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The order Zoantharia Rafinesque, 1815 (Cnidaria, Anthozoa: Hexacorallia): supraspecific classification and nomenclature

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Abstract

Many supraspecific zoantharian names have long and complicated histories. The present list is provided to advise researchers on the current state of supraspecific nomenclature of the zoantharians, particularly given the recent attention paid to the taxonomy, phylogeny, and biodiversity of this order. At the same time, several taxonomic issues brought to light by recent research are resolved. Details on the taxonomic and nomenclatural history of most groups are provided, along with appendices of invalid supraspecific names.

Keywords

zoantharians, family-group, genus-group, taxonomy, historical literature

Contents

Introduction

The Zoantharia are an order of Hexacorallia most closely related to the sea anemones (Actiniaria) (Kayal et al. 2013). They are found in most marine ecosystems. Despite their cosmopolitan distribution and high frequency in many ecosystems, compared to both Actiniaria and Scleractinia, research on this order has been relatively scant. This is due to both their high levels of intraspecific morphological variation (e.g. Burnett et al. 1997, Reimer et al. 2004, Ong et al. 2013) and the presence of incrustations in their body walls (for all zoantharian families except the Zoanthidae), which makes internal histological examination problematic (Reimer et al. 2010c). Taxonomic identification problems have been compounded by a general lack of utility in some traditionally used diagnostic characters (Sinniger et al. 2010a, Swain 2010). Thus, despite being common in many ecosystems (Karlson 1980), until very recently zoantharian taxonomy has been confused (Burnett et al. 1997).

However, recent molecular phylogenetic examination of zoantharians, combined with a reassessment of their taxonomy and diagnostic characters, has led to the group becoming somewhat ordered (Reimer et al. 2007a, 2008a, Reimer and Fujii 2010, Sinniger et al. 2010a, 2013, Fujii and Reimer 2011, 2013, Swain and Swain 2014; Swain et al. 2015), setting an example for the reorganization of other anthozoan groups. This follows in the footsteps of the database Biogeoinformatics of Hexacorallia (Fautin and Buddemeier 2008), which was established as a repository for taxonomic and nomenclatural information on the Hexacorallia (see also Fautin 2016).

The order Zoantharia (= Zoanthidea or Zoanthiniaria) is currently thought to be comprised of nine families—Abyssoanthidae Reimer and Fujiwara, in Reimer, Sinniger, Fujiwara, Hirano and Maruyama, 2007, Epizoanthidae Delage and Hérouard, 1910, Hydrozoanthidae Sinniger, Reimer and Pawlowski, 2010, Microzoanthidae Fujii and Reimer, 2011, Nanozoanthidae Fujii and Reimer, 2013, Neozoanthidae

Herberts, 1972, Parazoanthidae Delage and Hérouard, 1901, Sphenopidae Hertwig, 1882, and Zoanthidae Rafinesque, 1815 (Daly et al. 2007: 143, 144; Hoeksema and Reimer 2013).

There is also a bioinformatics rationale for the compilation of such a taxonomic listing. As electronic name-lists of available and valid names become increasingly accessible, the need to link such lists with nomenclators of names will become an imperative. To this end, listings such as the present one can provide clear linkages between valid names and the huge mass of historical names (most of which are synonyms and some being potentially valid), which will effectively reduce the historical 'synonymy load' (Low and Reimer 2012a: 83) and provide a clear list of available supraspecific names of Zoantharia for future researchers.

Additional notes for introductory text

All valid taxa are treated in the systematics section, with the taxon (genus and species) listed. Synonyms are also listed. Justification for these synonymies is given in the sections that follow (Appendices 1–3). We use the general term "zoantharian" to refer to species within this order, unless when quoting original text in which another term (usually "zoanthid") was used.

Statistics

A total of 16 family-group names are treated. Nine are considered to be valid, six are synonyms, and one is not referable to the order Zoantharia. A total of 102 names at the genus rank are treated. Of these, 28 names are considered to be valid, 38 to be synonyms, 19 are incorrect spellings, 18 are not referable to the order Zoantharia, and two—*Stephanidium* Hertwig, 1888, and *Triga* Gray, 1867—are of uncertain placement and validity (see Table 1).

Systematics

Phylum Cnidaria Hatschek, 1888

Cnidaria Hatschek, 1888 (in 1888–1891): 40.

Remarks. See discussion on the nomenclature of the phylum in Fautin and Daly (2009: 315).

Class Anthozoa Ehrenberg, 1831

Anthozoa Ehrenberg, 1831: 44.

Subclass Hexacorallia Haeckel, 1896

Zoantharia de Blainville, 1830: 274.
Hexacorallia Haeckel, 1896: 217.

Order Zoantharia Rafinesque, 1815

Zoanthia Rafinesque, 1815: 155.
Zoantharia Gray, 1832: 94.
Zoanthiniaria van Beneden, 1897: 150.
Zoanthidea Bourne, 1900: 58.

Diagnosis. Anthozoans with body walls usually incrusted with sand and/or other detritus (except for the family Zoanthidae), tentacles always arranged in two rows or cycles. Majority of species are colonial.

Remarks. Herein, we choose to use the name Zoantharia Rafinesque, 1815. Although Zoantharia Rafinesque, 1815, has identical spelling with the supraordinal name Zoantharia de Blainville, 1830, the latter name has fallen from common use—Hexacorallia Haeckel, 1896, being favoured. Furthermore, using the name Zoanthidea Bourne, 1900, can potentially cause confusion when used in the non-technical form "zoanthids" to denote members of the order, as it would be identical with the term "zoanthids" to denote members of the family Zoanthidae Rafinesque, 1815.

Suborder Brachycnemina Haddon and Shackleton, 1891

Brachycneminae Haddon and Shackleton, 1891a: 626.

Diagnosis. Zoantharians with the fifth mesenteries from the dorsal directive being incomplete.

Remarks. —Recent molecular phylogenetic research indicates the two suborders of Zoantharia may not be monophyletics (e.g. Fujii and Reimer 2013). Three families are currently assigned to Brachycnemina Haddon and Shackleton, 1891.

Neozoanthidae Herberts, 1972

Neozoanthidae Herberts, 1972: 137.

Type genus. *Neozoanthus* Herberts, 1972.

Gender. Masculine.

Diagnosis. Zooxanthellate, brachycnemic zoantharians with only partial incrustation in ectoderm, rarely extending to mesoglea, no incrustation around the top, oral ends of polyps (Herberts 1972).

Remarks. A monogeneric and monospecific family-group. This taxon was originally defined as "Zoanthaires à arrangement mésentérique de type brachycnémique et à sphincter endodermique" (Herberts 1972: 137). However, recent work has further divided zoantharian sphincter muscles into ten different basic types; that of Neozoanthidae is discontiguous endodermal (Swain et al. 2015). Thus, the above diagnosis has been slightly modified from that of Herberts' (1972).

Recent molecular phylogenetic work calls into the question the validity of this family, as molecular data derived from *Neozoanthus* specimens cluster within the Zoanthidae radiation (Reimer et al. 2011a). Incrustation does not extend to mesoglea and is only found in the ectoderm. The families Neozoanthidae and Zoanthidae are not synonymised herein, as the Neozoanthidae also has some phylogenetic relation with the Hydrozoanthidae and the relationships between these families will require additional research (Reimer et al. 2011a).

Neozoanthus Herberts, 1972

Neozoanthus Herberts, 1972: 137.

Type species. *Neozoanthus tulearensis* Herberts, 1972, by monotypy.

Gender. Masculine.

Diagnosis. As for family above.

Remarks. Molecular phylogenetic results (Reimer et al. 2011a) indicate that this genus appears to be very closely related to the genus *Isaurus* Gray, 1828 (a genus assigned to the family Zoanthidae). Three species included in this group are from the Indo-Pacific.

Sphenopidae Hertwig, 1882

Palythoidae (as "Palythoae") Duchassaing de Fonbressin and Michelotti, 1860: 37.
Sphenopidae Hertwig, 1882: 120.

Type genus. *Sphenopus* Steenstrup, 1856.

Gender. Masculine.

Diagnosis. Brachycnemic zoantharians with sand/detritus incrustation in the ectoderm and mesoglea.

Remarks. The family-group name Sphenopidae Hertwig, 1882, is currently threatened by the senior subjective synonym Palythoidae Duchassaing de Fonbressin and Michelotti, 1860. To maintain widespread and current usage of the former name, and in accordance with Article 23.9.2 (ICZN 1999: 28, 29), an application is being prepared to request the International Commission on Zoological Nomenclature to suppress the senior subjective synonym Palythoidae Duchassaing de Fonbressin and Michelotti, 1860, in favour of Sphenopidae Hertwig, 1882. See additional discussion in Appendix 3.

The family-group Sphenopidae was established by Hertwig (1882), with the inclusion of only the type genus, *Sphenopus* Steenstrup, 1856. Two genera are currently assigned to Sphenopidae Hertwig, 1882.

Sphenopus **Steenstrup, 1856**

Sphenopus Steenstrup, 1856: 37.

Type species. *Sabella marsupialis* Gmelin, 1791, by monotypy.

Gender. Masculine.

Diagnosis. Unitary (=solitary, non-colonial) brachycnemic zoantharians with sand/detritus incrustation in the ectoderm and mesoglea.

Remarks. Distinct, large unitary polyps found embedded in sandy habitats with the oral disc clear of, and not attached to substrate (Soong et al. 1999, Reimer et al. 2012b, 2015b). Recent molecular work has also indicated that this this genus-group may form a clade with some *Palythoa* spp. (Reimer et al. 2012b, Fujii and Reimer 2016).

Palythoa **Lamouroux, 1816**

Palythoa Lamouroux, 1816: 359.
Corticifera Le Sueur, 1817: 178.
Polythoa Schweigger, 1819: 100 [incorrect spelling].
Polythea Gistel, 1848: 181 [incorrect spelling].
Gemmaria Duchassaing de Fonbressin and Michelotti, 1860: 55.
Polythoa (*Corticithoa*) Andres, 1883a: 521, 535–538.
Polythoa (*Gemmithoa*) Andres, 1883a: 521, 532, 533.
Parapalythoa Verrill, 1900: 560.
Protopalythoa Verrill, 1900: 562.
Haplotella Stechow, 1919: 853.

Type species. *Palythoe* [*sic*] *stellata* Lamouroux, 1816 [= *Alcyonium mammillosum* Ellis, in Ellis and Solander, 1786], by subsequent designation by Haddon and Shackleton (1891b: 691) (see also discussion in Appendix 3).

Gender. Feminine.

Diagnosis. Colonial brachycnemic zoantharians with sand/detritus incrustation in the ectoderm and mesoglea. Currently, all species except for two described are zooxanthellate (Irei et al. 2015).

Remarks. Specimens examined with a sphincter muscle of linear mesogleal type (Swain et al. 2015).

Protopalythoa was originally separated from *Palythoa* based on primarily polyp shape. Pax (1910) recommended merging *Palythoa* and *Protopalythoa*, and he defined three groups; "immersae", "intermediae" and "liberae", which have no taxonomic rank (see Ryland and Lancaster 2003). In 1923, Carlgren adopted this inclusive nomenclature. Similarly, Burnett et al. (1997) discussed the need to merge these genera but retained *Protopalythoa*. Ryland and Lancaster (2003) also discussed this issue and argued to keep *Protopalythoa* citing additional characters (zooxanthellate eggs in *Protopalythoa*; afterwards potentially observed in *Palythoa* spp. (Shiroma et al. 2010)). Herein, based on the several recent molecular studies (Sinniger et al. 2005, Reimer et al. 2006, 2007b, 2012a), we formally synonymise *Palythoa* and *Protopalythoa*, with *Palythoa* having priority.

Although at least 272 species-group names have been established in the genera *Palythoa* and *Protopalythoa* in the literature (see Fautin and Buddemeier 2008), with more research, these species-group names will likely be found to be synonyms—the result of high level of intraspecific morphological variation (see Burnett et al. 1994, Reimer et al. 2006, Hibino et al. 2014).

Zoanthidae Rafinesque, 1815

Zoanthidae (as "Zoanthia") Rafinesque, 1815: 155.
Zoanthidae Gray, 1832: 95.

Type genus. *Zoanthus* Lamarck, 1801.

Diagnosis. Brachycnemic zoantharians with no or little sand/detritus encrustation. Continuous or divided marginal muscle, and zoanthinae larvae (Ryland and Lancaster 2003).

Remarks. All members of this family are zooxanthellate (with endosymbiotic *Symbiodinium* spp.), and are found in sub-tropical and tropical waters. Authorship of the family-group name Zoanthidae should be attributed to Rafinesque (1815), and not Gray (1832, 1840) (see Low and Reimer 2012a). Three genera are currently assigned to Zoanthidae Rafinesque, 1815.

Zoanthus Lamarck, 1801

Zoanthus Cuvier, 1800: tables 9–10 [*nomen nudum*].
Zoanthus (as "*Zoantha*") Lamarck, 1801: 363.

Mammillifera Le Sueuer, 1817: 177.
Actimastus Rafinesque, 1818: 271 [unnecessary replacement name]
Mamillifera Quoy and Gaimard, 1834: 169 [incorrect spelling]
Anthozoon Gistel, 1848: 181 [unnecessary replacement name]
Mammilifera Gistel, 1848: 181[incorrect spelling]
Polythoa (*Mammithoa*) Andres, 1883a: 521.
Polythoa (*Mammothoa*) Andres, 1883a: 533 [incorrect spelling].
Zoanthus (*Rhyzanthus*) Andres, 1883a: 538.

Type species. *Actinia sociata* Ellis, 1768, by monotypy.

Gender. Masculine.

Diagnosis. Zooxanthellate, absence of mineral incrustations in the column/coenenchyme (excluding superficial surface attachments) brachycnemic zoantharians with smooth, usually erect polyps—except in *Zoanthus praelongus* Carlgren, 1954 (see discussion below)—with no endodermal invaginations. Mesogleal sphincter muscle with clear distal and proximal sections, mesogleal canal system but no encircling sinus (Duerden 1898, Swain and Swain 2014).

Remarks. Species of the genus *Zoanthus* and *Acrozoanthus* have a double sphincter muscle, which is unique among zoantharians. Referred to in Swain et al. (2015) as discontiguous mesogleal type.

Despite over 150 species having been described in or assigned to this genus (see Fautin and Buddemeier 2008), many of the species-group names are likely to be synonyms—due to the high level of intraspecific morphological variation (see Burnett et al. 1995, 1997, Reimer et al. 2004). One species, *Zoanthus praelongus* Carlgren, 1954, has recumbent (non-erect) polyps (as in the genus *Isaurus*) but is clearly referable to *Zoanthus* (see Carlgren 1954, Muirhead and Ryland 1985, Reimer et al. 2008b).

Acrozoanthus Saville-Kent, 1893

Acrozoanthus Saville-Kent, 1893: 153, 154.

Type species. *Acrozoanthus australiae* Saville-Kent, 1893, by monotypy.

Gender. Masculine.

Diagnosis. Zooxanthellate, absence of mineral incrustations in the column/coenenchyme (excluding superficial surface attachments) brachycnemic zoantharians inhabiting the outside of eunicid worms, with a ‘budding’ method of asexual reproduction (Reimer et al. 2011b).

Remarks. Specimens examined with a discontiguous mesogleal sphincter muscle (Swain et al. 2015).

The genus *Acrozoanthus* has a long and complicated taxonomic history. Reimer et al. (2011b) discussed that “despite its very similar appearance, *Acrozoanthus australiae* was placed into a genus separate from *Zoanthus* due to the presence of an axial skeleton

(Saville-Kent 1893). Later it was shown that this skeleton was in fact a result of habitat preference as *Acrozoanthus* inhabits the outside of eunicid worm tubes, and the genus was subsequently merged back again into the genus *Zoanthus* (Haddon 1895). Subsequent to its original description, this species was not mentioned in literature again until its rediscovery by Ryland (1997), based on examination of a single specimen. Further work by Ryland and co-workers described the nematocysts of *Acrozoanthus australiae* (Ryland et al. 2004) and also an unusual 'budding' method of asexual reproduction (Ryland 1997), which was theorized to potentially confirm the placement of this species in its own genus".

Molecular phylogenetic data indicate that *Acrozoanthus* is within the *Zoanthus* (see Reimer et al. 2011b) monophyly. However, due to a need for more detailed investigations, we refrain from synonymising *Acrozoanthus* with *Zoanthus*.

Isaurus Gray, 1828

Isaura Lamouroux, in Audouin, Bourdon, de Candolle, d'Aubebard de Férussac, Deshayes, Deslongchamps, É. Geoffroy Saint-Hilaire, I. Geoffroy Saint-Hilaire, Guérin, Guillemin, de Jussieu, Kunth, Delafosse, Lamouroux, Latreille, Prévost, Richard and Bory de Saint-Vincent, 1826: 23 [*nomen oblitum*].
Isaurus Gray, 1828: 8 [*nomen protectum*]
Isaura Agassiz, 1845: 14 [unjustified emendation].
Antinedia Duchassaing de Fonbressin and Michelotti, 1866: 136.
Pales Gray, 1867: 8.
Panceria Andres, 1877: 221–226.
Polythoa (*Monothoa*) Andres, 1883a: 521.
Zoanthus (*Monanthus*) Andres, 1883a: 538, 549, 541, 543.
Isaua Volpi and Benvenuti, 2003: 72 [incorrect spelling].

Type species. *Isaurus tuberculatus* Gray, 1828, by monotypy.

Gender. Masculine.

Diagnosis. Zooxanthellate, absence of mineral incrustations in the column/coenenchyme (excluding superficial surface attachments) brachycnemic zoantharians with recumbent (non-erect) polyps. Often have tubercules (raised bumps = endodermal invagination) on the outer surface of polyps, except in *Isaurus maculatus* Muirhead and Ryland, 1985, which has a smooth polyp surface.

Remarks. Specimens examined with an orthogonally-reticulate mesogleal sphincter muscle (Swain et al. 2015).

Ryland and Lancaster (2003) recognised only three valid species in this genus, although 22 species have been described in or assigned to this genus.

Suborder Macrocnemina Haddon and Shackleton, 1891

Macrocneminae Haddon and Shackleton, 1891a: 626.

Diagnosis. Zoantharians with the fifth mesenteries from the dorsal directive being complete.

Remarks. As stated above, the two suborders of Zoantharia appear not to be monophyletic (Sinniger et al. 2005). Three families are currently assigned to Macrocnemina Haddon and Shackleton, 1891.

Epizoanthidae Delage and Hérouard, 1901

Mardoellidae Danielssen, 1890: 116, 117 [*nomen oblitum*].
Epizoanthinae Delage and Hérouard, 1901: 664 [*nomen protectum*].

Type genus. *Epizoanthus* Gray, 1867.

Diagnosis. Macrocnemic zoantharians with a simple mesogleal muscle (Sinniger and Häussermann 2009: 26).

Remarks. The family-group Epizoanthidae (as "Epizoanthinae") was established by Delage and Hérouard (1901: 664, 665) as monotypic, with the inclusion of only the type genus. Three genera are currently assigned to Epizoanthidae.

Recent molecular and morphological studies (e.g. Swain et al. 2015) suggest that this diagnosis should be revised following a complete revision of the suborder. Currently, molecular signatures such as those suggested in Sinniger et al. (2008) and in Sinniger et al. (2013) appear efficient to distinguish macrocnemic genera.

Epizoanthus Gray, 1867

Sidisia Gray, 1858: 489 [suppressed in Opinion 1689, ICZN 1992].
Epizoanthus Gray, 1867: 237 [conserved in Opinion 1689, ICZN 1992].
Carolia Gray, 1867: 239 [invalid name, junior homonym].
Polythoa (*Endeithoa*) Andres, 1883a: 521, 531.
Verrillia Andres, 1883a: 520, 545.
Zoanthus (*Corticanthus*) Andres, 1883a: 538, 541.
Mardoell Danielssen, 1890: 117–126.
Marodellia Blanchard, 1893: 130 [unjustified emendation]
Mardoella Bell, 1906: 762 [incorrect spelling].
Lirrevia Delphy, 1939: 270.

Type species. *Dysidea papillosa* Johnston, 1842, by monotypy (see also Opinion 1689, ICZN 1992).

Gender. Masculine.

Diagnosis. As for family but readily distinguishable from *Palaeozoanthus* by the presence of non-fertile micromesenteries (Sinniger and Häussermann, 2009: 26).

Remarks. Most species with reticulate mesogleal muscle, *E. illoricatus* Tischbierek, 1930 with simplified mesogleal sphincter muscle (Swain et al. 2015).

As discussed in Sinniger and Häussermann (2009: 26), this genus is characterised by the "[p]olyps usually strongly encrusted with sand particles. Species found on rocky substrata or gastropod shells often inhabited by pagurids; some cases of free-living species reported (*E. lindhali*, *E. vagus*). In colonial species, polyps linked by stolons or, in pagurid-associated species, by a continuous coenenchyme. No symbioses with *Symbiodinium* zooxanthellae".

Palaeozoanthus Carlgren, 1924

Palaeozoanthus Carlgren, 1924: 470–473.

Type species. *Paleozoanthus reticulatus* Carlgren, 1924, by original description and monotypy.

Gender. Masculine.

Diagnosis. Macrocnemic zoantharians with a simple mesogleal muscle, and fertile micromesenteries.

Remarks. This genus is monospecific, and is comprised of the type species *Paleozoanthus reticulatus*, which has not been encountered since it was first described. Due to similarities in sphincter muscles (Swain et al. 2015) further studies are needed to determine if this genus corresponds to *Terrazoanthus*.

Thoracactis Gravier, 1918

Thoracactis Gravier, 1918: 12.
Thoracactus Walsh, 1967: 49 [unjustified emendation and junior objective synonym].
Toracactis Herberts, 1972: 80 [incorrect spelling].

Type species. *Thoracactis topsenti* Gravier, 1918, by monotypy.

Gender. Masculine.

Diagnosis. Rudimentary sphincter muscles, azooxanthellate, with no mesogleal channels or lacunae, found on hexactinellid sponges.

Remarks. This is a monospecific genus comprised of only the type species *Thoracactis topsenti*. In describing *Thoracactis topsenti*, Gravier (1918) incorrectly identified it as an actinian (anemone) based on the lack of zooxanthellae, channels, gaps, or cell islets. Although currently placed in the family Epizoanthidae, based on the current understanding of the type species, this genus is referable to the family Parazoanthidae, although an examination of the type material will be necessary to confirm this (see Reimer et al. 2010a: 158).

Hydrozoanthidae Sinniger, Reimer and Pawlowski, 2010

Hydrozoanthidae Sinniger, Reimer and Pawlowski, 2010: 60.

Type genus. *Hydrozoanthus* Sinniger, Reimer and Pawlowski, 2010.

Diagnosis. "This family is erected to group former Parazoanthidae species sharing specific insertions and deletions in mt-16S rDNA, especially in the V5 region (as defined in Sinniger *et al.*, 2005) of this gene" and "Phylogenetically, species in this family are more closely related to brachycnemic zoanthids (especially from the genus *Palythoa*) than to other parazoanthids." (Sinniger et al. 2010a: 61).

Remarks. "This family groups several tropical and sub-tropical macrocnemic zoanthids; including species associated with hydrozoans and also several other non-hydrozoan associated species." (Sinniger et al. 2010a: 61). This family is currently comprised of two genera— *Hydrozoanthus* Sinniger, Reimer and Pawlowski, 2010, and *Terrazoanthus* Reimer and Fujii, 2010.

Hydrozoanthus Sinniger, Reimer and Pawlowski, 2010

Hydrozoanthus Sinniger, Reimer and Pawlowski, 2010: 60.

Type species. *Parazoanthus tunicans* Duerden, 1900, by original designation.

Gender. Masculine.

Diagnosis. A hydrozoanthid associated with hydrozoans.

Remarks. Examined species with branchiform endodermal sphincter muscle (Swain et al. 2015).

Terrazoanthus Reimer and Fujii, 2010

Terrazoanthus Reimer and Fujii, 2010: 20.

Type species. *Terrazoanthus onoi* Reimer and Fujii, 2010, by original designation.

Gender. Masculine.

Diagnosis. This genus is characterised by being a member of the Hydrozoanthidae that is found on rocky substrates (as opposed to being obligate symbionts with hydrozoans). Some species in this genus are also brightly coloured (see Reimer and Fujii 2010: 20).

Remarks. Sphincter muscle transitional, with distal half mesogleal and proximal half endodermal, with encrustations to endodermal surface of mesoglea (Swain and Swain 2014) (=meso-endo transitional [Swain et al. 2015]), although *T. minutus* (Duerden, 1898) has a simplified mesogleal sphincter muscle (Swain et al. 2015).

Described species currently referable to the genus *Terrazoanthus* are mainly from the East Pacific, with *T. minutus* from the Caribbean, and it is likely that several more undescribed species exist in the Atlantic (see Reimer et al. 2010a, 2012a) and in the Central Indo-Pacific region (Reimer et al. 2014b).

The diagnosis of *Terrazoanthus* is in need of revision with the placement of *T. patagonichus* (Carlgren, 1898) into this genus by Swain et al. (2015) as this species is associated with hydroids (McMurrich 1904).

Microzoanthidae Fujii and Reimer, 2011

Microzoanthidae Fujii and Reimer, 2011: 420, 421.

Type genus. *Microzoanthus* Fujii and Reimer, 2011.

Diagnosis. As discussed in Fujii and Reimer (2011: 421), this family is characterised by "[c]olonies attached to bottom side (downward facing side) of dead coral rubble, asperous stones, inside narrow cracks, or occasionally on dead coral rubble on muddy seafloor. Azooxanthellate, macrocnemic. Polyps connected by narrow stolon or solitary. Sand particles encrusted in column. Irregularly sized sand particles encrusted into ectoderm. Tentacles two to three times as long as expanded oral disc diameter. Edge of oral disc shaped in regular, repeating zig-zagged pattern".

Remarks. This is a monotypic family and comprises only the genus *Microzoanthus* Fujii and Reimer, 2011, with two species.

Microzoanthus Fujii and Reimer, 2011

Microzoanthus Fujii and Reimer, 2011: 420, 421.

Type species. *Microzoanthus occultus* Fujii and Reimer, 2011, by original designation.

Gender. Masculine.

Diagnosis. As for family (Fujii and Reimer 2011). Encircling sinus present just beneath ectodermal surface (Swain and Swain 2014).

Remarks. Examined specimens with spindly-cteniform endodermal sphincter muscle (Swain et al. 2015).

Currently two species, reported only from the Pacific Ocean (Fujii and Reimer 2013) and the Red Sea (Reimer et al. 2014c).

Nanozoanthidae Fujii and Reimer, 2013

Nanozoanthidae Fujii and Reimer, 2013: 512.

Type genus. *Nanozoanthus* Fujii and Reimer, 2013.

Diagnosis. "Well developed polyps connected by narrow stolon. Mineral particles encrusted in column from aboral end to the edge of the oral disc. Irregularly sized sand particles encrusted into ectoderm and slightly into mesoglea. Zig-zagged, white-colored pattern following outside edge of oral disc. Macrocnemic mesenterial arrangement. Sphincter muscle mesogleal. No lacunae or ring sinus. Zooxanthellate. Mitochondrial cytochrome oxidase subunit I and 16S ribosomal DNA sequences significantly differ from all other known zoanthid genera (Fig. 1, 2)." (Fujii and Reimer 2013).

Remarks. A monogeneric family. Molecular data position this family in an intermediate position between the Brachycnemina and Macrocnemina, although currently it is placed within Macrocnemina (Fujii and Reimer 2013).

***Nanozoanthus* Fujii and Reimer, 2013**

Nanozoanthus Fujii and Reimer, 2013: 512–515.

Type species. *Nanozoanthus harenaceus* Fujii and Reimer, 2013, by original designation.

Gender. Masculine.

Diagnosis. As for family above.

Remarks. This is a monospecific genus currently, with specimens reported from southern Japan, Western Australia, and the Red Sea (Reimer et al. 2015a). However, molecular data indicate that the European species *Isozoanthus sulcatus* (Gosse, 1859) likely also belongs to this genus (Fujii and Reimer 2013).

Parazoanthidae Delage and Hérouard, 1901

Savaliidae (as "Savalini") Nardo, 1844: 433.
Bergidae Verrill, 1865a: 147 [*nomen oblitum*].
Gerardidae Verrill, 1865a: 148.
Savagliidae Brook, 1889: 51, 74, 79.
Parazoanthidae Delage and Hérouard, 1901: 665 [*nomen protectum*].
Savaliidae Poche, 1914: 104.
Heterozoanthidae Pax and Müller, 1956: 3.

Type genus. *Parazoanthus* Haddon and Shackleton, 1891.

Diagnosis. As discussed in Sinniger and Häussermann (2009: 28), this family "[…] traditionally groups macrocnemic zoanthids possessing an endodermal sphincter. Member species are frequently associated with other organisms, which are used as substrata". Excludes species that form monophyly with Brachycnemina (Sinniger et al. 2010a).

Remarks. Precedence of Bergiidae Verrill, 1865, and *Bergia* Duchassaing de Fonbressin and Michelotti, 1860, and respectively Parazoanthidae Delage and Hérouard, 1901, and *Parazoathus* Haddon and Shackleton, 1891a, was reversed in Low and Reimer (2011a). In accordance with Article 23.9.2 (ICZN 1999: 28, 29), an application is being prepared to request that the International Commission on Zoological Nomenclature suppress the senior subjective synonyms Savaliidae Nardo, 1844, Gerardiidae Verrill, 1865, and Savagliidae Brook, 1889, in favour of Parazoanthidae Delage and Hérouard, 1901, to maintain current and widespread usage. See additional discussion in Appendix 3.

In addition to the type genus, *Parazoanthus* Haddon and Shackelton, 1891, twelve other valid genera are currently assigned to the family Parazoanthidae: *Antipathozoanthus* Sinniger, Reimer and Pawlowski, 2010, *Bergia* Duchassaing de Fonbressin and Michelotti, 1860, *Bullagummizoanthus* Sinniger, Ocaña and Baco, 2013, *Corallizoanthus* Reimer, in Reimer, Nonaka, Sinniger and Iwase, 2008, *Hurlizoanthus* Sinniger, Ocaña and Baco, 2013, *Isozoanthus* Carlgren, in Chun, 1903, *Kauluzoanthus* Sinniger, Ocaña and Baco, 2013, *Kulamanamana* Sinniger, Ocaña and Baco, 2013, *Mesozoanthus* Sinniger and Häussermann, 2009, *Savalia* Nardo, 1844, *Umimayanthus* Montenegro, Sinniger and Reimer, 2015, and *Zibrowius* Sinniger, Ocaña and Baco, 2013.

***Parazoanthus* Haddon and Shackelton, 1891**

Heterozoanthus Verrill, 1870: 371 [*nomen oblitum*].
Parazoanthus Haddon and Shackleton, 1891a: 653, 654 [*nomen protectum*].

Type species. *Palythoa axinella* Schmidt, 1862, by original designation.

Gender. Masculine.

Diagnosis. Originally described as well-developed canal system in the mesoglea of the column, forming a ring sinus. Zoantharians often associated with sponges but not Hydrozoa, lacking skeletal secretion (Sinniger et al. 2010a). Examined species with endodermal sphincter muscle (=branchiform endodermal muscle [Swain et al. 2015]), encrustations reaching to endodermal surface of mesoglea (Swain and Swain 2014).

Remarks. "The original morphological description of *Parazoanthus* mentions several characteristics such as diffuse endodermal sphincter, encircling sinus, endodermal canals, lacunae and cell-islets in the mesoglea, continuous ectoderm and body-wall incrusted with mineral particles, often with numerous sponge spicules present in the incrustations. As shown in Sinniger et al. (2005) and here, these morphological characteristics alone do not ascertain the monophyly of *Parazoanthus*. Morphological characteristics in zoanthids can often become artifactual due to both complications encountered in making thin cuttings of heavily sediment incrusted polyps, and in interpreting the results of such sections. In the past, the large majority of epizoic macrocnemic zoanthids were described as belonging to *Parazoanthus* despite clearly different ecologies in many cases.

Thus, the results of this study strongly suggest that only zoanthid species able to associate with sponges should remain in *Parazoanthus*, as the type species of this genus, *P. axinellae* from the Mediterranean Sea, is regularly associated with demosponges." (Sinniger et al. 2010a: 69).

There is a need for a new diagnosis of this genus-grouping. With the recent erection of *Umimayanthus* Montenegro, Sinniger and Reimer, 2015 and the resurrection of *Bergia* Duchassaing de Fonbressin and Michelotti, 1860 in Montenegro et al. (2015a), the genus *Parazoanthus* now consists only of the former phylogenetic grouping of *Parazoanthus* 'clade C' sensu Sinniger et al. (2010a) and is monophyletic (Montenegro et al. 2015a: 71). *Parazoanthus* can be distinguished from *Bergia* and *Umimayanthus* by 16S-rDNA sequences, lacking the unique 60 bp deletion of *Bergia* and the unique insertion and deletion of *Umimayanthus*. Thus, the molecular characters described in Sinniger et al. (2008, 2013) appear to be efficient in identifying to genus level and could be used as diagnostic characters.

Antipathozoanthus **Sinniger, Reimer and Pawlowski, 2010**

Antipathozoanthus Sinniger, Reimer and Pawlowski, 2010: 61.

Type species. *Gerardia macaronesicus* Ocaña and Brito, 2003, by original designation.

Gender. Masculine.

Diagnosis. Sinniger et al. (2010a: 63) originally diagnosed this genus as a group that "grows exclusively on antipatharians" and lacking skeletal secretion.

Remarks. No mesogleal canals or sinus, encrustation to outer mesoglea (Swain and Swain 2014), examined species with either branchiform endodermal or endo-meso transitional sphincter muscle (Swain et al. 2015).

Sinniger et al. (2010a: 63) discussed that "[t]he type species *A. macaronesicus* was originally included in the description of *Savalia* (*Gerardia*) *macaronesica* (Ocaña and Brito 2003), and later the description was amended and the authors suggested the possible placement of this species in a separate genus (Ocaña et al. 2007). The species name was accorded to the genus gender. Skeletal secretion (similar to *Savalia* spp.) was advanced by Ocaña and Brito (2003) as occurring in *Antipathozoanthus macaronesicus*, and this remains to be studied in detail in order to assess whether this is an isolated characteristic or if it is taxonomically informative at genus level."

It also appears at least one member of this genus can be found on gorgonian octocorals (Bo et al. 2012).

Bergia Duchassaing de Fonbressin and Michelotti, 1860

Bergia Duchassaing de Fonbressin and Michelotti, 1860: 54.

Type species. *Bergia catenularis* Duchassaing de Fonbressin and Michelotti, 1860, by subsequent designation by Duerden (1903: 496).

Gender. Feminine.

Diagnosis. "… can be distinguished from all other zoantharians including *Parazoanthus* spp., *Umimayanthus* spp. and *Epizoanthus* spp. by a unique deletion of 60 bp (from position 133 to 192 in our alignment) and several consecutive base substitutions in the 16S-rDNA region. These characters clearly separate this genus from all other genera inside the family Parazoanthidae, as well as from the genus *Epizoanthus*" (Montenegro et al. 2015a: 68).

Remarks. Long considered to be a junior subjective synonym of *Parazoanthus* Haddon and Shackelton, 1891, recent molecular and morphological work by Montenegro *et al.* (2015a) have shown that the type species, *Bergia catenularis* Duchassaing de Fonbressin and Michelotti, 1860, represents a generic-level monophyly and resurrected the genus-group name *Bergia* Duchassaing de Fonbressin and Michelotti, 1860, for this grouping.

This genus-grouping currently contains three species all found in the Atlantic Ocean, although there is evidence of undescribed species in the Pacific Ocean (Montenegro et al. 2015a: 68).

Examined species in this genus-grouping have either branchiform endodermal or simplified mesogleal sphincter muscles (Swain et al. 2015).

Bullagummizoanthus Sinniger, Ocaña and Baco, 2013

Bullagummizoanthus Sinniger, Ocaña and Baco, 2013: [9].

Type species. *Bullagummizoathus emilyacadiaarum* Sinniger, Ocaña and Baco, 2013, by original designation.

Gender. Masculine.

Diagnosis. Characteristic insertion/deletion pattern in the 16S V5 region sensu Sinniger et al. (2005) (Sinniger et al. 2013).

Remarks. Monospecific deep-sea genus, appears to be specifically epibiotic on paragorgiid octocorals, and described from and only reported from the Hawaiian Archipelago, although likely present throughout the Pacific (Sinniger et al. 2013).

Corallizoanthus Reimer, in Reimer, Nonaka, Sinniger and Iwase, 2008

Corallizoanthus Reimer, in Reimer, Nonaka, Sinniger and Iwase, 2008: 940.

Type species. *Corallizoanthus tsukaharai* Reimer, in Reimer, Nonaka, Sinniger and Iwase, 2008, by monotypy.

Gender. Masculine.

Diagnosis. Characterised by its association with living precious corals (Alcyonacea: Coralliidae), and unlike the gorgonian-associated genus *Savalia*, does not secrete its own scleroproteinous axis. Additionally, polyps are primarily but not always unitary (solitary; non-colonial) (see Reimer et al. 2008a: 940). Encrustations to center of mesoglea, sphincter muscle is cyclically transitional (Swain and Swain 2014, Swain et al. 2015).

Remarks. A monospecific genus thus far only reported from the Ryukyu Islands, Japan.

Hurlizoanthus Sinniger, Ocaña and Baco, 2013

Hurlizoanthus Sinniger, Ocaña and Baco, 2013: [7].

Type species. *Hurlizoanthus parrishi* Sinniger, Ocaña and Baco, 2013, by original designation.

Gender. Masculine.

Diagnosis. Macrocnemic genus associated with primnoids. Characteristic insertion/deletion pattern in the 16S V5 region sensu Sinniger et al. (2005) (Sinniger et al. 2013).

Remarks. Currently this deep-sea genus includes only one species, known from a few locations in the Hawaiian Archipelago (Sinniger et al. 2013).

Isozoanthus Carlgren, in Chun, 1903

Polythoa (*Taeniothoa*) Andres, 1883a: 521, 532 [*nomen oblitum*].
Isozoanthus Carlgren, in Chun, 1903: 520 [*nomen protectum*].

Type species. *Isozoanthus giganteus* Carlgren, in Chun, 1903, by monotypy (Articles 68.3, 68.3.1, ICZN, 1999: 71).

Gender. Masculine.

Diagnosis. Macrocnemic zoanthids with a marginal endodermal sphincter muscle (=cteniform endodermal [Swain et al. 2015]) and inconspicouous mesogleal ring-sinus.

Remarks. The genus *Isozoanthus* was first made available in Carlgren (in Chun 1903: 520). The type species by monotypy is *Isozoanthus giganteus* (first very briefly diagnosed and figured by Carlgren (in Chun, 1903: 520, unnumbered fig.). Carlgren's (in Nordgaard 1905: 159) use of "*Isozoanthus* (*Epizoanthus*) *arborescens*" and subsequent designation (i.e. Carlgren 1913: 39) of *Epizoanthus arborescens* (Danielssen, 1890) as type species are thus invalid (Article 67.2, ICZN, 1999: 66, 67) (see also Williams 2000: 195).

The status of this genus is currently very confused. With the utility of the characters of the sphincter muscle in zoantharians in question (see Swain 2010, Sinniger et al. 2010a), it is clear that more research is needed to clarify the diagnosis and taxonomic position of *Isozoanthus*. The taxonomy is further complicated by the recently described species (the hydroid-associated *Hydrozoanthus antumbrosus* (Swain, 2009) originally described within *Isozoanthus*), and the octocoral-associated *Isozoanthus primonodius* Carreiro-Silva, Braga-Henriques, Sampaio, de Matos, Porteiro and Ocaña, 2010) clearly belong to other genera based on ecology and morphology. Furthermore, only limited molecular data is available for the type species *Isozoanthus giganteus*. Data in Swain (2010) indicate that *Isozoanthus giganteus* is highly divergent from both the well-researched species of *Isozoanthus*—*Isozoanthus sulcatus* (Gosse, 1859)—and all known zoantharians. Recent work by Fujii and Reimer (2013) shows that *I. sulcatus* is likely within the Nanazoanthidae Fujii and Reimer, 2013. However, as additional information on *Isozoanthus giganteus* is lacking, the diagnosis is retained with the caveat that any assignment of species to this genus should include: 1) phylogenetic confirmation of a close relationship with *Isozoanthus giganteus*; and 2) the elimination of any possibility that the species in question does not belong to another parazoanthid genera based on morphology, ecological associations, and/or habitat.

Kauluzoanthus Sinniger, Ocaña and Baco, 2013

Kauluzoanthus Sinniger, Ocaña and Baco, 2013: [8].

Type species. *Kauluzoanthus kerbyi* Sinniger, Ocaña and Baco, 2013, by original designation.

Gender. Masculine.

Diagnosis. Polyps do not contract when fixed. Characteristic insertion/deletion pattern in the 16S V5 region sensu Sinniger et al. (2005) (Sinniger et al. 2013).

Remarks. Currently this genus comprises only one species, which was reported as parasitic on *Kulamanana haumeaae*.

Kulamanamana Sinniger, Ocaña and Baco, 2013

Kulamanamana Sinniger, Ocaña and Baco, 2013: 4.

Type species. *Kulamanamana haumaeaae* Sinniger, Ocaña and Baco, 2013, by original designation.

Gender. Feminine.

Diagnosis. Macrocnemic genus associated with octocorals and secreting a golden to dark brown scleroproteic skeleton. Ectoderm absent of mineral particles, with well-developed coenenchyme completely covering the host. Characteristic insertion/deletion pattern in the 16S V5 region sensu Sinniger et al. (2005) (Sinniger et al. 2013).

Remarks. The type species has been reported to live primarily on isidid corals (bamboo corals) (Sinniger et al. 2013: 6). Reported from the Hawaiian Archipelago, Line and Jarvis Islands, Palmyra Atoll, Kingman Reef, all in the Pacific (Sinniger et al. 2013).

Mesozoanthus **Sinniger and Häussermann, 2009**

Mesozoanthus Sinniger and Häussermann, 2009: 31, 32.

Type species. *Mesozoanthus fossii* Sinniger and Häussermann, 2009, by original designation and monotypy.

Gender. Masculine.

Diagnosis. "Macrocnemic with *Parazoanthus*-like growth-form. Well-developed polyps with long and pointed tentacles; polyps form clusters linked by a basal coenenchyme. DNA sequences significantly differ from those in other genera..." and "In contrast to *Parazoanthus*, members of *Mesozoanthus* usually occur in small patches and are not known to colonise demosponges. No symbioses with *Symbiodinium* zooxanthellae." (Sinniger and Häussermann 2009: 32).

Remarks. Only two species of this genus are known, from temperate waters along the west coast of the Americas.

Savalia **Nardo, 1844**

Savalia Nardo, 1844: 433, 434.
Savaglia Nardo: 1877: 674–676 [unjustified emendation].
Gerardia Lacaze-Duthiers, 1864a: 87.

Type species. *Gorgonia savaglia* Bertolini, 1819, by monotypy (Articles 68.3, 68.3.1, ICZN 1999: 71).

Gender. Masculine.

Diagnosis. No mesogleal canal system in the column. Secreting a black or dark brown horny skeleton, azooxanthellate.

Remarks. Examined species in this genus-grouping have branchiform endodermal or cyclical transitional sphincter muscle (Swain et al. 2015). Distinction from the other skeleton-secreting zoantharians such as *Kulamanamana* or potentially *Antipathozoanthus* can be made through habitat (shallow vs. deep-sea) and/or molecular signatures.

There has been historical and recent controversy over the correct name for this genus-group, and this is discussed in detail in Appendix 3.

Umimayanthus Montenegro, Sinniger and Reimer, 2015

Umimayanthus Montenegro, Sinniger and Reimer, 2015: 76.

Type species. *Umimayanthus chanpuru* Montenegro, Sinniger and Reimer, 2015, by original designation.

Gender. Masculine.

Diagnosis. "…can be distinguished from all zoantharians including *Parazoanthus* spp. by a highly conservative and unique insertion of 9 bp in length (from position 556 to 564 in alignment) and one deletion of 14 bp long (from position 574 to 587) in the mt 16S-rDNA region" (Montenegro et al. 2015b: 76).

Remarks. Specimens examined from this genus-grouping have a branchiform endodermal sphincter muscle (Swain et al. 2015).

"…exclusively associated with sponges, usually encrusting and cushion sponges, occasionally with massive sponges. Polyps generally scattered over the sponge surface, but can form defined stoloniferous chains in lines, or form groups of two to three connected polyps. Polyps may be solitary or connected to each other by a stolon through a thin but clearly visible coenenchyme either over or under the sponge surface. Polyps with sand particles and detritus incrusted in column. Tentacles equal or longer than the expanded oral disc diameter." (Montenegro et al. 2015b: 76).

This genus-group currently includes four described species; three in the Indo-Pacific and one in the Atlantic (Montenegro et al. 2015b).

Zibrowius Sinniger, Ocaña and Baco, 2013

Zibrowius Sinniger, Ocaña and Baco, 2013: [7].

Type species. *Zibrowius ammophilus* Sinniger, Ocaña and Baco, 2013, by original designation.

Gender. Masculine.

Diagnosis. "Sand incrusted, arborescent fan shaped colonies, golden skeleton, well developed coenenchyme completely covering the host, can be confused with *Kulamanamana*, but easily distinguished by the presence of sand incrustation in the ectoderm, characteristic insertion/deletion pattern in the 16S V5 region" sensu Sinniger et al. [2005] (Sinniger et al. 2013: 7)

Remarks. Until now, only reported from the Cross Seamount in the central Pacific Ocean.

Suborder *incerta sedis*

Remarks. Two families are currently not assigned to any suborder.

Abyssoanthidae Reimer and Fujiwara, in Reimer, Sinniger, Fujiwara, Hirano and Maruyama, 2007

Abyssoanthidae Reimer and Fujiwara, in Reimer, Sinniger, Fujiwara, Hirano and Maruyama, 2007: 258.

Type genus. *Abyssoanthus* Reimer and Fujiwara, in Reimer, Sinniger, Fujiwara, Hirano and Maruyama, 2007.

Diagnosis. "Sand/detritus/sediment-encrusted Zoantharia with unitary (noncolonial) free-living polyps, attached to hard substrates at abyssal (non-continental shelf deep-sea) depths surrounding methane cold seeps or other chemosynthetic ecosystems." Reimer and Sininger (2010: 454).

Remarks. A monogeneric family. Molecular data places this family in an unresolved position distant from the Brachycnemina and Macrocnemina.

Abyssoanthus Reimer and Fujiwara, in Reimer, Sinniger, Fujiwara, Hirano and Maruyama, 2007

Abyssoanthus Reimer and Fujiwara, in Reimer, Sinniger, Fujiwara, Hirano and Maruyama, 2007: 258.

Type species. *Abyssoanthus nankaiensis* Reimer and Fujiwara, in Reimer, Sinniger, Fujiwara, Hirano and Maruyama, 2007, by original designation and monotypy.

Gender. Masculine.

Diagnosis. As for family above.

Remarks. Two species known, both from waters around Japan. There may be additional species from the Mediterranean, in non-chemosynthetic environments (Sinniger et al. 2010b).

Family *incerta sedis*

Stephanidium Hertwig, 1888

Stephanidium Hertwig, 1888: 52.

Type species. *Stephanidium schulzii* Hertwig, 1888, by monotypy.

Gender. Neuter.

Diagnosis. Very small (diameter 1.5–2.2 mm, height 1 mm), unitary polyps, with microcnemes and macrocnemes, although their arrangement could not be clearly seen. Mesenteriel insertions make body wall to have a furrowed appearance, with spherical evaginations on the body wall above the area where the sphincter muscle is present. Twenty-six mesenteries.

Remarks. From the original description, possibly a species of zoantharian, but type material needs to be located and examined. We make no decision as to the validity of this genus and species in the event that the identification of this genus and species requires a reversal of precedence Article 23.9 (ICZN 1999: 27, 28) with a later (but more widely-used name). Also, the genus-group name *Stephanidium* Hertwig, 1888, is preoccupied by *Stephanidium* Ehrenberg, 1839 (*incerta sedis*).

Discussion

As can be seen from examining the nomenclatural and taxonomic history of the various supraspecific names in this paper, many taxa of the order Zoantharia have a confused history. However, over the past two decades, phylogenetic and detailed morphological examinations of zoantharians have resulted in a new understanding of the evolutionary relationships within the order (Sinniger et al. 2005, Reimer et al. 2007a, 2008a, Reimer and Fujii 2010, Sinniger et al. 2010a, 2013, Fujii and Reimer 2011, 2013; Swain et al. 2015). Combined with a recent effort to organize the nomenclature of zoantharians (Low and Reimer 2011a, b, 2012a, b), it can be said that much of the Zoantharia nomenclature is now stable, and generally reflects our current understanding of their evolutionary history.

However, as seen in this manuscript, there are still some nomenclatural issues that remain to be resolved. For example, the validity of the genera *Sphenopus* and *Acrozoanthus* still have to be thoroughly examined. Furthermore, it is clear from recent molecular phylogenetic results (Fujii and Reimer 2013) that the taxonomy and nomenclature of the suborders are in urgent need of a revision. Finally, at the ordinal level, it appears that Zoantharia is much closer to the Actiniaria (sea anemones) than has been previously thought (Fujii and Reimer 2013). As these two orders have been speculated to be basal cnidarians (Kayal et al. 2013), after clarification of their evolutionary history, subsequent nomenclatural amendment may be needed.

Additional work examining the utility of ecological and morphological traits of Zoantharia as diagnostic characters is needed to allow the linkage of current phylogenetic results with past literature (Swain et al. 2016). Despite, or perhaps due to its confused and challenging morphological taxonomy, the order Zoantharia is now among the most advanced hexacorallian order in terms of the use of molecular tools to clarify phylogenetic relationships between taxa at various taxonomic levels. As such, and despite potential and known differences in molecular evolution of other anthozoans (Stampar et al. 2014), Zoantharia is a potentially good model for clarifying the taxonomy of other hexacorallian orders and anthozoan groups.

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References

The question of nomenclatural priority (while correctly a minor and largely theoretical exercise) underpins the system of nomenclature currently in use. In this order-wide review of the supraspecies nomenclature and taxonomy, we have had to determine the relative priority of many synonyms, and have come across accurate date of publication information for much of the literature. Many of these references have a nomenclatural impact beyond the order Zoantharia, and these data are included for the benefit of the taxonomic community at large.

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Appendix 1

Nomenclator of family-group names in the Zoantharia Rafinesque, 1815

Names in **bold** and designated with an asterisk (*) are considered to be valid family-group names. Also refer to the genus-group names in the next section. Names marked with a † are invalid synonyms, or incorrect spellings (if further denoted by a "[*sic*]"). Additional names without either designation have been confused with the order Zoantharia at one time or another but have since been removed from this group.

***Abyssoanthidae** Reimer and Fujiwara, in Reimer, Sinniger, Fujiwara, Hirano and Maruyama, 2007: 258. Type genus *Abyssoanthus* Reimer and Fujiwara, in Reimer, Sinniger, Fujiwara, Hirano and Maruyama, 2007.

Bergidae Verrill, 1865. See Bergiidae Verrill, 1865.

†Bergidae [*sic*]. Incorrect subsequent spelling of Bergiidae Verrill, 1865 (e.g. Verrill 1869 [in 1868–1871]: 494; Duerden 1903: 495).

†Bergiidae Verrill, 1865a: 147. Type genus *Bergia* Duchassaing de Fonbressin and Michelotti, 1860. This family-group name was first established as "Bergidae" (an incorrect original spelling. *Bergia* Duchassaing de Fonbressin and Michelotti, 1860, was previously considered to be a junior subjective synonym of *Parazoanthus* Haddon and Shackleton, 1891, but has since been revalidated (see Montenegro et al. 2015a: 63–71). Bergiidae Verrill, 1865, and Parazoanthidae Delage and Hérouard, 1901, nevertheless remain subjective synonyms. Low and Reimer (2011a: 64, 65) enacted Article 23.9 (ICZN 1999: 27, 28) to reverse precedence between these family-group names, thereby making Bergiidae Verrill, 1865, a *nomen oblitum*, and Parazoanthidae Delage and Hérouard, 1901, a *nomen protectum*. Low and Reimer (2011a: 64, 65) incorrectly attributed the name Bergiidae to Verrill, 1869 (in 1868–1871), but the name should be attributed to Verrill (1865). The findings and action of Low and Reimer (2011: 64, 65) remain valid.

***Epizoanthidae** Delage and Hérouard, 1901: 664. Type genus *Epizoanthus* Gray, 1867. First described as the subfamily "Epizoanthinae". See also Mardoellidae Danielssen, 1890.

Gerardidae Verrill, 1865. See Gerardiidae Verrill, 1865a.

†Gerardidae [*sic*]. Incorrect subsequent spelling of Gerardiidae Verrill, 1865 (e.g., Verrill 1869 [in 1868–1871]: 499; Duerden 1903: 495).

†Gerardiidae Verrill, 1865a: 1484. Type genus *Gerardia* Lacaze-Duthiers, 1864. This family-group name was first established as "Gerardidae" (an incorrect original spelling). A subjective synonym of Parazoanthidae Delage and Hérouard, 1901. This family group name is a senior subjective synonym of Parazoanthidae Delage and Hérouard, 1901, and an application to the ICZN in accordance with Article 23.9.2 (ICZN 1999: 28, 29) is in preparation to suppress this name in favour of the more universally-accepted and -used name Parazoanthidae Delage and Hérouard, 1901. Also see discussion in Appendix 3.

†Heterozoanthidae Pax and Müller, 1956: 2. Type genus *Heterozoanthus* Verrill, 1870. The type genus is an objective synonym of *Parazoanthus* Haddon and Shackleton, 1891, making Heterozoanthidae Pax and Müller, 1956, a junior objective synonym of Parazoanthidae Delage and Hérouard, 1901 (Article 61.3.2 of the Code, ICZN 1999: 64) (see Low and Reimer 2012a: 83, 84).

***Hydrozoanthidae** Sinniger, Reimer and Pawlowski, 2010: 60. Type genus *Hydrozoanthus* Sinniger, Reimer and Pawlowski, 2010.

†Mardoellidae Danielssen, 1890: 116, 117. Type genus *Mardoell* Danielssen, 1890. The type genus is a subjective synonym of *Epizoanthus* Gray, 1867 (see Low and

Reimer, 2011b: 84, 85; Lwowsky, 1913: 603, 604). Mardoellidae Danielssen, 1890, is therefore a subjective synonym of Epizoanthidae Delage and Hérouard, 1901. Low and Reimer (2011b: 84) enacted Article 23.9 (ICZN 1999: 27, 28) to reverse precedence between these family-group names, thereby making Mardoellidae Danielssen, 1890, a *nomen oblitum*, and Epizoanthidae Delage and Hérouard, 1901, a *nomen protectum*.

***Microzoanthidae** Fujii and Reimer, 2011: 420, 421. Type genus *Microzoanthus* Fujii and Reimer, 2011.

***Nanozoanthidae** Fujii and Reimer, 2013: 512. Type genus *Nanozoanthus* Fujii and Reimer, 2013.

***Neozoanthidae** Herberts, 1972: 137. Type genus *Neozoanthus* Herberts, 1972.

Orinidae Verrill, 1869. See Oriniidae Verrill, 1869.

Oriniidae Verrill, 1869 (in 1868–1871): 494. Type genus *Orinia* Duchassaing de Fonbressin and Michelotti, 1860. This family-group name was first established as "Orinidae" (an incorrect original spelling). The type genus *Orinia* Duchassaing de Fonbressin and Michelotti, 1860, is a junior subjective synonym of *Rhodactis* Milne Edwards and Haime, 1851, which is currently assigned to the family Discosomidae Verrill, 1869 [Coralliomorpha] (see Fautin 2016: 25, 28, 38). Also see remarks under *Orinia* Duchassaing de Fonbressin and Michelotti, 1860, in Appendix 2.

Polythoae Duchassaing de Fonbressin and Michelotti, 1860. See Palythoidae Duchassaing de Fonbressin and Michelotti, 1860.

Palythoidae Duchassaing de Fonbressin and Michelotti, 1860: 37. Type genus *Palythoa* Lamouroux, 1816 (spelled as "*Polythoa*"). This family-group name was first established as "Polythoae" (based on "*Polythoa*", an incorrect subsequent spelling of *Palythoa* Lamouroux, 1816, see Appendix 3). A subjective synonym of Sphenopidae Hertwig, 1882, as the type species *Sphenopus* Steenstrup, 1856, and *Palythoa* Lamouroux, 1816, as assigned to the same family (see Appendix 3). Precedence between Palythoidae Duchassaing de Fonbressin and Michelotti, 1860, and Sphenopidae Hertwig, 1882, cannot be reversed and an application to the ICZN in accordance with Article 23.9.2 (ICZN, 1999: 28, 29) is in preparation to suppress the former name in favour of the latter name that is more widely accepted and used. Also see discussion in Appendix 3.

***Parazoanthidae** Delage and Hérouard, 1901: 665. Type genus *Parazoanthus* Haddon and Shackleton, 1891. See also the synonyms Bergiidae Verrill, 1865, Gerardiidae Verrill, 1865, Heterozoanthidae Pax and Müller, 1956, Savagliidae Brook, 1889, and Savaliidae Nardo, 1844. Also see discussion in Appendix 3.

†Savagliidae Brook, 1889: 51, 74, 79. Type genus *Savaglia* Nardo, 1877. A subjective synonym of Parazoanthidae Delage and Hérouard, 1901. This family group name is a senior subjective synonym of Parazoanthidae Delage and Hérouard, 1901, and an application to the ICZN in accordance with Article 23.9.2 (ICZN, 1999: 28, 29) is in preparation to suppress this name in favour of the more widely accepted and used name Parazoanthidae Delage and Hérouard, 1901. Also see discussion in Appendix 3.

†Savaliidae Nardo, 1844: 433. Type genus *Savalia* Nardo, 1844. This family-group name was first established at the rank of subfamily as "Savalini" (an incorrect original spelling). A subjective synonym of Parazoanthidae Delage and Hérouard, 1901. This family group name is a senior subjective synonym of Parazoanthidae Delage and Hérouard, 1901, and an application to the ICZN in accordance with Article 23.9.2 (ICZN, 1999: 28, 29) is in preparation to suppress this name in favour of the more universally-accepted and -used name Parazoanthidae Delage and Hérouard, 1901. Also see discussion in Appendix 3.

†Savaliidae Poche, 1914: 104. Type genus *Savalia* Nardo, 1844. Proposed as a replacement name for Savagliidae Brook, 1889. A junior objective synonym of Savaliidae Nardo, 1844, and Savagliidae Brook, 1889.

Savalini Nardo, 1844. See Savaliidae Nardo, 1844.

***Sphenopidae** Hertwig, 1882: 120. Type genus *Sphenopus* Steenstrup, 1856.

Zoanthia Rafinesque, 1815. See Zoanthidae Rafinesque, 1815.

***Zoanthidae** Rafinesque, 1815: 155. Type genus *Zoanthus* Lamarck, 1801. First established at the rank of subfamily as "Zoanthia" (an incorrect original spelling). Authorship of the family-group name Zoanthidae is conventionally attributed to Gray (1832: 95; 1840: 72), however Rafinesque's (1815) indication has priority (see Low and Reimer 2012a: 85).

Appendix 2.

Nomenclator of genus-group names in the Zoantharia Rafinesque, 1815

Names in **bold** and designated with an asterisk (*) are considered to be valid genus-group names. In accordance with Article 67.2 of the Code (ICZN 1999: 66, 67), all type species designations made herein are from among the "originally included nominal species". Names marked with a † are invalid synonyms, or incorrect spellings (if further denoted by a "[*sic*]"). Additional names without either designation have been confused with the order Zoantharia at one time or another but have since been removed from this group. The identity of two possible zoantharian genus-group name-*Stephanidium* Hertwig, 1888, and *Triga* Gray, 1867-will need to be resolved.

****Abyssoanthus*** Reimer and Fujiwara, in Reimer, Sinniger, Fujiwara, Hirano and Maruyama, 2007: 258. Type species *Abyssoanthus nankaiensis* Reimer and Fujiwara, in Reimer, Sinniger, Fujiwara, Hirano and Maruyama, 2007, by original designation; gender masculine.

****Acrozoanthus*** Saville-Kent, 1893: 153, 154, unnumbered fig. Type species *Acrozoanthus australiae* Saville-Kent, 1893, by monotypy; gender masculine.

†*Actimastus* Rafinesque, 1818: 271. Replacement name for *Mammillifera* Le Sueur, 1817. Type species *Mammillifera auricula* Le Sueur, 1817, by subsequent designation by Haddon and Shackleton (1891a: 626) (for *Mammillifera* Le Sueur,

1817); gender masculine. Unnecessary replacement name for and junior objective synonym of *Mammilifera* Le Sueur, 1817. Both *Actimastus* Rafinesque, 1818, and *Mammilifera* Le Sueur, 1817, are junior subjective synonyms of *Zoanthus* Lamarck, 1801, as the type species of both genus-group names is now considered to be a species of *Zoanthus* Lamarck, 1801 (see Appendix 3).

Anthozoanthus Carter, 1870: 449. Type species *Anthozoanthus parasiticus*, by monotypy; gender masculine. Not a zoantharian (see Carter 1870: 449). This name appears to be Deshayes manuscript name that was published by Carter (1870).

†*Anthozoon* Gistel, 1848: 181. Unnecessary replacement name and junior objective synonym of *Zoanthus* Lamarck, 1801; gender neuter.

†*Antinedia* Duchassaing de Fonbressin and Michelotti, 1864: 42 (also 1866: 136). Type species *Zoanthus tuberculatus* Duchassaing de Fonbressin, 1850, by monotypy; gender feminine. The type species *Zoanthus tuberculatus* Duchassaing de Fonbressin, 1850, is a junior subjective synonym and junior secondary homonym of *Isaurus tuberculatus* Gray, 1828. A subjective junior synonym of *Isaurus* Gray, 1828 (see Muirhead and Ryland 1985: 325).

†*Actinorhiza* Agassiz, 1846: 7. Unjustified emendation and junior objective synonym of *Actinorhyza* Blainville, 1830. See Appendix 3.

†*Actinorhysa* [*sic*]. Incorrect subsequent spelling of *Actinorhyza* Blainville, 1830, by Blainville (1834: 329). See Appendix 3.

† *Actinorhyza* Blainville, 1830: 295. Type species *Actinia sociata* Ellis, 1768 (see Appendix 3); gender feminine. An unnecessary replacement name for, and junior objective synonym of *Zoanthus* Lamarck, 1801. See also the incorrect subsequent spellings *Actinorhysa* Blainville, 1834, and *Actinorrhyza* Ehrenberg, 1834, and the unjustified emendation *Actinorhiza* Agassiz, 1844. See additional discussion in Appendix 3.

†*Actinorrhyza* [*sic*]. Incorrect subsequent spelling of *Actinorhyza* Blainville, 1830, by Ehrenberg (1834a: 269). See Appendix 3.

Actinocereus Blainville, 1830: 294. No type species designated (see Fautin et al. 2012: 20, 21); gender masculine. Placed in synonymy (in part) of *Hughea* Lamouroux, 1821, by Andres (1881: 336). Currently a genus-group name in the Actiniaria (see Fautin et al. 2012: 20–22; Fautin 2016: 54). *Actinocereus* Blainville, 1830, is now considered a synonym of *Cereus* Ilmoni, 1830, and the International Commission for Zoological Nomenclature was petitioned Fautin et al. (2012: 22) to suppress the former name in favour of the latter, and subsequenty ruled as such (ICZN 2014: 136, 137).

****Antipathozoanthus*** Sinniger, Reimer and Pawlowski, 2010: 61. Type species *Gerardia macaronesicus* Ocaña and Brito, 2003, by original designation; gender masculine.

Axinella O. Schmidt, 1862: 60. Type species *Axinella polypoides* O. Schmidt, 1862 (see Gazave et al. 2010). Not a zoantharian (see Gazave et al. 2010).

****Bergia*** Duchassaing de Fonbressin and Michelotti, 1860: 54. Type species *Bergia catenularis* Duchassaing de Fonbressin and Michelotti, 1860, by subsequent designation by Duerden (1903: 496); gender feminine. The type species was formerly assigned to the genus *Parazoanthus* Haddon and Shackleton, 1891a (see Duerden

1903: 496, Low and Reimer 2011a: 64), making *Bergia* Duchassaing de Fonbressin and Michelotti, 1860, a subjective synonym of *Parazoanthus* Haddon and Shackleton, 1891a. Low and Reimer (2011a) enacted Article 23.9 (ICZN 1999: 27, 28) to reverse precedence between these genus-group names, thereby making *Bergia* Duchassaing de Fonbressin and Michelotti, 1860, a *nomen oblitum*, and *Parazoanthus* Haddon and Shackleton, 1891a, a *nomen protectum*. Recent molecular and morphological work by Montenegro et al. (2015a: 63–71) have shown that the type species, *Bergia catenularis* Duchassaing de Fonbressin and Michelotti, 1860, represents a generic-level monophyly and resurrected the genus-group name *Bergia* Duchassaing de Fonbressin and Michelotti, 1860, for this grouping.

****Bullagummizoanthus*** Sinniger, Ocaña and Baco, 2013: 9. Type species *Bullagummizoanthus emilyacadiaarum* Sinniger, Ocaña and Baco, 2013, by original designation; gender masculine.

†*Carolia* Gray, 1867: 239. Type species *Zoanthus couchii* Johnston, in Couch, 1844, by monotypy; gender feminine. The type species is now assigned to the genus *Epizoanthus* Gray, 1867 (see Haddon and Shackleton 1891a: 644, 645), making *Carolia* Gray, 1867, a subjective synonym of *Epizoanthus* Gray, 1867. The name *Carolia* Gray, 1867, is an invalid junior homonym of *Carolia* Cantraine, 1838 (Mollusca), and the *Epizoanthus* Gray, 1867, is the valid name for this genus-group. See also *Epizoanthus* Gray, 1867.

†*Cavolinia* Schweigger, 1819: 99. No type species designated, for originally included species, see Appendix 3; gender feminine. *Cavolinia* Schweigger, 1819, is a junior homonym of *Cavolinia* Abildgaard, 1791, and is not a valid name (see Appendix 3). See also the unnecessary replacement name *Cynicus* Gistel, 1848.

****Corallizoanthus*** Reimer, in Reimer, Nonaka, Sinniger and Iwase, 2008: 940. Type species *Corallizoanthus tsukaharai* Reimer, in Reimer, Nonaka, Sinniger and Iwase, 2008, by original designation; gender masculine.

†*Corticanthus* Andres, 1883a: 538, 541. Type species *Epizoanthus paguriphilus* Verrill, 1882, herein designated (see Appendix 3); gender masculine. First proposed as a subgenus of *Zoanthus* Lamarck, 1801. The type species is now assigned to the genus *Epizoanthus* Gray, 1867 (see Appendix 3), making *Zoanthus* (*Corticanthus*) Andres, 1883, a junior subjective synonym of *Epizoanthus* Gray, 1867.

†*Corticifera* Le Sueur, 1817: 178, 179. Type species *Corticifera glareola* Le Sueur, 1817, by subsequent designation by Haddon and Shackleton (1891b: 692); gender feminine. The type species is now assigned to the genus *Palythoa* Lamouroux, 1816 (see Appendix 3), making *Corticifera* Le Sueur, 1817, a junior subjective synonym of *Palythoa* Lamouroux, 1816.

†*Corticithoa* Andres, 1883a: 521, 535–538. Type species *Alyconium tuberculosum* Esper, 1805, herein designated (see Appendix 3); gender feminine. First proposed as a subgenus of *Palythoa* Lamouroux, 1816. The type species, *Alcyonium tuberculosum*, is now assigned to the genus *Palythoa* Lamouroux, 1816 (see Appendix 3), making *Palythoa* (*Corticithoa*) Andres, 1883, a junior subjective synonym of *Palythoa* Lamouroux, 1816.

†*Cortificera*. Incorrect spelling of *Corticifera* Le Sueur, 1817, by Brandt (1835: 208).

†*Cynicus* Gistel, 1848: viii. Unnecessary replacement name for, and junior objective synonym of, *Cavolinia* Schweigger, 1819; gender masculine.

Edwardsia de Quatrefages, 1841: 427. Type species *Edwardsia beautempsii* de Quatrefages, 1842, by subsequent designation by Delphy (1938) (see Fautin 2016: 82); gender feminine. Not a zoantharian (see Fautin et al. 2007: 201, Williams 1981a: 326; Fautin 2016: 82, 83).

†*Endeithoa* Andres, 1883a: 521, 531. Type species *Zoanthus norvegicus* Koren and Danielssen, 1877, herein designated (see Appendix 3); gender feminine. First proposed as a subgenus of *Palythoa* Lamouroux, 1816. The type species is now assigned to the genus *Epizoanthus* Gray, 1867 (see Appendix 3), making *Palythoa* (*Endeithoa*) Andres, 1883, a junior subjective synonym of *Epizoanthus* Gray, 1867.

Epiactis Verrill, 1869 (in 1868–1871): 492. Type species *Epiactis prolifera* Verrill, 1869, by monotypy; gender feminine. Not a zoantharian (Fautin et al. 2007: 202; Fautin 2016: 85).

****Epizoanthus*** Gray, 1867: 237. Type species *Dysidea papillosa* Johnston, 1842, by monotypy; gender masculine. Placed on *Official List* and has priority over *Sidisia* Gray, 1858 (see Opinion 1689, ICZN 1992: 236). The subsequent designation of *Mammillifera incrustatus* Düben and Koren, 1847, as the type species of *Epizoanthus* Gray, 1867, by Haddon and Shackleton (1891a: 627) is not valid as this species was not amongst the species originally included in the description of *Epizoanthus* Gray, 1867, and does not qualify for selection as the type species (see Ryland and Muirhead 1991: 19, 20; and Article 69.2 of the Code, ICZN 1999: 72, 73). See also the synonyms *Carolia* Gray, 1867, *Lirrevia* Delphy, 1939: 270, *Mardoell* Danielssen, 1890, *Marodellia* Danielssen, 1890, *Palythoa* (*Endeithoa*) Andres, 1883, *Sidisia* Gray, 1858, *Verrillia* Andres, 1883, and *Zoanthus* (*Corticanthus*) Andres, 1883,

†*Gemmaria* Duchassaing de Fonbressin and Michelotti, 1860: 55. Type species *Gemmaria rusei* Duchassaing de Fonbressin and Michelotti, 1860, by subsequent designation by Haddon and Shackleton (1891a: 626). The genus-group name *Gemmaria* Duchassaing de Fonbressin and Michelotti, 1860, is preoccupied by *Gemmaria* McCrady, 1859 (Hydrozoa). Herein considered to be a junior subjective synonym of *Palythoa* Lamouroux, 1816 (See Appendix 3). See also the replacement names *Haplotella* Stechow, 1919, and *Protopalythoa* Verrill, 1900.

†*Gemmithoa* Andres, 1883a: 521, 532, 533. Type species *Mammillifera brevis* Duchassaing de Fonbressin, 1850, by monotypy; gender feminine. First proposed as a subgenus of *Palythoa* Lamouroux, 1816. The type species is now assigned to the genus *Palythoa* Lamouroux, 1816 (see Appendix 3), making *Palythoa* (*Gemmithoa*) Andres, 1883, a junior subjective synonym of *Palythoa* Lamouroux, 1816.

†*Gerardia* Lacaze-Duthiers, 1864a: 87. Type species *Leoipathes lamarcki* Haime, 1849, by monotypy; gender feminine. A subjective junior synonym of *Savalia* Nardo, 1844 (see Appendix 3). This genus-group name was also described as new in Lacaze-Duthiers (1864c: 175, 176), and appeared as a translation in Lacaze-Duthiers (1864b: 242).

†*Gerardina* [sic]. Incorrect spelling of *Gerardia* Lacaze-Duthiers, 1864, by H. Schmidt (1972: 452).

†*Haplotella* Stechow, 1919: 853. Replacement name for *Gemmaria* Duchassaing de Fonbressin and Michelotti, 1860, preoccupied by *Gemmaria* McCrady, 1859 (Hydrozoa). Type species *Gemmaria rusei* Duchassaing de Fonbressin and Michelotti, 1860, by typification of the preoccupied name; gender feminine. A junior objective synonym of *Gemmaria* Duchassaing de Fonbressin and Michelotti, 1860, and a junior subjective synonym of *Palythoa* Lamouroux, 1816 (see Appendix 3). See also *Gemmaria* Duchassaing de Fonbressin and Michelotti, 1860, *Parapalythoa* Verrill, 1900, and *Protopalythoa* Verrill, 1900.

†*Heterozoanthus* Verrill, 1870: 371. Type species *Palythoa axinellae* O. Schmidt, 1862, by subsequent designation by Low and Reimer (2012a: 84); gender masculine. As *Heterozoanthus* Verrill, 1870, and *Parazoanthus* Haddon and Shackleton, 1891, have the same type species, they are objective synonyms. Low and Reimer (2012a: 84) reversed precedence thereby making *Heterozoanthus* Verrill, 1870, a *nomen oblitum*, and *Parazoanthus* Haddon and Shackleton, 1891, a *nomen protectum*.

Hughaea [*sic*]. Incorrect spelling of *Hughea* Lamouroux, 1821, by Duchassaing de Fonbressin (1850: 9). Not a zoantharian (see *Hughea* Lamouroux, 1821).

Hughea Lamouroux, 1821: 89. Type species *Actinia calendula* Hughes, in Ellis and Solander, 1786, by monotypy; gender feminine. The type species, *Actinia calendula* was described by Ellis, in Ellis and Solander (1786: 7, 8, pl. 1, fig. 3) based on an unnamed cnidarian described and illustrated by Hughes (1750: 293, 294, pl. 24, fig. 1) that is clearly not a zoantharian (see also Ryland and Lancaster 2003: 411; Fautin 2016: 182). *Actinia calendula* Ellis, in Ellis and Solander, 1786, is currently considered to be assigned to the genus *Petalactis* Andres, 1883 (see Fautin 2016: 118), thereby making *Hughea* Lamouroux, 1821, a synonym of *Petalactis* Andres, 1883. Also see the unnecessary replacement name *Meto* Gistel, 1848.

Hughuea [*sic*]. Incorrect spelling of *Hughea* Lamouroux, 1821, by Gistel (1848: 181). Not a zoantharian (see *Hughea* Lamouroux, 1821).

****Hurlizoanthus*** Sinniger, Ocaña and Baco, 2013: 7. Type species *Hurlizoanthus parrishi* Sinniger, Ocaña and Baco, 2013, by original designation; gender masculine.

****Hydrozoanthus*** Sinniger, Reimer and Pawlowski, 2010: 60. Type species *Parazoanthus tunicans* Duerden, 1900, by original designation; gender masculine.

Iluanthos Forbes, 1840: 184. Type species *Iluanthos scoticus* Forbes, 1840, by monotypy; gender masculine. Fautin (2016: 97) considers the correct original spelling of this genus-group name to be "Ilyanthus" following Article 33.3.1 of the Code (ICZN 1999: 43). Not a zoantharian (Fautin et al. 2007: 209; Fautin 2016: 97).

†*Isaua* [*sic*]. Incorrect subsequent spelling of *Isaurus* Gray, 1828, by Volpi and Benvenuti (2003: 72).

†*Isaura* Agassiz, 1844: 14. Unjustified emendation and objective synonym of of *Isaurus* Gray, 1828, and junior homonym of *Isaura* Lamouroux, in Audouin, Bourdon, de Candolle, d'Aubebard de Férussac, Deshayes, Deslongchamps, É. Geoffroy Saint-Hilaire, I. Geoffroy Saint-Hilaire, Guérin, Guillemin, de Jussieu, Kunth, Dela-

fosse, Lamouroux, Latreille, Prévost, Richard and Bory de Saint-Vincent, 1826. See *Isaurus* Gray, 1828.

†*Isaura* Lamouroux, in Audouin, Bourdon, de Candolle, d'Aubebard de Férussac, Deshayes, Deslongchamps, É. Geoffroy Saint-Hilaire, I. Geoffroy Saint-Hilaire, Guérin, Guillemin, de Jussieu, Kunth, Delafosse, Lamouroux, Latreille, Prévost, Richard and Bory de Saint-Vincent, 1826: 23. Type species *Isaurus tuberculatus* Gray, 1828, by subsequent designation by Haddon and Shackleton (1891b: 682); gender masculine. An objective synonym of *Isaurus* Gray, 1828 (see Low and Reimer 2012b: 46). See *Isaurus* Gray, 1828.

****Isaurus*** Gray, 1828: 8. Type species *Isaurus tuberculatus* Gray, 1828, by subsequent designation by Haddon and Shackleton (1891b: 682); gender masculine. The name *Isaurus* Gray, 1828, is a replacement name for *Isaura* Lamouroux, in Audouin, Bourdon, de Candolle, d'Aubebard de Férussac, Deshayes, Deslongchamps, É. Geoffroy Saint-Hilaire, I. Geoffroy Saint-Hilaire, Guérin, Guillemin, de Jussieu, Kunth, Delafosse, Lamouroux, Latreille, Prévost, Richard and Bory de Saint-Vincent, 1826, which Gray (1828: 8) believed to be preoccupied (see Low and Reimer 2012b: 46). Low and Reimer (2012b: 47) reversed the precedence of *Isaura* Lamouroux, in Audouin, Bourdon, de Candolle, d'Aubebard de Férussac, Deshayes, Deslongchamps, É. Geoffroy Saint-Hilaire, I. Geoffroy Saint-Hilaire, Guérin, Guillemin, de Jussieu, Kunth, Delafosse, Lamouroux, Latreille, Prévost, Richard and Bory de Saint-Vincent, 1826, and *Isaurus* Gray, 1828, thereby maintaining current and prevailing usage of the latter name. See also the synonyms *Antinedia* Duchassaing de Fonbressin and Michelotti, 1864, *Pales* Gray, 1867, *Palythoa* (*Monothoa*) Andres, 1883, *Panceria* Andres, 1877, and *Zoanthus* (*Monanthus*) Andres, 1883.

****Isozoanthus*** Carlgren, in Chun, 1903: 520. Type species *Isozoanthus giganteus* Carlgren, in Chun, 1903, by monotypy; gender masculine. Williams (2000) enacted Article 23.9 of the Code (ICZN 1999: 27, 28) to reverse precedence of *Palythoa* (*Taeniothoa*) Andres, 1883, and *Isozoanthus* Carlgren, in Chun, 1903. See also *Palythoa* (*Taeniothoa*) Andres, 1883.

****Kauluzoanthus*** Sinniger, Ocaña and Baco, 2013: 8. Type species *Kauluzoanthus kerbyi* Sinniger, Ocaña and Baco, 2013, by original designation; gender masculine.

****Kulamanamana*** Sinniger, Ocaña and Baco, 2013: 4. Type species *Kulamanamana haumaeaae* Sinniger, Ocaña and Baco, 2013, by original designation; gender feminine.

†*Lirrevia* Delphy, 1939: 270. Replacement name for *Verrillia* Andres, 1883; gender feminine. *Lirrevia* Delphy, 1939, and *Verrillia* Andres, 1883, are thus subjective junior synonyms of *Epizoanthus* Gray, 1867. See also *Verrillia* Andres, 1883.

†*Mamillifera* [*sic*]. Incorrect spelling of *Mammillifera* Le Sueur, 1817, by Blainville (1830: 295).

†*Mammilifera* [*sic*]. Incorrect spelling of *Mammillifera* Le Sueur, 1817, by Gistel (1848: 181).

†*Mammillifera* Le Sueur, 1817: 177. Type species *Mammillifera auricula* Le Sueur, 1817, by subsequent designation by Haddon and Shackleton (1891a: 626); gender

feminine. The type species is now assigned to the genus *Zoanthus* Lamarck, 1801 (see Appendix 3), making *Mammillifera* Le Sueur, 1817, a junior subjective synonym of *Zoanthus* Lamarck, 1801. See also *Actimastus* Rafinesque, 1818.

†*Mammithoa* Andres, 1883a: 521. Type species *Mammillifera nymphaea* Le Sueur, 1817, herein designated (see Appendix 3); gender feminine. First proposed as a subgenus of *Palythoa* Lamouroux, 1816. The type species is now a junior subjective synonym of *Zoanthus pulchellus* Duchassaing de Fonbressin and Michelotti, 1864, which is currently assigned to the genus *Zoanthus* Lamarck, 1801 (see Appendix 3), making *Palythoa* (*Mammithoa*) Andres, 1883, a junior subjective synonym of *Zoanthus* Lamarck, 1801. See also the incorrect original spelling *Mammothoa* Andres, 1883.

†*Mammothoa* [*sic*]. An incorrect original spelling of *Mammithoa* Andres, 1883, by Andres, (1883a: 533–535; 1883b: 325–327; 1884: 318–320) (see Appendix 3).

†*Mardoell* Danielssen, 1890: 117–126. Type species *Mardoell erdmanni* Danielssen, 1890, by monotypy; gender feminine. The type species is assigned to the genus *Epizoanthus* Gray, 1867 (see Low and Reimer 2012a: 85, Lwowsky, 1913: 603, 604), making *Mardoell* Danielssen, 1890, a junior subjective synonym of *Epizoanthus* Gray, 1868. See also the incorrect emendation *Mardoellia* Blanchard, 1893.

†*Mardoella* [*sic*]. Incorrect spelling of *Mardoell* Danielssen, 1890, by Bell (1906: 762) and also in Neave's (1940: 43) *Nomenclator zoologicus* entry.

†*Mardoellia* Blanchard, 1893: 130. Type species *Mardoell erdmanni* Danielssen, 1890, by monotypy; gender feminine. Blanchard (1893: 130) incorrectly emended the genus-group name *Mardoell* Danielssen, 1890, to *Mardoellia* (see Low and Reimer 2012a: 84). *Mardoellia* Blanchard, 1893, is therefore a junior objective synonym of *Mardoell* Danielssen, 1890, and a junior subjective synonym of *Epizoanthus* Gray, 1867. See also *Mardoell* Danielssen, 1890.

****Mesozoanthus*** Sinniger and Häussermann, 2009: 31, 32. Type species *Mesozoanthus fossii* Sinniger and Häussermann, 2009, by original designation and monotypy; gender masculine.

Meto Gistel, 1848: 181. Replacement name for *Hughea* Lamouroux, 1821. Not a zoantharian (see remarks under *Hughea* Lamouroux, 1821).

****Microzoanthus*** Fujii and Reimer, 2011: 421. Type species *Microzoanthus occultus* Fujii and Reimer, 2011, by original designation; gender masculine.

†*Monanthus* Andres, 1883a: 538, 540, 541, 543. Type species *Isaurus tuberculatus* Gray, 1828, herein designated (see Appendix 3); gender masculine. First proposed as a subgenus of *Zoanthus* Lamarck, 1801. The type species is also the type species of *Isaurus* Gray, 1828, making *Zoanthus* (*Monanthus*) Andres, 1883, a junior objective synonym of *Isaurus* Gray, 1828 (see Appendix 3).

†*Monothoa* Andres, 1883a: 521. Type species *Panceria spongiosa* Andres, 1877, herein designated (see Appendix 3); gender feminine. The type species is now a junior subjective synonym of *Isaurus tuberculatus* Gray, 1828, (see Appendix 3), making *Palythoa* (*Monothoa*) Andres, 1883, a junior subjective synonym of *Isaurus* Gray, 1828.

Montlibaldia [*sic*]. Incorrect subsequent spelling of *Montlivaltia* Lamouroux, 1821, by Ehrenberg (1834a: 271).

Montlivaltia Lamouroux, 1821: 78. Type species *Montlivaltia caryophyllata* Lamouroux, 1821, by monotypy; gender feminine. Lamouroux (1821: 78) and Audouin (1826: 229) discussed the similarities of *Montlivaltia* Lamouroux, 1821, and *Palythoa* Lamouroux, 1816. *Montlivaltia* Lamouroux, 1821, is now considered to be a species of Scleractinia (see Stolarski and Roniewicz 2001: 1097).

****Nanozoanthus*** Fujii and Reimer, 2013: 512. Type species *Nanozoanthus harenaceus* Fujii and Reimer, 2013, by original designation; gender masculine.

****Neozoanthus*** Herberts, 1972: 137. Type species *Neozoanthus tulearensis* Herberts, 1972, by original designation and monotypy; gender masculine.

Orinia Duchassaing de Fonbressin and Michelotti, 1860: 54. Type species *Orinia torpida* Duchassaing de Fonbressin and Michelotti, 1860, by monotypy; gender feminine. The type species is considered to be a junior subjective synonym of *Actinia osculifera* Le Sueur, 1817 (see Cha 2007: 40; Fautin 2016: 38). As the type species of *Orinia* Duchassaing de Fonbressin and Michelotti, 1860, is currently a junior subjective synonym of a species assigned to *Rhodactis* Milne Edwards and Haime, 1851 (see Fautin 2016: 38), the former becomes a junior subjective synonym of the latter.

****Palaeozoanthus*** Carlgren, 1924: 470–473. Type species *Palaeozoanthus reticulatus* Carlgren, 1924, by original designation and monotypy; gender masculine.

†*Pales* Gray, 1867: 234, 235. Type species *Pales cliftoni* Gray, 1867, by monotypy; gender masculine. A subjective junior synonym of *Isaurus* Gray, 1828 (see Muirhead and Ryland, 1985: 325). The genus-group name *Pales* Gray, 1867, is also a junior homonym of *Pales* Meigen, 1800 (Diptera), *Pales* Robineau-Desvoidy, 1830 (Diptera), and *Pales* Koch, 1850 (Arachnida).

****Palythoa*** Lamouroux, 1816: 359. Type species *Palythoe* [*sic*] *stellata* Lamouroux, 1816 [= *Alcyonium mammillosum* Ellis, in Ellis and Solander, 1786], subsequent designation by Haddon and Shackleton (1891b: 691); gender feminine. See Appendix 3 for a discussion on the type species and its designation. Frequently incorrectly spelt as “Palythoe” (see Low and Reimer 2011b: 63). See also the synonyms *Cavolinia* Schweigger, 1819, *Corticifera* Le Sueur, 1817, *Cynicus* Gistel, 1848, *Palythoa* (*Corticithoa*) Andres, 1883, *Palythoa* (*Gemmithoa*) Andres, 1883, and the incorrect spellings *Palythoe* and *Polythoa*.

†*Palythoa* (*Corticithoa*) Andres, 1883. See *Corticithoa* Andres, 1883.

†*Palythoa* (*Endeithoa*) Andres, 1883. See *Endeithoa* Andres, 1883.

†*Palythoa* (*Gemmithoa*) Andres, 1883. See *Gemmithoa* Andres, 1883.

†*Palythoa* (*Mammithoa*) Andres, 1883. See *Mammithoa* Andres, 1883.

†*Palythoa* (*Mammothoa*) Andres, 1883. See *Mammothoa* Andres, 1883, and *Mammithoa* Andres, 1883.

†*Palythoa* (*Monothoa*) Andres, 1883. See *Monothoa* Andres, 1883.

†*Palythoa* (*Taeniothoa*) Andres, 1883. See *Taeniothoa* Andres, 1883.

†*Palythoaster* Haeckel, 1875: 44, pl. 1, fig. 5. Type species *Palythoa savignyi* Audouin, 1826, by monotypy; gender masculine. The type species *Palythoa savignyi* Audouin, 1826, is currently assigned to the genus *Palythoa* Lamouroux, 1816, making *Palythoaster* Haeckel, 1875, a junior subjective synonym of *Palythoa* Lamouroux, 1816 (see Appendix 3).

†*Palythoe* [*sic*]. An incorrect spelling of *Palythoa* Lamouroux, 1816 (see Low and Reimer 2011b: 63). See also *Palythoe* Lamouroux, 1812.

Palythoe Lamouroux, 1812: 188. Type species *Gorgonia muricata* Pallas, 1766, by subsequent designation by Low and Reimer (2011b: 64); gender not determined. Now a subjective synonym of *Muricea* Lamouroux, 1821 [Octocorallia] (Low and Reimer 2011b: 64). Not a zoantharian (Low and Reimer 2011b: 63). *Palythoe* is also sometimes used as an incorrect spelling of *Palythoa* Lamouroux, 1816 (see Low and Reimer 2011b: 63).

†*Playthoa* [*sic*]. Incorrect spelling of *Palythoa* Lamouroux, 1816, by various authors (e.g., Milliman et al. 1974: 162).

†*Panceria* Andres, 1877: 221–226. Type species *Panceria spongiosa* Andres, 1877, by monotypy; gender feminine. The type species is a subjective synonym of *Isaurus tuberculatus* Gray, 1828 (see Appendix 3), making *Panceria* Andres, 1877, a junior subjective synonym of *Isaurus* Gray, 1828.

†*Parapalythoa* Verrill, 1900: 560. Type species *Parapalythoa heilprini* Verrill, 1900, by monotypy. Herein considered to be a junior subjective synonym of *Palythoa* Lamouroux, 1816 (see Appendix 3). See also *Protopalythoa* Verrill, 1900.

****Parazoanthus*** Haddon and Shackleton, 1891a: 653, 654. Type species *Palythoa axinellae* O. Schmidt, 1862, by original designation; gender masculine. See also the synonyms *Bergia* Duchassaing de Fonbressin and Michelotti, 1860, *Gemmaria* Duchassaing de Fonbressin and Michelotti, 1860, *Heterozoanthus* Verrill, 1870, *Parapalythoa* Verrill, 1900, and *Protopalythoa* Verrill, 1900.

Peachia Gosse, 1855: 270, 271. Type species *Peachia hastata* Gosse, 1855, by subsequent designation by Carlgren (1949: 32); gender feminine. Not a zoantharian (Fautin et al. 2007: 220, 221; Fautin 2016: 47, 117).

Platyzoanthus Saville-Kent, 1893: 155. Type species *Platyzoanthus mussoides* Saville-Kent, 1893, by monotypy; gender masculine. Not a zoantharian (see Haddon 1898: 409, den Hartog 1980: 37, 39; Fautin 2016, 25, 28).

†*Polyphoa* [*sic*]. Incorrect spelling of *Palythoa* Lamouroux, 1816, by Danielssen (1890: 136). The Danish version of the same text on the same page is spelt "*Polythoa*" (see *Polythoa*).

†*Polythea* [*sic*]. Incorrect spelling of *Palythoa* Lamouroux, 1816, by Gistel (1848: 181).

†*Polythoa* [*sic*]. Incorrect spelling of *Palythoa* Lamouroux, 1816, by Schweigger (1819: 100). Also throughout Andres (1883a, b, 1884).

†*Protopalythoa* Verrill, 1900: 562. Replacement name for *Gemmaria* Duchassaing de Fonbressin and Michelotti, 1860, preoccupied by *Gemmaria* McCrady, 1859 (Hydrozoa). Type species *Gemmaria rusei* Duchassaing de Fonbressin and Michelotti, 1860, by typification of the preoccupied name; gender feminine. Verrill's (1900: 562) original designation of *Gemmaria variabilis* Duerden, 1898, as the type spe-

cies of this genus-group name is invalid (see Appendix 3). See also *Gemmaria* Duchassaing de Fonbressin and Michelotti, 1860.

†*Rhyzanthus* Andres, 1883a: 538, 541–544. Type species *Actinia sociata* Ellis, 1768, herein designated (see Appendix 3); gender masculine. First proposed as a subgenus of *Zoanthus* Lamarck, 1801. The type species is also the type species of the genus *Zoanthus* Lamarck, 1801, making *Zoanthus* (*Rhyzanthus*) Andres, 1883, a junior objective synonym of *Zoanthus* Lamarck, 1801.

†*Savaglia* Nardo, 1877: 674. Unjustified emendation of *Savalia* Nardo, 1844 (see Appendix 3). See *Savalia* Nardo, 1844.

****Savalia*** Nardo, 1844: 433, 434. Type species *Gorgonia savaglia* Bertolini, 1819, by monotypy; gender feminine. *Savalia savaglia* (Bertolini, 1819), and *Gerardia lamarcki* (Haime, 1849), are currently considered subjective synonyms (see Appendix 3). As each species is also the type species of its respective genus, the genera *Savalia* Nardo, 1844, and *Gerardia* Lacaze-Duthiers, 1864, are also subjective synonyms. As discussed in Poche (1914), the valid name for this taxon is *Savalia savaglia* (Bertolini, 1819), which agrees with the Principle of Priority (Article 23, ICZN 1999: 24) (see discussion in Appendix 3). The name *Savaglia* is an unjustified emendation of *Savalia* Nardo, 1844, by Nardo (1877).

Scolanthus Gosse, 1853: 157. Type species *Scolanthus callimorphus* Gosse, 1853, by monotypy. Not a zoantharian (see Manuel 1981: 266; Fautin 2016: 46, 129).

†*Sidisia* Gray, 1858: 489. Type species *Sidisia barleei* Gray, 1859, by subsequent monotypy; gender feminine. *Sidisia* Gray, 1858, was first proposed without the inclusion of any nominal species. In a subsequent paper, Gray (1859: 532) included *Sidisia barleei* Gray, 1859, as the only species in *Sidisia* Gray, 1858, and *Sidisia barleei* Gray, 1859, becomes the type species of *Sidisia* Gray, 1858, by subsequent monotypy (Article 69.3, ICZN, 1999: 73). Subjective synonym of *Epizoanthus* Gray, 1867. *Sidisia* Gray, 1858, was suppressed in favour of *Epizoanthus* Gray, 1867 (see Opinion 1689, ICZN 1992: 236).

Solanthus [*sic*]. Incorrect spelling of *Scolanthus* Gosse, 1853, by Gray (1867: 240).

†*Spenopus* [*sic*]. Incorrect spelling of *Sphenopus* Steenstrup, 1856, by Herberts (1972: 72, 80, 142).

†*Sphaenopus* [*sic*]. Incorrect spelling of *Sphenopus* Steenstrup, 1856, by Long, Poiner and Wassenberg (1995: 134).

****Sphenopus*** Steenstrup, 1856: 37. Type species *Sabella marsupialis* Gmelin, 1791, by original designation; gender masculine.

†*Stephanidium* Hertwig, 1888: 52. Type species *Stephanidium schulzii* Hertwig, 1888, by monotypy; gender neuter. From the original description, the type species is possibly a species of zoantharian, but the type material will need to be located and examined (also see Delage and Hérouard 1901: 662). Herein, we make no decision as to the validity of this genus and species in the event that the identification of this genus and species, but note that this genus-group name is preoccupied by *Stephanidium* Ehrenberg, 1839 (*incerta sedis*).

†*Taeniothoa* Andres, 1883a: 521, 532. Type species *Zoanthus sulcatus* Gosse, 1859, by subsequent designation by Williams (2000: 193); gender feminine. The type species is now assigned to the genus *Isozoanthus* Carlgren, in Chun, 1903 (see Williams 2000: 195), making *Palythoa* (*Taeniothoa*) Andres, 1883, a subjective synonym of *Isozoanthus* Carlgren, in Chun, 1903. Williams (2000: 195) enacted Article 23.9 (ICZN 1999: 27, 28) to reverse precedence between these genus-group names, thereby making *Palythoa* (*Taeniothoa*) Andres, 1883, a *nomen oblitum*, and *Isozoanthus* Carlgren, in Chun, 1903, a *nomen protectum*.

****Terrazoanthus*** Reimer and Fujii, 2010: 20. Type species *Terrazoanthus onoi* Reimer and Fujii, 2010, by original designation; gender masculine.

****Thoracactis*** Gravier, 1918: 12. Type species *Thoracactis topsenti* Gravier, 1918, by monotypy; gender masculine. Gravier (1918: 12, footnote) stated that the etymology of this name was from the Greek word "θοϱαξ, αχος" (= breastplate). It is also clear that Gravier (1918: 12) was using this word in combination with the ending "*-actis*" as commonly used for many other genera of Anthozoa, sea anemones in particular (e.g., *Amphiactis*, *Calliactis*, *Epiactis*, *Monactis*, *Paractis*; see Fautin 2016 for additional examples). In this context, the genus-group names ending with this suffix are to be treated in the same way as *Zoantha* and *Zoanthus* (see Low and Reimer 2012a: 85) in which Article 30.1.3 of the Code (ICZN 1999: 35) applies. The emendation of this name to *Thoracactus* by Walsh (1967: 49) is thus not justified. Also see the unjustified emendation *Thoracactis* by Walsh (1967: 49).

†*Thoracactus* Walsh, 1967: 49. Unjustified emendation (and junior objective synonym) of *Thoracactis* Gravier, 1918.

†*Toracactis* [*sic*]. Incorrect spelling of *Thoracactis* Gravier, 1918, by Herberts (1972: 80).

Triga Gray, 1867: 239. Type species *Triga philippinensis* Gray, 1867, by monotypy; gender feminine. McMurrich (1889: 125) stated that "in all probability this is a *Gemmaria*", considering it to be similar to *G. rusei* Duchassaing de Fonbressin and Michelotti, 1860, which is clearly a species of *Palythoa* Lamouroux, 1812. Heider (1899a: 283; 1899b: 133) cited McMurrich (1889) and agreed, placing this species in *Gemmaria*. Ryland and Lancaster (2003: 411) discussed that "[t]he solitary *Triga philippinesis* Gray, 1867, though tentatively referred to *Gemmaria* by McMurrich (1889), seems more likely to have been an actinian, but Gray's [1867] two-line diagnosis is insufficient even to determine the order with any certainty". The solitary and long polyps of this species would indicate a species belonging to the genus *Sphenopus* Steenstrup, 1856. The final identity of this genus-group name and its type species remain unresolved.

****Umimayanthus*** Montenegro, Sinniger and Reimer, 2015: 76. Type species *Umimayanthus chanpuru* Montenegro, Sinniger and Reimer, 2015, by original designation; gender masculine.

†*Verrillia* Andres, 1883a: 520, 545. Type species *Epizoanthus crassus* Verrill, 1869, by monotypy; gender feminine. The type species is currently assigned to the ge-

nus *Epizoanthus* Gray, 1867, making *Verrillia* Andres, 1883, a junior subjective synonym of *Epizoanthus* Gray, 1867 (see Appendix 3). *Verrillia* Andres, 1883, is preoccupied by *Verrillia* Stearns, 1873 (Scleractinia), and the name *Lirrevia* was proposed by Delphy (1939: 270) was proposed as a replacement name. See also *Lirrevia* Delphy, 1939.

****Zibrowius*** Sinniger, Ocaña and Baco, 2013: 7. Type species *Zibrowius ammophilus* Sinniger, Ocaña and Baco, 2013, by original designation; gender masculine.

†*Zoantha* Lamarck, 1801: 363. Type species *Actinia sociata* Ellis, 1768, by monotypy; gender feminine. This is an incorrectly Latinised spelling of a name derived from Greek and should be corrected to *Zoanthus* (see Article 30.1.3, ICZN 1999: 35). This name was first correctly emended by Tilesius (1809: 374, footnote) (see Low and Reimer 2012a: 85). See also *Zoanthus* Lamarck, 1801.

†*Zoanthella* van Beneden, 1897: 196. No type species designated. This name was established for zoantharian larvae of and is no longer in use as genus-group name (see Ryland et al. 2000: 191). Nevertheless, this name remains nomenclaturally available despite still being used as name for larvae.

†*Zoanthina* van Beneden, 1897: 200. No type species designated. This name was established for zoantharian larvae of and is no longer in use as genus-group name (see Ryland *et al.* 2000: 191). Nevertheless, this name remains nomenclaturally available despite still being used as name for larvae.

****Zoanthus*** Lamarck, 1801: 363. Type species *Actinia sociata* Ellis, 1768, by monotypy; gender masculine. The name *Zoanthus* is derived from the Greek words ζωο (zoo = animal) and ανθος (anthos = flower). According to Article 30.1.3 (ICZN 1999: 35), the Greek ending "-os" should be latinised to the Latin masculine *-us*. Cuvier (1800: tables 9, 10) first used the name "*Zoanthus*", but without the inclusion of species or a description and is a *nomen nudum*. Lamarck (1801: 363) next used the name *Zoantha* with the inclusion of *Actinia sociata* Ellis, 1768, the type species by monotypy. It is possible that Lamarck (1801) assumed that the gender of the Greek word for flower was feminine. Tilesius (1809: 394, footnote) first emended Lamarck's (1801) name to *Zoanthus*. This emendation is conventionally attributed to Cuvier (1816: 53) (see also Haddon and Shackleton 1891b, 676; Low and Reimer 2012a: 85). See also the synonyms *Actimastus* Rafinesque, 1818, *Actinorhyza* Blainville, 1830, *Anthozoon* Gistel, 1848, *Mammillifera* Le Sueuer, 1817, *Palythoa* (*Mammithoa*) Andres, 1883, *Zoanthus* (*Rhyzanthus*) Andres, 1883, and incorrect original spelling *Zoantha* Lamarck, 1801.

†*Zoanthus* (*Corticanthus*) Andres, 1883. See *Corticanthus* Andres, 1883**.**

†*Zoanthus* (*Monanthus*) Andres, 1883. See *Monanthus* Andres, 1883.

†*Zoanthus* (*Rhyzanthus*) Andres, 1883. See *Rhyzanthus* Andres, 1883.

†*Zooanthus* [*sic*]. Incorrect spelling of *Zoanthus* Lamarck, 1801 (e.g. Carlos et al. 1999: 1057, Kenny 2008: 78, Untawale and Dhargalkar 2002: 113).

Appendix 3.

Taxonomic and nomenclatural remarks on some previous unidentified or problematic family- and genus-group names in the Zoantharia Rafinesque, 1815

In this section, previously unidentified (or problematic) genus-group names have been grouped according to the senior synonym that they have been identified with. Two problematic groups of genus-group names are discussed last: 1) *Gemmaria* Duchassaing de Fonbressin and Michelotti, 1860, *Parapalythoa* Verrill, 1900, *Protopalythoa* Verrill, 1900, and *Haplotella* Stechow, 1919; and 2) *Savalia* Nardo, 1844, *Savaglia* Nardo, 1877, and *Gerardia* Lacaze-Duthiers, 1864.

Synonyms of *Epizoanthus* Gray, 1867 (Epizoanthidae) (I): *Corticanthus* Andres, 1883, and *Endeithoa* Andres, 1883

The genus-group name *Corticanthus* was proposed as a subgenus of *Zoanthus* Lamarck, 1801 by Andres (1883a: 538, 541, 544; 1883b: 330, 333, 336; 1884: 323, 326, 327, 329) with the inclusion of *Epizoanthus paguriphilus* Verrill, 1882, *Mammillifera anduzii* Duchassaing de Fonbressin and Michelotti, 1860, *Mammillifera conferta* Verrill, 1869, and *Mammillifera nitida* Verrill, 1869. *Epizoanthus paguriphilus*, is herein designated as the type species of *Zoanthus* (*Corticanthus*) Andres, 1883, making this genus-group name a subjective junior synonym of *Epizoanthus* Gray, 1867, as the type species is now assigned to the genus *Epizoanthus* (Pax and Müller, 1956: 12, 13; Reimer et al. 2010b: 730, 733, Walsh 1967: 45, 46).

The genus-group name *Endeithoa* was proposed as a subgenus of *Palythoa* by Andres (1883a: 521, 531; 1883b: 313, 323; 1884: 307, 316, 317) with the inclusion of *Zoanthus norvegicus* Koren and Danielssen, 1877, and *Zoanthus rubricornis* Holdsworth, 1861. *Zoanthus norvegicus* is herein designated as the type species of *Polythoa* (*Endeithoa*) making this genus-group name a subjective junior synonym of *Epizoanthus*, as the type species is now assigned to the genus *Epizoanthus* Gray, 1867 (Carreiro-Silva et al. 2011: 408, 413, Walsh 1967: 45).

Synonyms of *Epizoanthus* Gray, 1867 (Epizoanthidae) (II): *Lirrevia* Delphy, 1939, and *Verrillia* Andres, 1883

The genus-group name *Verrillia* was proposed by Andres (1883a: 520, 545; 1883b: 312, 337; 1884: 306, 330, 331) with the inclusion of only *Epizoanthus crassus* Verrill, 1869, the type species by monotypy (Article 68.3 of the Code; ICZN 1999: 71). *Epizoanthus crassus* Verrill, 1869, is currently assigned to the genus *Epizoanthus* Gray, 1867 (Lwowsky 1913: 560, Walsh, 1967: 39), and *Verrillia* is thus a junior subjective synonym of *Epizoanthus* Gray, 1867. *Verrillia* Andres, 1883, is not a valid name as it is a junior homonym of *Verrillia* Stearns, 1873, which was proposed for a genus of scleractinian coral. Delphy (1939: 269, 270) proposed the replacement name *Lirrevia*, which is an objective synonym of *Verrillia* Andres, 1883, and a junior subjective synonym of *Epizoanthus* Gray, 1867.

Synonyms of *Isaurus* Gray, 1828 (Zoanthidae): *Monanthus* Andres, 1883, *Monothoa* Andres, 1883, and *Panceria* Andres, 1877

Muirhead and Ryland (1985: 325) listed *Polythoa* (*Monothoa*) Andres, 1883, *Zoanthus* (*Monanthus*) Andres, 1883, and *Panceria* Andres, 1877, as synonyms of *Isaurus* Gray, 1828, but did not give details for this synonymy. Herein, type species are designated for *Polythoa* (*Monothoa*) Andres, 1883, and *Zoanthus* (*Monanthus*) Andres, 1883, to formally fix the identity of these genus-group names. The nomenclatural consequences of our type species designations are in agreement with the taxonomic conclusions of Muirhead and Ryland (1985).

The genus-group name *Monothoa* was proposed as a subgenus of *Palythoa* Lamouroux, 1816, by Andres (1883a: 521, 530, 537; 1883b: 313, 322, 329; 1884: 307, 315, 316, 322) with the inclusion of *Hughaea caraibeorum* Duchassaing de Fonbressin, 1850, *Mamillifera fulva* Quoy and Gaimard, 1834, *Mamillifera vanikorensis* Quoy and Gaimard, 1834, *Mamillifera viridifusca* Quoy and Gaimard, 1834, *Panceria spongiosa* Andres, 1877, and *Triga philippinensis* Gray, 1867. *Panceria spongiosa* Andres, 1877, is herein designated as the type species of *Polythoa* (*Monothoa*) Andres, 1883. *Panceria spongiosa* Andres, 1877, is currently considered to be a junior subjective synonym of *Isaurus tuberculatus* Gray, 1828 (Muirhead and Ryland, 1985: 326), and *Polythoa* (*Monothoa*) Andres, 1883, becomes a junior subjective synonym of *Isaurus* Gray, 1828.

The genus-group name *Monanthus* was proposed as a subgenus of *Zoanthus* Lamarck, 1801, by Andres (1883a: 538, 540, 541, 543; 1883b: 330, 332, 333, 335; 1884: 323, 325, 326, 328, 329) with the inclusion of *Isaurus tuberculatus* Gray, 1828, *Isaura neglecta* Duchassaing de Fonbressin and Michelotti, 1860, *Pales cliftoni* Gray, 1867, and *Palythoa savignyi* Audouin, 1826. *Isaurus tuberculatus* Gray, 1828, is herein designated as the type species of *Zoanthus* (*Monanthus*) Andres, 1883, thereby making *Zoanthus* (*Monanthus*) Andres, 1883, a junior objective synonym of *Isaurus* Gray, 1828, as they have the same type species (Article 61.3.3 of the Code, ICZN 1999: 64) (also see Low and Reimer 2012b: 47).

The genus-group name *Panceria* was proposed by Andres (1877: 221, 226) with the inclusion of *Panceria spongiosa* Andres, 1877, the type species by monotypy (Article 68.3 of the Code, ICZN 1999: 71). As discussed above, *Panceria spongiosa* Andres, 1877, is a junior subjective synonym of *Isaurus tuberculatus* Gray, 1828 and *Panceria* Andres, 1877, becomes a junior subjective synonym of *Isaurus* Gray, 1828.

Synonyms of *Palythoa* Lamouroux, 1816 (Sphenopidae) (I): *Cavolinia* Schweigger, 1819, and *Cynicus* Gistel, 1848

Schweigger (1819: 99, 100) proposed the genus-group name *Cavolinia* for two species of zoanthids: *Alcyonium mammillosum* Ellis, in Ellis and Solander, 1786 (incorrectly spelt as "*mamillosum*"), and *Cavolinia rosea* Schweigger, 1819 (an unnecessary replacement name for *Madrepora denudata* Cavolini, 1785). *Alcyonium mammillosum* Ellis, in Ellis and Solander, 1786, and *Madrepora denudata* Cavolini, 1785 (and therefore *Cavolinia rosea* Schweigger, 1819), are now assigned to the genus *Palythoa* Lamouroux, 1816 (see Milne Edwards 1857: 301, Ryland and Lancaster 2003: 410), making *Cavolinia* Schweigger, 1819, a junior subjective synonym of *Palythoa* Lamouroux, 1816.

No type species has been designated for *Cavolinia* Schweigger, 1819, and no designation is necessary as *Cavolinia* Schweigger, 1819, is an invalid junior homonym of *Cavolinia* Abildgaard, 1791 (Mollusca), and *Cavolinia* Bruguière, 1791 (Mollusca), and has been placed on the *Official Index of Rejected and Invalid Generic Names in Zoology* (see ICZN 1969: 28).

The replacement name *Cynicus* was proposed by Gistel (1848: viii) for *Cavolinia* Schweigger, 1819. *Cynicus* Gistel, 1848, is therefore an unnecessary replacement name for, and junior objective synonym of, *Cavolinia* Schweigger, 1819.

Synonyms of *Palythoa* Lamouroux, 1816 (Sphenopidae) (II): *Corticifera* Le Sueur, 1817, *Corticithoa* Andres, 1883, and *Gemmithoa* Andres, 1883

The genus-group name *Corticifera* was proposed by Le Sueur (1817: 178, 179) with the inclusion of *Corticifera flava* Le Sueur, 1817, and *Corticifera glareola* Le Sueur, 1817. Haddon and Shackleton (1891b: 692) designated *Corticifera glareola* Le Sueur, 1817, as the type species of *Corticifera* Le Sueur, 1817. As the type species of *Corticifera*, is currently assigned to genus *Palythoa*, *Corticifera*, is now a junior subjective synonym of *Palythoa* (see also Haddon and Shackleton 1891b: 692).

The genus-group name *Corticithoa* was proposed as a subgenus of *Palythoa* by Andres (1883a: 521, 535–538; 1883b: 313, 327–330; 1884: 307, 320–323) with the inclusion of *Alyconium tuberculosum* Esper, 1805, *Corticifera aggregata* Lesson, 1830, *Corticifera glareola* Le Sueur, 1817, *Gemmaria humilis* Verrill, 1869, *Mammillifera clavata* Duchassaing de Fombressin, 1850, *Mamillifera lutea* Quoy and Gaimard, 1834, and *Palythoa cinerea* Duchassaing de Fonbressin and Michelotti, 1864. *Alyconium tuberculosum* Esper, 1805, is herein designated as the type species of *Palythoa* (*Corticithoa*) Andres, 1883. *Alyconium tuberculosum*, is currently assigned to the genus *Palythoa* (see Reimer et al. 2006: 92, Ryland and Lancaster 2003: 409, 410, Walsh 1967: 19, 20). By this type species designation, *Palythoa* (*Corticithoa*) Andres, 1883, becomes a junior subjective synonym of *Palythoa*.

The genus-group name *Gemmithoa* was proposed as a subgenus of *Palythoa*, by Andres (1883a: 521, 532, 533; 1883b: 313, 324, 325; 1884: 307, 318) with the inclusion of *Mammillifera brevis* Duchassaing de Fonbressin, 1850, the type species by monotypy (Article 68.3 of the Code; ICZN 1999: 71). *Mammillifera brevis* Duchassaing de Fombressin, 1850, is now assigned to the genus *Palythoa* (see Walsh 1967: 5), making *Polythoa* (*Gemmithoa*) Andres, 1883, a junior subjective synonym of *Palythoa* Lamouroux, 1816.

Synonyms of *Palythoa* Lamouroux, 1816 (Sphenopidae) (III): *Palythoaster* Haeckel, 1875

Haeckel (1875: 44, pl. 1, fig. 5) proposed the name *Palythoaster* for a single species, *Palythoa savignyi* Audouin, 1826, the type species by monotypy (Article 68.3 of the Code, ICZN 1999: 71). Although the date on the title-page of the work by Haeckel is "1876", it was available in 1875 (see Leuckart 1875: 463).

Ehrenberg (1834a: 269; 1834b: 45) considered *Palythoa savignyi* Audouin, 1826, to be a valid species of zoantharian, but placed it in the genus *Hughea* Lamouroux, 1821. The genus *Hughea* Lamouroux, 1821, has long been confused for a genus of a zoantharian, which it is not (see Ryland and Lancaster 2003: 411; Appendix 2).

As discussed by Low and Reimer (2012b), the name *Palythoa savignyi* was proposed by Audouin (1826: 229) for an unnamed figured by Savigny (1811: pl. 2, fig. 1) from Egypt. Based on the figure and the other information provided by Savigny (1811) and Audouin (1826), we herein agree with the opinion of Ehrenberg (1834a: 269; 1834b: 45) in considering *Palythoa savignyi* Audouin, 1826, to be a valid species of zoantharian, but unlike this previous author, we consider it to be a species of *Palythoa* Lamouroux, 1816.

As the type species of the genus *Palythoaster* Haeckel, 1875, is considered to be a species of *Palythoa* Lamouroux, 1816, the former becomes a junior subjective synonym of the latter.

Synonyms of *Zoanthus* Lamarck, 1801 (Zoanthidae) (I): *Actimastus* Rafinesque, 1818, and *Mammillifera* Le Sueur, 1817

The genus-group name *Mammillifera* was proposed by Le Sueur (1817: 177, 178) with the inclusion of *Mammillifera auricula* Le Sueur, 1817, and *Mammillifera nymphaea* Le Sueur, 1817. *Mammillifera auricula* was designated as the type species of *Mammillifera* (see Haddon and Shackleton 1891a: 626). As the type species *Mammillifera auricula* is currently assigned to the genus *Zoanthus* Lamarck, 1801 (Duerden 1898: 334, Walsh 1967: 22, Reimer, et al. 2012a: 7), *Mammillifera* Le Sueur, 1817, and *Zoanthus* Lamarck, 1801, are subjective synonyms.

Rafinesque (1818: 271) proposed the name *Actimastus* to replace *Mammillifera* Le Sueur, 1817, stating that "*Mammillifera* of Lesueur, is rather too long; it is too much like *Mammillaria* in meaning and sense, and is composed of two Latin names united, which are tolerated in the specific nomenclature, but not often in the generic; lastly it has too much likeness to the classical name of Mammalia to be tolerated. It must then be changed into *Actimastus*; meaning radiated mammilla". As it is an unjustified emendation of *Mammillifera* Le Sueur, 1817 (Article 19.1 of the Code, ICZN 1999: 21), *Actimastus* Rafinesque, 1818, becomes a junior objective synonym of *Mammillifera* Le Sueur, 1817.

Synonyms of *Zoanthus* Lamarck, 1801 (Zoanthidae) (II): *Actinorhiza* Agassiz, 1846, and *Actinorhyza* Blainville, 1830

In a discussion on the genus *Zoanthus* Lamarck, 1801, Blainville (1830: 295) proposed the replacement name *Actinorhyza* for this genus-group stating only "[c]e genre, dans notre Système de nomenclature, pourroit ètre nommé Actinorhyse, *Actinorhyza*". We herein consider the name *Actinorhyza* Blainville, 1830, to be an unnecessary replacement name for, and junior objective synonym of, *Zoanthus* Lamarck, 1801. The type species is thus identical to that of *Zoanthus* Lamarck, 1801 (viz., *Actinia sociata* Ellis, 1768) (Article 67.8 of the Code, ICZN 1999: 68). In a later publication, Blainville (1834: 329) spelt the name as *Actinorhysa*, an incorrect subsequent spelling. Another incorrect subsequent spelling is *Actinorrhyza*, as used by Ehrenberg (1834a: 269).

Agassiz (1846: 7) proposed the unjustified emendation *Actinorhiza* for *Actinorhyza* Blainville, 1830, and the former is a junior objective synonym of the latter (Article 19.1 of the Code, ICZN, 1999: 21).

Synonyms of *Zoanthus* Lamarck, 1801 (Zoanthidae) (III): *Mammithoa* Andres, 1883, "*Mammothoa*" Andres, 1883, and *Rhyzanthus* Andres, 1883

The genus-group name *Mammithoa* was proposed as a subgenus of *Palythoa* Lamouroux, 1816, by Andres (1883a: 521, 533–535; 1883b: 313, 325–327; 1884: 307, 318–320). In the preliminary introduction to the newly proposed genus-group names, Andres (1883a: 521; 1883b: 313; 1884: 307) listed the name as *Polythoa* (*Mammithoa*) and included six species under this grouping: *Mammillifera auricula* Lesueur, 1817, *Mamillifera cingulata* Quoy and Gaimard, 1834, *Mammillifera nymphaea* Le Sueur, 1817, *Mammillifera univittata* Lorenz, 1860, *Mamillifera viridis* Quoy and Gaimard, 1834.

In a more detailed listing of the species included in the genus-group, the name was spelt as "*Mammothoa*" (Andres 1883a: 533–535; 1883b: 325–327; 1884: 318–320). As the genus-group names *Mammithoa* and *Mammothoa* were both used in the same publication (Andres 1883a: 521, 533–535), they were made available simultaneously and are both available names. First reviser action is herein taken to select *Mammithoa* Andres, 1883, as the correct original spelling (Article 24.2.3 of the Code, ICZN 1999: 30).

In this detailed listing of the genus-group name *Mammithoa* (incorrectly spelt as *Mammothoa*), Andres (1883a: 534, 535) discussed the included species as discussed above but with the name "*Polythoa* (*Mammithoa*) *nymphosa* Dana", being used in place of *Mammillifera nymphaea* Le Sueur, 1817. From the synonymy of "*Polythoa* (*Mammithoa*) *nymphosa* Dana", it is clear that the species-group name "*nymphosa* Dana" was a replacement for *nymphaea* Le Sueur, 1817. Although the species-group name *nymphosa* was attributed to Dana (see also Walsh 1967: 28), this species-group name was never used by Dana, and the authorship of *Polythoa* (*Mammithoa*) *nymphosa* should be attributed to Andres (1883a: 534, 535), and the name is herein considered an unnecessary replacement name for (and objective synonym of) *Mammillifera nymphaea* Le Sueur, 1817.

Mammillifera nymphaea Le Sueur, 1817, is herein designated as the type species of *Polythoa* (*Mammithoa*) Andres, 1883. *Mammillifera nymphaea* Le Sueur, 1817, is currently considered to be a subjective synonym of *Zoanthus pulchellus* Duchassaing de Fonbressin and Michelotti, 1864 (Acosta et al. 2005: 160, Duerden, 1898: 334, Reimer et al. 2012a: 7). *Zoanthus pulchellus* Duchassaing de Fonbressin and Michelotti, 1864, is currently assigned to the genus *Zoanthus* Lamarck, 1801 (Acosta et al. 2005: 160, Reimer et al. 2012a: 7, Walsh 1967: 29) and *Polythoa* (*Mammithoa*) Andres, 1883, therefore becomes a junior subjective synonym of *Zoanthus* Lamarck, 1801.

The genus-group name *Rhyzanthus* was proposed as a subgenus of *Zoanthus* Lamarck, 1801, by Andres (1883a: 538, 541–544; 1883b: 330, 334–336; 1884: 306, 330, 331) with the inclusion of *Actinia sociata* Ellis, 1768, *Zoanthus alderi* Gosse, 1859, *Zoanthus dubia* Lesueur, 1817, *Zoanthus mertensii* Brandt, 1835, and *Zoanthus solandri* Lesueur, 1817. *Actinia sociata* Ellis, 1768, is herein designated as the type species of *Zoanthus* (*Rhyzanthus*) Andres, 1883, thereby making this genus-group name an objective junior synonym of *Zoanthus* Lamarck, 1801, as they have the same type species (Article 61.3.3 of the Code, ICZN 1999: 64).

Gemmaria Duchassaing de Fonbressin and Michelotti, 1860, and its replacement names *Protopalythoa* Verrill, 1900, and *Haplotella* Stechow, 1919, junior subjective synonyms of *Palythoa* Lamouroux, 1816, as well as comments on *Parapalythoa* Verrill, 1900

The genus-group name *Gemmaria* was first proposed by Duchassaing de Fonbressin and Michelotti (1860: 55) with the inclusion of four nominal species: *Gemmaria rusei* Duchassaing de Fonbressin and Michelotti, 1860, *Gemmaria swiftii* Duchassaing de Fonbressin and Michelotti, 1860, *Mammillifera brevis* Duchassaing de Fonbressin, 1850, and *Mammillifera clavata* Duchassaing de Fonbressin, 1850. No type species was designated.

The identity of *Gemmaria* Duchassaing de Fonbressin and Michelotti, 1860, was debated by early workers. Duerden (1898: 353; 1903: 501) considered *Gemmaria swiftii* Duchassaing de Fonbressin and Michelotti, 1860, to be a species of *Parazoanthus* Haddon and Shackleton, 1891, and transferred this species to the genus. The assignment of *Gemmaria swiftii* Duchassaing de Fonbressin and Michelotti, 1860, to the genus *Parazoanthus* Haddon and Shackleton, 1891, remains the prevailing opinion (e.g. Ryland and Lancaster 2003: 410, Reimer et al. 2014a: 1, 3–7). *Mammillifera clavata* Duchassaing de Fonbressin, 1850, was considered by Reimer et al. (2012a: 8, 9) to be a valid species of *Palythoa* Lamouroux, 1816. The assignment of *Mammillifera brevis* Duchassaing de Fonbressin, 1850, to the genus *Epizoanthus* Gray, 1867, by workers such as Andres (1884: 311) was questioned by Haddon and Shackleton (1891b: 687), who nevertheless stated that "neither *G. swiftii* nor *G. brevis* would appear to belong to the same genus as the type species, nor is it certain that *G. clavata* does either".

It was probably for these reasons that Haddon and Shackleton (1891a: 626) designated *Gemmaria rusei* Duchassaing de Fonbressin and Michelotti, 1860, as the type species of *Gemmaria* Duchassaing de Fonbressin and Michelotti, 1860. The spelling of the type species, *Gemmaria rusei* Duchassaing de Fonbressin and Michelotti, 1860, requires some discussion. The International Commission on Zoological Nomenclature (ICZN 1998: 121, 122) ruled that the spellings of two genus- and species-group names derived from the surname Riise but earlier incorrectly spelled as Rüsei by Duchassaing de Fonbressin and Michelotti (see Bayer and Grasshoff 1997: 11) should be corrected. However, *Gemmaria rusei* Duchassaing de Fonbressin and Michelotti, 1860, was not one of the names that was ruled on. The spelling of the type species of *Gemmaria* Duchassaing de Fonbressin and Michelotti, 1860, should thus remain as *Gemmaria rusei* Duchassaing de Fonbressin and Michelotti, 1860 (but see also Ryland and Lancester 2003: 410).

The genus-group name *Gemmaria* Duchassaing de Fonbressin and Michelotti, 1860, is however not a valid name as it is a junior homonym of *Gemmaria* McCrady, 1859. The genus-group name *Gemmaria* was conditionally proposed by McCrady (1859: 151) for a new species of hydrozoan, *Zanclea gemmosa*, described in the same paper. Although the genus-group name *Gemmaria* McCrady, 1859, is currently considered to be a junior synonym of *Zanclea* Gegenbaur, 1856 (see Schuchert 2010: 487), it nevertheless remains an available name. *Gemmaria* Duchassaing de Fonbressin and Michelotti, 1860, therefore remains an invalid name as it is preoccupied by *Gemmaria* McCrady, 1859 (Article 53.2 of the Code, ICZN 1999: 57).

Realising this homonymy, Verrill (1900: 562) wrote: "*Protopalythoa* nom. nov. Type *G. variabilis* Duerden. *Gemmaria* Duch. and Mich., Corall. Antill., p. 55, 1860, (non McCready [*sic*], 1859)". As *Protopalythoa* Verrill, 1900, was explicitly proposed as a replacement name for *Gemmaria* Duchassaing de Fonbressin and Michelotti, 1860 (preoccupied by *Gemmaria* McCrady, 1859), the designation of *Gemmaria variabilis* Duerden, 1898, as the type species of *Protopalythoa* Verrill, 1900, is invalid.

Article 67.8 of the Code (ICZN 1999: 68) states that "[i]f an author publishes a new genus-group name expressly as a new replacement name (*nomen novum*) for a previously established name … both the prior nominal taxon and its replacement have the same type species, and type fixation for either applies also to the other, despite any statement to the contrary".

The type species of *Protopalythoa* Verrill, 1900, is therefore *Gemmaria rusei* Duchassaing de Fonbressin and Michelotti, 1860, as this is the type species of *Gemmaria* Duchassaing de Fonbressin and Michelotti, 1860 (as designated by Haddon and

Shackleton 1891a: 626). *Protopalythoa* Verrill, 1900, is therefore an objective synonym of *Gemmaria* Duchassaing de Fonbressin and Michelotti, 1860.

In their important paper on *Protopalythoa* Verrill, 1900, Ryland and Lancaster (2003: 410, 411) followed Verrill's (1900: 562) incorrect type species designation of *Gemmaria variabilis* Duerden, 1898, as the type species of *Protopalythoa* Verrill, 1900. Ryland and Lancaster (2003: 410, 411) stated: "*Gemmaria* Duchassaing and Michelotti, 1860, was introduced for *G. Rusei* nov., *Mamillifera clavata* Duchassaing, 1850, *G. swifti* nov. (= *Parazoanthus swifti*), and *M. brevis* Duchassaing, 1850, with no designation of type species. *Protopalythoa* Verrill, 1900 was a *nomen novum* because *Gemmaria* was preoccupied by *Gemmaria* McCrady, 1857 (cited as McCready, 1859), a hydroid. Verrill designated *Gemmaria variabilis* Duerden, 1898, as type species, on the grounds that *G. riisei* (sic: *G. rusei*) was unrecognisable and Duchassaing and Michelotti's other species were not congeners". Ryland and Lancaster (2003: 410, 411) considered the characters exhibited by *Gemmaria variabilis* Duerden, 1898 (and other congeners) to be sufficiently different from *Alcyonium mammillosum* Ellis, in Ellis and Solander, 1786 (an objective synonym of the type species of *Palythoa* Lamouroux, 1816), to require a genus-group of their own, for which they used *Protopalythoa* Verrill, 1900.

But what is the real identity of *Protopalythoa* Verrill, 1900? The identity of the genus-group *Protopalythoa* Verrill, 1900, then rests on the identity of its type species *Gemmaria rusei* Duchassaing de Fonbressin and Michelotti, 1860. Volpi and Benvenuti (2003: 66) listed the existence of a syntype of *Gemmaria rusei* Duchassaing de Fonbressin and Michelotti, 1860, at the Museo di Storia Naturale Università di Firenze (accession number: MZUF 847). Through the assistance of C. Volpi and S. Bambi, we have been able to examine high-resolution photographs of the syntype. The images clearly show a species of *Palythoa* Lamouroux, 1816, based on sampling information (depth, locality, etc.) and heavy sand encrustation of the polyps, and therefore *Gemmaria rusei* Duchassaing de Fonbressin and Michelotti, 1860, is referable to the genus *Palythoa* Lamouroux, 1816, as is currently defined.

Although the specific identity of *Gemmaria rusei* Duchassaing de Fonbressin and Michelotti, 1860, will require further research, we herein assign this species-group taxon to *Palythoa* Lamouroux, 1816. *Protopalythoa* Verrill, 1900, thus becomes a junior subjective synonym of *Palythoa* Lamouroux, 1816. Likewise, the preoccupied genus-group name *Gemmaria* Duchassaing de Fonbressin and Michelotti, 1860, as well as *Parapalythoa* Verrill, 1900 (discussed below), and *Haplotella* Stechow, 1919 (also discussed below), become junior subjective synonyms of *Palythoa* Lamouroux, 1816.

Verrill (1900: 562, 1907: 287) himself had already observed the close affinity between *Protopalythoa* Verrill, 1900, and *Palythoa* Lamouroux, 1816, stating "[t]he name *Gemmaria* having been preoccupied in Hydrozoa, it is necessary to give a new one to this group, if it is to be considered as really distinct from *Palythoa*, from which it seems to differ only in the fact that the zoöids are not united together laterally by coenenchyma, but only by stolons or based expansions. Some species of *Palythoa* are not thus united for more than half their height, or even less, and perhaps future discoveries may show a complete gradation between the two conditions" (Verrill 1900: 562). Similarly, Verrill (1907: 287) also discussed that: "[s]hould they [i.e., the species assigned to *Protopalythoa*] ultimately prove to be identical, it would probably be necessary to unite the genus *Protopalythoa* (= *Gemmaria* of many authors) to *Palythoa* … The only tangible difference between the two genera is the presence in the latter of a thick crust-like coenenchyma, uniting the polyps together laterally. But in this species they are often united for less than half their height".

Two other genus-group names need to be discussed. *Parapalythoa* Verrill, 1900, is another genus-group name that needs to be discussed in connection with *Gemmaria* Duchassaing de Fonbressin and Michelotti, 1860. Verrill (1900: 560) proposed the name *Parapalythoa* for specimens of "*Gemmaria Rusei*" described by McMurrich (1889: 124, 125) from Bermuda. Verrill (1900: 560) considered the material studied by McMurrich (1889) to be distinct from *Gemmaria rusei* Duchassaing de Fonbressin and Michelotti, 1860, and proposed that they should be called *Parapalythoa heilprini*. Although Verrill (1907: 283) later stated that the genus-group name *Parapalythoa* was an error for *Protopalythoa*, this statement has no bearing on the availability of the genus-group name *Parapalythoa*, and the name remains an available one, with *Parapalythoa heilprini* Verrill, 1900, being the type species by monotypy. Regardless of the validity of *Parapalythoa heilprini* Verrill, 1900, it is clear that Verrill (1900: 560) was intending to establish a new genus-group for a taxon similar to, but distinct from, *Gemmaria rusei* Duchassaing de Fonbressin and Michelotti, 1860. As discussed above, *Gemmaria rusei* Duchassaing de Fonbressin and Michelotti, 1860, is herein considered to be a species of *Palythoa* Lamouroux, 1816, and as the differences in the specimens of "*Gemmaria rusei*" described by McMurrich (1889: 124, 125) not being sufficient for a distinction at the genus-group level, we herein consider *Parapalythoa* Verrill, 1900, to also be a junior subjective synonym of *Palythoa* Lamouroux, 1816.

A final name that needs to be discussed in connection with *Gemmaria* Duchassaing de Fonbressin and Michelotti, 1860, is *Haplotella* Stechow, 1919. Stechow (1919: 853) proposed the name *Haplotella* as a replacement name for *Gemmaria* Duchassaing de Fonbressin and Michelotti, 1860, and has the same type species (see discussion above). *Haplotella* Stechow, 1919, is a junior objective synonym of *Gemmaria* Duchassaing de Fonbressin and Michelotti, 1860, and a junior subjective synonym of *Protopalythoa* Verrill, 1900, and *Parapalythoa* Verrill, 1900. The date of publication of *Haplotella* is conventionally cited as "1920", but in an abstract to the work that appeared in 1919, the following was stated: "Die Aktiniengattung "*Gemmaria*" Duchassaing et Michelotti 1861 erhält wegen Präokkupation durch ein Hydroidengenus den Namen *Haplotella*" (Stechow, 1919: 853). The date of publication of the name *Haplotella* is thus 1919.

In conclusion, the genus-group names *Gemmaria* Duchassaing de Fonbressin and Michelotti, 1860, *Parapalythoa* Verrill, 1900, *Protopalythoa* Verrill, 1900, and *Haplotella* Stechow, 1919, are all herein considered to be synonyms of *Palythoa* Lamouroux, 1816. Furthermore, the genus-group name *Protopalythoa* Verrill, 1900, can no longer be used by authors who consider *Gemmaria variabilis* Duerden, 1898 (and other related species) to be be sufficiently distinct to require a genus-group of its own (i.e. *Protopalythoa* sensu Ryland and Lancaster 2003). To resolve this, a new genus-group name will need to be established.

***Savalia* Nardo, 1844, is a senior subjective synonym of *Gerardia* Lacaze-Duthiers, 1864, with comments the family-group names Gerardiidae Verrill, 1865, Savagliidae Brook, 1889, and Parazoanthidae Delage and Hérouard, 1901**

The family-, genus- and species-group names for the zoantharian living on gorgonians in the Mediterranean area has been a matter of a long-running historical debate (reviewed in in Brook 1889: 79, 80, Bell 1891: 89–91; Carlgren 1895: 319–334, Roche and Tixier-Durivault 1951: 402–409).

At the species-group rank, the first available name to be applied to this taxon was "*Gorgonia Savaglia*" by Bertoloni (1819: 219). The name "savaglia" being the commonly used vernacular name for this animal (e.g., Imperato 1599: 724; Garencieres 1676: 5, Bell 1899: 90). Haime (1849: 225, note) later established "*Leiopathes Lamarcki*" (the species-group name being spelled with only one "i").

At the genus-group rank, Nardo (1844: 433, 434) and Lacaze-Duthiers (1864a: 87) respectively established the genus-group names *Savalia* (type species *Gorgonia savaglia* Bertoloni, 1819), and *Gerardia* (type species *Leoipathes lamarcki* Haime, 1849). Each species is the type species of its respective genus-group by monotypy (Article 68.3 of the Code, ICZN, 1999: 71). As a further complication, the genus-group name *Savaglia* was used by Nardo (1877), who was clearly intending to emend the spelling of *Savalia* Nardo, 1844.

Brook (1889: 79, 80) considered the valid binomial name for the species under consideration to be *Savaglia lamarcki* (Haime, 1849). The reason for for doing was given as: "Lacaze Duthiers was the first to show the true relations of this form, and its difference from the typical Antipathidae. Nardo, in 1843 [*sic*], gave the generic name *Savaglia* to the species described as *La Savaglia* by Donati in 1765, which he says is identical with *Leiopathes lamarcki*, Haime; in this case his name has priority over that of *Gerardia*, instituted by Lacaze Duthiers in 1864. This I gather from a more recent paper; I have not seen the original, and do not know if Nardo gave the species a specific, as well as a generic, name; there is no mention of one in his recent publication. I have, therefore, retained the specific name of Haime. Although it seems highly probable that Nardo's *Savaglia* is the same as *Gerardia*, Lacaze Duthiers, his description of the polyp does not agree with Lacaze Duthiers' observations on living specimens. Nardo states that the polyp has only fourteen tentacles, whereas the species in question has twenty-four" (Brook 1889: 79).

Bell (1891: 89–91) took the opposite position and considered the valid binomial name to be *Gerardia savalia* (Bertoloni, 1819). Bell (1891: 89–91) argued that the establishment of the genus-group name *Savalia* in Nardo (1844: 433, 434) was not 'legitimate' as "Nardo does not write out the full name or names of the species to be placed in this genus, but it is clear that had he done so he would have then written *Savaglia savaglia* (or *Savalia savalia*). This use of a specific for a generic name has been forbidden by the rules of the British Association. Meanwhile this species had become famous by the researches of Lacaze-Duthiers, who, conferring on it (in 1864) the generic name of *Gerardia*, retained for it the specific name of *lamarcki* given it by Haime (in 1849) when he called it *Leiopathes lamarcki*. … It is clear that there is no escape from the conclusion that the proper specific name of this Coral is *savalia*, and the generic *Gerardia* …".

In order to resolve the matter of the correct genus- and species- group names, a more detailed analysis of the description given by Nardo (1844: 433, 434). The description is given as follows: "*Sotto famiglia II.ª Savalini — Polipi a sedici tentacoli! Gen.* Savalia *N. … Fa meraviglia come sia sfuggito all'occhio deglie osservatori il bel lavoro del Donati V. sull'Antipate dell' Adriatico* Gorgonia savoglia [*sic*] *(Bertoloni) inserito nel primo volume del Giornale di Grisellino, ove vedesi esattamente descritto e figurato l'animale con i suoi sedici tentacoli. Non v'ha dubbio che una tale specie debbasi distinguere dal genere* Anthipathes. *Costituisee anzi a mio credere una sotto famiglia, come mostreró in più esteso lavoro relativo ai caratteri distintivi delle famiglie dei Zoofitarj*" (Nardo 1844: 433, 434).

This is translated as: "Subfamily 2. Savalini — Polyps with 16 tentacles. Genus *Savalia* N[obis]. … The fine work of V. Donati on Antipate [= black corals/zoophytes] of the Adriatic Sea in the first volume of the *Giornale di Grisellino* has long been overlooked by previous workers, in which *Gorgonia savoglia* [*sic*] (Bertoloni) was exactly described and figured as an animal with sixteen tentacles. There is not doubt that this species is deserving of a genus distinct from the genus *Anthipathes*. Indeed, as I will show in a more extensive work relating to the distinctive characteristics of the families of Zoofitarj, it constitutes a new subfamily".

The objection raised by Brook (1889: 79) for not using *Gorgonia savaglia* Bertoloni, 1819, as the species-group name is not tenable, as the only reason given is that he did "not know if Nardo gave the species a specific name" as Brook did not have access to the 1844 paper by Nardo. From the description by Nardo (1844: 433, 434), the genus-group name Savalia was clearly established for *Gorgonia savaglia* Bertoloni, 1819 (incorrectly spelled as "*savoglia*"). Virtually all recent authors consider *Gorgonia savaglia* Bertoloni, 1819, to be a subjective synonym of *Leiopathes lamarcki* Haime, 1849 (e.g. Roche and Tixier-Durivault 1951: 402, Ocaña et al. 1995: 155, Ocaña and Brito 2004: 170, Sinniger et al. 2005: 1124, 1125, Ocaña et al. 2007: 163–167). *Gorgonia savaglia* Bertoloni, 1819, has priority over *Leiopathes lamarcki* Haime, 1849, and the former is the valid species-group name.

The objections raised by Bell (1891: 90) for not accepting *Savalia* Nardo, 1844, are also not justified. Firstly, Nardo (1844: 433, 434) did indeed provide the name of the species he intended to be placed in *Savalia* Nardo, 1844 (as discussed above). Secondly, as already stated by Poche 1914: 104, tautomeric names (viz., "*Savaglia savaglia* / *Savalia savalia*") are not invalid on this basis alone (Articles 18 and 23.3.7 of the Code, ICZN 1999: 21, 26). As their respective type species are considered to be subjective synonyms (see above), the genus-group name *Savalia* Nardo, 1844, is a subjective synonym of *Gerardia* Lacaze-Duthiers, 1864 (see also Sinniger et al. 2013: [1], [2], [7]). As *Savalia* Nardo, 1844, has priority over *Gerardia* Lacaze-Duthiers, 1864, the former is the valid genus-group name.

At the family-group rank, three names have been proposed for *Savalia savaglia* (Bertoloni, 1819). As noted above, Nardo (1844: 433, 434) established the family-group name Savaliidae (as "Savalini") based on the genus-group name *Savalia* Nardo,

1844. Later, Verrill (1869 [in 1868–1870]: 499) established the family-group name Gerardiidae (as "Gerardidae"). Brook (1889: 79) wrote "Savagliidae, n[om]. n[ov]. (Gerardidae [*sic*], Verrill)". Brook (1889: 79, 80) based this family-group name based on the emended name *Savaglia* Nardo, 1877, as he did not have access to Nardo (1844) (discussed above). The family-group name Savagliidae proposed by Brook (1889: 79) is herein regarded to have been proposed independently of Savaliidae Nardo, 1844 (based on *Savalia* Nardo, 1844). As their respective type genera are synonyms (as discussed above), the family-group names Savaliidae Nardo, 1844, Gerardiidae Verrill, 1865, and Savagliidae Brook, 1889, are all synonyms.

The oldest and therefore valid family-group name for *Savalia savaglia* (Bertoloni, 1819) is therefore Savaliidae Nardo, 1844. The type genus of Savaliidae Nardo, 1844, (i.e., *Savalia* Nardo, 1844), is however currently assigned to the family Parazoanthidae Delage and Hérouard, 1901 (Sinniger et al. 2013: [2], [3]). This means that the family-group names Savaliidae Nardo, 1844, Gerardiidae Verrill, 1865, and Savagliidae Brook, 1889, are all subjective synonyms of Parazoanthidae Delage and Hérouard, 1901. To maintain current and widespread use of Parazoanthidae Delage and Hérouard, 1901, the best course of action would be to enact Article 23.9 of the Code (ICZN 1999: 27, 28) to reverse precedence between Parazoanthidae Delage and Hérouard, 1901, and the other three family-group names. This is not possible, however, as all three family-group names have been used after 1899, and Article 23.9.1.1 of the Code (ICZN 1999: 28) cannot be satisfied.

In accordance with Article 23.9.2 (ICZN 1999: 28, 29), an application is being prepared to request that the International Commission on Zoological Nomenclature suppress the senior subjective synonyms Savaliidae Nardo, 1844, Gerardiidae Verrill, 1865, and Savagliidae Brook, 1889, in favour of Parazoanthidae Delage and Hérouard, 1901, to maintain current and widespread usage.

Sphenopidae Hertwig, 1882, and the hitherto overlooked subjective synonym Palythoidae Duchassaing de Fonbressin and Michelotti, 1860

The family-group name Sphenopidae was established by Hertwig (1882: 120) for the genus *Sphenopus* Steenstrup, 1856. The name Sphenopidae Hertwig, 1882, had been used sporadically since it was established. Since it was reinstated by Ryland et al. (2000: 191, 192) for the genera *Sphenopus* Steenstrup, 1856, and *Palythoa* Lamouroux, 1816, however, the name Sphenopidae Hertwig, 1882, is now in current and widespread use (see references cited below).

This current and widespread use of the family-group name Sphenopidae Hertwig, 1882, is threatened by the hitherto overlooked subjective synonym Palythoidae Duchassaing de Fonbressin and Michelotti, 1860 (type genus *Palythoa* Lamouroux, 1816).

This family-group name was first established as "Polythoae" for "*Polythoa*", "*Bergia* n. g." and "*Gemmaria* n. g." (Duchassaing de Fonbressin and Michelotti, 1860: 37). That Duchassaing de Fonbressin and Michelotti (1860: 37) intended this to be a family-group name is evidenced by their use of "Zoanthidae" (containing "*Zoanthus*", "*Isaura*", "*Mammillifera*" and "*Orinia* n. g.") as a counterpart to "Polythoae". The name "*Polythoa*" is an incorrect subsequent spelling of *Palythoa* Lamouroux, 1816 (the first usage of which appears to be by Schweigger 1819: 100).

As type genus of Sphenopidae Hertwig, 1882, and of Palythoidae Duchassaing de Fonbressin and Michelotti, 1860, are considered to belong to the same family grouping (e.g., Ryland et al. 2000: 192; Reimer et al. 2012b: 45, 47, 49; Irei et al. 2015: 2, 3, 14–16; Reimer and Fujii 2016: 14, 19), both family-group names are therefore subjective synonyms.

To prevent the nomenclatural and taxonomic destabilisation that would result from the replacement of Sphenopidae Hertwig, 1882, with its subjective synonym Palythoidae Duchassaing de Fonbressin and Michelotti, 1860, as required by the Principle of Priority (Article 23, ICZN 1999: 24) requires that the oldest available name for the taxon under consideration must be used.

To mediate the Principle of Priority, Article 23.9.1 of the Code (ICZN 1999: 27) allows for a reversal of precedence of a junior synonym when the senior synonym has not been used as a valid name after 1899 (Article 23.9.1.1) and the junior synonym "has been used for a particular taxon, as its presumed valid name, in at least 25 works, published by at least 10 authors in the immediately preceding 50 years and encompassing a span of not less than 10 years" (Article 23.9.1.2).

Since 1899, the name Palythoidae has been used in three publications. The first usage was by Barel and Kramers (1977: 32) used the term "species of Palythoidae" for an unidentified zoantharian associated with echinoderms. From the context, it appears that Barel and Kramers (1977: 32) were reporting on material with close affinities to *Palythoa* Lamouroux, 1816.

As Ng & Low (2010:37, 38) have argued, "valid usage" of a name must be unambiguous and show clearly that the author[s] both considered it the correct name to be used and adopted the name. According to these criteria, the usage of "Palythoidae" by Barel and Kramers (1977: 32) cannot be considered to be valid.

The second usage was by Herberts (1972: 125) who stated: "La disposition brachynémique des mésentères est un autre caractère des Palythoidae". That Herberts (1972: 125) was not using "Palythoidae" as a valid family-group name is evidenced by the fact that the section in which the term "Palythoidae" appears is headed by "Zoanthidae" (p. 106), and in a diagram detailing the classification of zoantharians, "*Palythoa*", "*Isaurus*", "*Spenopus* [*sic*]" and "*Zoanthus*" are clearly placed in "Zoanthidae" (p. 142).

The third usage is by Pax and Müller (1957: 3, 4) in which they recognise the "Unterfamilie Palythoinae" under Epizoanthidae, and further provide a key for identifying this subfamily. Clearly, Pax and Müller (1957: 3, 4) were recognising the family-group name Palythoidae as vaild.

The name Palythoidae Duchassaing de Fonbressin and Michelotti, 1860, thus has been used as the valid name for the taxon is denotes since 1899 (and Article 23.9.1.1 of the Code cannot be fulfulled).

Article 23.9.1.2 of the Code is fulfilled as the family-group name Sphenopidae Hertwig, 1882, is in current and widespread usage, as evidenced by the 30 publications by 99 different authors over the past 34 years using Sphenopidae as a valid name for the taxon it denotes (viz., Nagabhushanam and Jothinayagam 1982: 17; Ryland et al. 2000: 191, 192; Ryland and Lancaster 2003: 407, 409, 415; Ryland and Lancaster 2004: 180; Ryland and Westphalen 2004: 411; Ryland et al. 2004: 1195, 1197; Acosta et al. 2005: 147–149, 151, 154, 160; Sinniger et al. 2005: 1122, 1125, 1126; Daly et al. 2007: 144; Sinniger et al. 2008: 1254, 1256, 1257; Fautin and Daly 2009: 356; Del Mónaco et al. 2010: 360; Reimer and Sinniger 2010: 251; Reimer et al. 2010c: 606, 616; Swain 2010: 2592; Reimer et al. 2011a: 983, 985, 987, 989, 991, 992; Cavallari et al. 2012: 25; Longo et al. 2012: [1]; Palmer et al. 2012: 3880; Reimer et al. 2012b: 43, 45, 47, 49; Rodríguez-Viera et al. 2012: 32; Costello et al. 2013: [2]; Fujii and Reimer 2013: 510, 516; Krishna and Gophane 2013: 210; Koupaei et al. 2014: 64; Alencar et al. 2015: 1113, 1114, 1121; Irei et al. 2015: 1, 2, 4, 6, 14–16, 20; Qin et al. 2015: 100; De la Cruz-Francisco et al. 2016: 24; Fujii and Reimer 2016: 11, 12, 14, 17, 19, 20; Risi and Macdonald 2016: 113).

As precedence of the family-group names Sphenopidae Hertwig, 1882, and Palythoidae Duchassaing de Fonbressin and Michelotti, 1860, cannot be replaced, the former will need to be replaced by the latter. To prevent resulting nomenclatural instability, and in accordance with Article 23.9.2 (ICZN 1999: 28, 29), an application is being prepared to request that the International Commission on Zoological Nomenclature suppress the senior subjective synonym Palythoidae Duchassaing de Fonbressin and Michelotti, 1860, in favour of Sphenopidae Hertwig, 1882, to maintain current and widespread usage.

The type species of *Palythoa* Lamouroux, 1816

The genus-group name *Palythoa* (with the simultaneous French vernacular 'Palythoé') was established by Lamouroux (1816: 359–362) with the inclusion of two species, which were rendered French vernacular: 'Palythoé Etoilée' and 'Palythoé Ocellée'. The second species causes no problems "*P. Ocellata* … Sol. et Ell., p. 180, n. 6, tab. 1, fig. 6 (*A. Ocellatum*) …" is listed. This is *Alcyonium ocellatum* Ellis, in Ellis and Solander, 1786, a synonym of *Alcyonium mammillosum* Ellis, in Ellis and Solander, 1786 (see Pax 1910a: 102; 1910b: 258; Acosta et al. 2005: 159). The French vernacular name 'Palythoé Etoilée', however, is not the translation of the name "*P*[*alythoa*] *Mamillosa* [*sic*] … Sol. et Ell., p. 179, n. 5, tab. 1, figs. 4–5 (*A. Mamillosum* [*sic*]) …" given in the synonymy.

On an unnumbered page of errata after page 559 of Lamouroux (1816) gives "[page] 361 … [line] 12 … *Mamillosa*, lisez *Stellata*", and the captions on page 558 to plate 14 (and on the plate itself) of Lamouroux (1816) gives "*Palythoe* [sic] *stellata*, p. 361. figure copiée dans Ellis". It is thus clear that it was the intention of Lamouroux (1816: 361, 558, unnumbered errata page, pl. 14, fig. 2, caption) to rename *Alcyonium* *mammillosum* Ellis, in Ellis and Solander, 1786, *Palythoa stellata*. *Palythoe* [*sic*] *stellata* Lamouroux, 1816, is also a junior objective synonym of *Alcyonium mammillosum* Ellis, in Ellis and Solander, 1786, as Lamouroux (1816: 361, 558, unnumbered errata page, pl. 14, fig. 2, caption) proposed the former as a replacement name for the latter.

Alcyonium ocellatum Ellis, in Ellis and Solander, 1786, and *Palythoa stellata* Lamouroux, 1816, are thus to be considered species originally included in the genus *Palythoa* Lamouroux, 1816, and were both eligible for fixation (Article 67.2 of the Code, ICZN 1999: 67).

The type species of the genus *Palythoa* Lamouroux, 1816, is accepted as *Alcyonium mammillosum* Ellis, in Ellis and Solander, 1786, by subsequent designation by Haddon and Shackleton (1891b: 691) (see Low and Reimer 2011b: 63). As Lamouroux (1816: 361, 558, unnumbered errata page, pl. 14, fig. 2, caption) proposed the replacement name *Palythoa stellata* for *Alcyonium mammillosum* Ellis, in Ellis and Solander, 1786, the latter cannot be considered an originally included species in the sense of Article 67.2 of the Code (ICZN 1999: 67).

Article 69.2.2 of the Code (ICZN 1999: 72) states that "[i]f an author designates as type species a nominal species that was not originally included (or accepts another's such designation) and if, but only if, at the same time he or she places that nominal species in synonymy with one and only one of the originally included species (as defined in Article 67.2), that act constitutes fixation of the latter species as type species of the nominal genus or subgenus".

Haddon and Shackleton (1891b: 691) wrote that "*Palythoa mammillosa* is evidently regarded by Lamouroux [1816] as the type species of the genus. He reproduces Solander's figure of this species, but not that of *P. ocellata*, of which he merely gives a description. Unfortunately a Latinized version of the French name '*Palythoé Etoillée*,' given by Lamouroux to *P. mammillosa*, has been added at the bottom of his plate—a circumstance which has given rise to some confusion".

Clearly, Haddon and Shackleton (1891b: 691) considered *Alcyonium mammillosum* Ellis, in Ellis and Solander, 1786, to be a synonym of *Palythoe* [*sic*] *stellata* Lamouroux, 1816, as well as the type species of *Palythoa* Lamouroux, 1816. The conditions of Article 69.2.2 of the Code (ICZN 1999: 72) are met and Haddon and Shackleton (1891b: 691) are deemed to have designated *Palythoe* [*sic*] *stellata* Lamouroux, 1816, as the type species of *Palythoa* Lamouroux, 1816. As both names are objective synonyms, the valid name for the species under discussion is *Palythoa mammillosa* (Ellis, in Ellis and Solander, 1786).

Table 1. An updated supraspecific classification of the Zoantharia. All valid genera and their type species are given. The numbers given in parentheses after each suborder and family represent the total number of families and genera, respectively, in each grouping. A total of one order, three suborders, nine families and twenty-seven genera are currently recognised in the Zoantharia.

ORDER ZOANTHARIA RAFINESQUE, 1815

- **1. SUBORDER BRACHYCNEMINA HADDON AND SHACKLETON, 1891 (3)**
  - **1. Neozoanthidae Herberts, 1972 (1)**
    - 1. *Neozoanthus* Herberts, 1972
      - *Neozoanthus tulearensis* Herberts, 1972
  - **2. Sphenopidae Hertwig, 1882 (2)**
    - 2. *Sphenopus* Steenstrup, 1856
      - *Sabella marsupialis* Gmelin, 1791
    - 3. *Palythoa* Lamouroux, 1816
      - *Palythoe* [*sic*] *stellata* Lamouroux, 1816
  - **3. Zoanthidae Rafinesque, 1815 (3)**
    - 4. *Zoanthus* Lamarck, 1801
      - *Actinia sociata* Ellis, 1768
    - 5. *Acrozoanthus* Saville-Kent, 1893
      - *Acrozoanthus australiae* Saville-Kent, 1893
    - 6. *Isaurus* Gray, 1828
      - *Isaurus tuberculatus* Gray, 1828
- **2. SUBORDER MACROCNEMINA HADDON AND SHACKLETON, 1891 (5)**
  - **4. Epizoanthidae Delage and Hérouard, 1901 (3)**
    - 7. *Epizoanthus* Gray, 1867
      - *Dysidea papillosa* Johnston, 1842
    - 8. *Paleozoanthus* Carlgren, 1924
      - *Paleozoanthus reticulatus* Carlgren, 1924
    - 9. *Thoracactis* Gravier, 1918
      - *Thoracactis topsenti* Gravier, 1918
  - **5. Hydrozoanthidae Sinniger, Reimer and Pawlowski, 2010 (2)**
    - 10. *Hydrozoanthus* Sinniger, Reimer and Pawlowski, 2010
      - *Parazoanthus tunicans* Duerden, 1900
    - 11. *Terrazoanthus* Reimer and Fujii, 2010
      - *Terrazoanthus onoi* Reimer and Fujii, 2010
  - **6. Microzoanthidae Fujii and Reimer, 2011 (1)**
    - 12. *Microzoanthus* Fujii and Reimer, 2011
      - *Microzoanthus occultus* Fujii and Reimer, 2011
  - **7. Nanozoanthidae Fujii and Reimer, 2013 (1)**
    - 13. *Nanozoanthus* Fujii and Reimer, 2013
      - *Nanozoanthus harenaceus* Fujii and Reimer, 2013
  - **8. Parazoanthidae Delage and Hérouard, 1901 (13)**
    - 14. *Parazoanthus* Haddon and Shackelton, 1891
      - *Palythoa axinella* Haddon and Shackelton, 1891
    - 15. *Antipathozoanthus* Sinniger, Reimer and Pawlowski, 2010
      - *Gerardia macaronesicus* Ocaña and Brito, 2003
    - 16. *Bergia* Duchassaing de Fonbressin and Michelotti, 1860
      - *Bergia catenularis* Duchassaing de Fonbressin and Michelotti, 1860

2. SUBORDER MACROCNEMINA HADDON AND SHACKLETON, 1891 (5) (Continued)

- 17. *Bullagummizoanthus* Sinniger, Ocaña and Baco, 2013
  - *Bullagummizoanthus emilyacardiarum* Sinniger, Ocaña and Baco, 2013
- 18. *Corallizoanthus* Reimer, *in* Reimer, Nonaka, Sinniger and Iwase, 2008
  - *Corallizoanthus tsukaharai* Reimer, *in* Reimer, Nonaka, Sinniger and Iwase, 2008
- 19. *Hurlizoanthus* Sinniger, Ocaña and Baco, 2013
  - *Hurlizoanthus parrishii* Sinniger, Ocaña and Baco, 2013
- 20. *Isozoanthus* Carlgren, in Chun, 1903
  - *Isozoanthus giganteus* Carlgren, in Chun, 1903
- 21. *Kauluzoanthus* Sinniger, Ocaña and Baco, 2013
  - *Kauluzoanthus kerbyii* Sinniger, Ocaña and Baco, 2013
- 22. *Kulamanamana* Sinniger, Ocaña and Baco, 2013
  - *Kulamanamana haumeaae* Sinniger, Ocaña and Baco, 2013
- 23. *Mesozoanthus* Sinniger and Häussermann, 2009
  - *Mesozoanthus fossii* Sinniger and Häussermann, 2009
- 24. *Savalia* Nardo, 1844
  - *Gorgonia savaglia* Bertolini, 1819
- 25. *Umimayanthus* Montenegro, Sinniger and Reimer, 2015
  - *Umimayanthus chanpuru* Montenegro, Sinniger and Reimer, 2015
- 26. *Zibrowius* Sinniger, Ocaña and Baco, 2013
  - *Zibrowius ammophilus* Sinniger, Ocaña and Baco, 2013

3. SUBORDER *INCERTA SEDIS* (1)

9. Abyssoanthidae Reimer and Fujiwara, in Reimer, Sinniger, Fujiwara, Hirano and Maruyama, 2007 (1)

- 27. *Abyssoanthus* Reimer and Fujiwara, *in* Reimer, Sinniger, Fujiwara, Hirano and Maruyama, 2007
  - *Abyssoanthus nankaiensis* Reimer and Fujiwara, *in* Reimer, Sinniger, Fujiwara, Hirano and Maruyama, 2007

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On the trapdoor spiders of Mexico: description of the first new species of the spider genus *Aptostichus* from Mexico and the description of the female of *Eucteniza zapatista* (Araneae, Mygalomorphae, Euctenizidae)

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Abstract

A new species of the spider genus *Aptostichus* Simon, 1891 is described from a cave in Huautla de Jiménez, Oaxaca, Mexico: *Aptostichus sabinae* **sp. n.** This species represents the first new species described from Mexico and the southernmost record in North America for the genus so far. *Aptostichus sabinae* **sp. n.** represents the forty-first species described for the genus, which has the highest species diversity in the family Euctenizidae. *Eucteniza zapatista* is redescribed based on five new males and the first known female from the Parque Nacional La Malinche (PNLM), Tlaxcala Mexico. *Eucteniza zapatista* is the fourth species of the genus where a female is known, and one of fourteen species described for the genus to date.

Keywords

Aptostichus, *Eucteniza*, Euctenizidae, new species, Mexico, taxonomy

Introduction

Currently, the trapdoor spider family Euctenizidae Raven, 1985 comprises 75 species described in seven genera: *Apomastus* Bond & Opell, 2002; *Aptostichus* Simon, 1891; *Entychides* Simon, 1888; *Eucteniza* Ausserer, 1875; *Myrmekiaphila* Atkinson, 1886; *Neoapachella* Bond & Opell, 2002; and *Promyrmekiaphila* Schenkel, 1950 (Bond and Godwin 2013, World Spider Catalog 2016). Previously, Euctenizinae was a subfamily that included all the North American cyrtaucheniid genera (Raven 1985); however, morphological and molecular cladistic analyses (Bond and Opell 2002, Bond and Hedin 2006, Bond et al. 2012, Hedin and Bond 2006), demonstrated that the family Cyrtaucheniidae Simon, 1889 was polyphyletic and Euctenizinae was recovered as monophyletic group, and was elevated posteriorly to family status by Bond et al. (2012). Among the euctenizid genera, *Aptostichus* has the highest species diversity with 40 species not including the species described herein (Bond 2012, World Spider Catalog 2016). The last taxonomic revision and phylogeny of the genus was made by Bond (2012), where 33 new species were described and classified in four species groups: *Atomarius, Hesperus, Simus,* and *Sierra*. All the species of *Aptostichus* are distributed in the southwestern United States, with only three records in Mexico, in Baja California (World Spider Catalog 2016). The genus *Eucteniza*, which previously was the type genus for the cyrtaucheniid subfamily Euctenizinae (Raven 1985, Bond and Hedin 2006), currently comprises 14 species. The taxonomic revision of the genus was made by Bond and Godwin (2013), where 12 new species were described. Most of the species are distributed in Mexico (13 species), mainly from Baja California, along to the Sierra Madre Oriental and central part of the Transmexican Volcanic Belt (Bond and Godwin 2013: fig. 1), and two species from Texas, United States: *Eucteniza ronnewtoni* Bond & Godwin, 2013, and *Eucteniza relata* (O. Pickard-Cambridge, 1895) which is distributed widely throughout Texas and Northern Mexico (Bond and Godwin 2013, World Spider Catalog 2016). Like most of the trapdoor spiders, the specimens are difficult to collect, and *Aptostichus* and *Eucteniza* are no exception. Specimens are rare, even in biological collections. Most of the species are described based only on male specimens. For example, in *Eucteniza*, only three species of 14 are described based on both sexes (World Spider Catalog 2016). The type species for the genus was originally described based on a juvenile specimen, *Eucteniza atoyacensis* Bond & Opell, 2002, considered by Bond and Godwin (2013) as a nomen dubium ((*Eucteniza mexicana* (O. Pickard-Cambridge, 1895)). In this work, a new species of the genus *Aptostichus* is described based on a male collected from a cave in Oaxaca, Mexico; additionally the female of *Eucteniza zapatista* is described for the first time from Parque Nacional La Malinche (PNLM), Tlaxcala, Mexico.

Material and methods

The specimens were collected and deposited in 80% ethanol and, labeled with their complete field data. For the descriptions the specimens were observed using a Zeiss

Discovery.V8 stereoscope. A Zeiss Axiocam 506 color camera attached to a Zeiss AXIO Zoom.V16 stereoscope was used to photograph the different structures of specimens. All structures photographed under the stereoscope were submerged in gel alcohol (available commercially as a hand cleaner). The firm consistency of the gel allows for the immobilization and positioning of the structure to be photographed. The structure suspended in the gel alcohol was covered with 80% liquid ethanol to minimize diffraction during examination and photography. All measurements in the descriptions are in millimeters (mm). Photographs were edited with Adobe Photoshop CS6.

The holotype specimen of *Aptostichus sabinae* sp. n. is deposited with its collection code in the Colección Nacional de Arácnidos (**CNAN**) of the Instituto de Biología UNAM (**IBUNAM**), Mexico City. The holotype of *Eucteniza zapatista* Bond & Godwin, 2013 was previously deposited in the American Museum of Natural History (**AMNH**), New York, U.S.A. The specimens of *E. zapatista* used for this work, are deposited with their collections codes in the collection of the Laboratory of Arachnology (**LATLAX**), Laboratorio Regional de Biodiversidad y Cultivo de Tejidos Vegetales of the Instituto de Biología UNAM (**IBUNAM**), Tlaxcala City. Morphological nomenclature and measurements follow Bond (2012) and Bond and Godwin (2013).

Abbreviations used in the description are:

B	bulb;
Cl, Cw	carapace length and width (widest part);
Cy	cymbium;
E	embolus;
LBl, LBw	labium length and width taken from the longest and widest points, respectively;
PTl, PTw	male palpal tibia length and width (widest part in dorsal view);
STRl, STRw	sternum length and width (widest part);
v	ventral;
p	prolateral.

Taxonomy

Family Euctenizidae Raven, 1985

Genus *Aptostichus* Simon, 1891

Type species. *Aptostichus atomarius* Simon, 1891.

Diagnosis. For updated diagnosis of the genus see Bond (2012): 29.

General description. For updated description of the genus see Bond (2012): 29.

Species groups. *Atomarius, Hesperus, Simus,* and *Sierra* (Bond 2012).

Composition. *Aptostichus aguacaliente* Bond, 2012; *A. angelinajolieae* Bond, 2008; *A. anzaborrego* Bond, 2012; *A. asmodaeus* Bond, 2012; *A. atomarius* Simon, 1891;

A. barackobamai Bond, 2012; *A. bonoi* Bond, 2012; *A. cabrillo* Bond, 2012; *A. cahuilla* Bond, 2012; *A. cajalco* Bond, 2012; *A. chavezi* Bond, 2012; *A. chemehuevi* Bond, 2012; *A. chiricahua* Bond, 2012; *A. dantrippi* Bond, 2012; *A. derhamgiulianii* Bond, 2012; *A. dorothealangeae* Bond, 2012; *A. edwardabbeyi* Bond, 2012; *A. elisabethae* Bond, 2012; *A. fisheri* Bond, 2012; *A. fornax* Bond, 2012; *A. hedinorum* Bond, 2012; *A. hesperus* (Chamberlin, 1919); *A. huntington* Bond, 2012; *A. icenoglei* Bond, 2012; *A. isabella* Bond, 2012; *A. killerdana* Bond, 2012; *A. lucerne* Bond, 2012; *A. mikeradtkei* Bond, 2012; *A. miwok* Bond, 2008; *A. muiri* Bond, 2012; *A. nateevansi* Bond, 2012; *A. pennjillettei* Bond, 2012; *A. sabinae* sp. n., *A. sarlacc* Bond, 2012; *A. satleri* Bond, 2012; *A. serrano* Bond, 2012; *A. sierra* Bond, 2012; *A. simus* Chamberlin, 1917; *A. sinnombre* Bond, 2012; *A. stanfordianus* Smith, 1908; and *A. stephencolberti* Bond, 2008. Total: 41 species.

Distribution. United States, Mexico.

Aptostichus sabinae sp. n.

http://zoobank.org/E78270D0-B3A8-4BC7-B2E3-FF617CBFA6A3
Figs 1–20

Type material. MEXICO: Oaxaca: 1♂ holotype (CNAN-T1121) from Cueva Li Nita (lat 18.14767°, lon -96.79844°, 1919 m), Municipio Huautla de Jiménez, 12-April-2014, J. Mendoza, J. Cruz, S. Davlantes, M. Minkton Cols.

Etymology. This species is dedicated to the María Sabina Magdalena García "María Sabina", a famous Mazatec shaman due to her traditional knowledge of healing and ceremonial use of hallucinogenic mushrooms who was born in 1894 in Huautla de Jiménez (municipality of the type locality), Oaxaca, Mexico.

Diagnosis. Males are easily distinguished from the other known species of *Aptostichus* by the combination of the following characters: 1) a very long, slender and sigmoidal unique embolus (Figs 8, 9, 10, 12); 2) massive ventral and prolateral spines on the palpal tibiae (Figs 8, 11); 3) retrolateral-ventral small finger-shaped projection on metatarsus I (Fig. 19, arrows Figs 17, 18); 4) by having many spines on tibiae and metatarsi III and IV (Fig. 20); and 5) a unique dorsal opisthosomal pattern (Fig. 1).

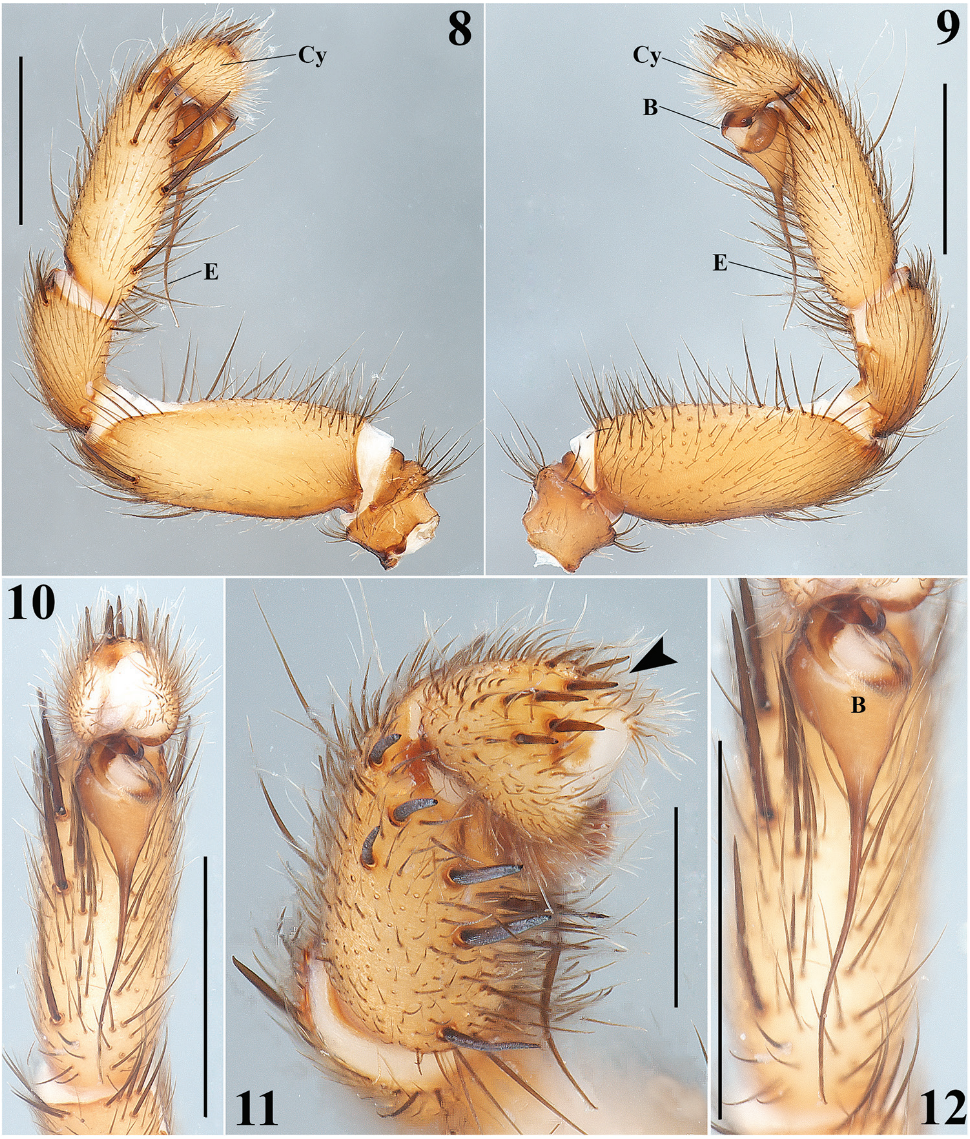
Description. Male (holotype): Specimen collected manually, preserved and observed in 80% ethanol. *Measurements:* Total length (prosoma + opisthosoma) 8.30. Carapace 3.84 long, 3.12 wide. Clypeus length 0.18. Diameter of AME 0.13, ALE 0.25, PME 0.18, PLE 0.23. Labium: LBl 0.23, LBw 0.53. Sternum: STRl 1.85, STRw 1.65. Leg lengths: I femur 2.75/ patella 1.80/ tibia 2.2/ metatarsus 1.88/ tarsus 1.36/ total 9.99; II- 2.50/ 1.64/ 1.88/ 1.68/ 1.24/ 8.94; III- 2.25/ 1.32/ 1.76/ 2.40/ 1.28/ 9.01; IV- 3.00/ 1.60/ 2.48/ 3.50/ 1.52/ 12.10. Leg formula: 4-1-3-2. *Prosoma:* Carapace longer than wide, with surface smooth, setose, pyriform shaped, light brown coloration (Figs 1, 3). Ocular region slightly elevated (Figs 3, 5, 6). Foveal groove slightly deep (Fig. 3). AER slightly procurved, PER slightly recurved (Figs 3, 6). Largest ALE, smallest AME (Fig. 6). Sternum longer than wide, nonagonal shaped, orange, more

Figures 1–4. *Aptostichus sabinae* sp. n. Male holotype: **1–2** Habitus, dorsal and ventral views respectively **3** Carapace, dorsal view **4** Prosoma, ventral view showing coxae, sternum, labium and endites (arrow indicates cuspules). Scale bars 0.5 mm (**1**, **2**), 0.2 mm (**3**, **4**).

setose towards posterior margin, without sigilla (Fig. 4). Labium wider than long, orange, with long setae anteriorly, without cuspules (Fig. 7). Endites long and setose, with an apical-prolateral conspicuous conical apophysis, with a patch of 11-13 small cuspules on proximal inner part on each endite (Fig. 7). *Chelicerae:* Promargin furrow

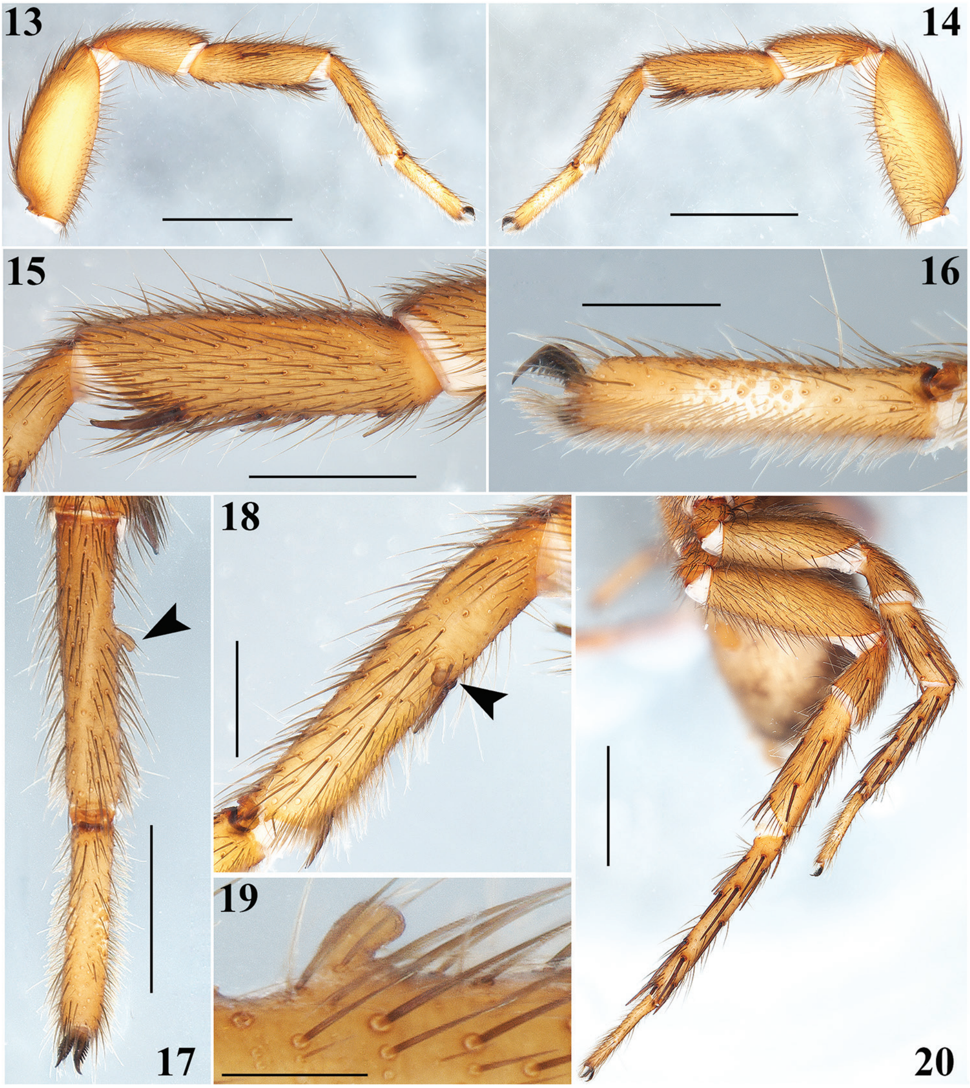
Figures 5–7. *Aptostichus sabinae* sp. n. Male holotype: **5** Chelicerae, lateral view **6** Ocular region **7** Endites, ventral view; detail of the cuspules. Scale bars 0.5 mm (**6**, **7**), 1 mm (**5**).

with 6 teeth, retromargin furrow with single row of very long setae. Rastellum consists of numerous long setae, but without stout spines. *Opisthosoma:* Longer than wide, setose, beige, with irregular brown pattern dorsally; ventrally with brown undefined lines, close to spinnerets (Figs 1, 2). Spinnerets beige. PMS small and rounded apically, single segment, with spigots. PLS long and conical apically, all 3 segments with spigots: basal segment length > median segment > distal segment. *Legs:* Light tarsal



Figures 8–12. *Aptostichus sabinae* sp. n. Male holotype: **8–9** Left palp, prolateral and retrolateral views respectively **10** Left palp, ventral view **11** Left palp, prolateral-apical view (arrow indicates apical spines on cymbium) **12** Detail of the bulb and embolus, ventral view. Scale bars 0.5 mm (**11**), 1 mm (**8–10**, **12**).

scopulae on all legs (Fig. 16). Tibiae, metatarsi and tarsi with trichobothria: Tibiae I-IV: two prolateral-dorsal rows with 9 trichobothria each, distal ones becoming larger; metatarsi I and II: one dorsal row with 12; metatarsi III: one dorsal row with 15; metatarsi IV: one dorsal row with 19; tarsi I: slightly staggered dorsal row with 10; tarsi II: slightly staggered dorsal row with 12; tarsi III: slightly staggered dorsal row with 10; tarsi IV: slightly staggered dorsal row with 11. Legs spination pattern: Tibiae



Figures 13–20. *Aptostichus sabinae* sp. n. Male holotype: **13–14** Left leg I, prolateral and retrolateral views respectively **15** Tibia I, retrolateral view **16** Tarsus I, retrolateral view**17** Metatarsus and tarsus I, dorsal view (arrow indicates the small finger-shaped projection on retrolateral-ventral part of metatarsus) **18** Metatarsus I, retrolateral view (idem) **19** Detail of the small finger-shaped projection on retrolateral-ventral part of metatarsus I. **20**, Spination pattern on legs III and IV. Scale bars 0.2 mm (**19**), 0.5 mm (**16**, **18**), 1 mm (**15**, **17**), 2 mm (**13**, **14**, **20**).

I: v(2+2+2) (one of the last spines -retrolateral- is massive) (Figs 14, 15), p(1) (Fig. 13); tibiae II: v(2+2+2), p(1+1); metatarsi I: v(2+1); metatarsi II: v(1+2+2), p(1). Leg III and IV spination pattern is illustrated in Figure 20. *Pedipalps:* Articles pale orange, slender, femora and tibiae with long setae ventrally (Figs 8, 9). Patellae with distal dorsal-prolateralspine. Tibiae with massive ventral and prolateral spines (Figs 8, 10–

12). Cymbium with seven dorsoapical spines (arrow, Fig. 11). Bulb pyriform, turned ventrally toward a concavity on ventral part of tibiae (Figs 8, 9, 10, 12). Embolus long, slender and sigmoidal, almost with the same length as tibiae (Figs 8, 9, 10, 12).

Female. Unknown.

Remarks. *Aptostichus sabinae* sp. n. resembles *Aptostichus asmodaeus* (Bond 2012: figs 127–132), from Contra Costa County, Mount Diablo State Park, California mainly in the shape of the retrolateral-ventral small finger-shaped projection on metatarsi I (arrows Figs 17, 18; Bond 2012: fig. 128). However, the spination pattern in leg I, the embolus and bulb shape (Figs 10, 12), the spination pattern on the ventral and prolateral part of palps tibiae (Fig. 11) (absent in *A. asmodaeus*; Bond 2012: figs 131, 132), and the opisthosoma dorsal pattern differ in both species (Bond 2012: figs 127–132). Following Bond (2012) and the synapomorphies that support each species groups, *Aptostichus sabinae* sp. n. does not fit into any of the groups. The *sierra* species group composed by four species is supported by two synapomorphies: long sternum and a long male metatarsus I (Bond 2012: figs 337, 338, 340), in *A. sabinae* the sternum is nonagonal shaped (Fig. 4) and the male metatarsus I is shorter (Figs 13, 14). The *simus* species group composed by eight species and supported by six synapomorphies: 1) absence of cuspules on male endites, present in *A. sabinae* (Fig. 7); 2) male palpal tibia stout (Bond 2012: figs 278, 287), in *A. sabinae* the palpal tibia is thinner (Figs 8, 9); 3) male palpal tibia spines short and positioned retrolaterally (Bond 2012: figs 278, 287), in *A. sabinae* the palpal tibia spines are long, scattered and positioned prolaterally (Figs 8, 9); 4) stout embolus (Bond 2012: figs 277, 306), *A. sabinae* has a long and thin embolus (Figs 10, 12); 5) embolus is dorsal - ventrally compressed (Bond 2012: figs 277), in *A. sabinae* is not (Figs 8, 9, 10, 12); and 6) retrolateral, distal most aspect of the cymbium formed as a distinct process (Bond 2012: fig. 277), absent in *A. sabinae* (Fig. 10). The *hesperus* species group, composed by thirteen species, is supported mainly by an offset retrolaretal rastellar spine (Bond 2012: fig. 189), which is absent in *A. sabinae* (Fig. 5). Also, four characters support the monophyly of this species group: 1) lighter carapace and 2) abdominal coloration, whereas in *A. sabinae* both colorations are darker than the other species of the group (Figs 1, 3); and 4) long and 5) sinuous spermathecal stalk, is unknown in *A. sabinae*. Finally, the *atomarius* species group, the most diverse and composed by fifteen species, is supported by three weak synapomorphies: 1) heavy carapace pubescence (Bond 2012: figs 101, 113), 2) dense female tarsal scopulae (38) and a distinct secondary spermathecal bulb. However, the carapace of *A. sabinae* has a slight carapace pubescence (Fig. 3), and the spermathecal bulb is unknown so far. Because to the synapomorphies explained above and mostly of them absent in *A. sabinae*, its placement within any of the species group proposed by Bond (2012) is uncertain. For that reason, we consider this new species as *inserta sedis* until the female of the species and more data and mainly new species from Mexico can be collected.

Natural history. The holotype specimen was hand collected inside a cave, in a temperate forest at 1919 m of elevation. Although the specimen was collected in a cave, it does not present any troglomorphism or adaptation to cave life, and so might be considered a trogloxene.

Distribution. Known only from the type locality (Fig. 53).

Genus *Eucteniza* Ausserer, 1875

Type species. *Eucteniza mexicana* Ausserer, 1875.

Diagnosis. For updated diagnosis of the genus see Bond and Godwin (2013): 36.

General description. For updated description of the genus see Bond and Godwin (2013): 36.

Composition. *Eucteniza cabowabo* Bond & Godwin, 2013; *E. caprica* Bond & Godwin, 2013; *E. chichimeca* Bond & Godwin, 2013; *E. coylei* Bond & Godwin, 2013; *E. diablo* Bond & Godwin, 2013; *E. golondrina* Bond & Godwin, 2013; *E. hidalgo* Bond & Godwin, 2013; *E. huasteca* Bond & Godwin, 2013; *E. mexicana* Ausserer, 1875; *E. panchovillai* Bond & Godwin, 2013; *E. relata* (O. Pickard-Cambridge, 1895); *E. ronnewtoni* Bond & Godwin, 2013, *E. rosalia* Bond & Godwin, 2013; and *E. zapatista* Bond & Godwin, 2013. Total: 14 species.

Distribution. Mainly from Baja California, along to the Sierra Madre Oriental and central part of the Transmexican Volcanic Belt (Bond and Godwin 2013: fig. 1), and with only one described species from Texas, United States.

Eucteniza zapatista Bond & Godwin, 2013

E. zapatista Bond & Godwin, 2013: 54, f. 48–52 (Dm)
Figs 21–51

Type data. MEXICO: Puebla: 1♂ holotype (EU012) (not examined), from Paso de Cortés (lat 19.1167°, lon -98.76676°, 3000 m), 18-July-1943, C. Bolivar Col. Holotype deposited in AMNH.

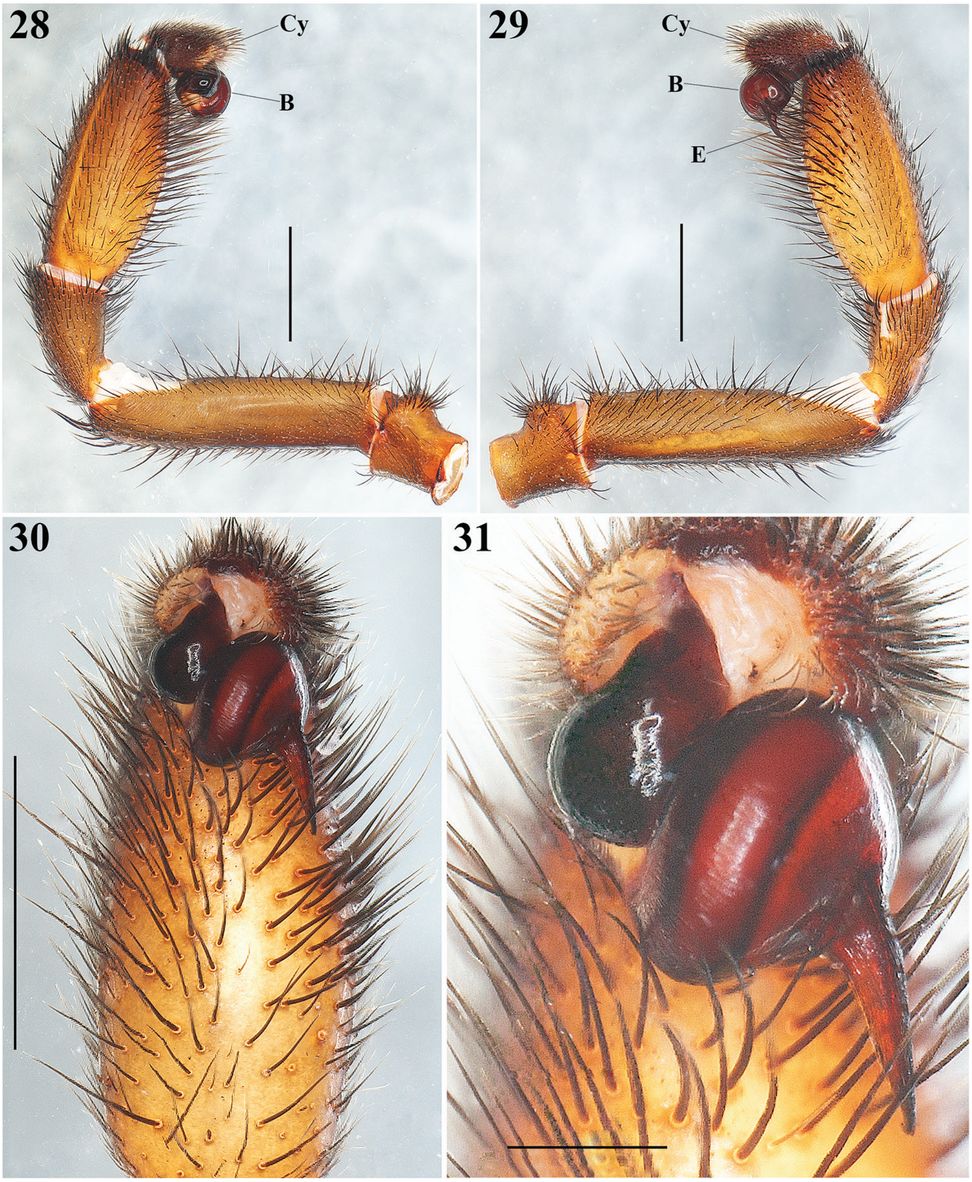
Material examined. MEXICO: Tlaxcala: 4♂♂ (LATLAX-Ara0031) (pitfall traps) from 1.5 km al Oeste de la Estación Científica del Parque Nacional La Malinche (PNLM) (lat 19.24544°, lon -98.00336°, 3250 m), Municipio Ixtenco, 25-April-2016, A. Valdez, M. Cortez, A. Juárez Cols. 1♂ (LATLAX-Ara0033) from Carretera Perimetral con entronque Albergue IMSS Parque Nacional La Malinche (PNLM), Municipio Ixtenco, 4-May-2016, A. Ramírez Col. 1♀ (LATLAX-Ara0032) (hand collected) from Parque Nacional La Malinche (PNLM) (hand collected), El Pasaje (lat 19.25304°, lon - 97.97942°, 3030 m), Municipio Ixtenco, 03-July-2016, V. Jiménez, A. Díaz Cols.

Diagnosis. Bond and Godwin 2013: "Male *Eucteniza zapatista* Bond and Godwin, 2013 leg I morphology is similar to *Eucteniza diablo* Bond and Godwin, 2013; however it lacks tarsal spines and has a more inflated or swollen tibia (Figs 32, 33, 36, 40–44). Males can be further distinguished from all other species by having an extensive patch of spines on the retrolateral distal aspect of the palpal tibia (Figs 28–30)". Also, ventrally tibia I with very stout and paired megaspines, close each other (Figs 36, 38). Females with similar spermathecae to *E. diablo*, however in *E. zapatista* the spermathecae has a dark stalk and the bulbs with porous sculpture (Fig. 49), whereas in *E. diablo* only the basal part of the bulbs is dark and the bulbs lack porous sculpture (Bond and Godwin 2013: fig. 36).

Figures 21–24. *Eucteniza zapatista* Bond & Godwin, 2013. Male: **21–22** Habitus, dorsal and ventral views respectively **23** Carapace, dorsal view **24** Prosoma, ventral view showing coxae, sternum, labium, and endites. Scale bars 0.5 mm (**23**, **24**), 1 mm (**21**, **22**).

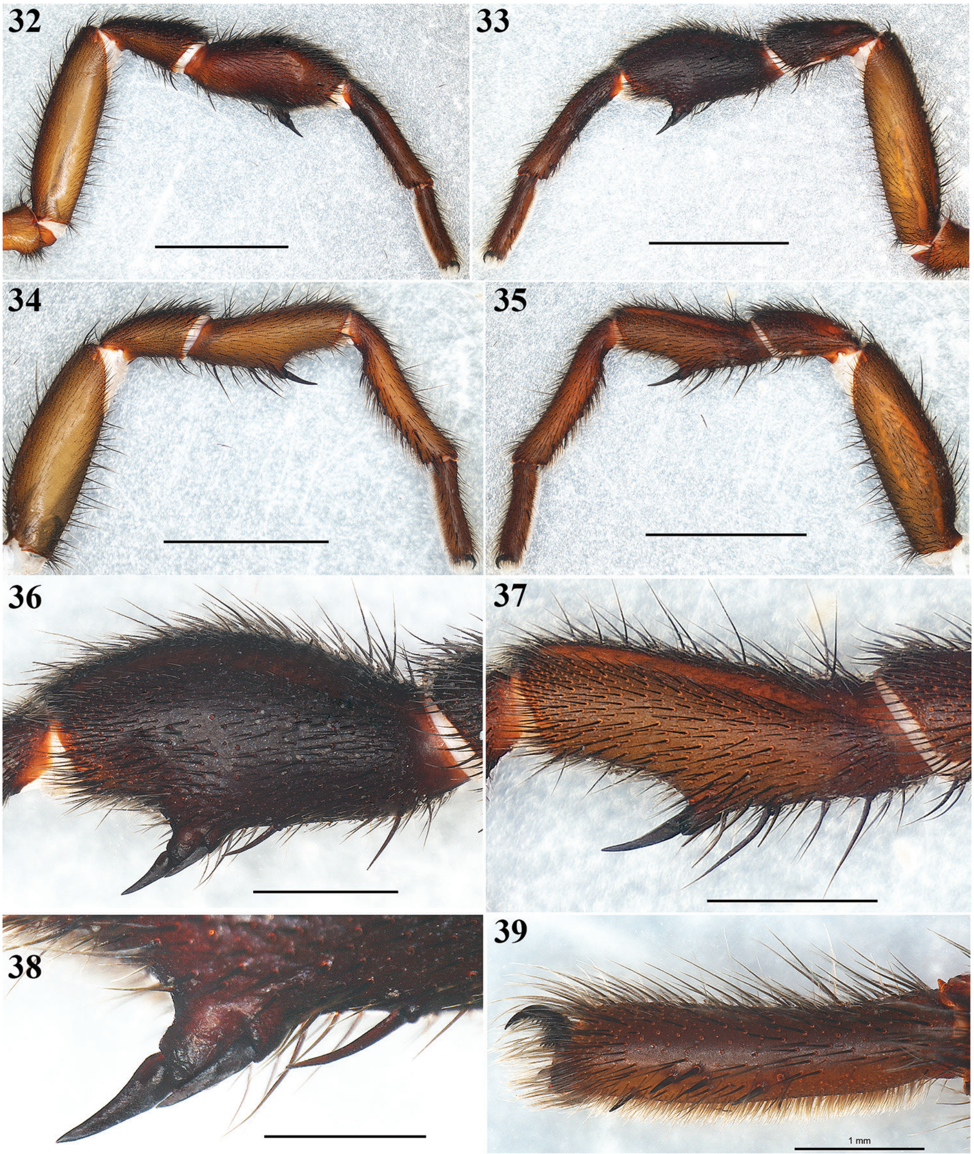
Figures 25–27. *Eucteniza zapatista* Bond & Godwin, 2013. Male: **25** Labium and endites, ventral view **26** Ocular region **27** Opisthosoma, ventral view, showing spinnerets. Scale bars 0.5 mm (**26**), 1 mm (**25**), 2 mm (**27**).

Redescription. Male: Specimen collected using pitfall traps, preserved and observed in 80% ethanol. *Measurements:* Total length (prosoma + opisthosoma) 17.68. Carapace 8.30 long, 7.40 wide. Clypeus length 0.80. Diameter of AME 0.46, ALE 0.40, PME 0.25, PLE 0.30. Labium: LBl 0.88, LBw 1.31. Sternum: STRl 4.70, STRw 4.25. Leg lengths: I femur 7.70/ patella 4.30/ tibia 5.90/ metatarsus 5.10/ tarsus 3.10/ total 26.10; II- 7.00/ 3.40/ 5.20/ 5.50/ 3.20/ 24.30; III- 5.90/ 3.30/ 3.75/ 5.90/ 3.70/ 22.55; IV- 7.20/ 3.80/ 6.00/ 6.50/ 3.70/ 27.20. Leg formula: 4-1-2-3. *Prosoma:* Cara-



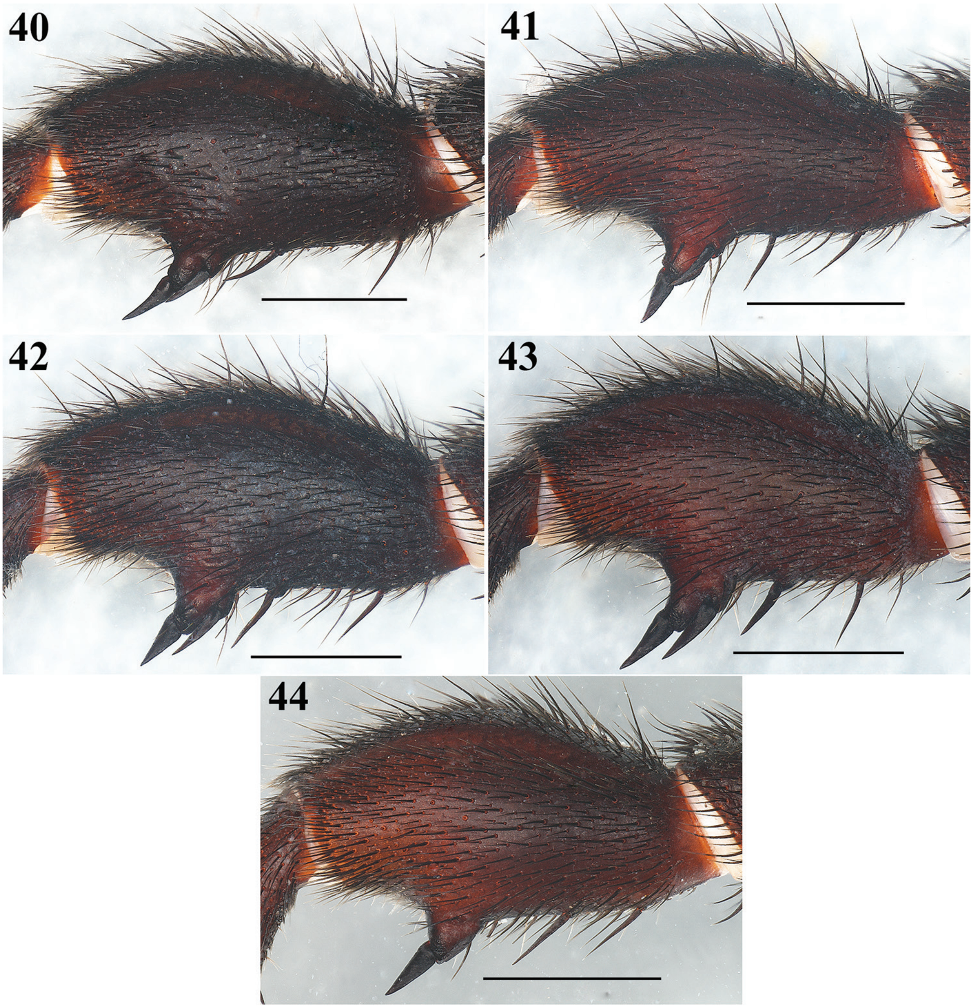
Figures 28–31. *Eucteniza zapatista* Bond & Godwin, 2013. Male: **28–29** Left palp, prolateral and retrolateral views respectively **30** Left palp, ventral view **31** Detail of the bulb and embolus, ventral view. Scale bars 0.5 mm (**31**), 2 mm (**28–30**).

pace longer than wide, protruding anteriorly, with surface smooth, setose in posterior part, hexagonal shaped, dark brown in anteriorly and lighter posteriorly (Figs 21, 23). Ocular region slightly elevated (Fig. 26). Foveal groove deep and procurved, U-shaped (Fig. 23). AER slightly procurved, PER recurved. Largest AME, smallest PME (Fig. 26). Sternum longer than wide, pyriform shaped, dark orange, setose, with sigilla



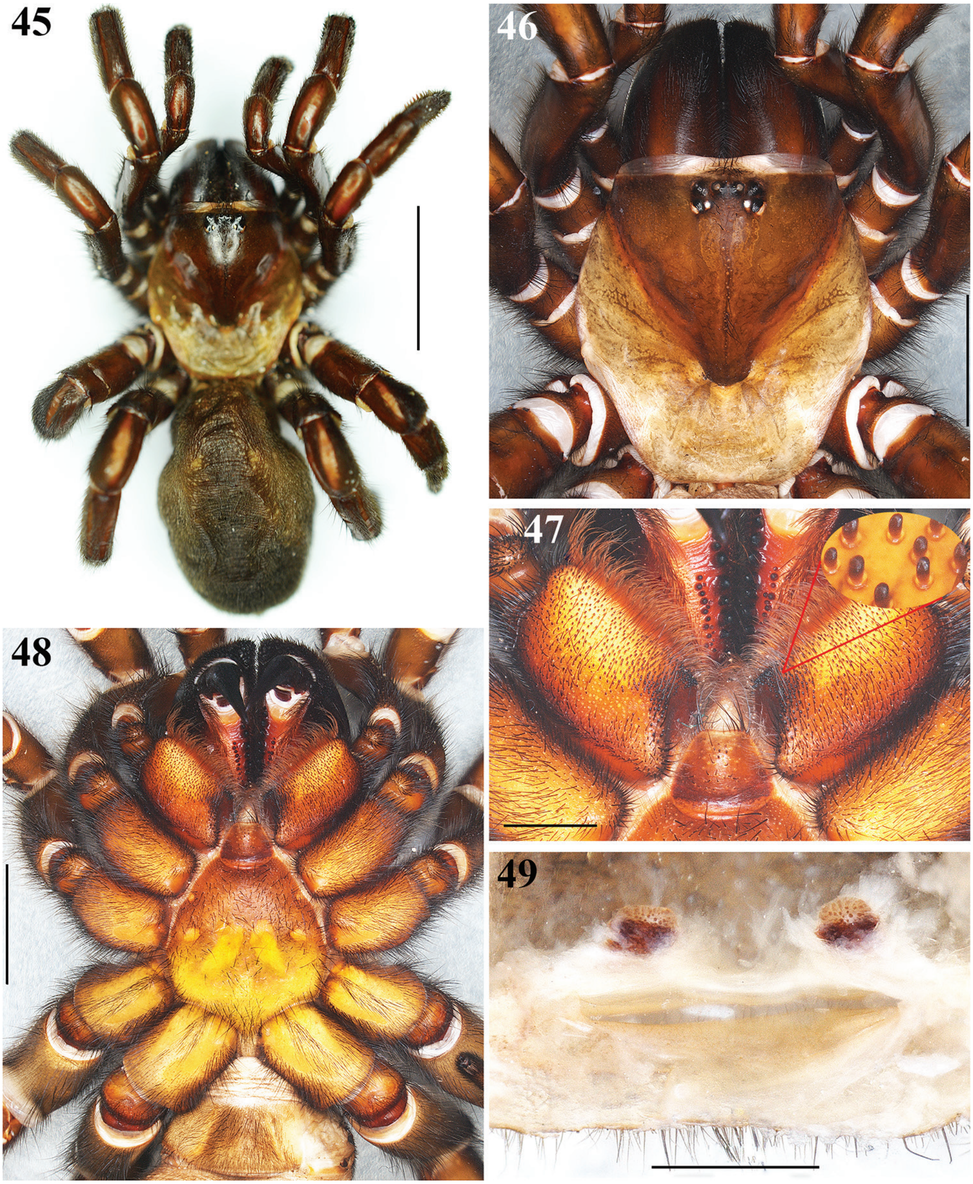
Figures 32–39. *Eucteniza zapatista* Bond & Godwin, 2013. Male: **32–33** Left leg I, prolateral and retrolateral views respectively **34–35** Left leg II, prolateral and retrolateral views respectively **36** Tibia I, retrolateral view **37** Tibia II, retrolateral view **38** Detail of the paired megaspines on tibia I **39** Scopulae on tarsus I, retrolateral view. Scale bars 1 mm (**38**, **39**), 2 mm (**36**, **37**), 5 mm (**32–35**).

(Fig. 24). Posterior sternal sigilla large and elongate, medial pair of anterior sigilla moderate in size, anterior pair small and marginal (Fig. 24). Labium wider than long, brown, with long setae anteriorly, without cuspules (Fig. 25). Endites long and setose, with an apical-prolateral inconspicuous conical apophysis, without cuspules (Fig. 25). *Chelicerae:* Promargin furrow with 7 teeth, retromargin furrow with approximately



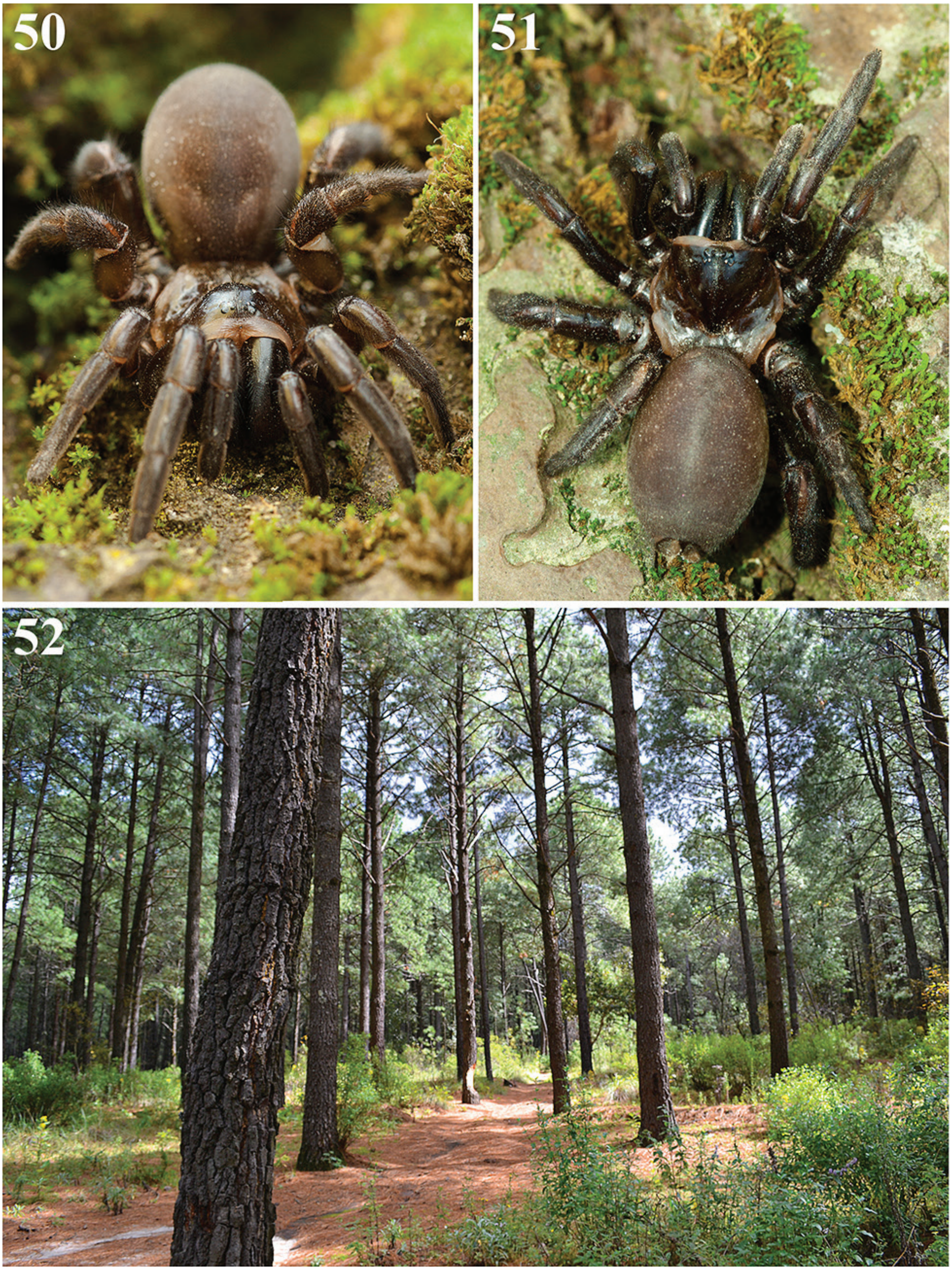
Figures 40–44. *Eucteniza zapatista* Bond & Godwin, 2013. Male: Morphological variation in the shape of the tibia I and macrospines of the five males collected for this study. Scale bars 2 mm.

18–20 small denticles. Rastellum consisting of 6-8 spines on a mound. *Opisthosoma:* Longer than wide, setose, gray, without pattern dorsally; lighter gray ventrally (Figs 21, 22). Spinnerets beige (Fig. 27). PMS small and rounded, single segment, with spigots. PLS long and conical, all 3 segments with spigots: basal segment length > median segment > distal segment. *Legs:* Very light tarsal scopulae on legs I, II, III (Fig. 39), absent in IV. Tibiae, metatarsi and tarsi with trichobothria, lacking pattern, only tarsi with slightly staggered dorsal row, variable in number. Legs spination pattern: Tibia I: with paired ventral megaspines (Figs 32, 33, 36) on prominent base (Fig. 38); tibiae II: with 1 thin and long megaspine (Figs 34, 35) on a slender base (Fig. 37); tibiae III and IV: scattered long spiniform setae; metatarsi and tarsi with scattered spination pattern. *Pedipalps:* Articles setose. Femora brown, long and cylindrical. Patellae brown, lighter



Figures 45–49. *Eucteniza zapatista* Bond & Godwin, 2013. Female: **45** Habitus dorsal **46** carapace, dorsal view **47** Endites, ventral view; detail of the cuspules **48** Prosoma, ventral view showing coxae, sternum, labium and endites **49** Spermathecae, dorsal view. Scale bars 1 mm (**49**), 2 mm (**47**), 5 mm (**46**, **48**), 10 mm (**45**).

ventrally (Figs 28, 29). Tibiae brown, lighter ventrally, long and cylindrical, widened in middle part (Figs 28, 29). Cymbium brownish and setose, without spines (Figs 28–30). Bulb oval, located toward internal part of the pedipalp (Figs 30, 31). Embolus short, thin and curved, pointing toward retrolateral part of the tibia (Figs 28–31).



Figures 50–52. 50, **51** Live female of *Eucteniza zapatista* Bond & Godwin, 2013 outside of her burrow (photos by Victor H. Jiménez Arcos) **52** Pine forest of the Parque Nacional la Malinche (PNLM), Tlaxcala, Mexico, where the specimens of *E. zapatista* used for this study were collected (photo by Alejandro Valdez Mondragón).

Description. Female. Similar to the male, differences: Specimen collected manually, preserved and observed in 80% ethanol. *Measurements:* Total length (prosoma + opisthosoma) 29.50. Carapace 12.20 long, 11.10 wide. Clypeus length 0.80. Diameter of AME 0.47, ALE 0.46, PME 0.23, PLE 0.43. Labium: LBl 1.31, LBw 1.87. Sternum: STRl 7.50, STRw 6.50. Leg lengths: I femur 9.10/ patella 5.10/ tibia 5.70/ metatarsus 4.30/ tarsus 2.50/ total 26.70; II- 7.60/ 5.10/ 4.80/ 4.00/ 2.20/ 23.70; III- 6.50/ 4.80/ 3.00/ 4.20/ 3.10/ 21.60; IV- 8.90/ 5.50/ 6.70/ 6.00/ 3.40/ 30.50. Leg formula: 4-1-2-3. *Prosoma:* Carapace markedly more anteriorly protruding than the male, small setae posteriorly, lighter brown anteriorly and posterior part markedly lighter color than the male (Figs 45, 46). Anterior part of ocular region more setose than the male. Sternum darker orange than the male (Fig. 48). Anterior pair of small and marginal sigilla more visible than the male (Fig. 48). Labium wider than long, brown, with long setae anteriorly, with nine cuspules (Fig. 47). Endites brown in retrolateral part, light orange toward prolateral part, with numerous cuspules (Fig. 47). *Chelicerae:* Promarginal furrow with nine teeth, retromarginal furrow with approximately 19 small denticles (Fig. 47). Rastellum consists of 5-7 spines on a mound. *Opisthosoma:* Setose, lighter gray toward anterior part, darker gray coloration than the male; ventrally, genital area dark brown (Fig. 48). Spinnerets dark brown. *Legs:* Short and stout legs compared with the male (Figs 45, 50, 51). Long and dense scopulae on metatarsi and tarsi I, II, absent in III and IV. Legs spination: Legs without megaspines; Tibiae I: v(1+1+1+1); tibiae II: v (1+1+1); tibiae III and IV: scattered long spiniform setae; metatarsi I and II: v(1+2); metatarsi III: v(2+2+1); metatarsi IV: scattered long spiniform setae; tarsi I and II: without spines; tarsi III and IV: with scattered spination pattern. *Pedipalps:* Articles stouter and darker coloration than the male, setose, with long and dense scopulae on tarsi. Tarsi with a single claw; spination pattern: v(1+1). Tibiae with scattered long spiniform setae. *Genital area:* Bulky, trapezoidal shape, setose, brown color (Fig. 48). Spermathecae with single oval bulbs, paired, with dark basal stalk, the bulbs seems to be porous (Fig. 49).

Variation. Males (N = 5): Cl 6.8–8.3, 7.62±0.62; Cw 6.5–7.3, 6.84±0.38; STRl 4.30–4.90, 4.60±0.25; STRw 3.80–4.30, 4.00±0.19; PTl 3.50–4.20, 3.90±0.27; PTw 1.5–1.8, 1.62±0.13; Tibiae I (length): 4.60–5.90, 5.18±0.55. There is variation in the width of the tibia I and in the position of the ventral megaspines; in three specimens megaspines are close together and in two the megaspines are separated (Figs 40–44).

Natural history. All specimens examined were collected in the PNLM, a temperate pine-oyamel forest at 3000-3250 m of elevation (Fig. 52). The four specimens (LATLAX-Ara0031) were collected using pitfall traps in a pine forest (Fig. 52). The specimen (LATLAX- Ara0033) was hand collected walking on the ground. The female (LATLAX- Ara0032) was hand collected from a vertical burrow of ~50-60 cm deep located at 2 m on a wall along road-cut in a pine forest, the female was also found in the bottom of the burrow (Figs 50, 51).

Distribution. MEXICO: Puebla, Tlaxcala (Fig. 53).

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Figure 53. Known distribution records of *Aptostichus sabinae* sp. n. (red) (Oaxaca state), and *Eucteniza zapatista* Bond & Godwin, 2013 (blue) (Tlaxcala and Puebla states).

Discussion

In general, to collect trapdoor spiders is a difficult task, and few species have been described using both males and females. Most of them are described using few specimens or even only the male holotypes. The females are more difficult to collect due to their fossorial nature, whereas males, during certain seasons of the year wander, making pitfall traps the best method or technique so far for their collection. As Bond (2012) said: "the most of the species can be collected only during certain times of the year and collecting typically requires that the burrows be excavated, an activity that is often very time-consuming". The best technique so far seems to be that one proposed by Bond (2012), where one must sometimes use a "scraping" technique to find burrows by removing the first few centimeters of topsoil, thereby exposing the silk lined burrow, however, this technique is not very effective in sandy desert habitats (Bond 2012: 6). In the case of the genus *Aptostichus*, the only way to find females in desert habitats seems to be after winter rains, when the spiders extend, or clean out their burrows, leaving a small mound of sand at the burrow entrance (Bond 2012).

Although the genus *Aptostichus* was expected to have a relatively restricted biogeographic distribution in the southwestern United States and Baja California peninsula in Mexico, where the species are found in different habitats ranging from Mediterranean climates to the arid Mojave and Colorado deserts (Bond 2012: figs 1–6); the genus seems to have a wide spread distribution in Mexico as well. The diversity of the genus in Mexico is unknown, and *Aptostichus sabinae* sp. n. represents the very first new species described from Mexico. Under sampled biogeographical provinces for this genus such as California and Baja California, Sonora, and the Mexican Montane biotic component and its provinces, as well as the Sierra Madre Occidental, Transmexican Volcanic Belt (TVB), Cuenca del Balsas, and the Sierra Madre del Sur where *Aptostichus sabinae* was collected, are some of the most biodiverse provinces in Mexico for different groups of mygalomorph (Mendoza 2014, Ortiz and Francke 2016) and araneomorph spiders (Valdez-Mondragón and Francke 2015).

As the genus *Aptostichus*, the genus *Eucteniza* in Mexico has been poorly collected in the Sierra Madre Occidental (Bond and Godwin 2013: fig. 1). Most species have been collected in Mexico, towards the Sierra Madre Oriental, three species in Baja California Sur, and a widespread species in Texas, United States. *Eucteniza* is currently composed of 14 species, most of which are described from the Sierra Madre Occidental. However, although three species have been recorded in the TVB including *Eucteniza zapatista*, this biotic province has been poorly collected, mainly towards temperate montane forests mountains of the states of Estado de México, Michoacán, North of Guerrero, Colima and Jalisco, where more collecting remains to be done. The TVB is located in the Mexican Transition Zone, a region of overlap between the Neartic and Neotropic biotic regions, which represents the most biodiverse region in North America (Halffter et al. 1995, Halffter 2003, Brooks 2005, Morrone 2005, 2014). The different vegetation types, altitude, and climates of the Mexican biotic components and their biogeographical provinces (Morrone 2004, 2005, 2014), hints at the possibility that the both genera have even greater diversity than currently described.

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RESEARCH ARTICLE

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Review of the genus *Promecidia* Lelej, 1996, with description of two new species from China (Hymenoptera, Mutillidae, Trogaspidiini)

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Abstract

Eleven species of *Promecidia* Lelej, 1996 are reviewed and keyed, and the diagnosis of the genus is given. The genus *Promecidia* is newly recorded from China and *P. abnormis* Lelej, **sp. n.** (China: Guangdong, Hainan) and *P. chui* Lelej & Xu, **sp. n.** (China: Yunnan, Hainan) are described and illustrated. New combination is proposed for *P. boopis* (Kohl, 1882), **comb. n.** (from the genus *Petersenidia* Lelej, 1996). New status is proposed for *P. saturnia* (Mickel, 1935), **stat. n.** and *P. samawangensis* (Mickel, 1935), **stat. n.**

Keywords

Key to species, mutillid wasps, new combination, new species, Oriental, Trogaspidiini

Introduction

Mutillidae currently include 217 genera and about 4300 described species (Lelej 2007; Lelej and Brothers 2008; Aguiar et al. 2013, updated). In the Palaearctic region 525 species in 61 genera and in the Oriental region 640 species in 64 genera are reported (Lelej 2002, updated; Lelej 2005). The mutillid fauna of China includes 158 species in 32 genera (Chen 1957; Lelej 2002, 2005; He 2004; Tu et al. 2014a, b, 2015), comprising both Palaearctic (northwards of 30°N) and Oriental (southwards of 30°N) taxa. Because of extreme sexual dimorphism, sex associations cannot be made using morphology alone; most species and some genera are known from one sex only. This has resulted in many taxonomic challenges and resulted in many synonyms recognized through matching of males and females.

The genus *Promecidia* Lelej, 1996 was described in the tribe Petersenidiini (as subtribe Petersenidiina) (Lelej 1996) but later when the presumed males of other species were associated and described (Lelej 2005) was placed in the tribe Trogaspidiini. Currently *Promecidia* includes eleven Oriental species which are known from one sex and only *Promecidia saturnia* (Mickel) and *P. chui* Lelej & Xu, sp. n. from both sexes. Both sexes of the genus were keyed as a part of the tribe Trogaspidiini (Lelej 2005). A key to males and females of this genus is given below.

Materials and methods

The following acronyms are used for the collections where type specimens and other materials are deposited:

CAS	California Academy of Sciences, San-Francisco, U.S.A.
HNHM	Hungarian Natural History Museum, Budapest, Hungary.
IBSS	Institute of Biology and Soil Science, Vladivostok, Russia.
MRSN	Museo Regionale di Scienze Naturali, Torino, Italy.
MSNG	Museo Civico di Storia Naturale "G. Doria", Genoa, Italy.
NHMW	Naturhistorisches Museum Wien, Vienna, Austria.
SCAU	Hymenopteran Collection of South China Agricultural University, Guangzhou, China.
SKYC	Seiki Yamane Collection at Kagoshima University, Kagoshima, Japan.
USNM	National Museum of Natural History, Smithsonian Institution, Washington, DC, U.S.A.

To study male genitalic characters, the male genitalia were extracted after being previously softened. The muscles were removed in a sodium hydroxide solution (NaOH 10%), several hours without heating; the genitalia were later placed in water to neutralize the NaOH and stored in micro vials filled with glycerin. Male genitalia were studied under a stereomicroscope in a depression slide.

Photographs of imagos and genitalia were taken with a digital camera Cool SNAP attached to Zeiss stereomicroscope Stemi 2000-CS and stacked using CombineZM software (Hadley 2008). The final illustrations were post-processed for contrast and brightness using Adobe® Photoshop® software. The terminology for morphology is based on the glossary provided by the Hymenoptera Anatomy Consortium (2013). The nomenclature of integument sculpture follows Harris (1979), morphological terms are from Brothers (1975) and Lelej (1985). The terminology of wing venation and cells follows Goulet and Huber (1993). Abbreviations are: **POL** postocellar (interocellar) distance between posterior ocelli which is measured dorsally, and **OOL** ocellocular distance between posterior ocellus and compound eye which is measured dorsally.

Systematics

Genus *Promecidia* Lelej, 1996

Figs 1–10

Promecidia Lelej, 1996b: 15, ♀; 2005: 80, ♂ & ♀; Lelej and Brothers 2008: 47, ♂ & ♀. Type species: *Promecidia yamanei* Lelej, 1996, ♀ (Malaysia, Sarawak), by original designation.

Gender. Feminine.

Diagnosis. MALE. Head very short, rounded posterad. Eye deeply notched inside. Prementum not tuberculate. Mandible bidentate, with weak subbasal widening beneath or subbasal tubercle (*P. abnormis*, *P. chui*) and without subbasal tooth on inner border (with weak subbasal widening in *P. chui*). Scape curved, rarely widened apically (*P. chui*), with two longitudinal carinae. Ocelli small, POL much shorter than OOL. Tegula not elongated. Mesoscutellum simple, not swollen nor conical. Metacoxa not dentate. Marginal cell of fore wing 1.5× longer than first submarginal cell. Metasomal tergum 2 with lateral felt line. Sternum 2 without lateral felt line. Metasomal sterna 8 (hypopygium) and 7 without strong carina, at most with weak submedian elevation or two submedian carinae on sternum 8 (in *P. chui*, *P. abnormis*) and blunt lateral tubercle on sterum 7 (in *P. abnormis*). Penial valves short, slightly asymmetrical, capitate apically. Volsella with long thin cuspis, stick-like digitus and tuberculate paracuspis. FEMALE. First flagellomere slightly flattened. Anterior part of clypeus with or without two teeth. Mandible slender, with inner preapical tubercle. Scutellar scale lacking. Propodeum dorsally with longitudinal median carina; posterolateral margin of propodeum dentate or serrate. Metasomal tergum 2 with two pale spots located transversely on basal half and with or without pale apical fringe, tergum 3 with pale band. Tergum 6 without distinct pygidial area, convex, smooth, shiny, basal part of tergum punctured, with long pale setae.

Species included. *Promecidia abnormis* Lelej, sp. n., ♂ (China: Guangdong, Hainan); *P. birmanica* (de Dalla Torre, 1897), ♂ (Myanmar); *P. bonthainensis* (André, 1896), ♂ (Indonesia: Sulawesi); *P. boopis* (Kohl, 1882), comb. n., ♀ (Indonesia: Sulawesi); *P. chui* Lelej & Xu, sp. n., ♂ & ♀ (China: Yunnan, Hainan); *P. mamblia* (Cameron, 1902), ♀ (Malaysia: Sabah, Sarawak); *P. ninnii* (Magretti, 1892), ♀ (Myanmar, Vietnam, Laos); *P. rubrocyanea* (Mickel, 1935), ♂ (Malaysia: Sabah); *P. saturnia* (Mickel, 1935), stat. n., ♂ & ♀ (Malaysia: Malay Peninsula; Singapore); *P. samawangensis* (Mickel, 1935), stat. n., ♂ (Malaysia: Sabah, Sarawak); *P. yamanei* Lelej, 1996, ♀ (Malaysia: Sarawak).

Sex association. The male of the type species has not been recognized; the presumed males of other species were associated and described by Lelej 2005: 196. The following pairs of species may eventually be recognized as opposite sexes: *Promecidia yamanei* Lelej, 1996, ♀, and *P. rubrocyanea* (Mickel, 1935), ♂ (both are from Borneo, with dark metallic blue metasoma); *P. boopis* (Kohl, 1882), ♀, and *P. bonthainensis* (André, 1896), ♂ (both are from Sulawesi); *P. mamblia* (Cameron, 1902), ♀, and *P. samawangensis* (Mickel, 1935), ♂ (both are from Sabah and Sarawak); *P. ninnii* (Magretti, 1892), ♀, and *P. birmanica* (de Dalla Torre, 1897), ♂ (both are from Myanmar and Vietnam).

Distribution. Oriental Region.

Comments. The male of *Promecidia* Lelej, 1996 has very short asymmetrical penial valves and definitely belongs to tribe Trogaspidiini. Based on similar penial valves, coupled with having the mandible not strongly excised beneath and simple mesoscutellum the male of *Promecidia* is related to that of Afrotropical *Spinulomutilla* Nonveiller, 1994 but differs by lacking strong lateral carinae on metasomal sterna 7 and 8 (with strong ones in *Spinulomutilla*) and by metacoxa (dentate in *Spinulomutilla*). The male of *Promecidia* is superficially similar with that of *Taiwanomyrme* Tsuneki, 1993 from the tribe Petersenidiini, but differs asymmetrical penial valves (symmetrical in *Taiwanomyrme*). Within the tribes Trogaspidiini and Petersenidiini the female of *Promecidia* easily differs by the absence of a scutellar scale (with more or less developed scutellar scale in other genera of these tribes) and absence of a pygidial area, metasomal tergum 6 glabrous, shiny, not carinate even apically (with more or less developed pygidial area, at least carinate apically in other genera of these tribes; if without pygidial area (*Orientidia* Lelej, 1996) then scutellar scale visible).

Key to species of *Promecidia*

1 Males (unknown in *P. boopis*, *P. mamblia*, *P. ninnii*, *P. yamanei*) **2**

– Females (unknown in *P. abnormis*, *P. bonthainensis*, *P. birmanica*, *P. rubrocyanea*, *P. samawangensis*) **8**

2 Mandible beneath with subbasal denticle; penial valves weakly elongate, apically widened **3**

– Mandible beneath basally slightly widened, without subbasal denticle beneath; penial valves shortened, apically capitate **4**

3 First flagellomere approximately equal in length to flagellomere 2; scape distinctly widened apically; metasomal sternum 8 with weak submedian elevation; sternum 7 without lateral tubercle; sternum 2 with median carina highest basally .... ***P. chui* Lelej & Xu, sp. n.**

– First flagellomere 1.4× flagellomere 2; scape not widened apically; metasomal sternum 8 with two submedian carinae; sternum 7 with blunt lateral tubercle; sternum 2 with strong median carina highest apically... ***P. abnormis* Lelej, sp. n.**

4 Mesosoma partly or predominantly reddish; metasoma black or dark metallic blue **5**

– Mesosoma black; metasoma black with segments 1–3 yellowish-orange........ .... ***P. birmanica* (de Dalla Torre)**

5 Metasoma dark metallic blue; metasomal tergum 3 with pale band; mesosoma (except sternum) ferruginous .... ***P. rubrocyanea* (Mickel)**

– Metasoma black **6**

6 Metasomal tergum 3 with pale band; mesosoma mostly black with pronotum, mesonotum and tegula ferruginous .... ***P. bonthainensis* (André)**

– Metasomal terga 3–4 with pale band 7

7 Mesosoma almost entirely ferruginous with black sterna .... ***P. saturnia* (Mickel)**

– Mesopleuron ventrally, propodeum and sterna black, other parts of mesosoma ferruginous .... ***P. samawangensis* (Mickel)**

8 Metasoma dark metallic blue .... ***P. yamanei* Lelej**

– Metasoma black **9**

9 Metasomal tergum 2 with apical pale fringe or narrow band **11**

– Metasomal tergum 2 without apical pale fringe **10**

10 Humeral angle of mesosoma prominently angulate; mesosoma dorsally with long black setae; larger species: 11.0 mm .... ***P. mamblia* (Cameron)**

– Humeral angle of mesosoma angulate but not prominent; mesosoma dorsally with long yellowish setae; smaller species: 5.6–7.6 mm ***P. saturnia* (Mickel)**

11 Posterolateral margin of propodeum dentate; metasomal terga 4 and 5 with black setae **12**

– Posterolateral margin of propodeum crenulate; metasomal terga 4 and 5 with rather dense golden setae .... ***P. chui* Lelej & Xu, sp. n.**

12 Tibiae and tarsi black; pale band on metasomal tergum 3 interrupted medially .... ***P. boopis* (Kohl)**

– Tibiae and tarsi ferruginous; pale band on metasomal tergum 3 entire .... ***P. ninnii* (Magretti)**

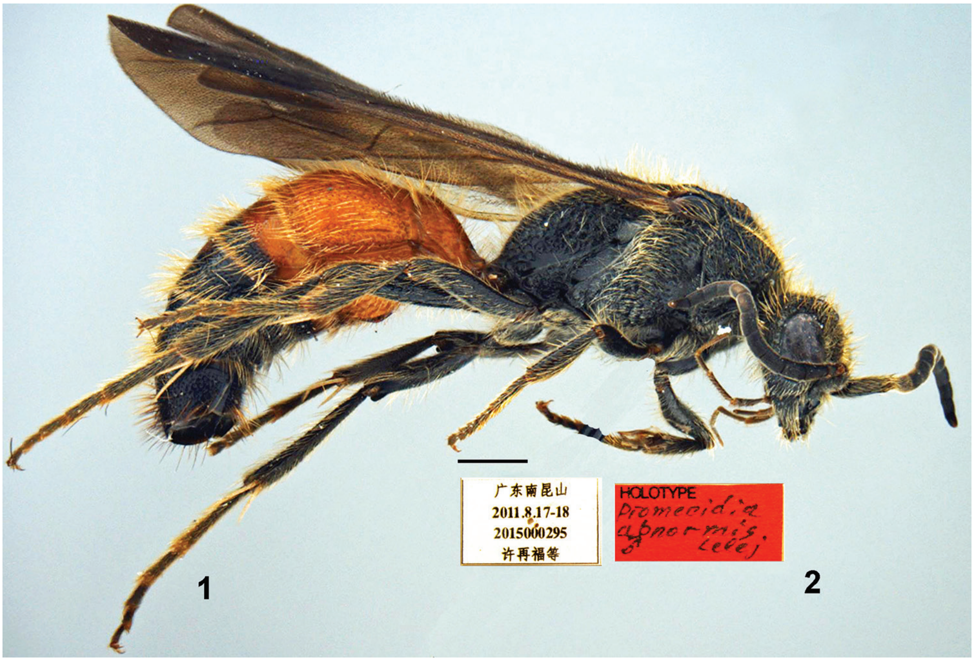
***Promecidia abnormis* Lelej, sp. n.**

http://zoobank.org/64E4361A-1D5E-42B9-9802-1ECCEF59C72F
Figs 1, 2, 6

Type material. Holotype (SCAU). CHINA: ♂, pinned, with genitalia and apical tergum and sternum in a separate micro vial, attached on the same pin, Guangdong, Nankunshan Provincial Nature Reserve, 17–18.VIII.2011, Zai-fu Xu & Hua-yan Chen, No. 2015000295.

Paratype. CHINA: ♂ (SCAU), Hainan, Jianfengling National Nature Reserve, 4–6.V.2008, Bo Qiu.

Diagnosis. MALE. Body length 8.5–10.2 mm. First flagellomere 1.2× flagellomere 2. POL:OOL = 0.36. Distance between outer ocellar margins equal to distance between posterior ocelli and posterior border of occiput. Mandible bidentate apically, with subbasal tooth on outer margin beneath. Metasomal sternum 2 (except apical third) with strong longitudinal median carina highest apically. FEMALE unknown.



Figures 1–2. *Promecidia abnormis* Lelej, sp. n., male, holotype. **1** Habitus, lateral view **2** labels. Scale bars 1 mm.

Description. MALE. Body length 8.5–10.2 mm. Black with ferruginous metasomal terga 1–2, sterna 1–3, and base of terga 3 and 4. Head, mandible and scape with yellowish, dense, subappressed setae; pronotum dorsally, mesoscutum, scutellum and metanotum medially with subappressed and erect golden setae, longer on scutellum and metanotum, posterodorsal margin of pronotum densely fringed; propleuron, mesopleuron, and propodeum laterally with whitish appressed and subappressed setae, denser on mesopleuron; posterior propodeal slope with whitish yellow, sparse, erect setae; dorsal propodeal slope with short appressed white setae; legs with dense pale yellow, suberect setae. Metasomal terga with appressed and erect yellowish setae, apically sparsely fringed with pale yellowish setae, sterna with sparse subappressed yellowish setae. Metasomal tergum 2 laterally with felt line, sternum 2 without lateral felt line.

Relation of head width and mesosoma width including tegulae 55:60; relation of maxillary palpus length and cardo length 5.0:1.5. Mandible bidentate apically, with subbasal tooth on outer margin beneath and dorsal carina extending from base to subapical tooth. Clypeus with median area subtriangularly raised, anterior margin with two denticles, distance between them much less than between denticle and base of mandible. Scape not widened apically, bicarinate beneath. First flagellomere 1.2× flagellomere 2; antennal scrobe carinate above. Ocelli small, POL:OOL = 0.36. Distance between outer ocellar margins equal to distance between posterior ocelli and posterior border of occiput. Frons and vertex with shallow dense punctures. Tegula large, not projecting scuto-scutellar suture, with smooth and shiny disc and posterior border. Mesoscutellum evenly convex. Notauli well developed, half length of mesoscutum. Parapsides poorly defined. Metanotum densely punctured, medially with deep glabrous area medially. Pronotum and mesopleuron with large, sometimes confluent punctures; mesoscutum with moderately coarse, more or less separated punctures; mesoscutellum with moderately coarse, somewhat confluent punctures; propleuron obscurely striato-punctate; inferior portions of metapleuron glabrous and shiny. Propodeum reticulate, more finely so laterally, and with larger reticulae dorsomedially.

Fore wing fuscous, first submarginal cell large, subtriangular, apically acute, 0.8× length of marginal cell; second submarginal cell receiving recurrent vein at midpoint; third submarginal cell less distinct than submarginal cell 2 and receiving recurrent vein at midpoint. Pterostigma length equal to distance between origin of RS_1 on *SC* and pterostigma.

Carina on metasomal sternum 1 well developed, straight, 0.8× length of sternum 1 in profile, straight; sternum 2 (except apical third) with strong longitudinal median carina highest apically. Terga 1–6 and posterior halves of sterna 3–6 with moderately fine, well separated punctures, larger on tergum 2; sternum 2 with large, moderately coarse, separated punctures; sternum 8 (hypopygium) and tergum 7 (except apical part) with moderately coarse, dense punctures; tergum 7 medially with longitudinal narrow glabrous area up to apical fourth where it with small punctures.

FEMALE. Unknown.

Etymology. The specific name is a Latin adjective meaning "abnormal", with reference to the unusual carina on metasomal sternum 2, like that of males of *Zeugomutilla* Chen, 1957.

Distribution. China (Guangdong, Hainan).

Promecidia birmanica (de Dalla Torre, 1897)

Mutilla birmanica de Dalla Torre, 1897: 16. New name for *Mutilla schlettereri* Magretti, 1892.

Mutilla schlettereri Magretti, 1892: 230, tab. 5, fig. 19, ♂, nom. praeocc., *nec* Morawitz, 1890, holotype, ♂, "Monti dei Carin–Chebá, Giugno 1888" [mountain area (1000–1200 m) in the Karen Hills of southeastern Myanmar, in the Tenasserim Mountain Range] (MSNG).

Promecidia birmanica: Lelej 2005: 80, ♂.

Promecidia ninnii: Lelej 2005: 81, part., ♂ (Laos, India: Assam).

Material examined. LAOS: 1 ♂ (MRSN). INDIA: 1 ♂ (CAS), Assam, Kohara, Kaziranga, 110 m, 7.X.1961, E.S. Ross, D.Q. Cavangaro. MYANMAR: 1 ♂ (IBSS), Palaing [16°32'28"N 97°57'34"E], V.1937, R. Perego. VIETNAM: 2 ♂ (IBSS), 70 km NE Saigon (now Ho Chi Minh), Ma de, VIII. 1994, Belyaeva.

Diagnosis. MALE. Body length 10.4–12.0 mm (holotype 12.0 mm). Mandible slightly widened beneath at base, without small subbasal denticle. Penial valves shortened, slightly longer than digitus, apically capitate. Mesosoma black. Metasoma black with segments 1–3 yellowish-orange. FEMALE unknown.

Distribution. Myanmar, India, Laos, Vietnam.

Comments. Possibly, this species is the male of *Promecidia ninnii* (Magretti, 1892). Both are distributed in Myanmar and Vietnam.

Promecidia bonthainensis (André, 1896)

Mutilla Bonthainensis André, 1896: 14, ♂, holotype, ♂: "Bonthain" (Indonesia: Sulawesi) (HNHM); Zavattari 1914: 96, ♂.
Timulla (*Trogaspidia*) *bonthainensis*: Mickel 1935: 257, ♂.
Promecidia bonthainensis: Lelej 2005: 81, ♂.

Material examined. INDONESIA: Sulawesi, holotype of *Mutilla bonthainensis* André (HNHM), ♂, "781. / 14. // S. Celebes / Bonthain / C. Riobbe 1884 // *M. bonta* / *nensis* / [sic!] det. André // Typus // Holotype / *Mutilla* ♂ / *bonthainensis* André / det. D.J. Brothers 1981 // *M.* / *thoracica* (Smith) / B. Petersen det. 1981".

Diagnosis. MALE. Body length 13.0 mm. Metasoma black. Metasomal tergum 3 with entire pale band. Mesosoma mostly black with pronotum, mesoscutum, mesoscutellum, metanotumn and tegula ferruginous. FEMALE unknown.

Distribution. Indonesia (Sulawesi) (André 1896).

Promecidia boopis (Kohl, 1882), comb. n.

Mutilla boopis Kohl, 1882: 478, ♀, syntypes: "Celebes" (Indonesia) (NHMW); Zavattari 1910: 8, ♀.
Timulla (*Trogaspidia*) *boopis*: Mickel 1935: 269, ♀.
Petersenidia boopis: Lelej 2005: 73, ♀.

Material examined. INDONESIA: 1 ♀ (IBSS), Sulawesi, Tomohon, Rurukan, Gn. Mahawu, 1150–1200 m, 30.XI.1999, A. Riedel; 1 ♀ (IBSS), Sulawesi, Kotamobagu, Matalibaru, Torosik, Gn. Tongara, 850–900 m, 9.XII.1999, A. Riedel.

Diagnosis. MALE unknown. FEMALE. Body length 6.4–9.0 mm. Metasoma black. Metasomal tergum 2 with apical pale fringe. Posterolateral border of propodeum dentate. Metasomal terga 4 and 5 with black setae. Tibiae and tarsi black. Pale band on metasomal tergum 3 interrupted medially.

Distribution. Indonesia (Sulawesi) (Kohl 1882).

Promecidia chui **Lelej & Xu, sp. n.**

http://zoobank.org/5CE6A276-4F51-47DC-A3CB-031353E076F6
Figs 3–5, 7–10

Type material. Holotype (SCAU). CHINA: ♂, pinned, with genitalia in a separate micro vial, attached on the same pin, Yunnan, Nabanhe National Nature Reserve, 19–23.VII.2011, Na-sen Wei & Zai-fu Xu, No. 2015000329.

Paratypes. CHINA: 2 ♂ (SCAU), with the same label as holotype; 3 ♂ (SCAU), Hainan, Bawangling National Nature Reserve, 7–11.VII.2006, Jiang-xian Liu and Li-qiong Weng; 2 ♂ (SCAU), same place, 9–10.VI.2007, Jie Zeng and Bing Xiao; 1 ♂ (SCAU), Wuzhishan Nature Reserve, 16–20.V.2007, Li-qiong Weng; 1 ♂ (IBSS), Jianfengling, 4–7.VI.2007, Jie Zeng; 1 ♀ (SCAU), Diaoluoshan National Nature Reserve, 16–17.VII.2006, Jiang-xian Liu and Li-qiong Weng; 2 ♂ (SCAU), Jiujialing, YPT, 18.VII.2010, Hua-yan Chen.

Diagnosis. MALE. Body length 6.8–11.9 mm. First flagellomere equal in length to flagellomere 2. Scape widened apically. Ocelli small, POL:OOL=0.6–0.65. Distance between outer ocellar margins 1.2–1.3× distance between posterior ocelli and posterior border of occiput. Mandible bidentate apically, with subbasal tooth on outer margin beneath, inner margin with weak subbasal widening. Metasomal sternum 2 basally with strong median carina highest basally. FEMALE. Body length 7.65 mm. Mesosoma and legs ferruginous red; flagellomeres 2–9 ferruginous ventrally. First flagellomere 1.33× flagellomere 2. Metasomal tergum 2 with two subcircular spots of yellowish setae anteriorly, separated by distance equal to their diameter. Tergum 6 convex, glabrous and shiny, without definite pygidial area.

Description. MALE. Body length 6.8–11.9 mm. Black except ferruginous metasomal terga 1–3 and sterna 1–3; tegula brownish. Frons, vertex, lateral area of clypeus and base of mandible with whitish dense subappressed setae; gena with whitish dense erect setae. Pronotum, propleuron with golden or whitish recumbent setae (posterior margin of pronotum densely fringed); mesonotum with sparse reddish (Yunnan) or white (Hainan) setae. Mesopleuron, lateral area of metanotum and dorsum of propodeum with whitish yellow, dense, appressed setae; posterior propodeal slope with whitish sparse erect setae; mesoscutellum and metanotum medially with erect yellowish setae; legs with yellowish dense suberect setae; lateral propodeal slope with few erect white setae. Metasomal tergum 2 with sparse yellowish setae; terga 3–4 with dense subappressed yellowish setae; terga 1–6 sparsely fringed apically; sterna 1–3 (1–4 in paratypes from Hainan) with sparse subappressed yellowish setae. Metasomal tergum 2 with felt line laterally, sternum 2 without lateral felt line.

Head width 0.84–0.92× mesosoma width including tegulae; relation of maxillary palpus length and cardo length 6.0:1.5. Mandible bidentate apically, with subbasal tooth on outer margin beneath and dorsal carina extending from base to subapical tooth; inner margin weakly widened subbasally. Clypeus subtriangularly raised

Figures 3–5. *Promecidia chui* Lelej & Xu, sp. n., male, holotype. **3** Habitus, lateral view **4** mandible, lateral view **5** labels. Scale bars 1 mm.

with median area concave and with anterior margin slightly notched, with transverse preapical carina with few setae. Scape widened apically, bicarinate beneath basally, upper (dorsal) carina complete and widened apically. First flagellomere equal in length to flagellomere 2; antennal scrobe carinate above. Ocelli small, POL:OOL=0.6–0.65. Distance between outer ocellar margins 1.2–1.3× distance between posterior ocelli and posterior border of occiput. Frons, vertex and gena with coarse dense punctures.

Tegula not projecting over scuto-scutellar suture, with smooth and shiny disc and posterior border. Mesoscutellum evenly convex. Metanotum densely punctured, with deep glabrous area medially. Pronotum and mesopleuron with dense, confluent punctures; mesoscutum with dense separated punctures; mesoscutellum with larger coarse, somewhat confluent punctures; propleuron, mesopleuron anterad, metapleuron glabrous. Propodeum reticulate, laterally more finely so, and dorsomedially with larger cells. Notauli well developed, ⅔ length of mesoscutum. Parapsides weaker and shorter than notauli.

Fore wings fuscous, first submarginal cell large, subtriangular, apically acute, 0.7× length of marginal cell; second submarginal cell receiving recurrent vein at midpoint; third submarginal cell less distinct than submarginal cell 2 and receiving recurrent vein at midpoint. Pterostigma length equal to distance between origin of RS_1 on SC and pterostigma.

Carina on metasomal sternum 1 well developed, 0.8× length of sternum 1 in profile, straight; sternum 2 basally with strong median carina highest basally. Terga 1–6 and posterior halves of sterna 3–6 with moderately fine, well separated punctures,

Figures 6–7. *Promecidia*, male genitalia, ventral view. **6** *P. abnormis* Lelej, sp. n., holotype **7** *P. chui* Lelej & Xu, sp. n., paratype from Hainan. Scale bars 0.5 mm.

larger on tergum 2; sternum 2 with larger, separated punctures; sternum 8 (hypopygium) and tergum 7 with moderately coarse, dense punctures; tergum 7 medially with narrow glabrous area widened apically.

FEMALE. Body length 7.65 mm. Black with brownish clypeus, palps pale, with ferruginous red mandible (except apex), scape, pedicel, flagellomere 1, legs, mesosoma; flagellomeres 2–9 ventrally ferruginous. Clypeus, gena, mandible with whitish, sparse, erect setae; frons and occiput with subappresseed golden-reddish setae; gena with subappressed whitish setae; dorsum of mesosoma with setae as those on frons; posterior propodeal slope and metasomal tergum 1 with erect whitish setae; metasomal tergum 2 with black dense, recumbent setae; apical fringe of terga 2–3 with yellowish, dense, appressed setae mixed with longer erect ones; terga 4–6 (except pygidial area) with darker and sparser brown setae; sterna 2–6 and legs with yellowish, sparse, erect setae. Metasomal tergum 2 in basal half with two subcircular spots of yellowish setae, separated by distance equal to their diameter; lateral felt line of tergum 2 whitish.

Figures 8–10. *Promecidia chui* Lelej & Xu, sp. n., female, paratype. **8** Habitus, dorso-lateral view **9** metasoma, dorsal view **10** metasomal terga 5 and 6, dorsal view. Scale bars 1 mm.

Relation of head width and mesosoma width 47:45 (pronotum): 42 (mesonotum): 37 (propodeum); relation of maxillary palp length and cardo length 3.5:1.5. Head distinctly narrowed behind eyes. Mandible with weak preapical tooth on inner margin. Clypeus posteriorly elevated into rather low, transversely arcuate ridge, with well developed median tubercle basally. First flagellomere 1.33× flagellomere 2; antennal scrobe distinctly carinate above. Eye ovate, strongly convex. Gena not carinate beneath, with tubercle on hypostomal carina closer to mandibular insertion. Frons, vertex and gena with moderately coarse, elongate punctures; vertex with two distinct tubercles located transversely on line of posterior eye borders.

Relation of mesosoma length to its width 55:37, widest on pronotum, narrowest propodeal spiracles. Mesosoma with lateral margins convergent posterad; crenulate, concavely curved, mesoscutum with lateral carina; humeral angles and pronotal lateral tubercle acute, latter prominent. Pleura depressed in center, sharply marked-off from anterior pronotal slope and dorsum of pro- to metanotum by marginal recurvature and from posterior propodeal slope by marginal tubercles; mesopleural suture carinate; dorsal and posterior propodeal slope in profile without definite bend. Dorsum of mesosoma with moderately coarse, deep punctures; posterior propodeal slope with coarser and shallower, elongate, strongly confluent punctures with tendency to rugosity; pleura glabrous.

Legs moderately long; meso- and metatibia each with one row of 5–6 spines and another one with three weak spines; tibio-tarsal relation of hind leg 37:15:11:9:5:7.

Metasomal sternum 1 with anterior arm of Y-shaped ridge moderately strong and posterior ones very weak. Anterior slope of tergum 1 with well separated punctures; dorsal surface of tergum 1 indefinite; tergum 2 with separate setiferous punctures mixed with dense micropunctures; terga 3–5 basally with separate punctures obscured by dense pale setae; tergum 6 (except pygidial area) with dense punctures; sternum 2 basally with median carina, with large separate punctures; posterior areas of sterna 3–6 with fine, separated punctures. Tergum 6 convex, glabrous and shiny, without definite pygidial area; lateral margins not carinate even apically.

Etymology. It is a great pleasure for us (A. Lelej and Z. Xu) to name this species after the well-known Chinese hymenopterist Prof. Chu Joo-tsu (1900–1981).

Distribution. China (Yunnan, Hainan).

Comments. The male and female are collected by the same collectors in July 2006 sites Hainan which are close to each other. There is no direct evidence to support the relationship.

***Promecidia mamblia* (Cameron, 1902)**

Mutilla mamblia Cameron, 1902: 79, ♀, holotype: "Kuching, Sarawak" (Malaysia) (The Natural History Museum, London, UK).
Timulla (*Trogaspidia*) *mamblia*: Mickel 1935: 268, ♀.
Petersenidia mamblia: Lelej 1996a: 93, ♀.
Promecidia mamblia: Lelej 2005: 81, ♀.

Material examined. MALAYSIA: 1 ♀ (SKYC), Sabah, Sepilok, forest, 21.VIII.1995, Sk. Yamane; 1 ♀ (IBSS), Sabah, Danum Valley, 30.IV.2000, C. Brühl.

Diagnosis. MALE unknown. FEMALE. Body length 9.6–11.0 (holotype) mm. Metasoma black. Metasomal tergum 2 without apical pale fringe. Humeral angle of mesosoma prominently angulate. Mesosoma dorsally with long black setae.

Distribution. Malaysia (Sabah, Sarawak). The record of this species from Perak (Zavattari 1914: 76) is doubtful (Mickel 1935) and probably belongs to a female of *Promecidia saturnia* (Mickel), which is distributed in the Malay Peninsula.

Promecidia ninnii (Magretti, 1892)

Mutilla Ninnii Magretti, 1892: 211, ♀, holotype: "Monti dei Carin–Chebà (900–1100 m. s./m.), Luglio 1888" [mountain area in the Karen Hills of southeastern Myanmar, in the Tenasserim Mountain Range] (MSNG); de Dalla Torre 1897: 66, ♀.
Promecidia ninnii: Lelej 2005: 81, ♀.

Material examined. VIETNAM: 1 ♀ (IBSS), Dong Nai, Ma Da, forest, 6.VI.1995, T. Sergeeva. THAILAND: 1 ♀ (IBSS), North-East Thailand, Nakornratchasima, Sakaerat lowland forest (DEF), 9.VII.1999, Sk. Yamane.

Diagnosis. MALE unknown. FEMALE. Body length 6.0 (holotype)–8.4 mm. Metasoma black. Metasomal tergum 2 with narrow apical pale band. Posterolateral border of propodeum dentate. Metasomal terga 4–5 with black setae. Tibiae and tarsi ferruginous. Pale band of tergum 3 entire.

Distribution. Myanmar, Thailand, Vietnam (Dong Nai). The record of this species from India (Assam, Lelej 2005) belongs to *P. birmanica* (de Dalla Torre, 1897) (above).

Comments. Possibly, this species is the female of *Promecidia birmanica* (de Dalla Torre, 1897); both are distributed in Myanmar and Vietnam.

Promecidia rubrocyanea (Mickel, 1935)

Timulla (*Trogaspidia*) *rubrocyanea* Mickel, 1935: 256, ♂, holotype, ♂, "British N. Borneo, Bettotan near Sandakan, August 20, 1927, C.B.K. and H.M.P." [C.B. Kloss and H.M. Pendlebury] (Malaysia: Sabah) (University of Minnesota, St. Paul).
Promecidia rubrocyanea: Lelej 2005: 81, ♂.

Material examined. No specimens examined.

Diagnosis (based on the original description of Mickel 1935). MALE. Body length 16.0 mm. Mandible slightly widened beneath at base, without small subbasal denticle beneath. Metasoma dark metallic blue. Mesosoma (except sternum) ferruginous. Metasomal tergum 3 with pale band. FEMALE unknown.

Distribution. Malaysia (Sabah) (Mickel 1935).

Promecidia samawangensis (Mickel, 1935), stat. n.

Timulla (*Trogaspidia*) *saturnia samawangensis* Mickel, 1935: 256, ♂, holotype, ♂: "British N. Borneo, Samawang near Sandakan", July17, 1927, C.B.K. and N.M.P." [C.B. Kloss and H.M. Pendlebury] (Malaysia: Sabah) (University of Minnesota, St. Paul).
Promecidia saturnia samawangensis: Lelej 2005: 81, ♂.

Material examined. No specimens examined.

Diagnosis (based on the original description of Mickel 1935). MALE. Body length 15 mm. Mandible beneath basally slightly widened, without small subbasal denticle beneath. Metasoma black. Metasomal terga 3–4 with pale band. Mesosoma ferruginous except mesopleuron ventrally, propodeum and sterna black. FEMALE unknown.

Distribution. Malaysia (Sabah, Sarawak) (Mickel 1935; Lelej 2005).

Remarks. The males of *Promecidia saturnia* and *P. samawangensis* differ in coloration, distribution and body length; therefore we consider these to be distinct species.

Promecidia saturnia (Mickel, 1935), stat. n.

Mutilla urania Smith, 1857: 83, ♂, *nec* ♀, "Borneo (Sarawak)".
Timulla (*Trogaspidia*) *saturnia saturnia* Mickel, 1935: 256, ♂, holotype, ♂: "Malay Peninsula, Mt. Ophir (labelled as ♂ of *Mutilla urania* Smith)" (Malaysia: Malacca) (Museum of Natural History, Oxford University).
Promecidia saturnia saturnia: Lelej 2005: 81, ♂.

Material examined. SINGAPORE: 1 ♂ & 1 ♀ (USNM), "Singapore, Coll. Baker" // "K". MALAYSIA: 1 ♂ (IBSS), "Pasoh Forest Res.[erve] / Negri S.[embilan] Malaysia / x.3.[19]79 sec.[ondary] for.[est] / P. & M. Becker"; 1 ♀ (IBSS), Selangor, Ulu Gombak, VII.1998, F. Ito; 1 ♀ (IBSS), Sabah, Danum Valley, 9.XI.1996, K. Eguchi.

Diagnosis. MALE. Body length 10.6–11.7 mm. Mandible beneath basally slightly widened, without small subbasal denticle beneath. Penial valves shortened, slightly longer than digitus, apically capitate. Metasoma black. Metasomal terga 3–4 with pale band. Mesosoma almost entirely ferruginous with black sterna. FEMALE. Body length 5.6–7.6 mm. Metasoma black. Metasomal tergum 2 without apical pale fringe. Humeral angle of mesosoma angulate but not prominent. Mesosoma dorsally with long yellowish setae.

Distribution. Malaysia (Malacca, Negeri Sembilan, Selangor, Sabah), Singapore.

Comments. Possibly the specimens from Singapore are taken *in copula* because they are with the same labels and marked by additional label "K". The specimens have been collected by C.F. Baker presumably during 1917–1918 when he was Director of Singapore Botanic Gardens (Ascher *et al.* 2016). The female of *P. saturnia* is related with that of *P. mamblia* (Cameron, 1902). The original description of the both sexes of *Mutilla urania* by Smith (1857) cited Sarawak, Borneo as the type locality. Mickel (1935) examined the syntypes in the Saunders Collection (Museum of Natural History, Oxford University) and found that both syntypes were labelled "Mt. Ophir", which is located in the Malay Peninsula. The material covered in Smith (1857–1858) paper came from Borneo, Mt. Ophir and Singapore. Possibly, the citation of the type locality as "Borneo" was an error and the correct type locality is Mt. Ophir, Malacca (Mickel 1935). According to Mickel (1935) both sexes of *M. urania* belong to different genera. The female was designated by Mickel as lectotype (holotype *sensu* Mickel

1935) of *urania* which currently belongs to the genus *Odontomutilla* Ashmead, 1899. For the male of *M. urania* (*sensu* Smith 1857) Mickel (1935) proposed a new name *Timulla* (*Trogaspidia*) *saturnia*, but really it was actually a new species based on the paralectotype of *M. urania*, which became the holotype of *T.* (*Trogaspidia*) *saturnia* which was later transferred to *Promecidia* Lelej, 1996 by Lelej (2005).

Promecidia yamanei **Lelej, 1996**

Promecidia yamanei Lelej, 1996b: 15, ♀, holotype, ♀: Malaysia, Sarawak (Malaysia: Sarawak) (SKYC); 2005: 81, ♀.

Material examined. MALAYSIA: Sarawak, holotype of *Promecidia yamanei* Lelej (SKYC), ♀, "Tower Region / Lambir N. P. / Miri, Sarawak / Malaysia // 17.viii.1995 / Sk. Yamane leg. // Holotype / *Promecidia* / *yamanei* Lelej, ♀". Other material. MALAYSIA: 1 ♀ (IBSS), Sarawak, Miri, Lambir National Park, Tower Region, 3.III.1997, Sk. Yamane.

Diagnosis. MALE unknown. FEMALE. Body length 9.0–12.0 mm. Metasoma dark metallic blue. Head and legs black, mesosoma ferruginous; flagellomeres 2–10 ventrally reddish. Metasomal tergum 2 with two small yellowish spots and narrow apical yellowish fascia interrupted medially, tergum 3 with broad yellowish or golden band.

Distribution. Malaysia (Sarawak).

Remark. Possibly, this species is the female of *Promecidia rubrocyanea* (Mickel, 1935) because both are from Borneo, with dark metallic blue metasoma (other species of *Promecidia* with black metasoma).

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RESEARCH ARTICLE

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Phylogeographic, morphometric and taxonomic re-evaluation of the river sardine, *Mesobola brevianalis* (Boulenger, 1908) (Teleostei, Cyprinidae, Chedrini)

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Abstract

The river sardine, *Mesobola brevianalis* (Boulenger, 1908), is the type species of *Mesobola* Howes, 1984. Standard phylogenetic analyses of partial sequences of the cytochrome oxidase I gene of individuals from populations across southern Africa that are currently identified as *M. brevianalis* showed that these populations represent four genetically distinct allopatric lineages. Furthermore, *Engraulicypris sardella* (Günther, 1868), the type species of *Engraulicypris* Günther, 1894, was convincingly nested amongst these clades. These findings support synonymisation of *Engraulicypris* and *Mesobola* **syn. n.**; restoration of *Engraulicypris gariepinus* (Barnard, 1943) **stat. rev.** for the lower Orange River population; description of two new species, *Engraulicypris ngalala* **sp. n.** and *Engraulicypris howesi* **sp. n.** from the Rovuma and Kunene river systems, respectively; affirmation of the synonymy of *Engraulicypris brevianalis* (Boulenger, 1908) **comb. n.** sensu stricto and *Engraulicypris whitei* van der Horst, 1934; and restoration of *Engraulicypris bredoi* Poll, 1945 **stat. rev.** and *Engraulicypris spinifer* Bailey & Matthes, 1971 **stat. rev.** from *Mesobola*. Discriminant function analysis of a truss network of five traditional morphometric measurements and 21 morphometric measurements that characterised the shape of the fishes was used to seek morphological markers for the genetically distinct populations. Only *E. gariepinus* was morphometrically distinctive, but live colouration differed between the lineages. Detailed taxonomic descriptions and an identification key for the species are provided.

Keywords

Phylogeography, morphometrics, nomenclature, *Mesobola*, *Engraulicypris*, new species, new combinations, new synonym

Introduction

The river sardine, *Mesobola brevianalis* (Boulenger, 1908), is a small, shoaling fish that favours the upper stratum of open waters particularly in rivers and dams in south central Africa (Engelbrecht & Mulder 1999), breeds in early summer, and feeds on planktonic crustaceans and insects (Hay et al. 2008). It is important for its potential as a food source for sympatric game and predatory fish, including indigenous nembwe (*Serranochromis robustus* (Günther, 1864)), silver catfish (*Schilbe intermedius* Rüppell, 1832) and tigerfish (*Hydrocynus vittatus* (Castelnau, 1861)), and introduced bass (*Micropterus* spp.) (Engelbrecht & Mulder 1999), and it is therefore used as bait by subsistence fisherman (Engelbrecht & Mulder 1999). However, little research has been done to inform the species' management, perhaps due to its low commercial potential (Engelbrecht & Mulder 1999).

Mesobola brevianalis falls under several fisheries jurisdictions, occurring in a number of southern African river systems, including the Kunene, lower Orange, Okavango and Zambezi River systems (van der Horst 1934, Barnard 1943, Bell-Cross 1965, Skelton 2001, Hay et al. 2008, Ramollo 2011). It is considered alien to the Lower Zambezi River, since they were introduced into the Nyamombe River, a tributary of the Mazowe River in Mozambique (Kadye 2008). River sardines have also been found in the eastern coastal rivers from the Mfolozi and Mkhuze rivers (Skelton & Whitfield 1989, Hay et al. 2008) to the Limpopo River (Olivier et al. 2009) in South Africa, and in the Rovuma River system in Mozambique.

Populations from different river systems show subtle differences in morphology or colouration that may indicate cryptic species, but this potentially significant geographical variation in the river sardine is not reflected in its taxonomy. *Mesobola brevianalis* was described as *Neobola brevianalis* Boulenger, 1908 based on specimens from the Mkuzi River, South Africa. It was transferred to its current genus, *Mesobola* Howes, 1984, as the type species of that genus (Howes 1984, Eschmeyer et al. 2016). *Engraulicypris whitei* van der Horst, 1934 was described from the Aapies River, a tributary of the Limpopo system, and later synonymized with *N. brevianalis* by Jubb (1963: 15, 26, Eschmeyer et al. 2016). Subsequently, *Engraulicypris gariepinus* Barnard, 1943 was described from the lower Orange River and also synonymized with *N. brevianalis* by Jubb (1967: 42, Eschmeyer et al. 2016). The status of these taxa was not assessed using contemporary quantitative methods.

A morphometric and phylogeographic study was therefore undertaken to assess the taxonomy of the biogeographically distinct populations of *M. brevianalis sensu lato* (i.e. including all taxonomic synonyms). Amongst other nomenclatural acts, the results support the synonymisation of *Engraulicypris* Günther, 1894 and *Mesobola* Howes, 1984 syn. n., the restoration of *E. gariepinus* Barnard, 1943 stat. rev., and the description of two new species of *Engraulicypris*.

Materials and methods

Specimens

Specimens identified as *Mesobola brevianalis* (Boulenger, 1908) were collected from twelve river systems from ten African countries (Fig. 1, Tables 1, 2). The fish were collected under permit by various methods including hand, seine netting and electrofishing device. Specimens were killed by over-dosing in a mixture of clove oil and water and when possible, photographs were taken of the left side of the fish to record its live colouration. The specimens were then fixed in 10% formalin and specimens collected in the same event were placed together into a container with a waterproof label bearing the date, sample number, location, details of the capture and preservation methods, the sample and specimen numbers (Tables 1, 2). In the laboratory, the fixed specimens were transferred through a series of dilutions up into 70% ethanol for long-term preservation.

When a fresh or ethanol-preserved fish was selected for genetic analysis, the entire caudal fin, or a muscle tissue sample taken between the end point of its dorsal fin and the beginning of its caudal fin, was placed in 95% ethanol in a separate microcentrifuge tube. The tissue samples and the whole specimens were catalogued into the South African Institute for Aquatic Biodiversity (SAIAB), Grahamstown.

Phylogenetic relationships

The relationships of the sampled populations identified as *M. brevianalis* and representatives of its near relatives in the Chedrini (Tang et al. 2010; Liao et al. 2012) were estimated using phylogenetic analysis of mtDNA sequences. Each tissue sample used for DNA extraction (Table 1) was dried completely before being placed in a new microcentrifuge tube. DNA was extracted using the DNeasy® blood and tissue kit (Qiagen, Valencia, CA) and the NucleoSpin® Tissue kit (Machery-Nagel GmbH & Co. KG) following the manufacturer's instructions for animal tissue isolation, except that the incubation period was 12 h to allow for complete tissue digestion and the final dilution step was performed with 50 µl (rather than 200 µl) nuclease-free distilled water during extraction with the DNeasy® kit to provide a higher concentration of DNA. The concentration and purity of each DNA extract was determined by using a NanoDrop 2000 Spectrophotometer. The DNA concentration, A260, A280, 260/280 and 260/230 values were documented to ensure that the DNA was sufficiently concentrated and pure.

A 658 basepair (bp) fragment of the protein-coding *Cytochrome Oxidase 1* (COI) mitochondrial gene was amplified using the LCOI490 and HCO2198 primer set (Folmer et al. 1994). The PCR conditions for this gene fragment were 94°C for 1 min, 45°C for 1.5 min, 72°C for 1.5 min, annealing of 94°C for 1 min, 50°C for 1.5 min and 72°C for 1 min for 40 cycles and a final elongation stage at 72°C for 5 min. The PCR products was electrophoretically separated on a 1% agarose gel at 80 V

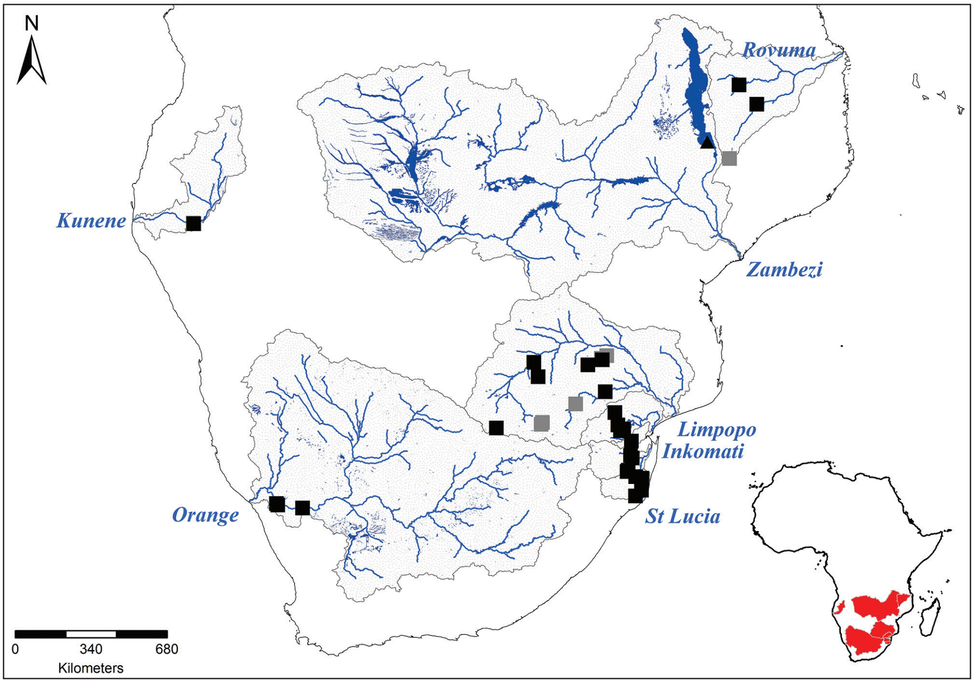


Figure 1. Map of the catchments and sampling sites in which the study species occur. p DNA and morphology: *E. sardella*; n DNA and morphology: *M. brevianalis s.l.*; n morphology only: *M. brevianalis s.l.* (Generated by H. Retief, Rhodes University).

for 30 min. Attempts to amplify the protein-coding *Recombination Activating Gene 1* (RAG1) nuclear gene failed, and although the 28S rRNA nuclear gene was amplified, it (predictably) showed no informative variation within *Mesobola*.

Sequencing by capillary electrophoresis was conducted by Macrogen Inc. (Seoul, South Korea) using the amplification primers. The forward and reverse nucleotide sequences were aligned using the ClustalX multiple sequence alignment module (Larkin et al. 2007) within the BioEdit sequence alignment software (Hall 2004) to form consensus sequences and deposited in Genbank (https://www.ncbi.nlm.nih.gov/Genbank) (Table 1).

The sister group to *Mesobola* is contentious (Howes 1980, 1984, Tang et al. 2010; Liao et al. 2012), so representative species of several genera, including *Chelaethiops* Boulenger, 1899, *Engraulicypris* Günther, 1894, *Neobola* Vinciguerra, 1895, *Opsaridium* Peters, 1854 and *Raiamas* Jordan, 1919, were chosen as outgroup taxa to root the phylogenetic analysis. The relevant additional sequences were either generated from tissue samples or downloaded from GenBank (https://www.ncbi.nlm.nih.gov/Genbank) (Table 1).

All of the sequences were aligned using ClustalX (Larkin et al. 2007) and saved in a Nexus-format file. MrModelTest (Nylander 2004) was used to access the model of best fit for the sequences using the Akaike Information Criterion (Akaike 1973), and

Table 1. Sample catalogue numbers and locality information for specimens from which DNA was extracted for phylogenetic analysis.

Taxon and Locality	Geocoordinates	SAIAB Catalogue Number	GenBank accession number
OUTGROUPS			
Neobola bottegoi			
Wabe River	7.44°N 40.17°E		HM224178
Chelaethiops congicus			
Malagarasi River	5.18°S 30.05°E	191919 DT10-A416	KX808580
Raiamas salmolucius			
Lulua River			JX197004.1
Opsaridium ubangiense			
Oubangui River	6.18°N 20.74°E		HM224193
Engraulicypris sardella			
Lake Malawi			JX196997
	14.12°S 34.93°E	191026	HM418189
		191026 DT13-M066	KX788904
		191026 DT13-M038	KX788905
INGROUP			
Mesobola brevianalis s.s.			
Albasini Dam	23.10°S 30.12°E	191910 RB12-Misc048	KX788875
		191910 RB12-Misc100	KX788876
Olifants River	24.19°S 30.82°E	190710 RB13-B066	KX788873
		190710 RB13-B094	KX788874
White Mbuluzi River	26.17°S 31.88°E	190657 RB13-B012	KX788888
		190657 RB13-B014	KX788889
Crocodile River	25.53°S 31.33°E	190670 RB13-B040	KX788899
		190670 RB13-B050	KX788900
Mlumati River	25.68°S 31.56°E	190621 RB13-B044	KX788896
		190621 RB13-B033	KX788897
	25.76°S 31.44°E	66145 S7	KX788898
Sabie River	25.02°S 31.21°E	190665 RB13-B062	KX788895
Usuthu River	26.86°S 31.91°E	66270	HM224176
		190635 RB13-B048	KX788883
Pongolo River	27.40°S 31.70°E	190682 RB13-B269	KX788884
		190682 RB13-B252	KX788885
	27.35°S 31.75°E	188141 RB13-B279	KX788886
		188141 RB13-B262	KX788887
Hluhluwe River	28.15°S 32.28°E	190719 RB13-B278	KX788880
		190719 RB13-B280	KX788881
		190719 RB13-B281	KX788882
Mfolozi River	28.39°S 32.04°E	190676 RB13-B294	KX788890
		190676 RB13-B259	KX788891
Mkhuze River	27.67°S 32.30°E	88674 PM09A211	KX788877
		88674 PM09A214	KX788878
	27.61°S 32.04°E	190643 RB13-B270	KX788879
Mesobola whitei topotypes			
Limpopo River	23.00°S 27.94°E	101196 A	KX788892
		101196 B	KX788894
	25.65°S 26.43°E	187259 KW12-AT410	KX788893

Taxon and Locality	Geocoordinates	SAIAB Catalogue Number	GenBank accession number
Mesobola gariepinus			
Orange River	28.87°S 18.61°E	78805 IRB-06-01	KX788901
	28.69°S 17.56°E	78822 IRB-06-03	KX788902
	28.75°S 17.61°E	78831 IRB-06-04	KX788903
Mesobola howesi sp. n.			
Kunene River	17.41°S 14.22°E	78759 A ES06_A_54	KX788912
		78759 B ES06_A_54	KX788913
Mesobola ngalala sp. n.			
Lake Chiuta	14.91°S 36.02°E	191029 DT13-M100	KX788906
Lucheringo River	11.82°S 36.22°E	74087 A N39	KX788909
		74087 B N39	KX788910
Rovuma River	12.60°S 36.94°E	73944 A N22	KX788907
		73944 B N22	KX788908
		73944 C N22	KX788911

Table 2. Sample catalogue numbers and locality information for specimens from which measurements were taken for morphometric analysis.

Species	Locality	Geocoordinates	SAIAB Catalogue number	Number of specimens
Engraulicypris sardella	Lake Malawi	14.12°S 34.93°E	191026	5
Mesobola brevianalis	Albasini Dam	23.10°S 30.12°E	191910	20
	Luvhuvhu River	22.90°S 30.70°E	82589	7
	Limpopo River	22.99°S 27.94°E	RB13-Limpopo1	9
	Mbwedi River	22.84°S 30.66°E	53570	4
	Mutshindudi River	22.86°S 30.69°E	53561	2
	Olifants River	24.67°S 29.62°E	61119	10
	–	24.18°S 30.82°E	RB13-Mes26	31
	White Mbuluzi River	26.16°S 31.87°E	RB13-Mes19	32
	Crocodile River	25.52°S 31.32°E	RB13-Mes22	33
	Mlumati River	25.68°S 31.56°E	RB13-Mes21	32
	Nkomati River	25.76°S 31.44°E	66145	18
	Sabie River	25.02°S 31.20°E	RB13-Mes23	15
	Mtindzekwa River	26.74°S 31.83°E	RB13-Mes23	31
	Usuthu River	26.86°S 31.91°E	66270	18
	Hluhluwe River	28.38°S 32.28°E	RB13-Mes04	39
	Mfolozi River	28.38°S 32.03°E	RB13-Mes02	5
	Mkhuze River	27.59°S 32.41°E	RB13-Mes05	60
Mesobola whitei syntypes	Aapies River	25.42°S 28.28°E	30041	9
Mesobola gariepinus	Orange River	28.69°S 17.56°E	78805	16
Mesobola howesi	Kunene River	17.41°S 14.22°E	78759	6
Mesobola ngalala	Lucheringo River	11.82°S 36.22°E	74087	4
	Rovuma River	12.60°S 36.94°E	73944	25
	Lake Chiuta	14.78°S 35.83°E	–	28
			Total:	**461**

the TrN+I+G model was selected and used to build a Bayesian inference tree in MrBayes (Huelsenbeck & Ronquist 2001) using a total of ten million generations (until the split frequency was below 0.05), with a tree sampled every 1000 generations. After examining the trace file, the first 20% of the sampled trees were discarded as burn-in. The Bayesian inference trees were viewed and annotated using TreeView (Page 1996).

Morphological characterization

The morphology and live colouration of representatives of each clade was examined in details for diagnostic traits; measures follow Howes (1980, 1984). Preserved specimens were each placed into a black- or white-based container (to provide contrast) filled with 70% ethanol and a photograph was taken of its left side using a Canon 550D SLR camera (18.1 megapixels) and 50 mm fixed macro lens. A scale bar was included in each photograph to calibrate measurements. Each specimen was then labelled with waterproof paper bearing its specimen number and photograph number, placed in a separate vial for further reference, and returned to its collecting lot.

The available type specimens of *M. brevianalis* and its synonyms, and of *E. sardella* were also examined using photographs supplied by the Natural History Museum, London (BMNH).

Based on these results, morphometric analysis of selected specimens (Table 2) from each major clade found in the phylogenetic analysis was used to find morphological features suitable for identification. The photographs were imported into the imaging software, AnalySIS Docu (Olympus Soft Imaging Systems: http://www.soft-imaging.net/) to measure six standard linear measurements: standard length (SL), orbit length, snout-to-orbit distance, and the lengths of the dorsal, anal and pelvic fins. A box truss network (Strauss & Bookstein 1982) of 21 measurements was used to capture the shape of each fish, based on ten landmark points (Fig. 2) that lay in areas of strong skeletal support, where distortion of soft tissue was likely to be minimal. All measurements were entered into a spreadsheet with each specimen's collection number, geographical origin (country, river, river system) and nomenclatural status (e.g. holotype, syntype). Measuring and transcription errors were sought using scatter plots and corrected.

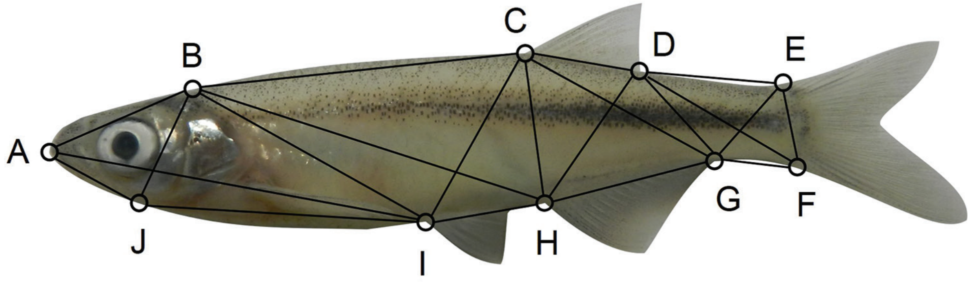


Figure 2. Truss network used for morphometric analysis, defined by ten landmarks **A–J**.

The measurement data were log-transformed to rectilinearise allometric variation (Strauss & Bookstein 1982), and a principal component analysis was used to seek morphological groups in the samples. A discriminant function analysis was performed to pinpoint diagnostic measurements of taxa defined by the genetic analysis. Both analyses were done using the Statistica 12 (http://www.statsoft.com/Products/STATISTICA-Features/Version-12) software package.

Taxonomy

Type specimens and their metadata were housed in the South African Institute for Aquatic Biodiversity, Grahamstown (SAIAB), the Albany Museum, Grahamstown (AMGT) and the Natural History Museum (BMNH), London. Photographs of the holotypes of *M. brevianalis* and *E. sardella* were received from the BMNH as the specimens were too fragile to transport. Catalogued SAIAB specimens of undescribed species was selected for description based on their physical condition (e.g. fin rays and scales intact) and whether they had associated genetic sequences.

Specimens were photographed with a scale bar. Measurements were made on each specimen with standard unbranded electronic digital callipers. The holotype photographs were measured using AnalySIS Docu software, but measurements that involved the width of the specimen including body width or inter-orbit length could not be measured or included in the description.

Meristic data, including fin ray counts, where gathered using a Leica Zoom 2000 microscope. Scale counts were made on a maximum of only three specimens because it required dyeing specimens with Alizarin Red for an average of five-to-ten minutes and then placing them directly into Acid Blue dye for a further five-to-ten minutes, after which visualising the scales was still very difficult. Because the dye did not wash out well, scale counts were not be made on type specimens. Vertebra counts were made on X-rays of some specimens including all holotypes except for the holotype of *E. sardella* for which no X-ray was available. A single specimen from each population was cleared and stained using standard methods (Taylor & van Dyke 1985), preserved in 70% glycerol, and dissected to count the gill rakers on both the ceratobranchial and epibranchial of the first gill arch.

The data were used to populate a character database in the DELTA software package (Dallwitz 1980, Dallwitz et al. 1993), which was used to generate the species descriptions and key.

Results and discussion

Phylogenetic relationships

The Bayesian phylogenetic analysis with a maximum-likelihood model showed that the biogeographically disparate populations identified as *M. brevianalis* represent inde-

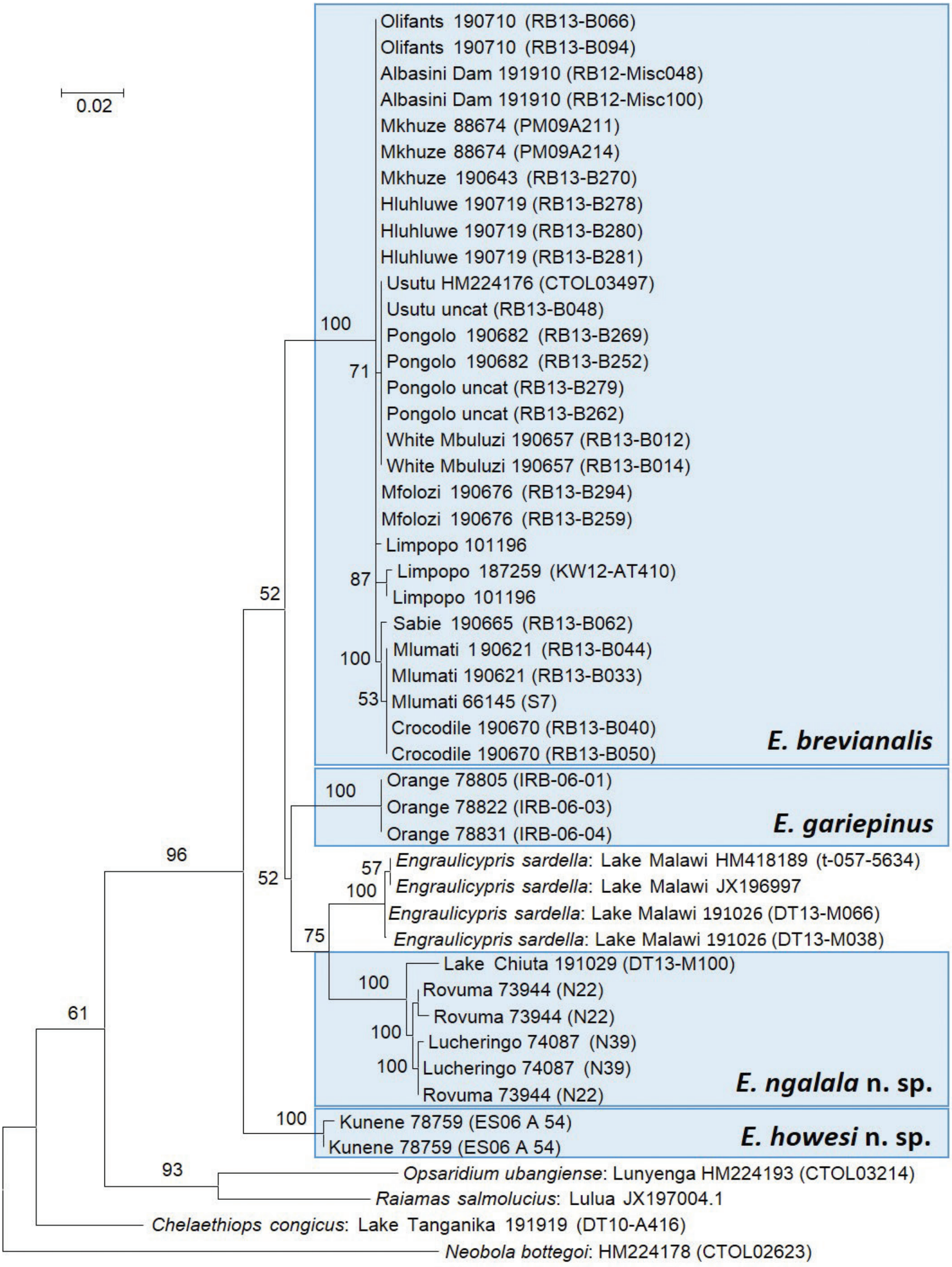


Figure 3. Maximum-likelihood phylogram based on partial sequences of the COI gene. Bootstrap support values were attained using a heuristic tree search and 1000 replicates. Numbers following locality names represent SAIAB catalogue numbers and GenBank accession numbers (in brackets). The shaded boxes enclose well-supported clades that were identified as populations of *Mesobola brevianalis* in the past. The scale bar represents the number of base substitutions per site.

pendent evolutionary clades (support values = 100% in all cases) with relative branch lengths (i.e. numbers of base substitutions per site) indicating larger average evolutionary divergence between the clades than within them (Fig. 3). These clades were collectively paraphyletic with respect to *E. sardella* (Fig. 3), but the monophyly of the whole ensemble received bootstrap support of 96%.

Support for relationships between the independent clades was weak, possibly suggesting a relatively rapid radiation, with the strongest evidence (p = 0.755) supporting a biogeographically plausible sister-group relationship between *E. sardella* from Lake Malawi and the population from the neighbouring Rovuma River system (Fig. 3). The Malawi Rift Basin began to form ~8.6 mya, in the Late Miocene (Delvaux 1995; Danley et al. 2012), cutting across the headwaters of the Palaeo-Rovuma River. This would provide a first approximation for the time of vicariance of these two clades.

The sister group to *Mesobola* remains uncertain for the same reasons that affected the study by Tang et al. (2010), which used four genes and many more taxa: limited taxon sampling within the African radiation of Chedrini and the involvement genera like *Raiamas* and *Opsaridium* that are potentially polyphyletic and not represented by their type species. The average evolutionary divergence between taxa is represented as number of base substitutions per site (Fig. 3).

Morphological identification

Although the phylogenetic analysis showed distinct populations within *Mesobola brevianalis sensu lato*, these could not be detected in a principal component analysis of the morphometric data. The first Eigenvector summarised 89% of the variance and its coefficients were all fairly similar in magnitude and uniform sign (Table 2), indicating that it summarised a general effect in the data, i.e. size, as is usual with morphometric analyses of organisms when variation in the sizes of specimens outweighs their variation in shape. Being orthogonal to the first axis, the remaining axes summarised variation in shape and allometry independent of gross differences in size. A plot of the second and third axes (Fig. 4) showed that populations from the Kunene River and eastern South Africa (including the syntypes of *E. whitei*) overlapped entirely in that morphospace, and partially overlapped those of the Rovuma and Orange rivers, which were mutually distinct. This supported the synonymization of *M. brevianalis* and *E. whitei*, which both occupy the Limpopo River system, and explains why most of the populations have not yet been recognised as distinct taxa. The second axis summarised 2.6% of the variance and differentiated the Rovuma and Orange River populations by emphasising truss measurements DE, DF, CD, DG and dorsal fin length (Table 3), which described the shapes of the caudal peduncle and the dorsal fin (Fig. 2). The third axis summarised 2.2% of the variance in morphology and emphasised eye length and the truss measurements AB, AJ and BJ (Table 3), which all described the head (Fig. 2), but did little to separate the populations further (Fig. 4). The remaining 24 axes collectively summarised only 6.1% of the variation and did not describe patterns that related to the populations.

Table 3. First three Eigenvectors of a principle component analysis of the morphometric data. Coefficients in bold lie outside the 95% confidence interval for the mean coefficient of each axis, and are therefore unusually influential in dispersing specimens on that axis.

Measurement	PCA			DFA		
	Factor 1	Factor 2	Factor 3	Root 1	Root 2	Root 3
A–B	-0.185	-0.158	**0.424**	0.101	-0.104	**0.470**
A–I	-0.199	0.002	0.171	0.041	0.012	0.315
A–J	-0.189	0.126	0.253	0.119	0.083	0.332
B–C	-0.196	0.043	-0.310	-0.070	0.094	0.291
B–H	-0.197	0.109	-0.154	0.001	0.100	0.310
B–I	-0.197	0.110	0.165	0.116	0.064	0.288
B–J	-0.189	-0.133	0.357	0.075	-0.056	0.419
C–D	-0.187	0.357	0.067	0.127	0.093	0.338
C–G	-0.197	0.183	0.018	0.100	0.090	0.303
C–H	-0.199	0.063	-0.148	0.019	0.098	0.286
C–I	-0.200	0.008	-0.169	-0.024	0.081	0.349
D–E	**-0.174**	**-0.570**	-0.094	-0.088	**-0.136**	0.273
D–F	-0.187	**-0.420**	-0.064	-0.045	-0.103	0.284
D–G	-0.196	0.287	-0.012	0.087	0.126	0.296
D–H	-0.199	0.129	-0.115	0.023	0.095	0.299
E–F	-0.198	0.084	0.038	0.076	-0.016	0.281
E–G	-0.201	-0.046	-0.074	0.004	0.038	0.295
F–G	-0.199	-0.072	-0.089	-0.009	0.037	0.276
G–H	-0.190	-0.138	-0.216	-0.067	0.026	0.272
H–I	-0.192	0.027	-0.126	-0.016	0.088	0.404
I–J	-0.189	-0.113	0.066	-0.055	-0.042	0.256
Caudal fin length	-0.193	0.006	-0.067	0.012	0.003	0.285
Caudal length	-0.202	-0.035	-0.103	-0.026	0.041	0.350
Dorsal fin length	-0.185	0.264	-0.168	0.005	0.107	0.259
Eye length	-0.187	-0.033	**0.413**	0.152	-0.071	0.295
Pelvic fin length	-0.186	-0.177	-0.198	-0.076	0.031	0.275
Snout-to-eye distance	-0.182	0.016	0.188	-0.002	0.020	0.409
Eigenvalue	24.070	0.695	0.595	2.557	1.412	0.810

Discriminant function analysis of the morphology of the genetically well-supported *Mesobola* populations and *E. sardella* successful assigned most specimens to their population of origin (Table 4; Fig. 5), although *Mesobola brevianalis sensu stricto* and *E. howesi* overlapped substantially in morphospace, at least on the first two canonical axes (Fig. 5). The first canonical axis tended to have negative weights for measurements along the body axis and positive weights for those across the body axis (Table 3; Fig. 5), thus describing the elongation of the body. The second axis contrasted measurements involving the dorsal fin with those of the caudal peduncle (Table 3; Fig. 5), while the third axis did showed no clear morphological pattern in its weights (Table 3).

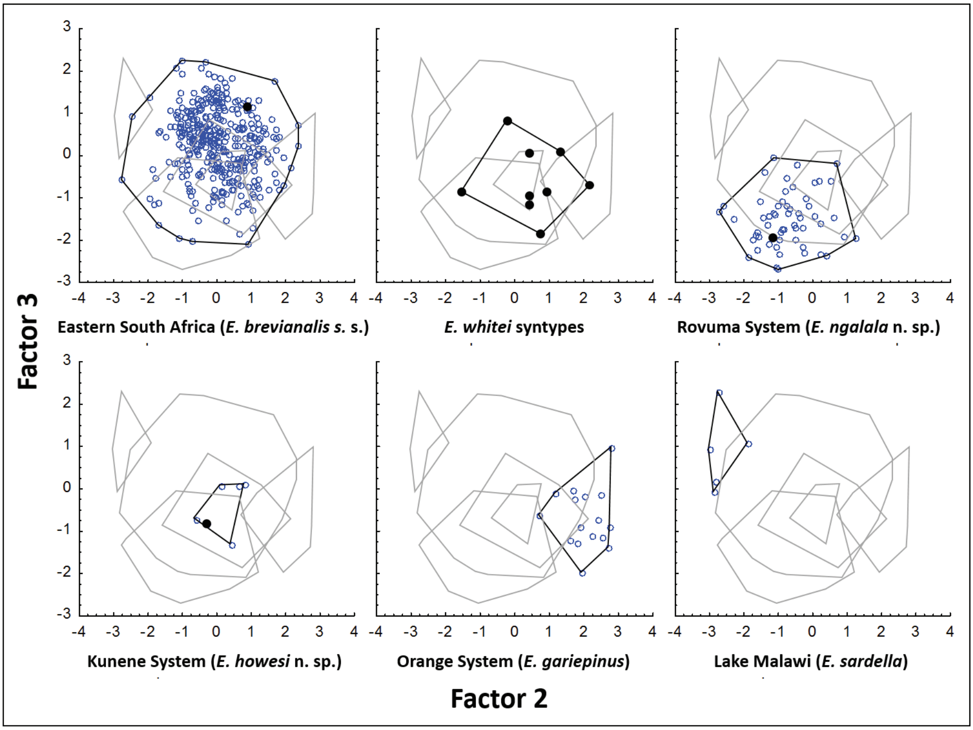


Figure 4. Plots of the second and third canonical axes of a principle component analysis of traditional and truss-based morphometric measurements of representative specimens of *E. sardella* and various populations referred to *Mesobola*, separated by taxon. Type specimens are marked with solid circles.

Table 4. Classification matrix resulting from a discriminant function analysis of the morphometric data. Cells in bold contain misclassifications.

True identity	Predicted classifications						Percent correct
	sardella	*brevianalis*	*whitei*	*gariepinus*	*ngalala*	*howesi*	
sardella	5	0	0	0	0	0	100.0
brevianalis	0	365	**1**	0	**2**	0	99.2
whitei	0	**1**	8	0	0	0	88.9
gariepinus	0	0	0	16	0	0	100.0
ngalala	0	**7**	0	0	50	0	87.7
howesi	0	0	0	0	0	6	100.0
Total	5	373	9	16	52	6	97.6

Taxonomy

Because *Engraulicypris pinguis* Günther, 1894 (= *E. sardella* (Günther, 1868): Lévêque & Daget 1984, Eschmeyer et al. 2016) is the type species of *Engraulicypris* by monotypy, we resolve the genus-level paraphyly evident in the phylogeographical analysis

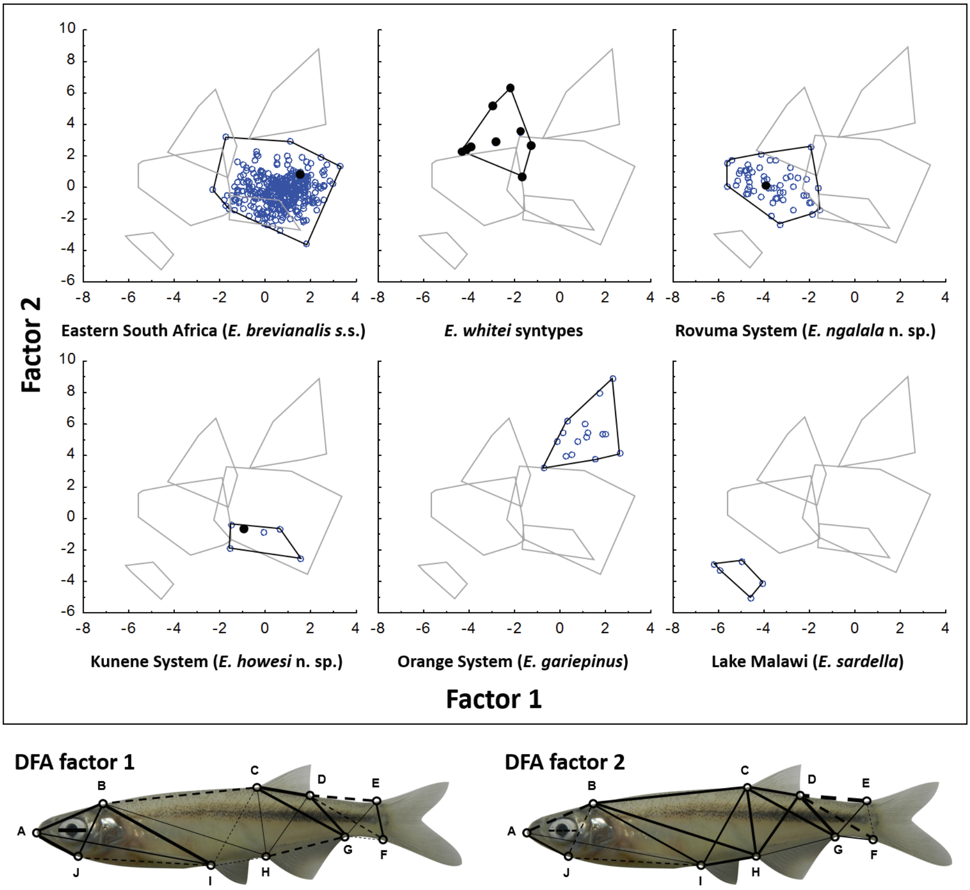


Figure 5. Plots of the first two canonical axes of a discriminant function analysis of traditional and truss-based morphometric measurements of representative specimens of *E. sardella* and various populations referred to *Mesobola*, separated by taxon. Type specimens are marked with a solid circle.

(Fig. 3) by synonymising *Engraulicypris* Günther, 1894 and *Mesobola* Howes, 1984 syn. n. and transferring *M. brevianalis* to *Engraulicypris brevianalis* (Boulenger, 1908) comb. n. We also restore two other species currently placed in *Mesobola* but originally placed in *Engraulicypris* by their authors (Eschmeyer et al. 2016): *Engraulicypris bredoi* Poll, 1945 stat. rev. and *Engraulicypris spinifer* Bailey & Matthes, 1971 stat. rev.

The species-level paraphyly in the phylogeographical analysis (Fig. 3) can be resolved by recognising the independent populations as species. In South Africa, specimens from the eastern populations of *Mesobola* grouped with specimens from the type locality of *E. brevianalis* (Fig. 3) and were somewhat phylogenetically intermingled with specimens from the western populations from which *M. whitei* was collected. These two species are therefore either synonymous or show incomplete lineage sorting or hybridization. The lower Orange River population can be recognised by restoring

E. gariepinus stat. rev. from synonymy with *M. brevianalis*. *Engraulicypris bredoi* and *E. spinifer* occur in Lake Albert and the Malagarasi River system, respectively (Lévêque et al. 1991), and are therefore unlikely to represent the Kunene and Rovuma River populations, for which there are thus currently no names available.

Descriptions

Engraulicypris Günther, 1894

Engraulicypris Günther, 1894: 626 (type species: *Engraulicypris pinguis* Günther, 1894 (= *Barilius sardella* Günther, 1868: Lévêque & Daget 1984, Eschmeyer et al. 2016))

= *Mesobola* Howes, 1984: 168 syn. n. (type species: *Neobola brevianalis* Boulenger 1908)

Diagnosis. With the synonymisation of *Mesobola* and *Engraulicypris*, Günther's (1894) diagnosis of *Engraulicypris* must be modified to include the species assigned to *Mesobola*. *Engraulicypris* is a genus of moderately small African chedrin barbs (*sensu* Tang et al. 2010; Liao et al. 2011, 2012) identified by a lack of a scaly lobe at the base of the pelvic or pectoral fin; a large mouth reaching the anterior border of the orbit or beyond; a dorsal fin origin originating behind midpoint of standard length, more or less above the origin of the anal fin; a pectoral fin not reaching the origin of the anal fin; and body colouration lacking vertical bars or bands. Osteological characters are discussed by Liao et al. (2011, 2012) for *Mesobola* and by Liao et al. (2012) for *Engraulicypris*.

Live colouration. (Fig. 6). Body without vertical bars or bands.

Etymology. *Engraulicypris* alludes to the anchovy-like form (eggraulis, -eos [eggraulis, -eos]; Greek) of these relatives of the carp (kyprinos [kyprinos]; Greek).

Distribution. Southern and Eastern Africa.

Engraulicypris brevianalis (Boulenger, 1908) comb. n.

Neobola brevianalis Boulenger, 1908. *Annals of the Natal Government Museum* 1(3): 281. Holotype: unsexed; "Mkuzi River, Zululand, Transvaal [sic]" [BMNH 1907.4.17.90] in formalin [BMNH].

= *Engraulicypris whitei* van der Horst, 1934. *Annals of the Transvaal Museum* 15(3): 281, unnumbered fig. Syntypes: 5 unsexed, Petronella [SAIAB 30040 ex TMP 15024]; 4 unsexed, Hammanskraal [SAIAB 30041 ex TMP 16022] in formalin [SAIAB].

Material examined. ***E. brevianalis*: Holotype**, BMNH No 1907.4.17: 90, SL 67 mm. "Mkuzi River, Zululand, Transvaal". [BMNH]. ***E. whitei*: Syntypes**, SAIAB 30040 (ex TM 15024) (5) and SAIAB 30041 (ex TM 16022) (4), "Aapies River (Limpopo System) near Petronella and near Hammanskraal (Transvaal)"**.** Other material, see Table 2.

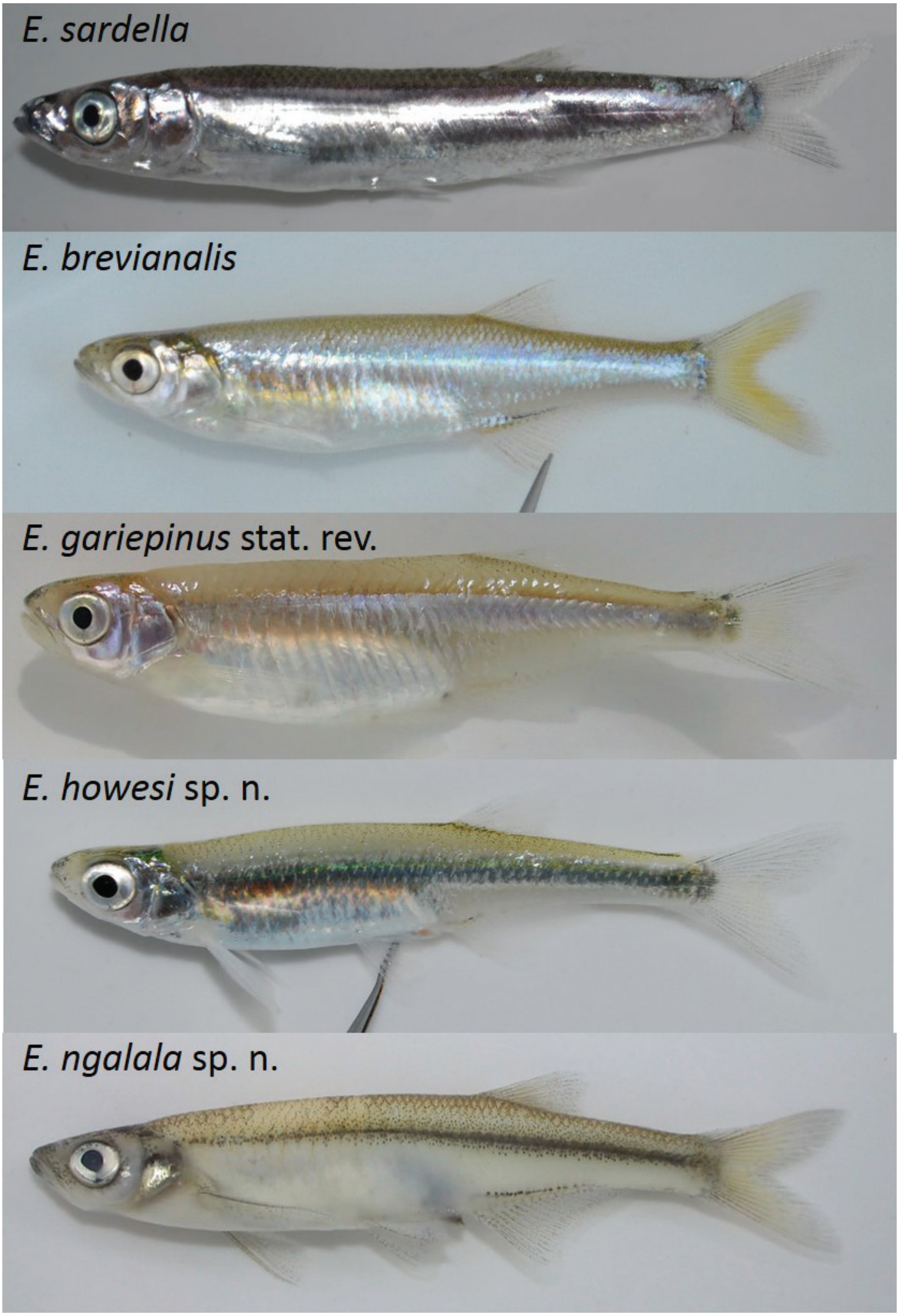


Figure 6. Photographs of fresh specimens of *Engraulicypris* species.

Diagnosis. Caudal fin membrane clear towards vivid yellow at fork; anal fin extending two thirds of length of caudal peduncle; caudal peduncle moderately long; operculum entirely (not partially) shiny; body midline silver (not black); iris dark to light grey (not white); head with tubercles along lower jaw and lower head in breeding males; snout rounded (not pointed), darker dorsally; pelvic fin melanophores absent.

Morphology. (Figs 6–8; Table 5). Maximum SL 75 mm. Body elongated; somewhat fusiform; laterally compressed. Maximum body depth at middle pelvic and pectoral fin origin. Pre-dorsal profile straight or slightly convex behind head. Head length 20% SL; with tubercles along lower jaw and lower head. Snout rounded; short; 30% of head length. Mouth terminal; slightly crescent-shaped with long anterior side; reaching anterior border of orbit. Nostrils large; level with dorsal margin of eye; separated from orbit by less than one orbit radius. Tubular anterior naris short; adjacent to open posterior naris. Eye lateral; visible from above and below (more prominent); diameter 35% of head length. First gill arch with 8+3 gill rakers on cerato- and epibranchial arms, respectively. Gill rakers long; pointed; widely-spaced. Pharyngeal bones in three rows. Pharyngeal teeth 4,3,2–2,3,4; robust and long; falcate.

Modal fin formulae in Table 5. Fins large in relation to body size. Dorsal fin closer to caudal fin than tip of snout; more or less above origin of anal fin; length 17% SL; posterior margin straight; rays soft; anterior-most branched fin ray longest. Pectoral fins largest; reaching $^1/_2$ to $^3/_4$ distance to base of pelvic fin; fin lacking lobe at base. Pelvic fins reaching $^2/_3$ distance to base of anal fin; relatively small; pointed; fin lacking a basal lobe. Anal fin moderately long; extending $^2/_3$ length of caudal peduncle; last unbranched ray longest. Ano-genital opening at anterior of base of anal fin. Caudal peduncle moderately long. Caudal fin forked; lobes with slightly concave interior and extending into point; upper lobe shorter.

Scales small to medium relative to body size; in regular rows; cycloid, slightly elongate; radially striate. Base of anal fin lacking sheath scales. Lateral line present; complete; dipping sharply towards ventral at tip of pectoral fin; joining midline at posterior of caudal peduncle; scale count 53–57 (n = 2) along lateral line, 18 around caudal peduncle.

Live colouration. (Fig. 6). Body silver, without vertical bars or bands. Dorsum pale brown with small dark brown melanophores, midline silver. Snout darker dorsally. Operculum entirely metallic silver. Iris dark to light grey. Dorsal fin membrane clear; rays clear with olive melanophores; fading towards tips. Caudal fin membrane clear, vivid yellow at fork; rays light olive; rays lighter towards tips; melanophores small, dark, fading towards rear. Anal fin rays clear; membrane clear; dark spotting above origin; melanophores dark olive fading towards tips. Pectoral fin membranes clear; rays clear; first ray with few dark melanophores. Pelvic fin rays clear; membrane clear.

Preserved colouration. (Fig. 7). Body and head white and silver with dark spotting sparse to densely packed towards caudal fin on midline and on dorsal surface. Scales on dorsal surface lightly pigmented. Ventral scale pigmentation as intense as dorsal surface. Dorsal surface of head lightly pigmented. Melanophores small, dark; clustered on rear of head, below orbit and on lips and snout; along midline, increasing

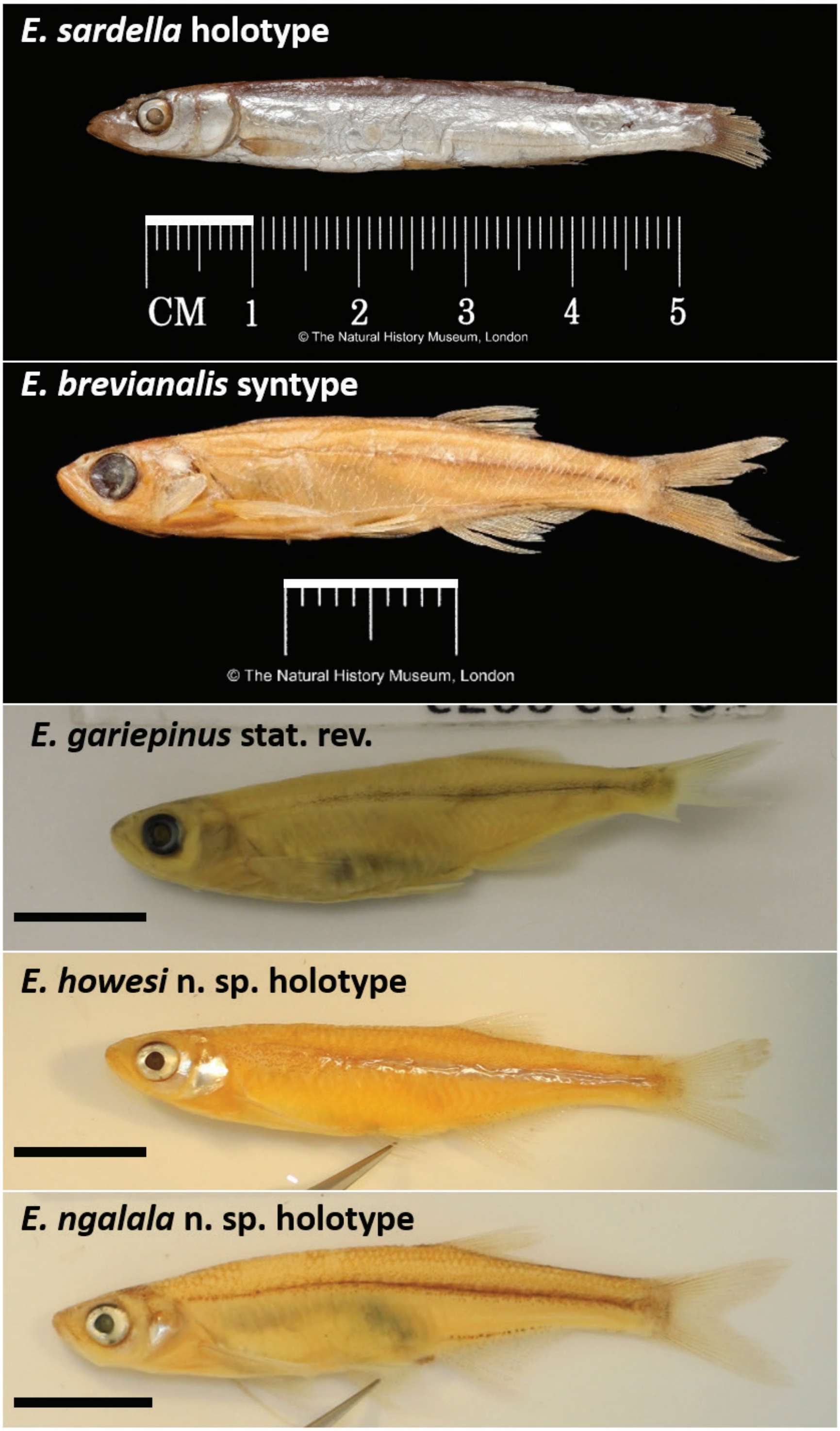
Table 5. Morphometric measurements and meristic counts for *Engraulicypris brevianalis*.

Measurement	n	Holotype	Max	Min	Mean	SD
SL	6	67.39	67.39	41.13	46.46	10.30
Head length (%SL)	6	16.56	24.57	19.74	21.20	1.86
Head depth (%HL)	6	11.59	86.24	69.80	74.61	6.09
Snout length (%HL)	6	3.53	37.96	21.29	32.95	5.96
Orbit diameter (%HL)	6	5.65	45.85	34.14	39.69	4.68
Postorbit length (%HL)	6	6.34	38.27	25.62	30.68	4.74
Inter-orbit length (%HL)	5	Unknown	47.19	36.40	44.52	4.59
Predorsal length (%SL)	6	44.35	65.80	62.36	64.00	1.33
Prepelvic length (%SL)	6	33.46	50.78	46.48	48.23	1.80
Dorsal fin Length (%SL)	6	12.32	18.64	16.01	17.55	0.97
Pectoral fin length (%SL)	6	13.40	22.32	19.88	21.66	0.99
Pelvic fin length (%SL)	6	8.98	13.66	11.37	12.31	0.97
Anal fin length (%SL)	6	12.08	17.92	14.33	16.07	1.33
Body depth (%SL)	6	14.27	23.54	20.53	21.96	1.10
Body width (%SL)	5	Unknown	13.46	10.69	12.08	1.05
Caudal peduncle length (%SL)	6	10.04	18.10	14.10	15.74	1.57
Caudal peduncle depth (%SL)	6	6.78	11.01	9.52	10.24	0.58
Meristics	n	Holotype	Range			
Dorsal-fin rays	5	Unknown	ii+8 (n = 5)			
Anal-fin rays	5	Unknown	iii+13 (n = 1), iii+14 (n = 3), iii+15 (n = 1)			
Pectoral-fin rays	5	Unknown	i+10 (n = 4), i+11 (n = 1)			
Pelvic-fin rays	5	Unknown	i+7 (n = 5)			
Lateral line scales	2	Unknown	53 (n = 1), 57 (n = 1)			
Caudal peduncle scale	2	Unknown	18 (n = 2)			
Scale rows lat. line-dorsal	2	Unknown	9 (n = 1), 11 (n = 1)			
Scale rows lat. line-pelvic	2	Unknown	2 (n = 2)			
Scale rows lat. line-anal	2	Unknown	2 (n = 2)			
Total vertebrae	5	37	37 (n = 1), 38 (n = 4)			
Abdominal vertebrae	5	19	18 (n = 2), 19 (n = 3)			
Caudal vertebrae	5	18	19 (n = 4), 20 (n = 1)			
Rib pairs	5	14	13 (n = 1), 14 (n = 3), 15 (n = 1)			

in intensity to caudal fin; browner on dorsal surface above midline; forming a small, dark line above anal fin. Operculum and posterior edge of orbit with silver sheen. Membranes between fin rays clear. Pelvic fin clear membranes and rays. Dorsal, caudal and pectoral fin membranes clear; rays with melanophores small, dark, widely-spaced; rays pale grey.

Etymology. '*Brevianalis*' alludes to the relatively short anal fin. '*Whitei*' honours Mr A. G. White, who collected the type specimens in the Aapies River near Petronella and Hammanskraal.

Distribution. Botswana, Zimbabwe, South Africa, Swaziland, Mocambique: Limpopo River, Incomati River, Pongolo River, St Lucia system, Mkhuze River.



E. sardella holotype

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E. brevianalis syntype

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E. gariepinus stat. rev.

E. howesi n. sp. holotype

E. ngalala n. sp. holotype

Figure 7. Photographs of preserved type specimens of *Engraulicypris* species. Scale bars = 1 cm.

Type locality. Mkuzi River (perhaps within 40 km east or west of 27°35'S 32°00'E), South Africa.

Biology. Pelagic species preferring close proximity to substrate and seeking out slacker areas such as backwater, eddies and pools below riffles. Occurs in shoals and prefers well-aerated, open water in flowing rivers (Skelton 2001), favouring the upper stratum (Engelbrecht & Mulder 1999). Feeds from water column on planktonic crustaceans and insects (e.g. midges and ants) (Skelton 2001). Caught at night with light. Breeding occurs in early summer (Skelton 2001). Found in dams where appears to propagate successfully with little predation and moves around in rivers according to seasonal flows. Appears to migrate up streams in spring to breed where it is found in tributaries.

Remarks. The specimen (SAIAB 66270) used by Liao et al. (2012) to represent a DNA sequence of *M. brevianalis* and is from the Usuthu River (Table 1), and does belong to that species (Fig. 3).

Engraulicypris gariepinus Barnard, 1943 stat. rev.

Engraulicypris gariepinus Barnard, 1943. *Annals of the South African Museum* **36**(2): 220. Syntypes: 2 unsexed (not located), “Orange River and Fish River” [SAM 18722–23] [lost].

Material examined. SAIAB 193617, 6 unsexed, 2 cleared & stained: SL 43–44 mm. Namibia, Orange River, Noordower, 28°44'50"S 17°36'32"E, 21 October 2006, R. Bills; SAIAB 78822, 7 unsexed, 2 cleared & stained: SL 39–41 mm. Namibia, Orange River, Felix Unite Camp, 28°41'19"S 17°33'20"E, 20 October 2006, R. Bills; 2 unsexed, SAIAB 78805, 42–47 mm. Namibia, Orange River, Houms River Camp Site, 28°52'5"S 18°36'42"E, 18 October 2006, R. Bills; SAIAB 74232, 10 unsexed, 2 cleared & stained: SL 29–41 mm. South Africa, Orange River, Pella Drift lower site, 28°57'47"S 19°6'36"E, 28 January 2004, R. Bills & N. Jones.

Diagnosis. Caudal fin membrane clear to pale orange towards midline; anal fin extending over three quarters of length of caudal peduncle; caudal peduncle short; operculum entirely (not partially) shiny; body midline silver (not black); iris dark to light grey (not white); head with tubercles along lower jaw and lower head in breeding males; snout rounded, with dense dark spotting on tip; pelvic fin melanophores absent.

Morphology. (Figs 6–8; Table 6). Maximum SL 46 mm. Body elongated; somewhat fusiform; laterally compressed. Maximum body depth before pelvic fin. Pre-dorsal profile straight or slightly convex behind head. Head length 21% SL; with tubercles along lower jaw and lower head. Snout rounded; short; 32% of head length. Mouth terminal; slightly crescent-shaped with long anterior side; reaching anterior border of orbit. Nostrils large; level with dorsal margin of eye; separated from orbit by less than one orbit radius. Tubular anterior naris short; adjacent to open posterior naris. Eye lateral; visible from above and below (more prominent); diameter 32 % of head length.

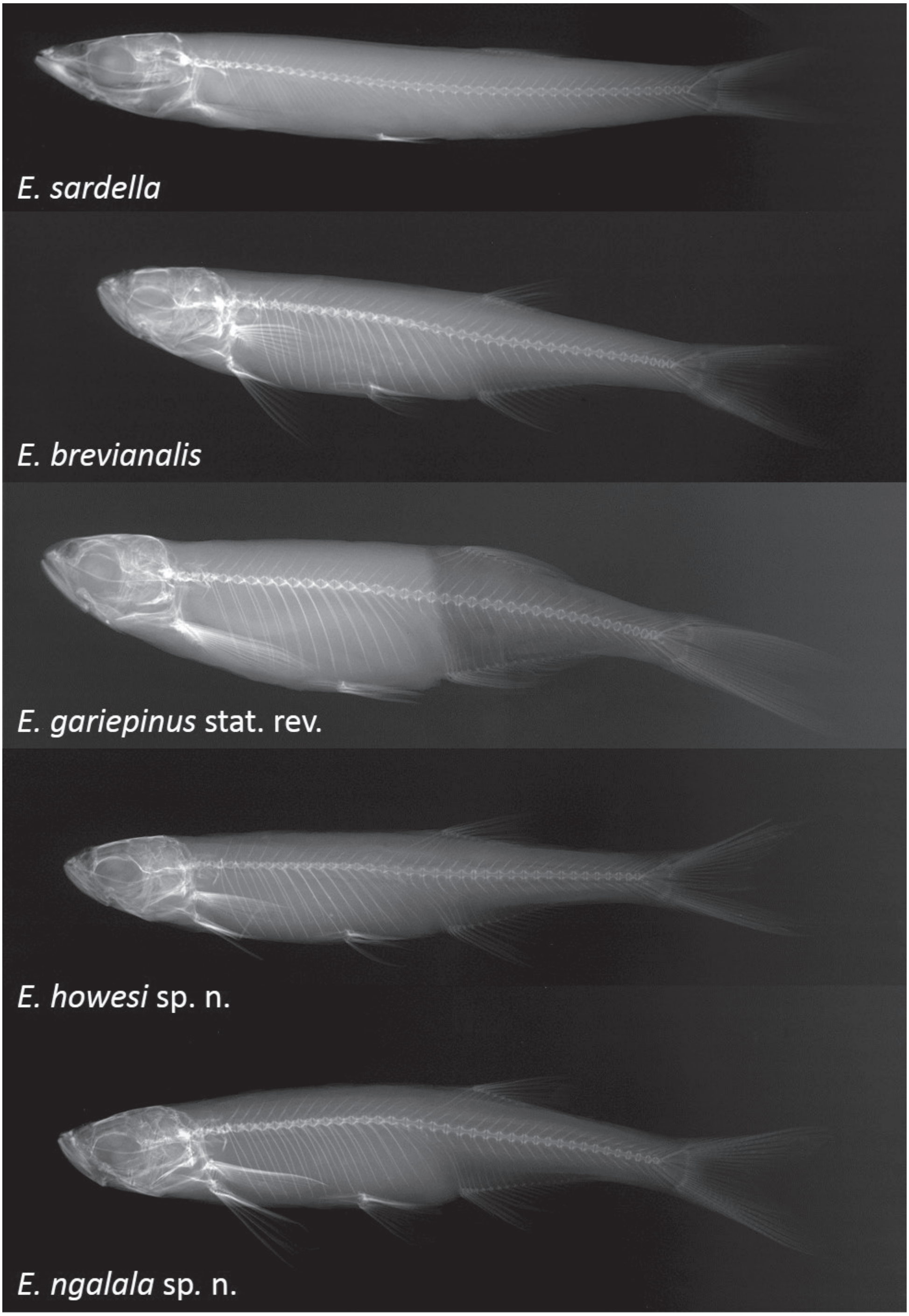

Figure 8. X-ray images of specimens of *Engraulicypris* species.

Table 6. Morphometric measurements and meristic counts for *Engraulicypris gariepinus*.

Measurement	n	Max	Min	Mean	SD
SL	20	46.61	28.76	38.36	5.41
Head length (%SL)	20	23.78	18.25	21.18	1.79
Head depth (%HL)	20	93.35	59.71	77.75	7.75
Snout length (%HL)	20	40.37	23.10	31.77	4.69
Orbit diameter (%HL)	20	50.35	36.89	40.27	3.32
Postorbit length (%HL)	20	38.75	27.56	33.06	3.03
Inter-orbit length (%HL)	20	48.23	27.79	38.10	5.68
Predorsal length (%SL)	20	68.09	62.17	64.83	1.71
Prepelvic length (%SL)	20	55.17	45.07	49.03	2.32
Dorsal fin Length (%SL)	20	20.39	15.19	17.00	1.37
Pectoral fin length (%SL)	20	25.04	21.60	22.90	1.00
Pelvic fin length (%SL)	20	14.25	11.80	12.79	0.68
Anal fin length (%SL)	20	18.45	14.38	16.41	1.12
Body depth (%SL)	20	25.64	18.39	21.81	1.91
Body width (%SL)	20	13.27	9.39	11.11	1.19
Caudal peduncle length (%SL)	20	16.64	11.13	13.95	1.52
Caudal peduncle depth (%SL)	20	9.84	7.13	8.18	0.79
Meristics	n	Range			
Dorsal-fin rays	20	ii+7 (n = 3), ii+8 (n = 17)			
Anal-fin rays	20	iii+14 (n = 4), iii+15 (n = 9), iii+16 (n = 7)			
Pectoral-fin rays	20	i+9 (n = 10), i+10 (n = 8), i+11 (n = 2)			
Pelvic-fin rays	20	i+7 (n = 19), i+8 (n = 1)			
Lateral line scales	2	49 (n = 1), 51 (n = 1)			
Caudal peduncle scale	2	14 (n = 1), 16 (n = 1)			
Scale rows lat. line-dorsal	2	11 (n = 2)			
Scale rows lat. line-pelvic	2	2 (n = 2)			
Scale rows lat. line-anal	2	2 (n = 2)			
Total vertebrae	12	36 (n = 1), 38 (n = 3)			
Abdominal vertebrae	12	17 (n = 1), 18 (n = 1), 19 (n = 10)			
Caudal vertebrae	12	19 (n = 3), 20 (n = 8), 21 (n = 1)			
Rib pairs	12	13 (n = 3), 14 (n = 7), 15 (n = 2)			

First gill arch with 7+3 gill rakers on cerato- and epibranchial arms, respectively. Gill rakers long; pointed; widely-spaced. Pharyngeal bones in three rows. Pharyngeal teeth 4,3,2–2,3,4; robust and long; falcate.

Modal fin formulae in Table 6. Fins large in relation to body size. Dorsal fin closer to caudal fin than tip of snout; more or less above origin of anal fin; length 17% SL; posterior margin straight; rays soft; anterior-most branched fin ray longest. Pectoral fins largest; reaching $^{1}/_{2}$ to $^{3}/_{4}$ distance to base of pelvic fin; fin lacking lobe at base. Pelvic fins reaching $^{2}/_{3}$ distance to base of anal fin; relatively small; pointed; fin lacking a basal lobe. Anal fin moderately long; extending over $^{3}/_{4}$ length of caudal peduncle;

last unbranched ray longest. Ano-genital opening at anterior of base of anal fin. Caudal peduncle short; half of length. Caudal fin forked; lobes pointed; upper lobe shorter.

Scales small to medium relative to body size; in regular rows; cycloid, slightly elongated; radially striate. Base of anal fin lacking sheath of enlarged, elongate scales. Lateral line present; complete; dipping drastically towards ventral at tip of pectoral fin; joins midline at posterior of caudal peduncle; scale count 49–51 (n = 2) along lateral line, 14–16 around caudal peduncle.

Live colouration. (Fig. 6). Body without vertical bars or bands. Dorsum transparent pale brown with melanophores concentrated around dorsal fin; midline silver. Snout with dense dark spotting on tip. Operculum entirely metallic silver. Iris dark to light grey. Dorsal fin membrane clear; rays clear; melanophores fading towards tips. Caudal fin membrane clear to pale orange towards midline; rays dark grey, lighter towards tips; melanophores small, dark, fading towards rear. Anal fin rays clear; membrane clear; pale orange spotting above origin; melanophores few to absent. Pectoral fin membranes clear; rays clear; first ray few dark melanophores. Pelvic fin rays clear; membrane clear.

Preserved colouration. (Fig. 7). Body and head orange with small dark brown spotting along dorsal surface, midline and above anal fin. Scales on dorsal surface lightly pigmented. Ventral scale pigmentation less intense than dorsal. Dorsal surface of head lightly pigmented. Melanophores small, dark; grouped on rear of head, below orbit, and on lips and snout; along midline, increasing in intensity to caudal fin; brownish on dorsal surface, darkening between origin of pectoral and dorsal fin; forming small dark line above anal fin. Membranes between fin rays clear. Pelvic fin clear membranes and rays.

Etymology. '*Gariepinus*' refers to the Gariep, a San name for the Orange River that means 'Great water'.

Distribution. South Africa, Namibia: Lower Orange River system, Fish River (Barnard, 1943).

Type locality. Orange River and Fish River, Namibia (Barnard, 1943).

Biology. This shoaling fish favours open, shallow water, normally occurring in slack pools and particularly below riffles. Populations found in the lower Orange and Fish Rivers are limited by the Augrabies and Fish River Falls. They are thought to feed mainly on small autochthonous invertebrates (planktonic crustaceans or insects), and are caught in large numbers where they occur. They are restricted to turbid waters, which provide protection from visual predators (R. Bills, pers. obs.).

Remarks. The two syntypes of *E. gariepinus* Barnard, 1943 were originally stored in the South African Museum, but were moved to the Albany Museum, Grahamstown, South Africa (AMG 106 and 1009) (Eschmeyer 2014). The Albany Museum fish collection has now been moved to SAIAB and these specimens have not been traced (I.R. Bills, pers. obs.). There is no 'exceptional need' (ICZN, Articles 75.2 and 75.3) for a neotype, since there is only one species of *Mesobola* in the topotypical river system, and the species is sufficiently physically distinctive that even if another species was introduced, they would be easy to distinguish on the basis of published descriptions.

Engraulicypris howesi **Riddin, Bills & Villet, sp. n.**

http://zoobank.org/0476418B-6254-48D1-B336-69A8A4C56D33

Holotype. SAIAB 201623, unsexed, SL 43 mm, "Olushandja Dam at channel outlet, Kunene River System, Namibia, 17°25'53"S 14°38'36"E, 16 April 2015, R. Bills, V. Bills & R. van Zeeventer, D-net". In 70% ethanol [SAIAB]

Paratypes. SAIAB 39012, 11 unsexed, SL 21–43 mm, 30 May 1992, C. Hay, N. James & P. Skelton; SAIAB 78759, 7 unsexed, SL 28–37 mm, Kunene River at Hippo Pool below Ruacana Waterfall, Namibia, 17°24'24"S 14°13'1"E, 21 August 2006, E. Swartz & Kramer; SAIAB 38961, 14 unsexed, SL 29–35 mm, 27, Kunene River, Namibia,17°38'33"S 14°21'67"E, 27 May 1992, C. Hay, N. James & P. Skelton, SAIAB 35340, 6 unsexed, 2 cleared & stained, Kunene River below Ruacana Falls, Namibia, 13 January 1991, B. van der Waal [SAIAB].

Diagnosis. Anal fin extending over three quarters of length of caudal peduncle; caudal peduncle short; operculum entirely (not partially) shiny; body midline silver (not black); iris dark to light grey (not white); head with tubercles along lower jaw and lower head in breeding males; snout rounded; pelvic fin melanophores absent.

Morphology. (Figs 6–8; Table 7). Maximum SL 43 mm. Body elongated; somewhat fusiform; laterally compressed. Maximum body depth midway along body. Predorsal profile straight or slightly convex behind head. Head length 23% of SL; with tubercles along lower jaw and lower head. Snout rounded; short; 29% of head length. Mouth terminal; slightly crescent-shaped with long anterior side; reaching anterior border of orbit. Nostrils large; level with dorsal margin of eye; separated from orbit by less than one orbit radius. Tubular anterior naris short; adjacent to open posterior naris. Eye lateral; visible from above and below (more prominent); diameter 41% of head length. First gill arch with 8+3 gill rakers on cerato- and epibranchial arms, respectively. Gill rakers long; pointed; widely-spaced. Pharyngeal bones in four rows. Pharyngeal teeth 5,3,2,1–1,2,3,5; slender and long; falcate.

Modal fin formulae in Table 7. Fins large in relation to body size. Dorsal fin closer to caudal fin than tip of snout; more or less above origin of anal fin; length 14% of SL; posterior margin straight; rays soft; anterior-most branched fin ray longest. Pectoral fins largest; reaching $^1/_2$ to $^3/_4$ distance to base of pelvic fin; fin lacking lobe at base. Pelvic fins reaching $^2/_3$ distance to base of anal fin; relatively small; pointed; fin lacking a basal lobe. Anal fin moderately long; extending $^2/_3$ length of caudal peduncle; last unbranched ray longest. Ano-genital opening at anterior of base of anal fin. Caudal peduncle moderately long; depth half of length. Caudal fin forked; lobes pointed; upper lobe shorter.

Scales small to medium relative to body size; in regular rows; cycloid; radially striate; rounded, slightly elongate. Base of anal fin lacking sheath of scales. Lateral line present; complete; dipping sharply towards ventral at tip of pectoral fin; joins midline at posterior of caudal peduncle; scale count 51–52 (n = 2) along lateral line, 14 around caudal peduncle.

Table 7. Morphometric measurements and meristic counts for *Engraulicypris howesi*.

Measurement	N	Holotype	Max	Min	Mean	SD
SL	20	42.84	42.84	21.90	33.35	5.03
Head length (%SL)	20	21.62	25.04	21.43	22.76	1.11
Head depth (%HL)	20	64.25	74.52	56.81	65.62	5.61
Snout length (%HL)	20	25.27	34.30	21.22	28.53	3.95
Orbit diameter (%HL)	20	37.80	46.29	32.49	40.62	3.42
Postorbit length (%HL)	20	37.37	43.86	29.95	36.34	4.01
Inter-orbit length (%HL)	20	32.07	43.25	5.79	33.35	8.38
Predorsal length (%SL)	20	62.61	67.19	62.61	64.78	1.33
Prepelvic length (%SL)	20	46.27	51.11	40.37	47.48	2.57
Dorsal fin Length (%SL)	20	16.15	17.63	9.52	14.30	2.43
Pectoral fin length (%SL)	20	20.12	24.16	15.50	18.86	2.17
Pelvic fin length (%SL)	20	11.83	14.19	9.05	12.06	1.19
Anal fin length (%SL)	20	15.90	16.80	9.22	13.69	2.16
Body depth (%SL)	20	18.49	20.42	14.22	17.83	1.59
Body width (%SL)	20	10.04	10.96	5.82	9.36	1.46
Caudal peduncle length (%SL)	20	18.98	18.98	13.15	15.91	1.52
Caudal peduncle depth (%SL)	20	9.45	9.86	7.01	8.51	0.92
Meristics	n	Holotype	Range			
Dorsal-fin rays	20	ii+8	ii+6 (n = 2), ii+7 (n = 6), ii+7 (n = 12)			
Anal-fin rays	20	iii+13	iii+13 (n = 9), iii+14 (n = 6), iii+15 (n = 5)			
Pectoral-fin rays	20	i+10	i+8 (n = 2), i+9 (n = 17), i+10 (n = 1)			
Pelvic-fin rays	20	i+7	i+6 (n = 1), i+7 (n = 17), i+8 (n = 2)			
Lateral line scales	2	Unknown	51 (n = 1), 52 (n = 1)			
Caudal peduncle scale	2	Unknown	14 (n = 2)			
Scale rows lat. line-dorsal	2	Unknown	9 (n = 2)			
Scale rows lat. line-pelvic	2	Unknown	2 (n = 2)			
Scale rows lat. line-anal	2	Unknown	2 (n = 2)			
Total vertebrae	11	38	38 (n = 3), 39 (n = 7), 40 (n = 1)			
Abdominal vertebrae	11	19	19 (n = 10), 20 (n = 1)			
Caudal vertebrae	11	19	19 (n = 4), 20 (n = 7)			
Rib pairs	11	14	13 (n = 5), 14 (n = 6)			

Live colouration. (Fig. 6). Body without vertical bars or bands. Dorsum transparent brown with melanophores concentrated around dorsal fin and caudal peduncle; midline silver. Snout darker dorsally. Operculum entirely metallic silver. Iris white to light grey. Dorsal fin membrane clear; rays clear with dark melanophores. Caudal fin membrane clear; rays dark brown to black, lighter towards edge; melanophores lighter towards tip. Anal fin rays clear; membrane clear; few dark spots above origin; melanophores absent. Pectoral fin membrane clear; rays clear; first ray with few dark melanophores. Pelvic fin rays clear; membrane clear.

Preserved colouration. (Fig. 7). Body and head orange with small dark brown spots along dorsal surface, midline and above anal fin. Scales on dorsal surface lightly pigmented. Ventral scale pigmentation less intense than dorsal. Dorsal surface of head lightly pigmented. Melanophores small, dark; grouped on rear of head, below orbit, and on lips and snout; along midline, increasing in intensity to caudal fin; browner on dorsal surface, darkening between origin of pectoral and dorsal fin; forming small dark line above anal fin. Operculum with silver sheen. Side of body with silver sheen extending from pectoral fin to anal fin origin. Membranes between fin rays white to clear towards end. Pelvic fin clear membranes and rays. Dorsal, caudal and pectoral fin membranes white to clear; rays with small, widely-spaced, melanophores fading towards edges; rays pale brown to clear.

Etymology. This species is named in honour of Gordon John Howes (1938-2013), whose studies of the osteology of the Danioninae (Howes 1980, 1984) laid the foundations of their modern classification. The epithet is a genitive noun.

Distribution. Namibia, Angola: Cunene River system.

Type locality. Olushandja Dam at channel outlet (17°25’53”S 14°38’36”E), Kunene River System, Namibia.

Biology. Very little is known of the biology of this species. Individuals appear to favour turbid, rocky, river regions where they can gather in pockets of recirculating currents. The holotype and some paratypes were collected in the shallow, turbid Olushandja Dam in the Namibian upper reaches of the system. They feed on drifting invertebrate larvae and adults and plankton.

Engraulicypris ngalala Riddin, Villet & Bills, sp. n.

http://zoobank.org/5A3FD50F-25DF-49B8-86BD-EB911A238DFF

Holotype. SAIAB 74087 A, GenBank KX788909, unsexed, SL 40 mm. “Lucheringo River, Singa Hunting Camp, Mozambique, 11°48'56"S 36°13'15"E, 25 August 2003, I.R. Bills, seine net”. In 70% ethanol [SAIAB].

Paratypes. SAIAB 193064, 2 unsexed, SL 42-45 mm, collected with holotype; SAIAB 73944, 29 unsexed, 2 cleared & stained, SL 18–29 mm, Rovuma River below Chamba, Mozambique, 12°35'47"S 36°56'8"E, 19 August 2003, I.R. Bills; SAIAB 39269, 11 unsexed, 1 cleared and stained, SL 42–53 mm. Lake Chiuta at Mthubula Beach, Malawi, 14°78'33"S 35°83'33"E, 13 July 1992, P. Skelton & D. Tweddle [SAIAB].

Diagnosis. Operculum shiny only on ventral posterior edge and small area at posterior edge of orbit (not entire area); body midline black (not silver); head with tubercles along lower jaw and lower head in breeding males; snout rounded (not pointed); iris white to light grey (not dark grey) with a few melanophores; pelvic fin melanophores present, dark and widely dispersed.

Morphology. (Figs 6–8; Table 8). Maximum SL 51 mm. Body elongated; somewhat fusiform; laterally compressed. Maximum body depth midway along body. Predorsal profile straight or slightly convex behind head. Head length 18% of SL; with tubercles along lower jaw and lower head. Snout rounded; short; 33% of head length.

Table 8. Morphometric measurements and meristic counts for *Engraulicypris ngalala*.

Measurement	n	Holotype	Max	Min	Mean	SD
SL	20	40.03	50.46	19.37	43.95	2.90
Head length (%SL)	20	7.59	22.79	16.90	18.44	1.26
Head depth (%HL)	20	5.67	77.08	56.85	73.59	2.75
Snout length (%HL)	20	2.54	40.91	15.34	33.10	3.28
Orbit diameter (%HL)	20	3.47	46.01	30.50	43.01	2.67
Postorbit length (%HL)	20	2.54	38.22	22.50	33.18	3.24
Inter-orbit length (%HL)	20	2.68	43.41	21.26	39.13	2.46
Predorsal length (%SL)	20	25.35	68.23	62.27	64.10	1.82
Prepelvic length (%SL)	20	19.27	51.15	42.62	47.72	2.34
Dorsal fin Length (%SL)	20	5.43	19.27	11.89	14.04	1.81
Pectoral fin length (%SL)	20	8.88	23.15	19.29	21.84	0.98
Pelvic fin length (%SL)	20	5.01	17.66	10.57	13.20	1.53
Anal fin length (%SL)	20	6.31	17.52	12.66	14.57	0.97
Body depth (%SL)	20	7.46	20.68	13.89	18.37	0.99
Body width (%SL)	20	3.43	9.26	3.05	8.07	0.69
Caudal peduncle length (%SL)	20	5.98	18.31	12.82	15.89	1.32
Caudal peduncle depth (%SL)	20	3.24	10.13	5.33	8.46	0.64
Meristics	n	Holotype	Range			
Dorsal-fin rays	20	ii+7	ii+7 (n = 15), ii+8 (n = 5)			
Anal-fin rays	20	iii+14	iii+13 (n = 3), iii+14 (n = 6), 3+15 (n = 9), iii+16 (n = 2)			
Pectoral-fin rays	20	i+10	i+ 8 (n = 3), i+9 (n = 11), i+10 (n = 6)			
Pelvic-fin rays	20	i+7	i+6 (n = 2), i+7 (n = 17), i+8 (n = 1)			
Lateral line scales	2	Unknown	51 (n = 1), 52 (n = 1)			
Caudal peduncle scale	2	Unknown	14 (n = 1), 16 (n = 2)			
Scale rows lat. line-dorsal	2	Unknown	9 (n = 2)			
Scale rows lat. line-pelvic	2	Unknown	2 (n = 2)			
Scale rows lat. line-anal	2	Unknown	1 (n = 1), 2 (n = 1)			
Total vertebrae	14	38	38 (n = 2), 39 (n = 1)			
Abdominal vertebrae	14	19	19 (n = 12), 20 (n = 2)			
Caudal vertebrae	14	19	19 (n = 4), 20 (n = 10)			
Rib pairs	14	14	14 (n = 1), 15 (n = 13)			

Mouth terminal; slightly crescent-shaped with long anterior side. Nostrils large; level with dorsal margin of eye; separated from orbit by less than one orbit radius. Tubular anterior naris short; adjacent to open posterior naris. Eye lateral; visible from above and below (more prominent); diameter 43% of head length. First gill arch with 13+3 gill rakers on cerato- and epibranchial arms, respectively. Gill rakers long; pointed; widely-spaced. Pharyngeal bones in four rows. Pharyngeal teeth 5,3,2,1–1,2,3,5; slender and long; falcate.

Modal fin formulae in Table 8. Fins large in relation to body size. Dorsal fin closer to caudal fin than tip of snout; more or less above origin of anal fin; length 14% of

SL; posterior margin straight; rays soft; anterior-most branched fin ray longest. Dorsal and anal fin point parallel. Pectoral fins largest; reaching $^1/_2$ to $^3/_4$ distance to base of pelvic fin; fin lacking lobe at base. Pelvic fins reaching $^2/_3$ distance to base of anal fin; relatively small; pointed; fin lacking a basal lobe. Anal fin moderately long; extending $^2/_3$ length of caudal peduncle; last unbranched ray longest. Ano-genital opening at anterior of base of anal fin. Caudal peduncle moderately long; depth half of length. Caudal fin forked; lobes slightly concave interior lobe into point; upper lobe shorter.

Scales small to medium relative to body size; in regular rows; cycloid; radially striate; rounded, slightly elongate. Base of anal fin lacking sheath of enlarged, elongate scales. Lateral line present; complete; dipping sharply towards ventral at tip of pectoral fin; joins midline at posterior of caudal peduncle; scale count 51–52 (n = 2) along lateral line, 14-16 (n = 3) around caudal peduncle.

Live colouration. (Fig. 6). Body and head white ventrally with pale brown dorsal surface. Body midline black; colouration without vertical bars or bands. Dorsal surface with ubiquitous melanophores. Snout with dense dark spotting on tip. Operculum shiny only on ventral posterior edge and small area at posterior edge of orbit. Iris white to light grey with a few melanophores. Dorsal fin membrane clear; rays clear with dark melanophores. Caudal fin membrane clear to pale orange towards midline; rays dark brown to black, lighter towards edge; melanophores abundant and fading towards tips. Anal fin rays clear; membrane clear; pale orange spotting above origin; melanophores dark brown fading towards tips. Pectoral fin membranes clear; rays clear; first ray with abundant dark melanophores. Pelvic fin rays clear; membrane clear.

Preserved colouration. (Fig. 7). Body and head pale yellow with dark brown spotting on dorsal surface and midline. Scales on dorsal surface lightly pigmented. Ventral scale pigmentation less intense than dorsal. Dorsal surface of head lightly pigmented. Melanophores small, dark; grouped on rear of head, below orbit, and on lips and snout; along midline, increasing in intensity to caudal fin; browner on dorsal surface, darkening between origin of pectoral and dorsal fin; forming small dark line above anal fin. Operculum and posterior base on orbit with silver sheen. Membranes between fin rays white to clear towards end. Pelvic fin clear membranes with melanophores on first ray. Dorsal, caudal and pectoral fin rays with melanophores small, widely-spaced, fading towards edges; pale brown to clear.

Etymology. In the Cyao language spoken in the Niassa region of northern Mozambique, the name '*ngalala*' denotes any, small, compressed, silvery fish, including *Mesobola* and species of *Brycinus* Valenciennes, 1850 and *Hemigrammopetersius* Pellegrin, 1926. The epithet is treated as a nominative singular noun in apposition.

Distribution. Mozambique, Malawi: Rovuma River system and Lake Chiuta.

Type locality. Lucheringo River below rapids at Singa hunting camp (11°48'56"S 36°13'15"E), Mozambique.

Biology. This species is found in ecological conditions very similar to those characteristic of *E. gariepinus* (Bills 2004). It favours big rivers, gathering in slack, turbid and shallow regions with sandy, rocky or muddy substrates. In Lake Chiuta specimens were caught in reed beds along the margins. The Lake Chiuta and Rovuma River stocks may differ ecologically because Lake Chiuta offers a lacustrine pelagic and benthic prey community (copepods, etc.) that is not found in the Rovuma River channel, where fish would predominantly have access to invertebrate drift.

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Golden jackal (*Canis aureus*) in the Czech Republic: the first record of a live animal and its long-term persistence in the colonized habitat

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Abstract

A golden jackal (*Canis aureus*) individual was recorded ~40 km east of Prague in the Czech Republic. It is the first record of a living golden jackal in the country; up to now several individuals have been recorded but all of them were either shot dead or killed by a vehicle. The observed animal was documented by camera traps set up for research of carnivore diversity in different habitats in the study area. It was first photographed on 19 June 2015, and in total there were 57 records made by 12 traps until 24 March 2016 when the animal was still present in the area. Forty-nine of the 57 records were made in a shrubby grassland over an area of ~100 ha, 39% of sightings were during the day and 61% in the night. There were two distinct peaks in the circadian activity of the animal, from 4 to 10 a.m., and from 6 p.m. to midnight. We also review the verified records of the golden jackal in the Czech Republic, some of which were only published in local hunting magazines. However, the observation reported in this paper represents the first evidence of a long-term occurrence in Europe of the same golden jackal individual, that persisted for at least nine months and over winter, northwest of Hungarian-Austrian border where the population has been known to reproduce.

Keywords

Golden jackal, Habitat, Persistence, Range expansion

Introduction

Ongoing global change is bringing about shifts in species distributions that include both the spread of populations of invading species and range expansions or contractions of native biota (e.g. Thuiller et al. 2008; Walther et al. 2009; Langham et al. 2015). In Europe this is typically reflected in species moving from the south-eastern part of the continent to the north-west, most often in response to increasing temperatures that allow organisms to colonize areas that were previously unsuitable. Examples cover a wide range of plants and animals (e.g. Walther et al. 2007; Robinet and Roques 2010), including vertebrates. One species that has received much attention because of its range expansion in recent decades is the golden jackal (e.g. Arnold et al. 2012; Šálek et al. 2014; Trouwborst et al. 2015).

The golden jackal (*Canis aureus* L.) is a canid that was traditionally considered native to northern Africa and southern Eurasia, with natural distribution ranging from north of Tanzania in Africa to the Middle-East to Thailand in Asia (Sillero-Zubiri et al. 2004, Jhala and Moehlman 2008). Yet, current genomic analyses (Koepfli et al. 2015) provide a robust evidence of a deep divergence between the Eurasian clade of *Canis aureus* s. str. and the African populations (including those from North Africa) that form a sister clade to *Canis lupus*, which is to be thus referred as a separate species, *Canis anthus*. This work thus confirmed taxonomic separation based on cranial morphological features, suggested first by Spassov (1989).

In Europe, golden jackals naturally occur in the southeastern part of the continent, the Balkan Peninsula (Demeter and Spassov 1993; Krystufek et al. 1997; Stoyanov 2012), but in recent decades the species has started expanding towards the northwest. After undergoing a population decline and local extinctions in the Pannonian region in the mid-20th century, conservation measures and lowered hunting pressure has resulted in the species not only starting to recolonize its former range, but also to spread northwards to regions of Europe where it has never occurred naturally (Krystufek et al. 1997; Lapini et al. 2009; Krofel 2009; Mihelič and Krofel 2012; Trouwborst et al. 2015). During the first decade of the present millennium it became a common and regularly reproducing species in Hungary and East Austria (Szabó et al. 2009) and there have been reports of it occurring as far to the north as Denmark (http://cphpost.dk/news/european-jackal-found-in-denmark.html) and Estonia (http://goldenjackalaround.blogspot.com/2013/03/golden-jackal-survey-in-w-estonia.html), and to the west as Netherlands in 2016 (http://www.wageningenur.nl/nl/Expertises-Dienstverlening/Onderzoeksinstituten/Alterra/show/Eerste-goudjakhals-gezien-in-Nederland.htm). All records documenting the range expansion are very recent (2015, 2013 and 2016, respectively), reported on internet news servers, and refer to dead animals. Overall spread towards the regions in Europe located beyond this species' historical native range is summarized in the most recent review of the golden jackal historical and current distribution that also deals with the legal status of the species in EU (Trouwborst et al. 2015).

Several factors are assumed to have promoted the dispersal of golden jackals during recent decades. Climate change could play a role by reducing dispersal barriers due to unsuitable climatic conditions in the north of Europe, as suggested for other species (e.g. Walther et al. 2007, 2009). However, the effect of this factor should not be overestimated for a representative of such a highly adaptive guild of carnivores, and a direct evidence of how climate change might have affected this species' spread is missing. Other suggested factors are human-caused changes in the overall character of landscapes (Šálek et al. 2014), the lack of natural predators, particularly wolves (*Canis lupus*) (Giannatos 2004; Arnold et al. 2012), and also a high degree of ecological tolerance in golden jackal individuals (Banea et al. 2012; Šálek et al. 2014). The golden jackal is omnivorous and can survive in various habitats ranging from arid environments to evergreen forests and it also seems to be able to migrate through high-elevation areas (Sillero-Zubiri 1996). Last but not least, it should be remembered that the observed range expansion is essentially favoured by a pronounced capability of the species for a long-distance leptokurtic disperal. Rutkowski et al. (2015) report a number of records of long-distance movements and demonstrate a dual origin of the population in Baltic region recently established first by immigrants of the Caucasian haplotype followed by those of the south-eastern European origin.

In this paper we (i) report the first occurrence of a living individual of the golden jackal in the Czech Republic, and (ii) provide details on this animal's persistence in the study area over a period of nine months. To put our observation in a wider geographical context, we (iii) review the available reports on the occurrence of golden jackal in the Czech Republic and the neighbouring countries, with the aim of separating reliable records from those not supported by rigorous evidence.

Golden jackal in the Czech Republic and neighbouring countries: historical overview

The golden jackal came to the Czech Republic from the south, probably through Austria. The first record in Austria is from Styria in 1987 (Humer 2006) and some of the later observations refer to localities close to the Czech-Austrian border (Hoi-Leitner and Kraus 1989; Bauer and Suchentrunk 1995). In Slovakia, the first record is allegedly from 1947; Feriancová-Masárová and Hanák (1965) report a find of furs of one adult and three young animals in a fur collection point in Bratislava to where they were brought from the Žitný ostrov island on the Danube river; however, the observation remains only anecdotal, unconfirmed by a physical evidence (Hell and Bleho 1995). Later on, an individual was shot near Čierna nad Tisou, eastern Slovakia, in the spring of 1989 (Mošanský 1995) but was at first mistaken for a fox and only later recognized as a golden jackal, documented by an incomplete skull. Another record is a shot animal from the Tríbeč Mountain, February 1995, identified based on skull (see details in Hell and Bleho 1995). At least four other animals were shot between 1989 and 2001 and there were some unconfirmed sightings from central Slovakia in 2008 (Arnold et al. 2012). Concerning arrival to other countries neighbouring the Czech Republic, the golden jackal first appeared in Germany in 1996 (Möckel 2000) and the first record in Poland is from 13 April 2015 – a carcass was found in western Poland near German border. There were a couple more confirmed observations documented by photographs in eastern Poland later that year (Kowalczyk et al. 2015). All of these records refer to occasional observations with no sign of a long-term persistence of the animals in sites where they were spotted. Of the European regions to which golden jackals migrated, they are known to reproduce only in Hungary and Austria with the first evidence of reproduction in the latter country reported in the Austrian-Hungarian border area near the Neusiedler See lake (Arnold et al. 2012, Herzig-Straschil 2007).

The first, albeit unconfirmed, report of the golden jackal's presence in the Czech Republic is from May of 1998, of two individuals reportedly sighted in central Bohemia near Kropáčova Vrutice, district Mladá Boleslav (Suchomelová 1999). The first confirmed record, however, comes from eight years later (19 March 2006) when a carcass of an adult golden jackal was found by the side of the road near Podolí village, close to town of Uherské Hradiště in Moravia, the eastern part of the country (Koubek and Červený 2007). The next two individuals were also found as a result of road kill, one of them again in Moravia, near Brno, in December 2010 (Forejtek et al. 2011), and the third one in Václavice, central Bohemia, in 2011 (Kadlec 2012). In July 2014 a golden jackal was shot in northern Moravia and later stuffed and put in a museum in Nový Jičín (Hudeček and Jakubec 2014); in the same region, another individual was shot by a hunter near Otice on 16 January 2014 (http://www.nowiny.pl/96628-myslal-ze-strzela-do-psa.html), unfortunately this internet record cannot be considered verified. Beside these, numerous other unconfirmed sightings were made in various parts of the Czech Republic – Anděra (2014) mentions 10 non-verified reports between 2004–2012, all of them but one in the easternmost part of the Czech Republic. Other allegedly new sightings are occasionally reported on internet (e.g., http://www.rozhlas.cz/zpravy/priroda/_zprava/v-lesich-a-na-loukach-v-okoli-sternberka-se-objevili-sakali--1542857). The complete overview of the golden jackal's verified finds in the Czech Republic is presented in Table 1.

Table 1. Overview of verified published records of golden jackal (*Canis aureus*) in the Czech Republic. The records always refer to a single animal. Bohemia is the western and Moravia eastern part of the Czech Republic. See Fig. 1 for location of the finds.

Year	Location	Evidence	Reference
2006 (March)	Podolí (distr. Uherské Hradiště, southern Moravia)	Road kill	Koubek and Červený 2007
2010 (December)	Klobouky u Brna (distr. Brno, southern Moravia)	Road kill	Forejtek et al. 2011
2011 (September)	Václavice[1] (distr. Benešov, central Bohemia)	Road kill	Kadlec 2012
2014 (July)	Kunín (distr. Nový Jičín, northern Moravia)	Shot	Hudeček and Jakubec 2014
2015–2016	Milovice (distr. Nymburk, central Bohemia)	Photographs	this study

[1] This location is erroneously given as Vranovice in Anděra (2014).

Methods

We used UOVision UV535 Panda camera traps with a motion sensor and infrared night flash that allows for monitoring animals without disturbing them. In May–June 2015 we placed 73 camera traps so as to cover a range of habitats in a relatively untransformed landscape in central Bohemia, ~40 km east of Prague, ~6 km north-east of the town of Lysá nad Labem, near Milovice (Fig. 1). The total size of the area monitored with camera traps is estimated at 709 ha. The photos were being downloaded approximately once a month from June 2015 to March 2016. The focus of the project was to survey carnivores in general, with no primary focus on golden jackal. The results thus represent a random sampling of its presence in the study area over the sampled period.

Results

The site in which the golden jackal was observed is located approximately 2 km from the nearest village and is surrounded by forests and fields (the average distance from the nearest settlement of the camera traps which recorded the animal was 1.99 km, range 1.60–2.46 km). There is a golf course and an airport nearby. It is not a remote and quiet area and the region is quite densely populated.

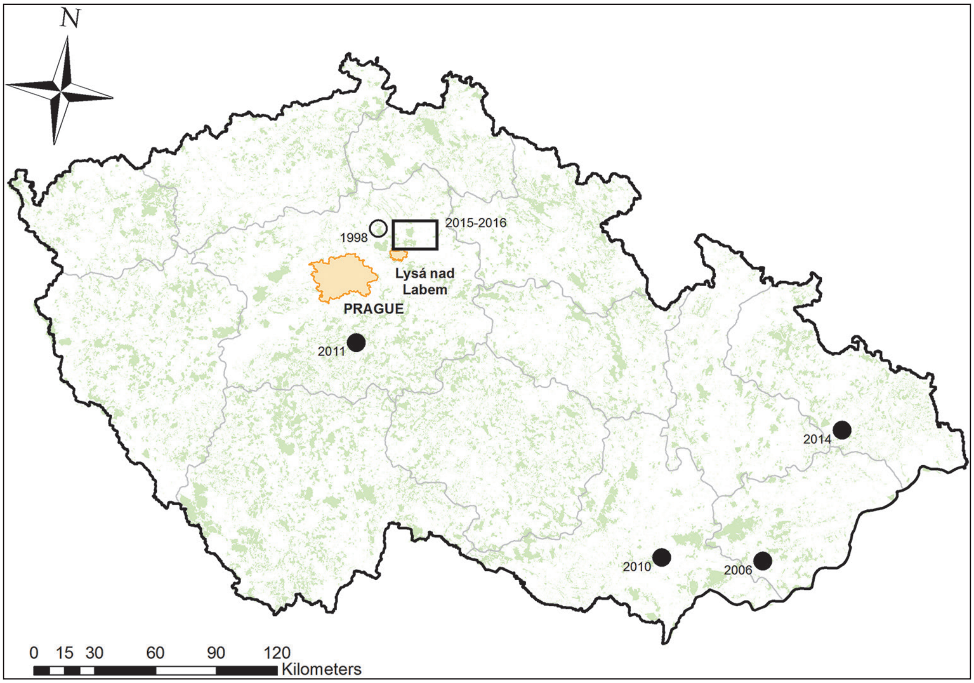

Figure 1. Location of the study area in central Bohemia, western part of the Czech Republic (black rectangle). Previous records relating to dead animals (solid circles), and the first unconfirmed observation (empty circle) are also shown. The records are given by the year of observation, see details in Table 1.

Figure 2. Photographs of a golden jackal (*Canis aureus*) individual in the summer (**A**) and winter (**B**).

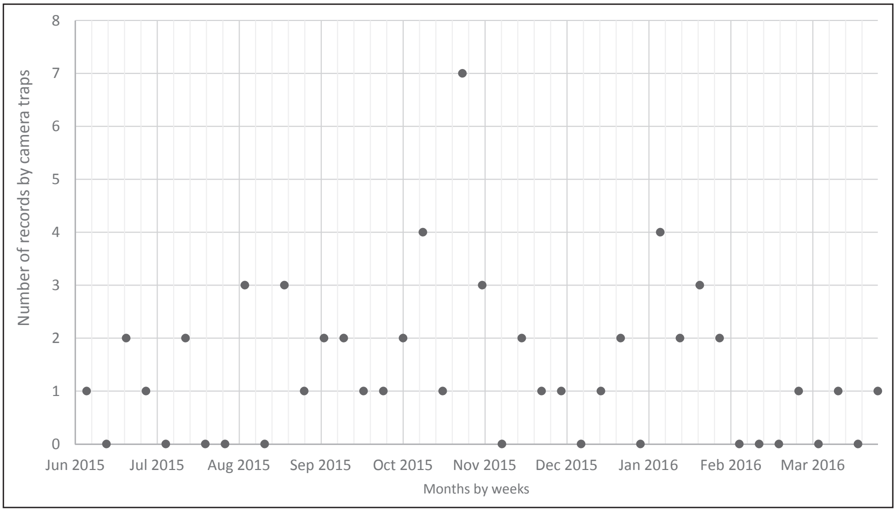

Figure 3. Distribution of the records of golden jackal. The numbers of photographs per week are given.

The photographs made it possible to determine that the animal was a golden jackal based on morphological characteristics, size and coloration (Fig. 2). We also recorded an individual howling back to the recoding of golden jackal around midnight for about 30 seconds (see Suppl. material 1 for the record). Our determination was verified by Boris Krystufek (personal comm.). It is highly likely that the observed animal was one individual, an adult, the sex of which cannot be determined based on photographs. N. Spassov (in litt.) suggested that in certain respects the observed individual differs from the mean phenotype of the species, namely by its long legs and ears, white spot in the fingers from the front left foot (at a summer photograph; Fig. 2A), and a non-typical winter coloration with the long tail position (Fig. 2B).

The first photo of a golden jackal's individual was taken on 19 June 2015 at 8:51 (Fig. 2). Since then the animal was photographed 57 times, by 12 camera traps, with records rather evenly distributed over the sampled period that spanned over 10 months

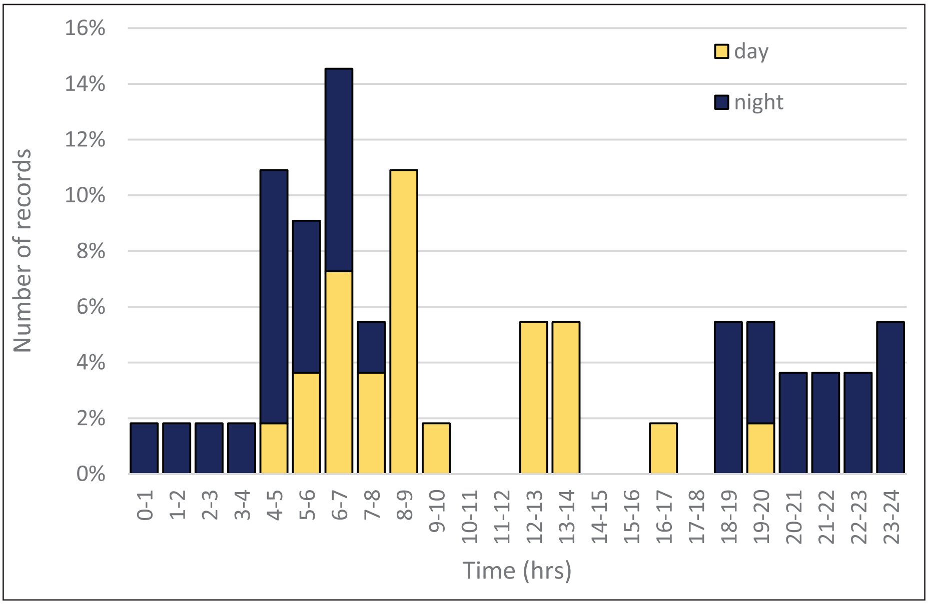

Figure 4. Distribution of the golden jackal (*Canis aureus*) individual's circadian activity over the study period. Records from the whole monitoring period were pooled and related to the time of the day in which the photographs were taken.

or 40 weeks, until March 2016 (Fig. 3), when the animal was still present in the monitored area. Forty-nine records were made in a shrubby steppe-like grassland with hawthorn (*Crataegus* sp. div.) and blackthorn (*Prunus spinosa*) dominating the shrub layer with varying cover; in some places the cover is quite dense, some parts are more open with grass (Fig. 2). The remaining eight records were in a nearby deciduous forest. The animal was being observed over an area of ~100 ha, with 39% of sightings (22) during the day and 61% (35) in the night. There are two distinct peaks in the circadian activity, at dusk and dawn. The animal was most active between 4 and 7 a.m., with as many as 32% of all records made within these two hours (Fig. 4).

Discussion

Systematic sampling reveals long-term persistence: on the way to establishment of golden jackal in the Czech Republic?

Recently, records of the golden jackal individuals have started to be reported from various European regions with increasing frequency, suggesting an ongoing range expansion of this species from the area of its native distribution towards north-west of the continent (Trouwborst et al. 2015). Our observation is the first report of a living animal in the Czech Republic where the four animals previously recorded were road kill or shot. More importantly, it is the only evidence of the long-term persistence of a living animal in the same area available for the region north-west of Hungary and its border with Austria where the species is known to reproduce (Szabó et al. 2009) – earlier records across Europe are mostly vagrants (Trouwborst et al. 2015). Due to systematic random sampling across a large section of the landscape, we were able to prove that the golden jackal individual in our study area, most likely a single individual, occurred on at least ~100 ha area, for eight months so far, and it is still present there at the time of us reporting this find, as of September 2016. In good agreement with literature records, most of activity appeared during night hours, the repeated exploratory behaviour (e.g. controls of badger hole entrance) was recorded also at daytime, surprisingly even around noon.

Although the winter that the animal in our study area survived was rather mild, reports from more northerly located regions of Europe, such as Denmark or Estonia, indicate that this would not be a necessary condition for survival. Moreover, the golden jackal is assumed to be highly adaptive (Šálek et al. 2014) which makes him well suited for establishment in the rather heavily used and densely populated central European landscape.

It is important to note that until now the occurrence in the Czech Republic has been demonstrated by incidental records only, no systematic search was undertaken and the actual distribution of the species is generally unknown. Nevertheless, it is almost certain that the population size of the golden jackal in this country is much higher than previously thought (see Anděra 2014). This, together with the obvious capability for long-term persistence and survival in a suitable habitat as documented in our paper, allows us to predict that the establishment of golden jackal in the Czech Republic in the near future is very probable, and so is the spread of this species further to the north-west. The animal we report here will be further monitored within the ongoing project focused on recording the carnivore diversity in the study area. It remains to be seen whether we will be able to observe the initial phase of establishment. The differences in phenotype of the observed individuals from mean character state of the species evokes a question to which degree a hybridization with domestic dog has been included in the expansion history of the species. Regarding a minute genetic distance between both the species (e.g. Agnarsson et al. 2010) obviously no genetic barrier against hybridization does exist and a lack of social control on alien species mating during a leptokurtic dispersal can be expected as well. Multiple cases of jackal hybridization with domestic dog are well known (e.g. Leonard et al. 2014, Galov et al. 2015).

Nativity, conservation and legislation: Neither flesh nor red herring?

With the recent expansion of the golden jackal, there has been much discussion about whether or not to treat it as an alien species in countries it recently colonized. Although the recent expansion of the golden jackal in the Baltic countries has generated concerns about its possible negative effects on other wildlife species and livestock via predation or transmission of pathogens, and has led to it being labelled as a potentially invasive alien species, the prevailing opinion in other countries does not support this attitude (Banea et al. 2015; Rutkowski et al. 2015; Science for Environment Policy 2016).

Although some authors argue that invasion is an ecological process, the key feature of which is introduction by humans and subsequent spread, and impact should not be part of the definition (Blackburn et al. 2011), the IUCN definition for an invasive species requires that it has an impact on environment in the new range (IUCN 2000). The golden jackal in the Czech Republic and elsewhere in Europe does not meet the IUCN requirement for an invasive species; all the animals are assumed to have arrived on their own, with intentional release not implicated. Other definitions from the field of invasion biology, based on introduction pathways, do not necessarily require intentional introduction but the process of introduction needs to be related to humans – according to Hulme et al. (2008), a species that arrived without human intervention from an area where it is native should be treated as native. The available evidence is therefore in favour of considering the golden jackal as a species that naturally expands its distribution, making use of the changing conditions.

The latter statement indicates that the conclusion about the golden jackal's nativity (which implies legal protection which has become an issue recently; Science for Environment Policy 2016) has a flip side – if it is not alien to central Europe, is it native? This begs the question to what extent the expansion is natural? The factors driving or facilitating the golden jackal's expansion are still not entirely clear although land use changes, as well as climate change, are most likely implicated (Giannatos 2004; Arnold et al. 2012; Šálek et al. 2014). Moreover, it is also suggested that the expansion might be easier in current landscape where wolves, natural intra-guild predators of golden jackals, are uncommon or absent (Giannatos 2004; Arnold et al. 2012). However, this argument is rather speculative because in central European temperate landscapes the two species differ in their habitat preferences. This allows for quasi-supported speculation that had it not been for the indirect effect of humans, the golden jackal might not have reached that far to the northwest of Europe where it is currently present. It is not the primary aim of this article to deal with this issue that has been recently thoroughly reviewed in Trouwborst et al. (2015) but we think it is worth pointing out that opinions about this species' status in Europe may continue to differ region by region in the future, with good reasons on both sides.

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Supplementary material 1

Goledn jackal's howling record

Authors: Klára Pyšková, David Storch, Ivan Horáček, Ondřej Kauzál, Petr Pyšek

Data type: multimedia

Explanation note: Recording of an individual howling back to the recording of golden jackal. Recorded on 15 September 2015 around midnight.

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RESEARCH ARTICLE

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Tosanoides obama, a new basslet (Perciformes, Percoidei, Serranidae) from deep coral reefs in the Northwestern Hawaiian Islands

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Abstract

The new species *Tosanoides obama* is described from two specimens collected at a depth of 90–92 m off Kure Atoll and Pearl and Hermes Atoll, Northwestern Hawaiian Islands. It differs from the other two species of this genus in life color and in certain morphological characters, such as number of pored lateral-line scales, pectoral-fin rays, snout length, anterior three dorsal-fin spine lengths, dorsal-fin profile, and other characters. There are also substantial genetic differences from the other two species of *Tosanoides* ($d \approx 0.10$ in mtDNA cytochrome oxidase I). The species is presently known only from the Northwestern Hawaiian Islands within the Papahānaumokuākea Marine National Monument.

Keywords

Mesophotic Coral Ecosystem, Closed-Circuit Rebreather, Endemic, Papahānaumokuākea Marine National Monument, President Obama

Introduction

Since 2009, the National Oceanographic and Atmospheric Administration (NOAA) has conducted annual research cruises to the Northwestern Hawaiian Islands led by the third author (RKK) involving advanced mixed-gas diving operations to explore and document mesophotic coral ecosystems (MCEs; coral-reef habitat at depths of 30–150 m) within the Papahānaumokuākea Marine National Monument. In addition to conducting quantitative surveys of fishes (e.g., Kane et al. 2014, Kosaki et al. 2016), exploratory deep dives have focused on documenting species occurrence records in an effort to develop comprehensive checklists of fishes from each major reef and island within the Monument. During one such deep dive on 5 June 2016 off Kure Atoll, the first author (RLP) observed a small pink fish that at first appeared to be a juvenile *Pseudanthias thompsoni* (Fowler, 1923), but had a prominent red spot on the posterior portion of the dorsal fin. After capturing a brief video clip of this fish, as well as a second similar individual that lacked the spot on the dorsal fin (YouTube 2016), the specimen with the spot was collected alive. The following day, the second author (BDG) observed a group of three individuals of the same fish (one with the red spot on the dorsal fin, and two without) at a depth of 90 m off Pearl and Hermes Atoll, and collected one of the individuals (lacking the spot) alive.

The specimens represent an undescribed species within the serranid subfamily Anthiadinae Poey, 1861 (commonly spelled Anthiinae, but see van der Laan et al. 2014, 2016 and *Discussion* section below), within the genus *Tosanoides* Kamohara, 1953. The genus currently includes two nominal species, both considered valid and both from the tropical and subtropical northwestern Pacific: *Tosanoides filamentosus* Kamohara, 1953 (type species), and *T. flavofasciatus* Katayama & Masuda, 1980. Herein we describe the third member of the genus, *Tosanoides obama*, based on morphologic and genetic differences compared with the other two known species.

Methods

Specimens were collected with hand nets during deep dives using mixed-gas, closed-circuit rebreathers.

Standard length (SL) was measured from the tip of the snout to the caudal-fin base. Total length (TL) was measured from the tip of the snout to the posterior edge of the filamentous extensions on the caudal fin. Head length was measured from the tip of the snout to the posterior-most edge of the fleshy flap near the upper end of the gill opening. Body depth is the greatest depth of body measured as a vertical from the ventral edge of the abdomen to the upper edge of scaled fleshy sheath of the dorsal fin (typically from about fourth or fifth dorsal spine). Width of the body is the maximum width. Snout length is the distance from the tip of the snout to the closest point on the bony orbit. Predorsal length is the distance from the tip of the snout to the angle formed by the scaled fleshy sheath at the insertion point of the first dorsal-fin spine, when erected. Preanal length is the distance from the tip of the snout to angle formed by the scaled fleshy sheath at the insertion point of the first anal-fin spine, when erected. The base of the dorsal fin is measured from the extreme base of the first dorsal-fin spine to the extreme base of the last dorsal-fin soft ray. The base of the anal fin is measured from the extreme base of the first anal-fin spine to the extreme base of the last anal-fin soft ray. Orbit diameter is the maximum diameter of the bony orbit. Interorbital width is the width of the bony interorbital space. Depth of the caudal peduncle is the least depth. Pelvic-fin spine length was measured from the extreme base of the pelvic-fin spine to its distal tip. Pelvic fin length is the length of the first ray from its extreme base to the distal tip of the filamentous extension. Length of spines and soft rays of dorsal and anal fins were measured from the extreme base to the most distal tip. Caudal-fin length is defined as the difference between TL and SL. Pectoral-fin length was measured as the longest fin ray, from its extreme base to its tip.

The last dorsal- and anal-fin soft rays are branched to the base and were counted as a single ray. Caudal-fin ray counts include small unsegmented and rudimentary rays. Pectoral-fin ray counts include first two and last two unsegmented and rudimentary rays. Lateral-line scale counts include only those scales with pores. Scale row counts above and below lateral line to origins of dorsal and anal fins (respectively) include small truncate scales at bases of respective fins. Vertebral counts include the first vertebra fused to the skull, and the last vertebra fused to the hypural plate.

All counts and measurements except vertebrae were made directly from specimens. Measurements were made using dial calipers with +/- 0.05 mm precision. Lengths of dorsal- and anal-fin spines and soft rays were made with the aid of a bright light transmitted from behind the fins to reveal the position of their extreme bases. Gill-raker count for the holotype was obtained by removing the first gill arch from the right side of the specimen (not counted on the paratype). Vertebral counts were made from x-radiographs.

Head length, depth of body, width of body, snout length, predorsal length, preanal length, length of dorsal-fin and anal-fin bases, orbit diameter, interorbital width, caudal-peduncle depth, and lengths of fin spines and rays are expressed as percent of SL. Counts and measurements for the paratype, if different from the holotype, are presented in parentheses after the value for the holotype.

Description template and wording modified from Katayama and Masuda (1980) for consistency.

The holotype has been deposited at the Bernice Pauahi Bishop Museum fish collection, Honolulu (BPBM), and the paratype has been deposited at the U.S. National Museum of Natural History, Washington, D.C. (USNM).

Fresh tissue samples were obtained from the holotype and paratype. DNA barcodes (cytochrome c oxidase I; COI) were sequenced following the protocol described in Copus et al. (2015). Barcode of Life Database (BOLD) identifiers for DNA sequences are presented along with museum catalog numbers for type material and non-type specimens.

Taxonomy

Tosanoides obama Pyle, Greene & Kosaki, sp. n.

http://zoobank.org/18C72D73-00C3-40E4-B27F-FA7748A1251E

Figs 1–6

Type locality. Northwestern Hawaiian Islands, Kure Atoll, north side, 28.4918°N, 178.2879°W.

Holotype. BPBM 41315, male, Barcode of Life TOSOB001-16 (submitted to GenBank), 43.2 mm SL, Northwestern Hawaiian Islands, Kure Atoll, north side, 28.4918°N, 178.2879°W, 90 m, 5 June 2016, R. L. Pyle, aboard NOAA ship *Hiʻialakai* (Cruise: HA-16-04), hand nets, limestone bottom with small holes. Found in association with a single presumed female (not collected).

Paratype. USNM 440451, immature, Barcode of Life TOSOB002-16 (submitted to GenBank), 28.4 mm SL, Northwestern Hawaiian Islands, Pearl and Hermes Atoll, northwest side, 27.9095°N, 175.9359°W, 92 m, 6 June 2016, B. D. Greene, aboard NOAA ship *Hiʻialakai* (Cruise: HA-16-04), hand nets, limestone bottom with small holes. Found in association with two other individuals, one presumed male and one presumed female (not collected).

Diagnosis. A species of *Tosanoides* (*sensu* Katayama & Masuda, 1980) distinguished by the following combination of characters: fourth or fifth dorsal spine the longest, dorsal-fin soft rays 17; anal-fin soft rays 8; pored lateral-line scales 33 or 34; head 2.9–3.0 in SL; body depth 2.8–2.9 in SL; color in life pink or yellowish pink on head and body, slightly darker dorsally fading ventrally; snout and region immediately dorsal to eye bright yellow, with a thin bright yellow band extending dorsally on either side of nape; a thin bright yellow horizontal stripe extending horizontally from posterior middle edge of eye posteriorly across most of operculum, continuing as a series of irregular oblong spots on midline of body from just posterior to gill opening to a point approximately one-fourth to one-half of pectoral fin; a second thin bright yellow stripe extending posteriorly from lower jaw across maxilla just ventral to eye and continuing horizontally across operculum and base of pectoral fin; dorsal fin pink or yellowish pink with darker pink regions on membranes, and a bright magenta margin extending from tip of first dorsal fin posteriorly on anterior half of soft dorsal fin; males with a large circular ocellate spot covering posterior one-third of soft dorsal fin, bluish magenta on perimeter and dark red with faint yellow stripes centrally; anal and pelvic fins magenta or yellow; caudal fin translucent yellow, more pale and translucent medially and distally, with bright magenta margins extending along margins of both lobes.

Description. Dorsal fin X,17, last soft ray branched to base; anal fin III,8, last soft ray branched to base; pectoral-fin rays 14; pelvic-fin rays I,5; principal branched caudal rays 14, upper procurrent unbranched caudal rays 6, lower procurrent unbranched caudal rays 4; pored lateral-line scales 33 (34); scale rows above lateral line to origin of dorsal fin 3 (4); scale rows below lateral line to origin of anal fin 14 (13); gill rakers on upper limb 10, on lower limb 22; vertebrae 26 (10+16).

Figure 1. Holotype of *Tosanoides obama* (BPBM 41315), collected at a depth of 90 m off Kure Atoll, Northwestern Hawaiian Islands. Photo by R. L. Pyle.

Figure 2. Paratype of *Tosanoides obama* (USNM 440451), collected at a depth of 92 m off Pearl and Hermes Atoll, Northwestern Hawaiian Islands. Photo by R. L. Pyle.

Body ovoid, compressed, its greatest depth 2.88 (2.84) in SL, the width just posterior to gill opening 2.00 (2.50) in depth; head length 2.88 (2.96) in SL; snout short, its length 7.14 (6.40) in head; orbit diameter 2.88 (2.67) in head; interorbital convex, the least bony width 3.57 (3.43) in head; least depth of caudal peduncle 2.83 (2.59) in head.

Mouth large, oblique and protractile; lower jaw not projecting beyond the upper when mouth closed; maxilla 2.08 (2.04) in head, expanded distally, reaching below posterior border of pupil, slightly diagonal, the gape forming an angle of about 20° to the horizontal, supramaxilla absent. A pair of nostrils on either side of head, close together, directly in front of eye, anterior nostril in a membranous tube with an elevated posterior edge, posterior nostril with a slight rim anteriorly. Teeth in upper jaw villiform, forming a band broader anteriorly with a pair of canines on each side and another pair of canines slightly posteriorly and internally directed backward, an outer row of about 10 slender canines on each side of jaw curved forward; lower jaw with a patch of villiform teeth anteriorly; one canine on each side anteriorly facing forward and a second canine on each side curved forward, an outer row of about 15 slender canines like those of the upper jaw, posterior ones pointing forward; small teeth on vomer and palatines, teeth on vomer in a triangular band; tongue pointed, smooth. Preopercle with a round angle, upper limb serrate with about 25 spinules, lower limb smooth; opercle with two flat spines, upper one longest and at apex; subopercle and interopercle smooth. Gill rakers long and numerous, with 10 rakers on the upper limb and 22 on the lower limb, longest raker much longer than gill filament.

Dorsal fin very slightly notched, inserted slightly posterior to dorsal end of gill opening, its base 1.76 (1.67) in SL; first dorsal-fin spine 4.29 (4.17) in head, second dorsal-fin spine 3.33 (3.43) in head, third dorsal-fin spine 3.06 (2.91) in head, fourth dorsal-fin spine the longest, 2.68 (2.40) in head, fifth dorsal-fin spine 2.88 (2.40) in head, last dorsal-fin spine 3.06 (2.67) in head; membranes between anterior dorsal-fin spines mildly incised, progressively less so posteriorly; longest dorsal soft ray (seventh or eighth) 1.32 (1.92) in head. Anal fin originating below base of second dorsal soft ray; second anal spine slightly stronger than the third; length of first anal-fin spine 5.77 (4.80) in head, second anal-fin spine 2.54 (1.96) in head, third anal-fin spine 2.50 (1.85) in head; posterior margin of anal fin rounded; length of longest anal soft ray (fifth or sixth) 1.70 (1.48) in head. Pectoral fins subsymmetrical, longer than head, reaching a vertical at base of third anal soft ray, their length 2.63 (2.49) in SL; caudal fin deeply convex, upper and lower lobes each with two filamentous extensions on their outermost principle rays; pelvic spine 2.00 (1.88) in head; first soft ray of pelvic fin with a filamentous extension (broken in holotype), its length (1.67), in SL.

Scales moderately large, ctenoid; 3 (4) in a series from origin of dorsal fin to lateral line, 14 (13) from origin of anal fin to lateral line; head closely scaled except for lips and tip of snout anterior to nostrils; dorsal and anal fins with small scales basally, a single row on spinous portion of dorsal fin, reaching distally about 1/5 of distance to outer margin posteriorly on soft portions of dorsal and anal fins; about 7 or 8 vertical scale rows on base of caudal fin; scales on pectoral fins basally, extending posteriorly on lower half of pectoral fin approximately one third distance to posterior margin. Lateral line high, concurrent with back, forming an angle below last several dorsal rays and extending along middle of caudal peduncle to base of caudal fin.

Color in life as in Figures 1–6. This species is sexually dichromatic. Male (holotype; Figures 1, 3–5): body and head pink, slightly darker dorsally fading ventrally; snout and region immediately dorsal to eye bright yellow, with a thin bright yellow band extending dorsally on either side of nape from dorsal edge of eye to about one-third to

Figure 3. Holotype of *Tosanoides obama* immediately prior to collection, at a depth of 90 m off Kure Atoll, Northwestern Hawaiian Islands. Cropped frame from video by R. L. Pyle.

Figure 4. Holotype of *Tosanoides obama* (upper left) alongside presumed female (lower right, not collected) immediately prior to collection of the holotype, at a depth of 90 m off Kure Atoll, Northwestern Hawaiian Islands. Both fish retreated into the same hole moments after this image was captured. Cropped frame from video by R. L. Pyle.

one-half distance to origin of dorsal fin; nape pink; a thin bright yellow stripe extending horizontally from posterior middle edge of eye across most of operculum, continuing as a series of irregular oblong spots on midline of body from just posterior to gill opening to a point approximately one-fourth to one-third of pectoral-fin length; a second thin bright yellow stripe extending posteriorly from lower jaw across maxilla just ventral to eye and continuing horizontally across operculum and base of pectoral fin; a very thin faint yellow stripe along anterior two thirds of lateral line; dorsal fin pink with a bright magenta margin extending from tip of first dorsal-fin spine to anterior half of soft dorsal fin, a large circular ocellate spot covering posterior one-third of soft dorsal fin, extending from base of fin to outer margin, broadly bluish magenta on perimeter and dark red with faint yellow stripes centrally; anal fin magenta except for anterior base; pelvic fins translucent magenta with a pale blue pelvic spine; caudal fin translucent yellow, paler and translucent medially and distally, with bright magenta margins extending along dorsal and ventral margins; live male held under duress in captivity (Figure 5) paler pink over most of body, with faded coloration on median fins and pelvic fins, central portion of ocellate spot bright yellow with thin red lines corresponding to soft dorsal-fin rays. Immature (paratype, Figures 2, 6) and presumed female (Figure 4) fish: body and head yellowish pink, fading ventrally on abdomen and chest; snout and region immediately dorsal to eye bright yellow, with a dusky yellow band extending dorsally on either side of nape from dorsal edge of eye to origin of dorsal fin; nape with a magenta stripe extending from a point just dorsal to snout horizontal to midline of eye and extending dorsally along nape, tapering to a point at origin of dorsal fin; a thin bright yellow stripe extending horizontally from posterior middle edge of eye across most of operculum, continuing as a series of irregular oblong spots on midline of body from just posterior to gill opening to a point approximately one-third to one-half of pectoral-fin length; a second thin bright yellow stripe extending posteriorly from lower jaw across maxilla just ventral to eye and continuing horizontally across operculum and base of pectoral fin; dorsal fin yellowish pink with darker pink regions on membranes between dorsal-fin spines and basally on soft portion of fin; a bright magenta margin extending from tip of first dorsal-fin spine to anterior half of soft dorsal fin; anal fin yellow with pink blotches; pelvic fins translucent yellow anteriorly, white posteriorly, spine bright magenta; caudal fin translucent yellow, paler and translucent medially and distally, with bright magenta dorsal and ventral margins; live immature fish held under duress in captivity (Figure 6) darker pink over most of body.

Color in alcohol uniformly pale yellow except for eye, which is black.

Morphometric data for selected characters of type specimens are provided in Table 1.

Distribution. *Tosanoides obama* is known on the basis of two specimens and three additional individuals observed at a depth of 90–92 m at Kure Atoll and Pearl and Hermes Atoll, within the Northwestern Hawaiian Islands. Gooding (1980) listed a single individual of *T. filamentosus* among the fishes collected during a series of trawls at depths of 140–170 fathoms (256–311 m) in 1975–1979 at Hancock Seamount (located approximately 360 km northwest of Kure Atoll). This record appears to represent the only basis for subsequent reports of this species in or near the Hawaiian

Figure 5. Holotype of *Tosanoides obama* shortly after collection, alive in a holding tank aboard the NOAA Ship *Hi'ialakai*. Photo by R. L. Pyle.

Figure 6. Paratype of *Tosanoides obama* shortly after collection, alive in a holding tank aboard the NOAA Ship *Hi'ialakai*. Photo by R. L. Pyle

Archipelago (e.g., Humphreys et al. 1984, Uchida and Uchiyama 1986, Mundy 2005, Hart and Pearson 2011). Unfortunately, the fish reported by Gooding was not preserved, therefore there is no way to determine whether it was correctly identified as *T. filamentosus*, or perhaps was an individual of *T. obama*, or a different species.

T. obama is the only coral-reef fish species endemic to the Papahānaumokuākea Marine National Monument (which includes part of Hancock Seamount), although further exploration of MCEs in nearby regions may yet reveal its presence elsewhere. This is consistent with the observation that fish assemblages on deep coral reefs have proportionally more endemic species than on shallow reefs (Pyle 1996, Kane et al. 2014, Kosaki et al. 2016).

Habitat and ecology. Two groups of *T. obama* have been observed in nature; one consisting of two individuals (the male holotype and an apparent female), and the other consisting of three individuals (an apparent male, an apparent female, and the immature paratype). Both groups were found living among small holes in a hard limestone bottom covered with crustose calcareous algae, in areas of apparent ancient shorelines (undercut limestone ledges adjacent to sandy bottom). General habitat characteristics are evident in Figures 3, 4, as well as the videos cited in the bibliography as YouTube (2016). Both sites are characterized by comparatively dense populations of endemic reef-fish species [primarily *Pseudanthias thompsoni* (Fowler, 1923), *Chromis strusakeri* Randall & Swerdloff, 1973, *Caprodon unicolor* Katayama, 1975, and several other endemic labrids, chaetodontids, and pomacanthids]. Quantitative ecological surveys of mesophotic fish assemblages at the northern end of the archipelago indicate that these assemblages are numerically dominated by small-bodied, endemic planktivorous species (Fukunaga et al. 2016). The known habitat and likely trophic habits of *T. obama* are consistent with this pattern.

Etymology. We name this species *obama* (a noun in apposition) in honor of Barack H. Obama, 44th President of the United States, in recognition of his efforts to protect and preserve the natural environment, particularly through his decision to expand the Papahānaumokuākea Marine National Monument several weeks after the discovery of this new species.

Morphological comparisons. The morphology of this species is consistent with the diagnosis for the genus *Tosanoides* as presented by Katayama and Masuda (1980). Compared with *Pseudanthias* Bleeker, 1871 (the only other genus it resembles), *T. obama* shares with the other two species of *Tosanoides* fewer pored lateral line scales (30–34, compared with 35–52) number of anal soft rays (8, compared with 6–7), and unbranched pectoral fin rays.

Tosanoides obama is more similar morphologically to *T. flavofasciatus* (Figure 7) than to *T. filamentosus*, primarily on the basis of proportional dorsal-fin spine lengths (third or fourth dorsal spine the longest in *flavofasciatus*, compared with first dorsal spine the longest in *filamentosus*). *Tosanoides obama* differs from both species of *Tosanoides* in number of pored lateral-line scales (33–34, compared with 30–32), number of pectoral-fin rays (14, compared with 13), shorter snout length (6.40–7.14 in head, compared with 4.66–5.86 for *T. filamentosus* and 2.27–2.89 for *T. flavofasciatus*),

Table 1. Morphometric and meristic data for selected characters of type specimens of *Tosanoides obama*. Values of morphometric data (other than TL and SL) are represented as % of SL.

	Holotype	**Paratype**
Morphometrics	BPBM 41315	USNM 440451
Sex	Male	Immature
Total length (TL) in mm	61.5	41.0
Standard length (SL) in mm	43.2	28.4
Head length	35	34
Body depth	35	35
Body width	17	14
Snout length	4.9	5.3
Predorsal length	34	36
Preanal length	65	62
Base of dorsal fin	57	60
Base of anal fin	19	21
Orbit diameter	12	13
Interorbital Width	10	10
Caudal Peduncle Depth	12	13
Pelvic Spine	17	18
Pelvic Fin	32	60
First Dorsal Spine length	8.1	8.1
Second Dorsal Spine length	10	10
Third Dorsal Spine length	11	12
Fourth Dorsal Spine length	13	14
Fifth Dorsal Spine length	12	14
Last Dorsal Spine length	11	13
Longest Dorsal Ray length	26	18
First Anal Spine length	6.0	7.0
Second Anal Spine length	14	17
Third Anal Spine length	14	18
Longest anal ray length	20	23
Caudal fin length	42	44
Pectoral fin length	38	40
Meristics		
Dorsal Spines	X	X
Dorsal rays	17	17
Anal Spines	III	III
Anal Rays	8	8
Pectoral Rays	14	14
Caudal Rays	6+7+7+4	6+7+7+4
Pored lateral line scales	33	34
Dorsal scale rows	3	4
Ventral scale rows	14	13
Gill rakers	10+22	-

Figure 7. *Tosanoides flavofasciatus*, BPBM 40858, Palau Islands. Photo by R. L. Pyle

anterior three dorsal-fin spine lengths (4.29–4.17, 3.33–3.43 and 3.06–2.91 in head, compared with 2.03–1.84, 2.24–2.15 and 2.66–2.30 in head for *T. filamentosus*, and 3.57–3.21, 2.86–2.82 and 2.67–2.52 in head for *T. flavofasciatus*), and in dorsal-fin profile (slightly notched in *T. obama*). *Tosanoides obama* also differs from both other *Tosanoides* species in having far less scalation on the median fins (only basally, compared with one half or more of fins), and in the third anal-fin spine (approximately equal to second anal-fin spine, compared with a shorter and less stout third anal-fin spine relative to second anal-fin spine). *Tosanoides obama* additionally differs from *T. filamentosus* in having a longer anal-fin base (4.81–5.14 in SL, compared with 5.35–5.40), broader bony interorbital space (3.43–3.57 in head, compared with 4.44–4.63), and longer third anal-fin spine (1.85–2.50, compared with 2.55–3.19). *Tosanoides flavofasciatus* additionally differs from *T. obama* in having a deeper body (2.29-2.69 in SL, compared with 2.84–2.88).

The three species can also be easily distinguished from each other on the basis of life color.

Based on the five observed individuals of *T. obama*, none of which were larger than the holotype, this species appears to be much smaller than the other two, adults of which are typically 55–85 mm SL.

Genetic comparisons. Vertebrate mtDNA barcode (cytochrome oxidase I) sequences obtained from the holotype and paratype of *T. obama* reveal 9.5–10% uncorrected sequence divergence when compared with the other two described species of *Tosanoides*. This is somewhat higher than many species-level divergences in other fish taxa (e.g., Johns and Avise 1998, Bellwood et al. 2004, Fessler and Westneat 2007, Randall and Rocha 2009, Rocha 2004, Rocha et al. 2008, Pyle and Kosaki 2016). The accepted mtDNA clock rate of approximately 2% per million years in fishes (Bowen et al. 2001, Reece et al. 2010) indicates divergence between these species on the order of 5 million years. Nevertheless, based on a preliminary genetic analysis, *T. obama* has closer genetic affinities to both *Tosanoides* species than to representatives of eight other Indo-Pacific anthiadine genera (including *Luzonichthys* Herre, 1936, *Nemanthias* Smith, 1954, *Odontanthias* Bleeker, 1873, *Plectranthias* Fowler, 1935, *Pseudanthias* Bleeker, 1871, *Sacura* Jordan & Richardson, 1910, *Serranocirrhitus* Watanabe, 1949, and *Tosana* Smith & Pope, 1906). On this basis, as well as morphological comparisons, we are confident in assigning the new species to the genus *Tosanoides* until a more exhaustive investigation of phylogenetic relationships among the species in this subfamily is completed.

Discussion. *Tosanoides obama* is another example of several new fish species that have been discovered on deep coral reefs over the past several decades, mostly involving the use of modern mixed-gas closed-circuit rebreather diving technology (Pyle 1996, 2000). In recent years there has been increased attention focused on mesophotic coral ecosystems (MCEs), coral-reef habitat at depths of approximately 30–150 m in tropical regions worldwide (Hinderstein et al. 2010, Baker et al. 2016). Many more new species of fishes and other reef-associated marine organisms are likely to be discovered as a result of continued exploratory work in this poorly documented environment.

The fish subfamily Anthiinae (Anthiadides Poey, 1861, type genus *Anthias* Bloch, 1792, stem *Anthi-*), is a homonym of the beetle subfamily Anthiinae (Anthies Bonelli, 1813, type genus *Anthia* Weber, 1801, stem *Anthi-*). According to Article 55.3 of the International Code of Zoological Nomenclature (ICZN 1999), homonymous family-group names in current use based on similar (but not identical) genus-group names must be referred to the Commission for a ruling to remove homonymy. A case is currently in preparation to formally resolve this homonymy through application to the ICZN. Until an Opinion is issued, we follow van der Laan et al. (2014, 2016) and Carvalho-Filho (2016) in using the spelling “Anthiadinae” to represent the subfamily for this new species, instead of the more commonly used (but homonymous) spelling “Anthiinae”.

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