"; (b) "Calymmus / asperulus / Type Pasc"; (c) on white circle with orange border "Type"; (d) "Pascoe. / Coll. / 93–60."; (e) on blue paper "Tenebrionid Base / Aaron D. Smith / Catalog # 14322"; (f) on red paper, "LECTOTYPE / Calymmus / asperulus Pascoe / det. ADSmith 2015" (BMNH).

Additional material examined. Two specimens, both from Colombia. One female labeled "P'to. Berrio / Ant. Colomb" (FMNH) and one male labeled "Colombia" (HNHM).

Diagnosis. *Wattius asperulus* can be separated from *W. cucullatus* and the West Indian members of the genus based on the following character combination: Frontoclypeal suture strongly incised, frons shallowly depressed anterior to eyes and raised into near vertical ridge above eyes to cranial apex; pronotal horn strongly produced, apex expanded and spatulate in males, prosternal process raised behind coxae; wings fully developed, meso- and metacoxae separated by more than mesocoxal width; femora lacking smooth rounded callosities; outer margins of tibia flat with two indistinct rows of callosities, apical spine present on all tibia in males, all male femora lacking rounded protuberances.

Discussion. Wattius asperulus was synonymized under W. cucullatus by Champion (1886). Champion's rationale was that the separation between W. cucullatus and W. asperulus could not be maintained based on the variability displayed in the specimens, which ranged from Mexico to Argentina, available to him. However, a large series of BMNH specimens identified as W. cucullatus by Champion, and corresponding to many of the localities listed in the Biologia Centrali-Americana, represents an estimated seven Wattius species that are only now being described (Smith in prep.).



Figures 5-6. Wattius asperulus (Pascoe), Lectotype. 5 Dorsal habitus 6 Lateral habitus.

Wattius andersoni Smith & Sanchez, sp. n. http://zoobank.org/BEACFF8C-FC13-4C3B-8707-BFE54973D0F5 Figures 7–9

Type material. HOLOTYPE (male) labeled: (a) "CUBA: Cienfuegos / Mayari, 2 km E. / 21.96651 -80.11497, 842m / 18.v.2013, R.Anderson / 2013-017X, hardwood forest"; (b) "WORLD / WEEVIL / DATABASE / WWD0104144"; (c) "Tenebrionid Base / Aaron D. Smith / Catalog # 14681"; (d) on red paper, "HOLOTYPE / Wattius / andersoni / Smith & Sanchez 2015" (CMNC). PARATYPE (male) labeled: (a) "CUBA: Topes de Col- / lantes, Sierra de / Trinidad, I.V. prov. / June 11, 1959"; (b) "M. W. Sanderson



Figure 7. Distribution map of West Indian *Wattius* spp. Red squares = *W. andersoni* sp. n., green triangles = *W. emmabaconae* sp. n., purple circles = *W. viatorus* sp. n.

/ C59-25"; (c) " Tenebrionid Base / Aaron D. Smith / Catalog # 14154"; (d) on yellow paper, "PARATYPE / Wattius / andersoni / Smith & Sanchez 2015" (CMNC).

Diagnosis. *Wattius andersoni* can be separated from the other West Indian members of the genus based on the following character combination: apterous, meso- and metacoxae separated by less than mesocoxal width; pronotal horn reduced, barely projecting past medial anterior margin of pronotum.

Description (Male). Length 5.4–5.7 mm, width 2.5–2.7 mm (n = 2 specimens). Body, excepting antennae, eyes, underside of head, scutellum, tarsi, and coxae generally coated with thin shellac, often capturing debris on surface. Color ferruginous to black. **Head:** Frons and clypeus with dense foveae, shallow to absent on clypeus, each fovea with one decumbent scale-like setae near center. Sharp setose tubercle with minute pit at apex present above eye, setae curved towards tubercle apex. Frontoclypeal suture distinct, deeply impressed; clypeus with sharp lip along anterior margin, margin straight. Epistoma between eye and clypeus raised, with one or more tubercles. Deep

impression present around eye from epistoma to apex. Eye reniform; emarginate at epistoma anteriorly, lobes subequal in size, with smooth triangular callus posterior to dorsal lobe on head. Labrum with transverse medial ridge, long golden setae present from ridge to anterior margin on dorsal surface, margin straight with lateral setae on vertical surface. Mandible bifid at apex; maxillary palp four segmented, apical segment securiform; mentum trapezoidal, widest at anterior margin, faint medial longitudinal ridge present, more defined in anterior half. Antenna with distinct three segmented club, club lighter than preceding segments and tomentose, antennomeres 10 and 11 partially fused but with sinus clearly visible; antennomere 3 approximately 1.7× length of antennomere 4, antennomeres 4–8 subequal in length. **Prothorax:** Pronotal disc convex, widest near middle;



Figures 8-9. Wattius andersoni sp. n., Holotype (male). 8 Dorsal habitus 9 Lateral habitus.

densely foveate, each fovea with one decumbent scale-like setae near center; moderately tuberculate, each tubercle bearing apical minute pit and covered in scale-like setae curved towards apex; anterior fourth of pronotum with short stout medial horn, horn margin straight; posterior fourth of pronotum with slight medial depression near scutellum; lat-

eral margin distinct and crenulate; anterior apices produced and acute, posterior apices acute, not projecting. Hypomeron densely deeply foveate, each fovea with one decumbent scale-like setae. Prosternum anterior to coxa short, less than length of coxal cavity, medially depressed well below height of prosternal process; prosternal process raised between coxa, apex subacute, projecting behind coxa. Pterothorax: Apterous. Elytron gradually widening to posterior third, before sharply sloping and tapering caudad; stria weakly indicated by deep elongate oval to rounded punctures, interstria with somewhat regularly spaced tubercles and decumbent scale-like setae, tubercle structure as described for those on head and pronotum; 4th, 7th, and 10th interstria with tubercles forming short costae near elytral base. Scutellum glabrous and impunctate, conspicuously lacking shellac coating compared to elytron and pronotum, ~1.6× as wide as long, U-shaped. Mesoventrite short, anteriorly weakly emarginate behind prosternal process, mesocoxal cavities open. Metaventrite short, separating meso- and metacoxal cavities by less than mesocoxal cavity length. All ventrites on the pterothorax with shallow indistinct punctures, often obscured by shellac, and decembent scale-like setae. Legs: Mesotrocantin exposed; femora lacking spines or other protrusions, sculpturing finely transversely rugose, with decumbent scale-like setae emerging from shallow folds; tibia clothed in decumbent scale-like setae, outer margins with indistinct rows of elongate smooth callosities, inner apical margin with socketed spurs greatly reduced to absent at base of acute weakly curved spine, small patch of golden setae present near anterior apex of protibia; tarsal formula 5-5-4, venter of distal tarsomere on all legs with sparse golden setae, venter of all other tarsomeres clothed with dense long golden setae. Abdomen: Ventrites weakly longitudinally rugose, clothed in sparse decumbent scale-like setae; abdominal intercoxal process broader than prosternal process, anterior margin straight; intersegmental membranes concealed; ventrite 5 lacking submarginal groove; abdominal defensive reservoirs present; sternite viii weakly sclerotized and setose, deeply medially emarginate, emargination V-shaped; parameres fused, sharply acuminate to apex and curved ventrad.

Female. Unknown. Based on an examination of other species in the genus, the female is likely to be very similar to the male, except lacking apical spines on the tibia and emargination on sternite viii.

Distribution. Both specimens were found above 750m in elevation in the Parque Natural Topes de Collantes, Cuba.

Etymology. The species epithet honors Robert S. Anderson, weevil expert, avid field researcher, and collector of the holotype.

Wattius emmabaconae Smith & Sanchez, sp. n. http://zoobank.org/DCD9DB2E-0D6B-4A69-BB10-691C6D34D822 Figures 7, 10–13

Type material. HOLOTYPE (male) labeled: (a) "DOMINICAN REP: Prov / Barahona, nr.Filipinas. / Mt. Tutu; 26-VI-7-VII- / 1992; P.E. Skelley / day catch, beating"; (b) "OSUC 524311"; (c) "Tenebrionid Base / Aaron D. Smith / Catalog # 13781"; (d) on



Figures 10-11. Wattius emmabaconae sp. n., Holotype (male). 10 Dorsal habitus 11 Lateral habitus.

red paper, "HOLOTYPE/ Wattius / emmabaconae / Smith & Sanchez 2015". (OSUC). ALLOTYPE (female) labeled: (a) "DOMINICAN REPUBLIC/ Dajabon Prov. Los Cerezos./ 14km NW of Rio Limpio / 608-Fresh cut wood/ 19°18'42.9"N 71°36'36.6" W/ 29 June 2010 S.Lingerfelter" ; (b) "Tenebrionid Base / Aaron D. Smith / Catalog # 13780"; (c) on red paper, "ALLOTYPE / Wattius / emmabaconae / Smith & Sanchez". (SEMC) Paratype (male) labeled: (a) "DOMINICAN Rep. :Prov / Barahona. nr. Filipinas. / Larimar Mine: 26-VI-7- / VII-1992: Woodruff & / Skelly. at light"; (b) "OSUC 524312"; (c) "Tenebrionid Base / Aaron D. Smith / Catalog # 13779"; (d) on yellow paper, 'PARATYPE / Wattius / emmabaconae / Smith & Sanchez 2015". (OSUC)

Diagnosis. *Wattius emmabaconae* can be separated from the other West Indian members of the genus based on the following character combination: flight wings fully developed, meso- and metacoxae separated by more than mesocoxal width; pronotal



Figures 12-13. Wattius emmabaconae sp. n., Allotype (female). 12 Dorsal habitus 13 Lateral habitus.

horn strongly produced, apex strongly expanded and bifurcate in males; femora with smooth rounded callosities; outer margins of tibia with two distinct rows of elongate smooth callosities, males lacking apical spine.

Description (Male). Length 8.0–8.4 mm, width 2.8–3.3 mm (n = 2 specimens). Body, excepting antennae, eyes, underside of head, scutellum, tarsi, and coxae generally coated with thin shellac, often capturing debris on surface. Color ferruginous to black. **Head:** Frons and clypeus with dense shallow foveae, shallow to absent on clypeus, each fovea with one decumbent scale-like setae near center. Sharp setose tubercle with minute pit at apex present above eye, setae curved towards tubercle apex; one or more similar tubercles present between apex of eye and frontoclypeal margin. Frontoclypeal suture distinct, deeply impressed; clypeus with sharp lip along anterior margin, margin straight. Epistoma between eye and clypeus raised, with one or more sharp tubercles. Deep impression pre-

sent around eye from epistoma to apex. Eye reniform; emarginate at epistoma anteriorly, ventral lobe larger than dorsal, with micro-granulate triangular callus posterior to middle of eye. Labrum with transverse medial ridge, long golden setae present from ridge to anterior margin on dorsal surface, margin straight with setae on vertical surface. Mandible bifid at apex; maxillary palp four segmented, apical segment securiform; mentum trapezoidal, widest at anterior margin, medial longitudinal ridge present, forming anteriorly facing tooth near front margin. Antenna with distinct three segmented club, club lighter than preceding segments and tomentose, antennomeres 10 and 11 fused, with sinus visible near lateral edges, segment 9 darker at base and lightening towards apex and lateral margins; antennomere 3 approximately 1.2× length of antennomere 4, antennomeres 4-8 subequal in length. Prothorax: Pronotal disc weakly convex, widest anterior to middle; densely, nearly confluently, shallowly foveate, each fovea with one decumbent scale-like setae near center; moderately tuberculate, forming irregular V-shaped pattern from near scutellum to anterior fourth, each tubercle bearing apical minute pit and covered in scalelike setae curved towards apex; anterior fourth of pronotum giving rise to raised medial horn, horn gradually sloping towards head, strongly expanded and bifid in apical third of length; posterior fourth of pronotum with slight medial depression, lacking tubercles, near scutellum; lateral margin distinct and crenulate; anterior apices strongly produced and acute, posterior apices acute, not projecting. Hypomeron densely shallowly foveate, each fovea with one decumbent scale-like setae. Prosternum anterior to coxa approximately as long as coxal cavity, medially nearly level with prosternal process; prosternal process raised between coxa, apex acute, projecting behind coxa. Pterothorax: Wings fully developed. Elytron parallel sided to posterior fourth, before sharply sloping and tapering caudad; stria weakly indicated by deep rounded punctures, interstria with somewhat regularly spaced tubercles and decumbent scale-like setae, tubercle structure as described for those on head and pronotum; 4th, 7th, and 10th interstria with tubercles forming weak costae, tubercles between 4th and 7th interstria and elytron suture occasionally forming irregular transverse costae. Scutellum glabrous and impunctate, width approximately 1.4× length, nearly V-shaped. Mesoventrite short, sparsely setose, anteriorly weakly emarginate behind prosternal process with submedial rows of rounded tubercles anterior to mesocoxal cavities, mesocoxal cavities open. Metaventrite long, separating meso- and metacoxal cavities by more than mesocoxal cavity length, sparsely setose with decumbent scale-like setae, impunctate. All other ventrites on the pterothorax micro-granulate, often obscured by shellac, with decembent scale-like setae. Legs: Mesotrocantin exposed; femora lacking spines or other protrusions, sculpturing finely transversely rugose with irregular smooth callosities on distal laterad half, decumbent scale-like setae emerging from shallow folds throughout; tibia clothed in decumbent scale-like setae, outer margins with two distinct rows of elongate smooth callosities, inner apical margin with socketed spurs and apical spine vestigial to absent, small patch of golden setae present near anterior apex of all tibia; tarsal formula 5-5-4, venter of distal tarsomere on all legs with sparse golden setae, venter of all other tarsomeres clothed with dense long golden setae. Abdomen: Ventrites smooth, clothed in sparse decumbent scale-like setae; abdominal intercoxal process subequal in width to prosternal process, anterior margin with small medial projection; intersegmental membranes concealed; ventrite 5 lacking submarginal groove; abdominal defensive reservoirs present; sternite viii weakly sclerotized and setose, deeply medially emarginate, emargination V-shaped; parameres fused, weakly acuminate to apex and curved ventrad.

Female. Similar to male, horn very weakly expanded and bifid at apex.

Distribution. Known from only two localities in the Dominican Republic on Hispaniola.

Etymology. The specific epithet is in honor of Emma C. Bacon and was chosen by her loving partner Christiaan Harden, a generous contributor to the authors' ongoing biodiversity studies.

Wattius viatorus Smith & Sanchez, sp. n.

http://zoobank.org/7E9D769E-76D0-4BDF-A1EE-78B7C2D2ED71 Figures 7, 14–17

Type material. HOLOTYPE (male) labeled: (a) "Cayamas / 29.5 Cuba"; (b) "EASchwarz / Collector"; (c) "Tenebrionid Base / Aaron D. Smith / Catalog # 14184"; (d) on red paper "HOLOTYPE / Wattius / viatorus / Smith & Sanchez 2015" (USNM). ALLO-TYPE (female) labeled: (a) "Cayamas / 23.5 Cuba"; (b) "EASchwarz / Collector"; (c) "Tenebrionid Base / Aaron D. Smith / Catalog # 14183"; (d) On red paper "ALLOTYPE / Wattius / viatorus / Smith & Sanchez 2015" (USNM). PARATYPES (49 specimens) (all bearing the label "PARATYPE / Wattius / viatorus / Smith & Sanchez 2015" on yellow paper and the database label "Tenebrionid Base / Aaron D. Smith / Catalog # ", for convenience tenebrioniDBase catalog numbers are listed as TB# without quotations). PARATYPE (female) labeled: (a) "Cayamas / 24.5 Cuba"; (b) "EASchwarz / Collector"; (c) TB# 14155; (USNM). PARATYPE (male) labeled: (a) "Cayamas / 25.5 Cuba"; (b) "EASchwarz / Collector"; (c) TB# 14156; (USNM). PARATYPE (male) labeled: (a) "Cayamas / 12.3 Cuba"; (b) "EASchwarz / Collector"; (c) TB # 14157; (USNM). PARATYPE (male) labeled: (a) "Cayamas / 7.2 Cuba"; (b) "EASchwarz / Collector"; (c) TB # 14158; (USNM). PARATYPE (male) labeled: (a) "Cayamas / 26.2 Cuba"; (b) "EASchwarz / Collector"; (c) TB # 14159; (USNM). PARATYPE (male) labeled: (a) "Cayamas / 8.5 Cuba"; (b) "EASchwarz / Collector"; (c) TB# 14160; (USNM). PARATYPE (male) labeled: (a) "Cayamas / 8.5 Cuba"; (b) "EASchwarz / Collector"; (c) TB# 14161; (USNM). PARATYPE (female) labeled: (a) "Cayamas / 10.2 Cuba"; (b) "EASchwarz / Collector"; (c) TB# 14162; (USNM). PARATYPE (male) labeled: (a) "Cayamas / 10.6 Cuba"; (b) "EASchwarz / Collector"; (c) TB# 14163; (USNM). PARATYPE (male) labeled: (a) "Cayamas / 11.3 Cuba"; (b) "EASchwarz / Collector"; (c) TB # 14164"; (USNM). PARATYPE (male) labeled: (a) "Cayamas / 15.3 Cuba"; (b) "EASchwarz / Collector"; (c) TB# 14165; (USNM). PARATYPE (male) labeled: (a) "Cayamas / 15.3 Cuba"; (b) "EASchwarz / Collector"; (c) TB # 14166; (USNM). PARATYPE (female) labeled: (a) "Cayamas / Cuba, Baker"; (b) "4175"; (c) TB# 14167; (USNM). PARATYPE (male) labeled: (a) "BAHAMAS: ANDROS ID. / London Ridge, 2.7 mi. N., / 0.8 mi. E., Forfar Field /Stn., 30.IV.1994-012, / R.S. Anderson, high / interior coppice"; (b) TB # 14169; (WIBF). PARATYPE (female) labeled: (a) "BAHAMAS: ANDROS ID. / London Ridge, 2.7 mi. N., / 0.8 mi. E., Forfar Field /Stn., 30.IV.1994012, / R.S. Anderson, high / interior coppice"; (b) TB # 14170; (WIBF). PARATYPE (female) labeled: (a) "BAHAMAS: ANDROS ID. / London Ridge, 2.7 mi. N., / 0.8 mi. E., Forfar Field /Stn., 30.IV.1994-012, / R.S. Anderson, high / interior coppice"; (b) TB # 14171; (WIBF). PARATYPE (female) labeled: (a) "BAHAMA IS; N. Andros Is. / Atala Coppice, 10 km WNW / Stafford Creek town / 13.VI.1983"; (b) "Collector: / B.D. Valentine / and family"; (c) "OSUC 524309"; (d) TB # 14172. PARATYPE (male) labeled: (a) "Cienfuegos / 3-22-39 CUBA / J.C. Biddley"; (b) TB # 14173; (CUIC). PARATYPE (female) labeled (a) "BAHAMAS: ANDROS ID. / Fresh Creek, Androsia / Factory, 26.IV.1994-006 / R.S. Anderson beating / interior dry coppice"; (b) TB # 14168; (WIBF). PARATYPE (male) labeled (a) "South Bimini Isl. / Bahamas, B.W.I. / August 15, 1951 / C.& P.Vaurie"; (b) TB # 14175; (AMNH). PARATYPE (male) labeled (a) "BAHAMAS: ANDROS ID. / London Ridge, 2.7 mi. N., / 0.8 mi. E., Forfar Field / Stn., 30. IV. 1994-012, / R.S. Anderson, high / interior coppice"; (b) TB # 14179; (WIBF). PARATYPE (male) labeled (a) "BAHAMAS: ANDROS ID. / London Ridge, 2.7 mi. N., / 0.8 mi. E., Forfar Field / Stn., 30. IV. 1994-012, / R.S. Anderson, high / interior coppice"; (b) TB # 14179; (WIBF). PARATYPE (female) labeled (a) "BAHAMAS: ANDROS ID. / London Ridge, 2.7 mi. N., / 0.8 mi. E., Forfar Field Stn., / 5-6.V.1994, R.S. Anderson, / high interior coppice beating"; (b) TB # 14180; (WIBF). PARATYPE (female) labeled (a) "South Bimini Isl. / Bahamas, B.W.I. / July 23,1951 / C. & P. Vaurie"; (b) TB # 13782.; (AMNH). PARATYPE (female) labeled (a) "South Bimini Isl. / Bahamas, B.W.I. / August 15,1951 / C. & P. Vaurie"; (b) TB# 14176.; (AMNH). PARATYPE (male) labeled (a) "South Bimini Isl. / Bahamas, B.W.I. / July 23,1951 / C. & P. Vaurie"; (b) TB# 13783.; (AMNH). PARATYPE (female) labeled (a) "South Bimini Isl. / Bahamas, B.W.I. / August 18,1951 / C. & P. Vaurie"; (b) TB # 14177.; (AMNH). PARATYPE (female) labeled (a) "South Bimini Isl. / Bahamas, B.W.I. / July 5,1951 / C. & P. Vaurie"; (b) TB # 14178".; (AMNH). Two PARATYPES (female) (CMNC) labeled (a) "Guanahacabibes / Pen., P.R.Cuba / July 3-4,1956 / C.&P.Vaurie"; (b) TB#'s 14181, 14182. PARATYPE (female) labeled (a) "BAHAMAS: ANDROS ID. / Fresh Creek, Androsia / Factory, 26.IV.1994-006 / R.S. Anderson beating / interior dry coppice"; (b) TB # 14684.; (CMNC). Two PARATYPE (female) (CMNC) labeled (a) "BAHAMAS: ANDROS ID. / London Ridge, 2.7 mi. N., / 0.8 mi. E., Forfar Field / Stn., 28.IV.1994-011, / R.S. Anderson, high / interior coppice beat"; (b) TB #'s 14682, 14683. Two PARATYPES (male) and one (female) (CMNC) labeled (a) "BAHAMAS: ANDROS ID. / London Ridge, 2.7 mi. N., / 0.8 mi. E., Forfar Field / Stn., 30.IV.1994-012, / R.S. Anderson, high / interior coppice"; (b) TB#'s 14685, 14686, 14687. Three PARATYPES (male) and one (female) (ZMHB) labelled (a) "Hist.-Coll (Coleoptera) / Nr. 46143 / Bolitophagus spec. / Cuba, Muller / Zool. mus. Berlin"; (b) TB #'s 14758, 14759, 14760, 14761. Seven PARATYPES (unknown sex) labeled (a) "Liho? Del Infierno? / Agosto 15/28"; (b) "Field Mus. Nat. His. / 1966 / A. Bierig Colln. / Acc. Z - 13812"; (c) TB# 14763, 14765, 14766.; (FMNH). Two PARATYPES (unknown sex) labeled (a) "Rm 14, Vinales / Agosto 14/28"; (b) "Field Mus. Nat. His. / 1966 / A. Bierig Colln. / Acc. Z - 13812"; (c) TB# 14764; (FMNH).

Diagnosis. *Wattius viatorus* can be separated from the other West Indian members of the genus based on the following character combination: flight wings fully devel-



Figures 14–15. Wattius viatorus sp. n., Holotype (male). 14 Dorsal habitus 15 Lateral habitus.

oped, meso- and metacoxae separated by more than mesocoxal width; pronotal horn strongly produced, apex expanded and bifurcated in males; femora lacking smooth rounded callosities; outer margins of tibia lacking distinct rows callosities, apical spine present on all tibia in males.

Description (Male). Length 4.4–6.4 mm, width 1.8–2.6 mm (n = 44 specimens). Body, excepting antennae, eyes, underside of head, scutellum, tarsi, and coxae generally coated with thin shellac, often capturing debris on surface. Color ferruginous to black. **Head:** Frons and clypeus with dense deep foveae, somewhat shallower on clypeus, each fovea with one decumbent scale-like setae near center. Rounded setose tubercle lacking minute pit at apex present above eye, setae curved towards tubercle apex; tubercles absent between apex of eye and frontoclypeal margin. Frontoclypeal suture distinct, deeply impressed; clypeus with sharp lip along anterior margin, margin straight. Epistoma between eye and clypeus raised, rarely with one or two low tuber-



Figures 16–17. Wattius viatorus sp. n., Allotype (female). 16 Dorsal habitus 17 Lateral habitus.

cles weakly indicated. Deep impression present around eye from epistoma to apex. Eye reniform; emarginate at epistoma anteriorly, ventral lobe larger than dorsal, with micro-granulate and punctate triangular callus posterior to middle of eye. Labrum with transverse medial ridge, long golden setae present from ridge to anterior margin on dorsal surface, margin straight with setae on vertical surface. Mandible bifid at apex; maxillary palp four segmented, apical segment securiform; mentum trapezoidal, widest at anterior margin, medial longitudinal ridge present, strongest near anterior margin. Antenna with distinct three segmented club, club lighter than preceding segments and tomentose, antennomeres 10 and 11 fused, with sinus visible near lateral edges; antennomere 3 approximately $1.3 \times$ length of antennomere 4, antennomeres 4-8 subequal in length. **Prothorax:** Pronotal disc weakly convex, widest anterior to middle; densely, nearly confluently, deeply foveate, each fovea with one decumbent scale-like setae; densely tuberculate submedially, each tubercle bearing apical minute

pit and covered in scale- like setae curved towards apex; anterior fourth of pronotum giving rise to raised medial horn, horn gradually sloping towards head, strongly expanded and either distinctly bifid or weakly medially emarginate in apical third of length; posterior fourth of pronotum with slight medial depression, lacking tubercles, near scutellum; lateral margin distinct and crenulate; anterior apices strongly produced and acute, posterior apices acute, not projecting. Hypomeron densely deeply foveate, each fovea with one decumbent scale-like setae. Prosternum anterior to coxa approximately as long as coxal cavity, medially nearly level with prosternal process; prosternal process raised between coxa, apex acute, projecting behind coxa. Pterothorax: Wings fully developed. Elytron parallel sided to posterior fourth, before sharply sloping and tapering caudad; stria weakly indicated by deep rounded punctures, interstria with somewhat regularly spaced tubercles and decumbent scale-like setae, tubercle structure as described for those on head and pronotum; 4th, 7th, and 10th interstria with tubercles forming weak costae, tubercles between 4th and 7th interstria and elytron suture occasionally forming irregular transverse costae. Scutellum glabrous and impunctate, ~1.4× wider than long, U- to approximately pentagonal in shape. Mesoventrite short, sparsely setose, distinctly emarginate behind prosternal process and forming submedial ridges anterior to mesocoxal cavities, mesocoxal cavities open. Metaventrite long, separating meso- and metacoxal cavities by more than mesocoxal cavity length, transversely rugose, sparsely setose with decumbent scale-like setae, moderately shallowly punctate around base of setae. All other ventrites on the pterothorax micro-granulate, often obscured by shellac, with decembent scale-like setae. Legs: Mesotrocantin exposed; femora lacking spines or other protrusions, sculpturing finely transversely rugose, lacking callosities, decumbent scale-like setae emerging from shallow folds throughout; tibia clothed in decumbent scale-like setae, outer margins lacking distinct rows of elongate smooth callosities, inner apical margin with socketed spurs vestigial to absent at base of small apical spine, patch of golden setae present on apical spines of all tibia; tarsal formula 5-5-4, venter of distal tarsomere on all legs with sparse golden setae, venter of all other tarsomeres clothed with dense long golden setae. Abdomen: Ventrites clothed in sparse decumbent scale-like setae, base of setae set in moderately sized punctures; abdominal intercoxal process wider than prosternal process, anterior margin straight to weakly rounded; intersegmental membranes concealed; ventrite 5 lacking submarginal groove; abdominal defensive reservoirs present; sternite viii weakly sclerotized and setose, deeply medially emarginate, emargination V-shaped; parameres fused, sharply acuminate to apex and weakly curved ventrad.

Female. Similar to male, but lacking apical tibial spine and horn not as strongly expanded and/or bifid at apex.

Distribution. Cuba, Bahamas: South Bimini and North Andros Islands. Label data indicates that specimens have been collected between sea level and 20 meters in elevation.

Etymology. The species epithet is a noun in apposition from the Latin *viator*, meaning traveler or tourist, due to the distribution of the species on multiple islands considered to be vacation destinations.

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MONOGRAPH



Three new species of *Hagnagora* Druce, 1885 (Lepidoptera, Geometridae, Larentiinae) from Ecuador and Costa Rica and a concise revision of the genus

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Abstract

Three new *Hagnagora* Druce species (Geometridae, Larentiinae) are described: *Hagnagora richardi* Brehm, **sp. n.** from Ecuador, *H. hedwigae* Brehm, **sp. n.** from Ecuador, and *H. mirandahenrichae* Brehm, **sp. n.** from Costa Rica. A checklist of taxa assigned to *Hagnagora* is provided. *Hagnagora* is provisionally divided into six clades: the *anicata* clade (6 species), the *buckleyi* clade (3 species), the *croceitincta* clade (3 species), the *buckleyi* clade (3 species) and *H. subrosea* (1 species). Two taxa are revived from synonymy: *H. catagrammina* Druce, **stat. rev.** and *H. luteoradiata* Thierry-Mieg, **stat. rev.** Two taxa are reinstated from subspecies to species level: *H. acothysta* Schaus, **stat. rev.** and *H. jamaicensis* Schaus, **stat. rev.** Four taxa are provisionally removed from *Hagnagora*: "*Hagnagora*" *ignipennis*, "*Hagnagora*" *nesenata*, "*Hagnagora*" *vittata*, and "*Hagnagora*" *ceraria*. After these changes, the genus *Hagnagora* now comprises 20 valid species.

Keywords

Taxonomy, Hagnagora, Costa Rica, Ecuador

Introduction

The Neotropical genus Hagnagora was invented by Druce (1885a) and described by Druce (1885b). So far, it comprised 23 described taxa, with 16 valid species (Parsons et al. 1999, Brehm and Sullivan 2005, Sullivan 2011). One species, H. mortipax Butler, was subdivided into three subspecies. Eighty-three percent of all taxa had been described by 1913, followed by one taxon described in 1927 and three over the last decade. This pattern appears typical for Neotropical geometrid genera (Brehm et al. 2011). The assignment of taxa to Hagnagora is largely based on the Lepidoptera card index of the Natural History Museum in London (NHM), and subsequently from the catalogue of geometrid moths (Parsons et al. 1999). During identification work on Ecuadorian and Costa Rican geometrid moths, it became obvious that Hagnagora - like most Neotropical geometrid genera - requires revision. In this paper, I attempt to solve some of the most urgent taxonomic problems of the genus. I describe three new species, revive two species from synonymy, transfer two species from subspecies to species level, and provisionally exclude four taxa from the genus. With one exception, all known taxa assigned to Hagnagora are illustrated. I also include available molecular genetic data (COI gene) in order to aid species identification. This consice revision will be a basis of future taxonomic work that will be required, e.g. with regard to the question whether Hagnagora is monophyletic or consists of two separate lineages.

Species identities and Barcode of Life Data Systems

Species delimitation and description of Lepidoptera has traditionally focused on their external morphology, mostly wing patterns. These formed the basis of all original descriptions of taxa assigned to Hagnagora in past centuries. The latest three species descriptions additionally contain not only colour plates, but also illustrations of male and female genitalia (Brehm and Sullivan 2005, Sullivan 2011). Additionally, molecular genetic information is available for these three taxa in the form of sequence data for the 658 bp fragment of the mitochondrial Cytochrome Oxidase I gene ("COI-barcodes"). A system of unique Barcode Index Numbers (BINs) has been established by Barcode of Life Data Systems (www.boldsystems.org) (Ratnasingham and Hebert 2013). It usually allows a quick and reliable assignment of specimens to other specimens in the system, whether identified to species or higher taxonomic level. Barcoding of all type specimens is an ultimate goal that would greatly increase the reliability of identifications, particularly in poorly studied tropical regions, and in cryptic and 'difficult' arthropod taxa. However, while barcoding of old type specimens is possible and relatively cheap (Strutzenberger et al. 2012), financial and bureaucratic constraints are still impeding a large-scale molecular analysis of type specimens in museums. In this paper, assignment of barcodes to described species was therefore performed by careful comparison of type

material with freshly collected material, and all respective specimens are illustrated. The assignments are working hypotheses until original types are eventually barcoded. Twelve different BINs are assigned to different *Hagnagora* species in this paper, thus covering a substantial part of the known taxa. In one case, one BIN has been assigned to two taxa that nonetheless are treated as morphologically separate species.

To accelarate the taxonomic progress and following a recently reached consensus amongst geometrid taxonomists (Forum Herbulot 2014), this study focuses not on extensive species descriptions, but on diagnostic characters and the synthesis of illustrated external characters, genitalia structures and COI barcodes.

Methods

Moths were pinned and dissected following established techniques (Lafontaine 2004, Hünefeld et al. 2011). Genitalia slides were embedded in Euparal, stained with Chlorazol Black, and digitised using an Olympus dotSlide system with 10x magnification. Adult moths were photographed in raw format using a 60 mm Nikkor macro lens mounted on a Nikon D700 camera. Photos were adjusted and colour plates were mounted using Photoshop and InDesign software (Adobe Systems, San José, USA).

Sequencing of the barcode fragment of the COI gene was carried out at the Canadian Center for DNA barcoding in Guelph, Ontario. Barcode sequences were compared by nearest neighbour analyses (Kimura 2 parameter), as implemented on the Barcode of Life Data Systems website (Ratnasingham and Hebert 2007). The resulting trees represent preliminary hypotheses of taxa groupings and can form the basis of future phylogenetic work. Fig. 1 shows a summary tree of all available taxa with barcode data. It visualizes similarities and differences in the COI gene between the different taxa and it was instrumental in differentiating four of the six provisional larger clades indentified within *Hagnagora*.

The following acronyms are used for institutions in which the specimens are deposited:

CISEC	Colección de Invertebrados del Sur del Ecuador, Universidad Tecnica Par-
	ticular Loja, Ecuador
NHM	Natural History Museum, London, UK
PMJ	Phyletisches Museum, Jena, Germany
RCGB	Research Collection Gunnar Brehm, Jena, Germany
SMF	Senckenberg Museum, Frankfurt a. M., Germany
SMNS	Staatliches Museum für Naturkunde, Stuttgart, Germany
USNM	National Museum of Natural History [formerly United States National
	Museum], Washington D.C., USA
ZSM	Zoologische Staatssammlung, München, Germany



Figure 1. Summary tree of the available molecular genetic data based on genetic COI 'barcodes' using the Kimura 2 parameter implemented in BOLD systems. Four out of six clades are represented by the barcode data; no data were available for the *buckleyi* clade and for *H. subrosea.* "*Hagnagora*" mesenata groups outside *Hagnagora* sensu stricto. The species name is followed by the individual identification number and the Barcode Index Number (BIN). HT: Holotype, PT: Paratype.

Results and Discussion

Distribution and Biology

Species previously assigned to *Hagnagora* were described from a wide range of Central and South American countries ranging from Mexico and Jamaica (17–18° N) to Chile (Valdivia province, ca. 39° S). Table 1 provides an overview of all taxa. The southernmost type locality of any *Hagnagora* species considered in this paper is Valparaíso in Chile (33° S) for *H. discordata*, but this record needs confirmation. Judging from their type localities, most species have a predominantly montane distribution. This includes the three recently described Costa Rican species (Brehm and Sullivan 2005, Sullivan 2011), as well as species described from the Colombian, Ecuadorian, Peruvian and Chilean Andes and mountains in SE Brazil.

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BIN		ou	ou	ou		assigned: BOLD:AAA7285	BOLD:AAA7283	BOLD:AAI1951	BOLD:AAE6775	BOLD:AAI1950	BOLD:AAA7284		assigned: BOLD:AAI6476		assigned: BOLD:AAE6774	BOLD:AAF7723		assigned: BOLD:AAA0650	(ou)	
Type Locality		[Imbabura, Intag] Intaj	Nicaragua: Chontales; Panama: Volcán de Chiriqui; Bugaba, 800–1500 fi	[Pastaza] Sarayacu		Bogotá	Alajuela Province: Volcan Poás, Alajuela Province	Zamora-Chinchipe	Heredia, Braulio Carrillo	Zamora-Chinchipe	Tapantí National Park, Cartago Province, 1275m; Volcan Poás, Alajuela Province, 2500m, Villa Mills, Cartago Province, 2841m		Loja (surroundings)	Cuschi [Cushi]	Mexico: Coatepec; Panama: Chiriqui	Guanacaste		۰.	Bogotá	
Country		Ecuador (north)	Nicaragua, Panama	Ecuador (east)		[Colombia]	Costa Rica	Ecuador	Costa Rica	Ecuador	Costa Rica		[Ecador, (south)]	Peru (cast)	Mexico, Panama	Costa Rica		Costa Rica	[Colombia]	
Described in		Hagnagora	Hagnagora	Hagnagora		Heterusia	Hagnagora	Hagnagora	Hagnagora	Hagnagora	Hagnagora		Polythrena	Heterusia	Heterusia			Scordylia	Heterusia	
Year		1885	1885	1885		1875	2011	this paper	2005	this paper	2011		1892	1908	1893	this paper		1872	1897	
Author		Druce	Druce	Druce		Felder & Rogenhofer	Sullivan	Brehm	Brehm & Sullivan	Brehm	Sullivan		Dognin	Bastelberger	Druce	Brehm		Butler	Warren	
Taxon	1 buckleyi clade (3 sp)	buckleyi	catagrammina stat. rev.	lex	2 anicata clade (6 sp)	anicata	elianne	hedwigae sp. n.	marionae	richardi sp. n.	unnia	3 <i>croceitincta</i> clade (3 sp)	croceitincta	epimena	clustimena	mirandahenrichae sp. n.	4 mortipax clade (4 sp)	mortipax	flavipectus	

Types	SТ?	ST?		ST?	ST	ST		ST?		ST	ST	ST	ST
Museum	NNNN	NNNN		MHN	MHN	MNSU		MHN		NNNN	MHN	۸.	۰.
BIN	no	no		ou	assigned: BOLD:AAA7267	assigned: BOLD:AAA7267		no		no	assigned: BOLD:AAH4713	380 bp fragment	ou
Type Locality	Parana, Castro	Volcan Sta. Maria		Bogota	Valparaíso	۷.		Carabaya, Oconeque, 7000 ft	1 the genus: <i>"Hagnagora"</i>	Bogotá, 2800–3200 m	۰.	Provincia de Valdivia	ñ.
Country	[Brazil]	Guatemala		[Colombia]	[Chile]	Costa Rica, Bolivia		Peru (south east)	ally removed fron	Colombia	Chile	Chile	Chile
Described in	Heterusia	Scordylia		Heterusia?	Scordylia	Heterusia		Cophocerotis	pecies provision	Heterusia	Heterusia	Euclidia	Phalaena
Year	1901	1927		1875	[1858]	1892		1909	S	1913	1875	1859	1782
Author	Schaus	Schaus		Felder & Rogenhofer	Guenée in Boisduval & Guenée	Thierry-Mieg		Warren		Dognin	Felder & Rogenhofer	Philippi	Molina
Taxon	acothysta stat. rev.	guatica	5 ephestris clade (3 sp)	ephestris	discordata	l <i>uteoradiata</i> stat. rev.	6 subrosea	subrosea		ignipennis	mesenata	vittata	ceraria

Caterpillars of *Hagnagora* are only known for *H. mortipax* and *H. luteoradiata* from NW Costa Rica (Janzen and Hallwachs 2014; http://janzen.bio.upenn.edu/caterpillars/database.lasso). Both species' caterpilars were recorded on *Clethra mexicana* DC. (Ericales, Clethraceae) (Figs 42, 43). One species excluded in this paper from *Hagnagora*, i.e. "*Hagnagora*" vittata, was reared in captivity on *Fuchsia magellanica* LAM. (Onagraceae) (King and Parra 2011). King and Parra (2011) also described the morphology of the egg and larva of "*Hagnagora*" vittata.

Hagnagora imagines mandatorily fold their wings vertically while resting in the same way as most butterflies (Fig. 41). They share this behaviour with genera such as *Callipia* Guenée and *Erateina* Doubleday (personal observations), whereas most geometrids display different resting positions. *Hagnagora* species are frequently observed at night and are readily attracted to artificial light sources (Brehm 2002, Brehm and Sullivan 2005), while both diurnal and nocturnal activity has been recorded for *H. marionae* and "*Hagnagora*" vittata (Brehm and Sullivan 2005, King and Parra 2011). Furthermore, both mud puddling and diurnal activity of *Hagnagora mortipax* has been observed in Peru (www.flickr.com/photos/76033499@N00/15919107346/). Apart from these isolated observations, little is known about the behaviour and ecology of *Hagnagora* moths.

Hagnagora: a monophyletic genus?

Druce (1885a) described *Hagnagora buckleyi* and *H. lex*, and shortly defined the genus together with the description of *H. catagrammina* (Druce 1885b). Druce (1885b) established *Hagnagora* largely by comparison with *Anemplocia splendens* (Druce, 1885) due to differences in the wing shape. The colourful *H. buckleyi* clade shares an apparently unique combination of wing pattern characters (Figs 2–6): The forewings have an orange transversal band, and the hindwings display fields of metallic blue between the veins. Notably, Druce (1893) did not include *H. clustimena* Druce, *H. discordata* Gn, and *H. mortipax* Butler in *Hagnagora*, but assigned them to *Heterusia* Hübner. Recent molecular genetic studies have shown that *Heterusia* sp. and *Hagnagora mortipax* are closely related, but do not form a monophyletic group (Sihvonen et al. 2011). Parsons et al. (1999), following the card index of the Natural History Museum, transferred several species previously assigned to *Heterusia* to *Hagnagora*.

All species assigned to *Hagnagora* in this revision share distinct wing patterns including a conspicuous white or yellow transversal band or blotch on the forewing. In addition, members of the clades *anicata*, *ephestris* and *mortipax* share a striated pattern on the hindwing underside. The *croceitincta* clade and *H. subrosea* show remnants of this striation, but the members of the *buckleyi* clade display distinctly different hindwing patterns. Molecular genetic data are available for all groups, but unfortunately with the exception of the *buckleyi* clade and *H. subrosea*. In a genetic dataset including more than 1,400 species of Ecuadorian geometrid species, the six recorded *Hagnagora* species representing four different clades form a single cluster (Brehm et al. 2013). This strongly suggests that at least these four clades form a monophyletic group (see also Fig. 1). Further molecular genetic data and genitalia dissections are required for members of the *buckleyi* clade to test whether the entire group represents a monophyletic taxon or possibly consists of two distinct lineages.

Taxonomy of Hagnagora

An overview of all taxa is provided in Table 1, and an overview of new type specimens and reference specimens with Bardode Index Numbers (BINs) and GenBank Accessions is provided in Table 2.

1 buckleyi clade

Hagnagora buckleyi Druce, 1885 no assigned BIN

Figs 2, 3

Type locality. Ecuador, Intaj [possibly Intag, Imbabura province].

Remarks. Druce (1885a) described *H. buckleyi* and *H. lex.* The upper- and undersides of the wings in *H. buckleyi* are very similar, with the colour of the hindwings generally being paler. The forewings feature a deep orange transversal band on a dark brown background, and the hindwings show metallic blue fields between the veins, with three located on the upperside between M_3 and CuA_2 and one in the cell, and eight between all veins on the underside. The pattern of the female is similar, with the blue fields extending further on the forewing, including the blotch between veins CuA_2 and A. In the female, metallic blue scales are also present at the base of the forewing at both the wing upper- and underside.

Distribution. North-western Ecuador.

Diagnosis. The largest species of the clade. The extension of the blue fields is significantly larger than in *H. lex*. The orange transversal band on the forewing is more saturated and more rounded than in *H. catagrammina*. Form and extension of the metallic blue blotches are different from those in *H. catagrammina* (Figs 2–3, 5–6).

Hagnagora catagrammina Druce, 1885, stat. rev.

no assigned BIN Figs 5, 6

Type locality. Nicaragua: Chontales; Panama: Volcán de Chiriqui; Bugaba, 800–1500 ft. Remarks. Druce (1885b) described *catagrammina* in the same year, but separately from *H. buckleyi* and *H. lex*. The taxon was put in synonymy with *buckleyi* by Parsons et



Figures 2–6. 2 *Hagnagora buckleyi* Druce male, lectotype **a** dorsal view **b** ventral view **3** *H. buckleyi* female, paralectotype **a** dorsal view **b** ventral view **4** *H. lex* Druce male, lectotype **a** dorsal view **b** ventral view **5** *H. catagrammina* Druce male, lectotype **a** dorsal view **b** ventral view **6** *H. catagrammina* Druce female, paralectotype (paraLT) **a** dorsal view **b** ventral view.

Species	Voucher number	GenBank Accession	Туре	BIN
marionae	GB 014	AM051082.1	paratype	BOLD:AAE6775
anicata	ID 16016	HQ576490	BIN reference	BOLD:AAA7285
elianne	07-CRBS-1029	no	holotype	BOLD:AAA7283
unnia	06-CRBS-0049	no	holotype	BOLD:AAA7284
richardi	ID 18080	KT208284	holotype	BOLD:AAI1950
richardi	ID 15855	KT208285	paratype	BOLD:AAI1950
richardi	ID 16285	JF859087	paratype	BOLD:AAI1950
richardi	BC ZSM Lep 04774	no	paratype	BOLD:AAI1950
richardi	ID 17328	GU671808	paratype	BOLD:AAI1950
richardi	ID 16119	JF858934	paratype	BOLD:AAI1950
richardi	ID 17863	HM380148	paratype	BOLD:AAI1950
hedwigae	ID 17397	HM432223	holotype	BOLD:AAI1951
croceitincta	ID 16293	JF859094	BIN reference	BOLD:AAI6476
clustimena	10-SRNP-112230	JF846078	BIN reference	BOLD:AAE6774
mirandahenrichae	12-SRNP-103819	no	holotype	BOLD:AAF7723
mirandahenrichae	07-SRNP-103401	JQ566645	paratype	BOLD:AAF7723
mirandahenrichae	07-SRNP-103498	JQ566696	paratype	BOLD:AAF7723
mirandahenrichae	11-SRNP-102035	JQ545536	paratype	BOLD:AAF7723
mirandahenrichae	11-SRNP-102036	JQ545537	paratype	BOLD:AAF7723
mirandahenrichae	12-SRNP-105462	no	paratype	BOLD:AAF7723
mortipax	ID 17240	GU671855	BIN reference	BOLD:AAA0650
discordata	BC ZSM Lep 44128	no	BIN reference	BOLD:AAA7267
luteoradiata	ID 16725	HQ576573	BIN reference	BOLD:AAA7267
mesenata	АҮК-04-0533-2	KF491827	BIN reference	BOLD:AAH4713
vittata	BC LP 0092	no	BIN reference	no BIN

Table 2. Voucher specimens (types and reference specimens for Barcode Index Numbers (BINs) with identification numbers, GenBank Accession numbers and BINs.

al. (1999). As noted by Druce, *catagrammina* is closely related to the other two species of the clade and particularly similar to *H. buckleyi*. In agreement with Druces' original description of the three taxa, I revive the species from synonymy with *H. buckleyi* due to small but overall significant differences of the wing patterns. The morphological differences hint to different species, particularly given the experience from many other species complexes of Neotropical Geometridae in which often more subtle differences – ideally combined with results from genitalia morphology and barcoding – can be observed in different species.

Distribution. Central America, from Nicaragua to Panama.

Diagnosis. The extension of the blue blotches is significantly larger than in *H. lex.* The transversal band on the forewing is paler and straighter than in *H. catagrammina.* Form and extension of the metallic blue blotches are different from those in *H. buckleyi* (Figs 2–3).

Hagnagora lex Druce, 1885

no assigned BIN Fig. 4

Type locality. Ecuador (east), [Pastaza], Sarayacu.

Remarks. *Hagnagora lex* was described by Druce (1885a) together with *H. buck-leyi*. While *buckleyi* was collected on the western slopes of the Andes, *H. lex* originates from the Amazon slopes of the Eastern Andes.

Distribution. Eastern Ecuadorian Andes (Pastaza: Sarayacu).

Diagnosis. Smaller than *H. buckleyi* and of similar size to *H. catagrammina*. The extension of the blue blotches is significantly smaller than in *H. buckleyi*. The form of the transversal band on the forewing is similar to that in *H. buckleyi*, but the band does not stretch as far towards the wing margins. *H. lex* is the species with the smallest extensions of metallic blue blotches on the underside, with the upperside completely devoit of these blotches.

2 anicata clade

Hagnagora anicata (Felder & Rogenhofer, 1875)

BIN: BOLD:AAA7285 Figs 7, 8

Type locality. [Colombia], Bogotá.

Remarks. *H. anicata* was re-described with a description also of the male genitalia, by Sullivan (2013). The lectotype is illustrated in Fig. 7. A series of specimens collected in southern Ecuador (1999–2013) (Fig. 8) is indistinguishable from *H. anicata* and therefore regarded as conspecific. The female (Fig. 12) is larger than the



Figures 7–11. *7 Hagnagora anicata* (F&R), male lectotype **a** dorsal view **b** ventral view **c** valvae **d** aedeagus **8** *H. anicata* (F&R), male from Ecuador as reference specimen with Barcode Index Number (BIN) **a** dorsal view **b** ventral view **c** valvae **d** aedeagus **9** *H. richardi* sp. n., male holotype **a** dorsal view **b** ventral view **c** valvae **d** aedeagus **9** *H. richardi* sp. n., male holotype **a** dorsal view **b** ventral view **c** valvae **d** aedeagus **10** *H. unnia* Sullivan, male **a** dorsal view **b** ventral view. **II** *H. marionae* Brehm & Sullivan, male **a** dorsal view.

male. A living specimen is shown in Fig. 41 in the typical resting position of these beautiful moths.

Distribution. Apart from its Colombian type locality, *H. anicata* has recently been collected and barcoded from sites in southern Ecuador to central Bolivia at elevations ranging from 2000 to 2920 m a.s.l.

Diagnosis. Most species of the *H. anicata* clade are very similar, and the most reliable current method for diagnosis is the COI barcode. *H. anicata* tends to be smaller than the other species occurring sympatrically, namely *H. richardi* and *H. hedwigae*. The wing length of the male (holotype) is only 17.5 mm in comparison to 19 mm in the male holotype of *H. richardi*. The structures of the female signum are also more complex than in *H. richardi*, but similar to those in *H. hedwigae*. The uncus of the male is smaller and shorter than in *H. richardi*. Aedeagi of the known males are (*H. anicata* and *H. richardi*) similar. COI barcode: The minimum observed distance to the presumbably most closely related species (*H. hedwigae*) is 3.1%.

Hagnagora elianne Sullivan, 2011

Not figured (very similar to *H. unnia*) BIN (paratype): BOLD:AAA7283 Voucher 07-CRBS-1029

Type locality (holotype). Costa Rica: Alajuela Province, Poás Volcano National Park, 2500 m.

Remarks. *H. elianne* was described and illustrated by Sullivan (2011). The species closely resembles the other species in the *H. anicata* clade, particularly *H. unnia*.

Distribution. The species has recently been collected and barcoded in Honduras (Cortes Province) and in several provinces of Costa Rica at elevations ranging from 1480 to 2840 m a.s.l.

Diagnosis. Males are on average slightly larger than males in *H. unnia* and can be distinguished from *H. anicata* by a swollen as opposed to a gently tapered distal half of the uncus and by the absence of a moderately large, upcurved spine at the end of the costa in *H. elianne* (Sullivan 2011). Females may be distinguished from females of *H. unnia* by their longer, more complex signum. COI barcode: The minimum observed distance to the presumably most closely related species (*H. unnia*) is 5.0%.

Hagnagora unnia Sullivan, 2011 BIN (paratype): BOLD:AAA7284 Voucher 06-CRBS-0049 Fig. 10

Type locality (holotype): Costa Rica, Cartago Province, Tapantí National Park, 1275 m. **Remarks.** *H. unnia* was recently described and illustrated by Sullivan (2011).

Distribution. The species is known from several provinces in Costa Rica at elevations ranging from 587 to 2840 m a.s.l.

Diagnosis. The species closely resembles other species of the *H. anicata* clade, particularly *H. elianne*; see there for a diagnosis. COI barcode: The minimum observed distance to the presumably most closely related species (*H. elianne*) is 5.0%.

Hagnagora marionae Brehm & Sullivan, 2005

BIN (paratype): BOLD:AAE6775 GenBank Accession: AM051082 Fig. 11

Type locality. Costa Rica, Heredia province, Braulio Carrillo National Park, Volcán Barva, 2730 m a.s.l.

Remarks. H. marionae was described and illustrated by Brehm and Sullivan (2005).

Distribution. The species has been collected only at two high mountain areas in Costa Rica at elevations > 2500 m a.s.l.

Diagnosis. The species resembles the other species of the *H. anicata* clade, but is easily distinguished by large orange-yellow blotches on the forewing. Males have a spatula-shaped uncus. COI barcode: The minimum observed distance to the presumably most closely related species (*H. richardi*) is 6.6%.

Hagnagora richardi Brehm, sp. n.

http://zoobank.org/406E12C4-4231-49F2-BE51-61E504E395F7 BIN (holotype): BOLD:AAI1950 Voucher ID 18080 GenBank Accession: KT208284 Figs 9, 13

Type material. Holotype: male (Fig. 9): Ecuador, Loja province, Parque Nacional Podocarpus, Cajanuma, 04°06.85'S, 79°10.47'W, 2916 m, 20 November 2008, G. Brehm leg. (ID 18080, genitalia preparation, barcode sequence 658 bp) (PMJ).



Figures 12–14. 12 *H. anicata* (F&R), female from Ecuador as reference specimen with Barcode Index Number (BIN) **a** dorsal view **b** ventral view **c** genitalia **13** *H. richardi* sp. n., female, paratype **a** dorsal view **b** ventral view **c** genitalia **14** *H. hedwigae* sp. n., female, paratype **a** dorsal view **b** ventral view **c** genitalia.

Paratypes: (deposited in CISEC, PMJ, RCGB, ZSM) 4 males, 2 females. 1 female: same as holotype but 04°06.86'S, 79°10.46'W, 2897 m, F. Bodner leg. (ID 15855, barcode sequence 658 bp); 1 female (Fig. 13): Ecuador, Zamora Chinchipe, Reserva Biológica San Francisco, 03°58.72'S, 79°04.44'W, 2180 m, 16 November 2008, F. Bodner leg. (ID 16285, barcode sequence 658 bp); 1 male same as previous but 28 October 1999, D. Süßenbach leg. (BC ZSM Lep 04774, barcode sequence 529 bp); 1 male: same as previous but 03°59.65'S, 79°04.10'W, 2670 m, G. Brehm leg. (ID 17328, barcode sequence 658 bp); 1 male as previous but 03°59.68'S, 79°04.10'W, 2677 m, 18 November 2008 (ID 16119, barcode sequence 658 bp); 1 male as previous but 25 November 2008 (ID 17863, barcode sequence 621 bp).

Description. As illustrated in Figs 9, 13. The wing length of the holotype (male) is 19 mm. The wing length of a female paratype (Fig. 13) is 21 mm.

Distribution. Only known from a small region around Podocarpus National Park, provinces Zamora-Chinchipe and Loja, Ecuador, with an observed elevational range of 2180–3021 m a.s.l. Apart from the **Type locality** and nearby sites, specimens were collected at elevations at ca. 3000 m at Cerro Toledo in the same National Park (04°23'S, 79°07'W). However, this record is not fully reliable because genitalia preparation or barcoding was not conducted for these specimens.

Diagnosis. Closely resembles other species of the *H. anicata* clade. On average significantly larger than *H. anicata*, but the female has about the same size as *H. hedwigae*. The uncus of the male is larger and broader than in *H. anicata*. The signum of the bursa copulatrix is less complex than in *H. anicata* and *H. hedwigae*. Easily distinguishable from *H. marionae* by the cream-white colour of the blotches on the forewing. COI barcode: The minimum observed distance to the presumably most closely related species (*H. marionae*) is 6.6%.

Etymology. *Hagnagora richardi* is named in honour of Richard Philipp from Jena, Germany, in recognition of his and his parents' support for the taxonomy of Neotropical geometrid moths.

Hagnagora hedwigae Brehm, sp. n.

http://zoobank.org/91A46B5D-DF10-42A8-97B2-46E0D5D7E086 BIN (holotype): BOLD:AAI1951 Voucher ID 17397 GenBank Accession HM432223 Fig. 14

Type material. Holotype: female (Fig. 14): Ecuador, Loja province, Reserva Biológica San Francisco, 03°59.68'S, 79°04.10'W, 2677 m, 25 November 2008, G. Brehm leg. (ID 17397, genitalia preparation, barcode sequence 595 bp) (PMJ).

Description. As illustrated in Fig. 14.
Distribution. Only a single female is known from *H. hedwigae* collected in southern Ecuador (2677 m). The wing length of the holotype (female) is 21 mm (same size as *richardi*).

Diagnosis. Resembles most closely *H. anicata* and *H. richardi*, but is larger than *H. anicata*, and the signum of the bursa copulatrix is more complex than in *H. richardi*. COI barcode: The minimum observed distance to the presumably most closely related species (*H. anicata*) is 3.1%.

Etymology. *Hagnagora hedwigae* is named in memory of Hedwig Seppelt (*1919 in Baumgarten, Silesia; † 2013 in Korschenbroich, Germany). Mrs Seppelt loved nature, and she took care that birds, small animals and insects found a habitat in her garden. The name is given in recognition of support for the taxonomy of Neotropical geometrid moths provided by her daughter-in-law Irmgard and her son Winfried Seppelt.

3 croceitincta clade

Hagnagora croceitincta (Dognin, 1892)

BIN: BOLD:AAI6476 Figs 15–17

epimena (Bastelberger, 1908): Type locality. Peru (east), Cuschi [Cushi]

Type locality. [Ecador, (south)], Loja surroundings.

Remarks. *H. croceitincta* was described by Dognin from southern Ecuador where it has recently been collected in montane forests (Brehm 2002). As one of the largest known *Hagnagora* species, it is conspicuously coloured, with orange, dark brown and white patterns. The taxon *epimena* (Bastelberger) remains in synonymy because the lectotype specimen (Fig. 16) does not show any particular differences to the type specimen of *H. croceitincta* (Fig. 15).

Distribution. Recently collected and barcoded specimens were sampled from central Colombia to southeastern Peru at elevations between 1750 and 2540 m a.s.l.

Diagnosis. On average larger than the closely related species *H. clustimena* and *H. mirandahenrichae*: Forewing length of the female holotype reaches 23 mm in comparison to about 20 mm in the other species. On the forewing, the white transversal blotch does not stretch to the costal margin as seen in the other two species, and the apical, dark-brown area reaches beyond veins 1A+2A. The species is also generally more vividly coloured than the other species in this clade, with white spots on the forewing between veins CuA₂ and 1A+2A and around M₃ on the upperside of the hindwing. COI barcode: The minimum observed distance to the presumably most closely related species (*H. mirandahenrichae*) is 7.1%.



Figures 15–22. 15 *Hagnagora croceitincta* (Dognin) female, holotype **a** dorsal view **b** ventral view 16 *H. epimena* (Bastelberger) male, lectotype **a** dorsal view **b** ventral view 17 *H. croceitincta* male from Ecuador as reference specimen with Barcode Index Number (BIN) **a** dorsal view **b** ventral view 18 *H. clustimena* (Druce) female, lectotype **a** dorsal view **b** ventral view 19 *H. clustimena* female from Costa Rica as reference specimen with Barcode Index Number (BIN) **20** *H. clustimena* male from Costa Rica as reference specimen with Barcode Index Number (BIN) **20** *H. clustimena* male from Costa Rica as reference specimen with Barcode Index Number (BIN) **a** dorsal view **b** ventral view **c** valvae **d** aedeagus **21** *H. mirandahenrichae* Brehm sp. n. male, holotype **a** dorsal view **b** ventral view **c** valvae **d** aedeagus **22** *H. mirandahenrichae* female, paratype **a** dorsal view **b** ventral view **c** genitalia.

Hagnagora clustimena (Druce, 1893)

BIN: BOLD:AAE6774 Figs 18–20

Type locality. Mexico: Coatepec.

Remarks. *H. clustimena* was originally assigned by Druce to *Heterusia* and then transferred to *Hagnagora* by Parsons et al. (1999). *H. clustimena* and *H. croceitincta* appear to occur allopatrically.

Distribution. Besides the type specimens described by Druce from Mexico and Panama, recently collected and barcoded specimens were sampled in Honduras and Costa Rica between 850 and 1550 m a.s.l.

Diagnosis. On average smaller than *H. croceitincta* and slightly larger than *H. mirandahenrichae* (see *H. croceitincta*). The white transversal blotch on the forewing stretches to the costal margin and the apical dark-brown area reaches vein CuA_2 , as also observed in *mirandahenrichae*. *H. clustimena* is slightly paler than *H. mirandahenrichae*. The male genitalia of both species are similar, but the valves are broader and differently shaped to *mirandahenrichae*. COI barcode: The minimum observed distance to the presumably most closely related species (*H. mirandahenrichae*) is 4.6%.

Hagnagora mirandahenrichae Brehm, sp. n.

http://zoobank.org/4C4FF729-5872-412A-BEF4-2428DA894237 BIN (holotype) BOLD:AAF7723 Figs 21–22

Type locality. Costa Rica, Área de Conservación Guanacaste, Guanacaste province.

Type material. Holotype: male (Fig. 21): Costa Rica, Guanacaste province, Área de Conservación Guanacaste, Sector Santa Maria, Mirador Santa Maria, 10.766° N, 85.301°W, 920 m a.s.l., 20 June 2012, S. Rios & R. Franco leg. (voucher 12-SRNP-103819, genitalia preparation, barcode sequence 658 bp) (PMJ).

Paratypes: (deposited in PMJ, USNM) 5 males, 1 female. Costa Rica, Guanacaste province, Área de Conservación Guanacaste, Sector Pitilla, Estacion Pitilla, 10.989° N, 85.426° W, 675 m a.s.l.; 1 female (Fig. 22) 16 May 2007, F. Quesada & R. Franco leg. (voucher 07-SRNP-103401, genitalia preparation, barcode sequence 658 bp), 1 male same as previous but 17 May 2007 (voucher 07-SRNP-103498), 2 males, 02 Apr 2011, H. Cambronero & S. Rios leg. (vouchers 11-SRNP-102035 and 11-SRNP-102036, barcode sequences 658 bp), 1 male 12 November 2012, R. Franco & H. Cambronero leg. (voucher 12-SRNP-105462).

Description. As illustrated in Figs 21, 22.

Distribution. Only known from sectors Santa Maria and Pitilla from Área de Conservación Guanacaste, province Guanacaste, NW Costa Rica, at elevations ranging from 675–920 m a.s.l., and therefore with a lower elevational range than *H. clustimena* (observed: 850–1550 m a.s.l.).

Diagnosis. Easily distinguished from *H. croceitincta* by its wing patterns (see diagnosis in that species). The yellow ground colour of *H. mirandahenrichae* is slightly more intensive than in *H. clustimena*. The male genitalia of both species are similar, but the valves of *mirandahenrichae* are narrower and have a different shape to *clustimena*. COI barcode: The minimum observed distance to the presumably closest relative, *H. clustimena*, is 4.6%.

Etymology. *Hagnagora mirandahenrichae* is named in honour of Ms. Miranda Henrich of California in recognition of her and her mother's critical support for understanding the taxonomy and biodiversity development of the Área de Conservación Guanacaste (ACG) in northwestern Costa Rica, where this species has been found by the ACG caterpillar inventory (Janzen et al. 2014).

4 mortipax clade

Hagnagora mortipax (Butler, 1872) BIN: BOLD:AAA0650 Figs 23–25

flavipectus (Warren, 1897): Type locality. [Colombia], Bogotá.

Type locality. Costa Rica.

Remarks. *H. mortipax* is one of the earliest described species in the genus and among the smallest *Hagnagora* species. Together with *H. luteoradiata* it also has the largest known geographical range. The taxon *flavipectus* remains in synonymy because it falls within the confirmed geographical range of *mortipax* and shows no significant deviations from the type specimen of *mortipax*. In comparison to the type specimen, the extension of the large white blotch on the forewing is smaller in Ecuadorian specimens, where it does not reach the costal margin. Since the barcode sequences of Costa Rican and Ecuadorian populations are nearly identical, all respective specimens are treated as members of the same species, and slight differences in wing patterns are regarded as geographical variability.

Distribution. Recently sampled and barcoded material is either from Costa Rica (Fig. 24) or Ecuador (Fig. 25), from elevations ranging from 540–2180 m a.s.l., and additional material from Ecuador falls within the same elevational range (Brehm 2002).

Diagnosis. The upper side of the wing in *H. mortipax* has a dark brown base colour with a large cream-white blotch on the forewing. This blotch almost reaches the outer margin, also either reaching the costal margin (Costa Rican specimens), or scantily not (Ecuadorian specimens). The white blotch is narrower in *H. jamaicensis* (Fig. 27), and significantly smaller, and separated from the outer margin, in *H. acothysta* from Brazil. All three species are significantly larger than *H. guatica*.

Hagnagora jamaicensis (Schaus, 1901), stat. rev. no assigned BIN Fig. 27

Type locality. Jamaica.



Figures 23–29. 23 *Hagnagora moripax* (Druce) male, lectotype **a** dorsal view **b** ventral view 24 *H. mortipax* male from Costa Rica as reference specimen with Barcode Index Number (BIN) **a** dorsal view **b** ventral view 25 *H. mortipax* male from Ecuador as reference specimen with Barcode Index Number (BIN) **a** dorsal view **b** ventral view 26 *H. flavipectus* (Warren) male, holotype **a** dorsal view **b** ventral view 27 *H. mortipax jamaicensis* (Schaus) male, lectotype **a** dorsal view **b** ventral view (photo USNM) 28 *H. mortipax acothysta* (Schaus) female, lectotype **a** dorsal view **b** ventral view (photo USNM) 29 *H. guatica* (Schaus) female, lectotype **a** dorsal view (photo USNM).

Remarks. Originally described as a *Heterusia* species by Schaus (1901), this taxon was down-ranked as a subspecies of *mortipax* by Parsons et al. (1999). In my view, the significantly different wing pattern in *jamaicensis* justifies Schaus' original species rank, but further evidence from barcoding is desirable in order to consolidate its species status.

Distribution. Jamaica.

Diagnosis. In contrast to the other taxa in the *mortipax* clade, this species displays a very narrow, cream-white transversal band on the forewings. The striation on the underside of the hindwing is reduced in comparison to *mortipax* and *acothysta*.

Hagnagora acothysta (Schaus, 1901), stat. rev.

no assigned BIN Fig. 28

Type locality. [Brazil], Parana, Castro.

Remarks. Together with *jamaicensis*, Schaus (1901) originally placed this species in the genus *Heterusia*. It was then ranked down as a subspecies of *mortipax* by Parsons et

al. (1999). The major characteristic of *acothysta* is the reduction of the white transversal band (found both in *mortipax* and *jamaicensis*) to a smaller blotch that reaches about half the area found in *mortipax*. As in *jamaicensis*, further evidence from barcoding is desirable for the consolidation of the species status.

Distribution. Brazil.

Diagnosis. Unlike *mortipax* and *jamaicensis*, this species shows no white transversal band on the forewing, but rather a reduced blotch that reaches only about 50% of the size observed in *mortipax*.

Hagnagora guatica (Schaus, 1927)

no assigned BIN Fig. 29

Type locality. Guatemala, [Quetzaltenango Department], Volcán Sta. Maria.

Remarks. Schaus described *guatica* as belonging to *Scordylia* Gn (a junior synonym of *Heterusia*). The wing pattern of *guatica* strongly resembles that of other members in the *mortipax* clade, but the species lacks the typical striation on the underside of the hindwing. Further evidence from barcoding and the study of the genitalia will help to better understand the relationships of this species with other species of the *mortipax* clade.

Distribution. Guatemala.

Diagnosis. By far the smallest *Hagnagora* species. The species lacks the typical striation on the underside of the hindwing found in all other members of the *mortipax* clade.

5 ephestris clade

Hagnagora ephestris (Felder & Rogenhofer, 1875)

no assigned BIN Fig. 30

Type locality. [Colombia], Bogota.

Remarks. Felder & Rogenhofer described this species from Colombia. It closely resembles *H. discordata* and *H. luteoradiata*. Parsons et al. (1999) put *luteoradiata* in synonymy with *ephestris*, but freshly collected material from Costa Rica and Ecuador shows that *luteoradiata* consistently lacks yellow blotches on the hindwing. It appears therefore to be more likely that *ephestris* is a junior synonym of *discordata*, and an increased knowledge of COI sequences could help to solve this question. Given the current state of knowledge, it appears to be the most appropriate solution to revive *luteoradiata* from synonymy and to treat the other two taxa as full species.

Distribution. Colombia.



Figures 30–35. 30 *Hagnagora ephestris* (F&R) male, lectotype **a** dorsal view **b** ventral view **31** *H. discordata* male, lectotype **a** dorsal view **b** ventral view **32** *H. discordata* male (ZSM Lep 44128) from Brazil as reference specimen with Barcode Index Number (BIN) (photo ZSM) **33** *H. luteoradiata* (T-M) male, lectotype **a** dorsal view **b** ventral view **34** *H. luteoradiata* (T-M) male from Costa Rica (CR) as reference specimen with Barcode Index Number (BIN) **a** dorsal view **b** ventral view **35** *H. luteoradiata* (T-M) male from Ecuador as reference specimen with Barcode Index Number (BIN) **a** dorsal view **b** ventral view.

Diagnosis. Both *ephestris* and *discordata* show a pronounced yellow blotch on the hindwings that is absent in *luteoradiata*. Different from *discordata*, the yellow transversal band on the forewing of *H. ephestris* reaches the outer margin of the wing. Moreover, the band is broader than in *discordata*, whereas the yellow field of the hindwing is narrower, particularly in the proximate half of the wing.

Hagnagora discordata (Guenée [1858])

BIN: BOLD:AAA7267 (together with *luteoradiata*) Figs 31, 32

Type locality. [Chile], Valparaíso [possibly incorrect locality].

Remarks. The oldest described *Hagnagora* species, assigned by Guenée to *Scordylia* Gn (= *Heterusia*). The **Type locality**, given as Valparaíso, [Chile], requires confirmation. The cool-dry climate of this Chilean lowland region differs strongly from the wet montane habitats where other *Hagnagora* species are typically found.

Distribution. Apart from the doubtful type locality in Chile, recently collected specimens were sampled in Santa Catarina, Brazil (27°S), at elevations of 1300 m a.s.l.

Diagnosis. Both *discordata* and *ephestris* show a pronounced yellow blotch on the hindwings that is absent in *luteoradiata*. The yellow transversal band on the forewing is narrower than in *ephestris*, and it does not reach the outer margin of the wing. The yellow blotch on the hindwing is much broader than in *H. discordata*. COI barcode: The minimum observed distance of Brazilian *H. discordata* is 2.3% to *H. luteoradiata* from Costa Rica and 2.6% to *H. luteoradiata* from Ecuador. These short distances suggest a relatively young split within this species clade.

Hagnagora luteoradiata (Thierry-Mieg, 1892), stat. rev. BIN: BOLD:AAA7267 (together with discordata) Figs 33-35

Type locality. Costa Rica.

Remarks. *H. luteoradiata* was put in synonymy with *H. ephestris* by Parsons et al. (1999). However, *luteoradiata* specimens consistently do not show any yellow blotches on the hindwing as observed in *ephestris* and *clustimena*. Barcoded specimens from Costa Rica (Fig. 34) and Ecuador (Fig. 35) are genetically very similar (distance only ca. 1.1%) and, together with the highly similar appearance, are therefore regarded as conspecific. The *ephestris* type specimen from Bogotá, Colombia, falls within the geographical range of the *luteoradiata* specimens, but shows a different wing pattern, i.e. a prominent yellow blotch on the hindwing and a different shape of the blotch of the forewing. The taxon *luteoradiata* is therefore revived from synonymy.

Distribution. Costa Rica to Ecuador. Observed elevational range in Ecuador 1800-2890 m and 560-1480 m in Costa Rica.

Diagnosis. The most prominent difference is the absence of any yellow blotches on the hindwing that are present both in *ephestris* and *discordata*. The transversal yellow band on the forewing is broader than in *discordata*, and has a different shape than in *ephestris*.

6 subrosea

Hagnagora subrosea (Warren, 1909) no assigned BIN Fig. 36

Type locality. Peru (south east), Carabaya, Oconeque, 7000 ft.



36a-b subrosea female, lectotype

37 ignipennis male, lectotype

Figures 36-40. 36 Hagnagora subrosea (Warren) female, lectotype a dorsal view b ventral view 37 "Hagnagora" ignipennis (Dognin) male, lectotype dorsal view 38 "Hagnagora" mesenata (F&R) male, lectotype (LT) a dorsal view b ventral view 39 "Hagnagora" mesenata male (AYK-04-0533-2) from Chile as reference specimen with Barcode Index Number (BIN) **a** dorsal view **b** ventral view (photo K Mitter) 40 "Hagnagora" vittata (Philippi) male (m) (BC LP 0092) from Chile as reference specimen with 380 bp COI fragment, dorsal view (photo LE Parra).

Remarks. Warren originally assigned *subrosea* to *Cophocerotis* Warren, but the genus-defining type species, *C. jaspeata* (Dognin), does not show the two prominent white transversal bands of the forewing present in *subrosea*. Parsons et al. (1999) transferred the species to *Hagnagora*. Barcoding and genitalia dissections of fresh specimens from this species are required, but judging from the two transversal bands, *subrosea* might indeed be associated with the *croceitincta* clade.

Distribution. Peru.

Diagnosis. *H. subrosea* has a unique combination of a pale brown wing colour with two white transversal bands on the forewings not found in any other species of *Hagnagora*.

Species excluded from Hagnagora

The following species are provisionally removed from the genus *Hagnagora* and set in quotation marks, following the convention applied by Parsons et al. (1999). "*Hagnagora*" *ignipennis* (Fig. 37) from Colombia lacks most of the characteristics typical for *Hagnagora*, notably transversal bands on the forewing. "*Hagnagora*" *mesenata*, "*Hagnagora*" *vittata* and "*Hagnagora*" *ceraria* (Figs 38–40) appear to be closely related to each other, but the wing pattern and particularly the wing shape diverge strongly from other species treated as "true" *Hagnagora* in this paper. A full barcode sequence is available for "*Hagnagora*" *vittata*. Both sequences reveal that these species are probably not congeneric with "true" *Hagnagora*. It is possible that the clades around *ignipennis* and *vittata* represent undescribed Larentiinae genera, and both cases require closer examination and a thorough revision of Neotropical Larentiinae.

"Hagnagora" ignipennis (Dognin, 1913)

no assigned BIN Fig. 37

Type locality. Colombia, Bogotá, 2800-3200 m.

"Hagnagora" mesenata (Felder & Rogenhofer, 1875) assigned BIN: BOLD:AAH4713 of voucher specimen AYK-04-0533-2 from Chile GenBank Accession: KF491827 Figs 38, 39

Type locality. Chile.



Figures 41–43. *Hagnagora* living specimens **41** *Hagnagora anicata* (?), Ecuador, Zamora Chinchipe, Estación Biológica San Francisco, 22 November 2008 in typical resting habitus, but alert because of disturbance by the photographer. The tympanal organ at the base of the abdomen is well visible **42** *Hagnagora luteoradiata* from Costa Rica **a** young caterpillar (09-SRNP-31840-DHJ458869) **b** caterpillar in last instar (09-SRNP-31840-DHJ458860) **43** *Hagnagora mortipax* caterpillar from Costa Rica **a** dorsal view (14-SRNP-3240-DHJ487561) **b** lateral view (14-SRNP-3240-DHJ487557).

"Hagnagora" vittata (Philippi, 1859)

no BIN assigned but 380 bp COI fragment of voucher specimen BC LP 0092 from Chile Fig. 40

ceraria (Molina, 1782): Type locality. Chile

Type locality. Chile, Provincia de Valdivia.

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